UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

EFFETS DU CLIMAT PASSÉ ET FUTUR SUR LA CROISSANCE RADIALE DE QUATRE ESPÈCES D'ARBRES DOMINANTES (PEUPLIER FAUX-TREMBLE, BOULEAU BLANC, ÉPINETTE NOIRE, ET PIN GRIS) DE LA FORÊT BORÉALE MIXTE ET CONIFÉRIENNE DE L'OUEST DU QUÉBEC, CANADA

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JIANGUO HUANG

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EFFECTS OF CLIMATE AND OF POTENTIAL FUTURE CLIMATE ON RADIAL GROWTH OF FOUR DOMINANT BOREAL TREE SPECIES (TREMBLING ASPEN, PAPER BIRCH, BLACK SPRUCE AND JACK PINE) IN THE MIXED AND CONIFEROUS BOREAL FOREST OF WESTERN QUÉBEC, CANADA

THESIS

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PREFACE

The present thesis is comprised of seven parts, including the General Introduction, the Chapter I, Chapter II, Chapter III, Chapter IV, the General Conclusion, and an Appendix I presenting a publication associated with my Ph.D study. All the papers and contexts involved in the thesis together are my original contributions to my Ph.D in Environmental Science that I pursued and accomplished at Université du Québec en Abitibi-Témiscamingue, Canada. The Chapters I-IV are correspondingly based on the following four publications:

1. Huang J.G., Tardif J., Denneler B., Bergeron Y., and Berninger F (2008). Tree-ring evidence extends the historic northern range limit of severe defoliation by insects in the aspen stands of western Quebec, Canada. *Canadian Journal of Forest Research*, **38**:2535-2544. (**I**mpact **F**actor 2008: **1.434**)
2. Huang J.G., Tardif J., Bergeron Y., Denneler B., Berninger F., and Girardin M. (2010) Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Global Change Biology*, **16**:711-731. doi:10.1111/j.1365-2486.2009.01990.x (**IF** 2008: **5.876**)
3. Huang J.G., Bergeron Y., Berninger F., Zhai L.H., Tardif J., and Denneler B. Impact of future climate on radial growth of the four dominant boreal tree species along a latitudinal gradient in the eastern Canadian boreal forest. (in preparation to *Global Change Biology*) (**IF** 2008: **5.876**)
4. Huang J.G., Bergeron Y., Zhai L.H., and Denneler B. Variations in intra-annual radial growth (formation of the xylem) of black spruce along a latitudinal gradient in western Quebec. (in preparation to *Trees-Structure and Function*) (**IF** 2008: **1.629**)

The Appendix I publication was the result of my Ph.D Synthesis Exam, which is often done during the second year of the Ph.D study through writing a 50-pages report to answer a hot question associated more or less with the candidate's study field within three months from the Ph.D committee. It aims to assess if a Ph.D candidate in Environmental Sciences is eligible for doing this Ph.D at University of Quebec. The Appendix I paper is listed as following:

5. Huang J.G.**,** Bergeron Y., Denneler B., Berninger F., and Tardif J. (**2007**) Response of forest trees to increased atmospheric CO_2. *Critical Reviews in Plant Sciences*, **26(5)**: 265-283. DOI:10.1080/07352680701626978 (**IF** 2008: **6.206**)

The leading author developed all the experimental designs with Dr. Yves Bergeron and the late Dr. Bernhard Denneler, and conducted all the fieldwork with Dr. Denneler. The leading author conducted all the laboratory work of Chapters I and II. The leading author conducted all data analyses as well as wrote the five manuscripts and the thesis. Dr. Bergeron constantly financed, supervised, and discussed all PhD project, and commented the early versions of the manuscripts of all five papers and the thesis. Dr. Jacques Tardif guided the data analysis work in the Chapter I, and discussed and commented the early versions of the manuscripts of the four papers and the thesis. Dr. Frank Berninger discussed and commented the early versions of the manuscripts of the four papers and the thesis. Dr. Martin P. Girardin (Canadian Forest Service) calculated Canadian drought code data used in the Chapter II and commented the early version of it. Ms. LiHong Zhai (UQAM) calculated Canadian drought code data and processed large sets of climate change scenarios data in the Chapter III, and conducted all the laboratory work and provided key help on data analysis for Chapter IV, as well as discussed and commented the early versions of these two chapters. The comments and suggestions from all the coauthors greatly improved the quality of the papers, and are much appreciated.

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RÉSUMÉ

Afin d'aborder la question centrale du mode d'influence des changements climatiques sur la croissance des arbres dans le contexte du réchauffement global, nous avons utilisé une analyse dendrochronologique pour passer en revue systématiquement les réponses de quatre espèces ligneuses dominantes de la forêt boréale - *peuplier faux-tremble, bouleau blanc, épinette noire,* et *pin gris* – aux variations climatiques passées et futures le long d'un large gradient latitudinal s'étendant de 46 à 54ºN au niveau de la forêt boréale de l'est du Canada. Les chronologies de cernes issues de 34 peuplements forestiers disposés spatialement à un degré d'intervalle ont été reconstruites le long du gradient. De plus, une approche basée sur l'étude anatomique du bois a été utilisée pour mieux comprendre la formation intra-annuelle de xylème chez *l'épinette noire* sous les climats prédominant actuellement (saisons de croissance 2005 et 2006) le long d'un gradient allant approximativement de 47.5°N à 50°N dans l'est du Canada.

Du fait que les peuplements étudiés du *peuplier faux-tremble* et *bouleau blanc* étaient fréquemment défoliés par des insectes comme la livrée des forêts (*Malacosoma disstria* Hubner), les périodes de défoliations sévères dues aux insectes ont été identifiées par la mise en évidence de cernes pâles/étroits chez les espèces hôtes et ensuite comparées avec la chronologie des espèces non hôtes dans le chapitre I. Quelques épidémies majeures sont survenues avec une synchronicité relativement étroite à l'échelle régionale mais au stade initial de l'épidémie, l'intensité et l'étendue de cette dernière variaient dans l'espace. Par exemple, les épidémies des années 1950 ont été observées de 1951 à 1952 à 46°N, de 1953 à 1954 à 47°N et de 1954 à 1956 à 48°N. D'autres épidémies importantes comme celles de 1964 et 1980 étaient assez bien synchronisées aux latitudes nordiques. Les épidémies observées dans les peuplements de peuplier faux-tremble à la latitude 54°N fournissent des preuves manifestes que des défoliations sévères causées par les insectes surviennent beaucoup plus au nord qu'au niveau de la limite de l'aire de répartition couramment rapportée, soit entre 49°N et 51°N, dans le cas du plus important défoliateur du peuplier, la livrée des forêts. Les valeurs de cernes pâles identifiant les épidémies sévères ont ensuite été utilisées pour corriger le bruit, ce qui a permis de mettre en évidence les signaux climatiques qui pourraient servir aux futures études portant sur l'interaction climat-croissance.

Les chronologies corrigées des largeurs de cernes de 16 feuillus et de celles de 18 conifères ont été transformées en composantes principales (CP) et analysées à l'aide d'une corrélation par 'bootstrap' au cours de la période 1950-2003 pour identifier les facteurs climatiques restreignant la croissance radiale et les détails de l'association croissance radiale-climat le long du gradient. Pour toutes les espèces confondues, ce sont les températures estivales passées (influences négatives) et les températures

actuelles de janvier et de mars-avril (influences positives) qui ont montré les relations avec la croissance radiale les plus fortes le long du gradient. Combinée aux facteurs climatiques spécifiques aux espèces ou aux sites identifiés, notre étude a suggéré que les conditions hydriques durant l'année précédant la croissance radiale ont joué un rôle prépondérant dans la régulation positive de la croissance du *peuplier faux-tremble,* tandis que la température de janvier et les conditions hydriques de la saison de croissance ont eu un impact positif sur la croissance du *bouleau blanc.* Par ailleurs, *l'épinette noire* et *le pin gris* étaient tous deux positivement affectés par l'hiver et le printemps de l'année en cours, ou par les températures de la saison de croissance dans sa globalité et ce, à travers toute l'étendue de notre corridor. En raison des impacts des divers facteurs climatiques sur la croissance, ces espèces boréales ont montré des réponses contrastées au réchauffement récent dans la zone de transition, où *le bouleau blanc, l'épinette noire*, et *le pin gris* seraient les espèces les plus sensibles comparativement au *peuplier faux-tremble* qui serait l'espèce la moins sensible.

Au chapitre trois -en se basant sur les modèles empiriques développés, les modèles dynamiques et ceux locaux sont construits à partir des deux hypothèses suivantes: (1) La croissance future des peuplements au niveau des latitudes nordiques pourrait être prédite par les relations croissance-climat établies pour les peuplements actuellement localisés au niveau des latitudes sud, étant donné que les conditions de croissance des arbres pourraient changer au cours du temps avec le réchauffement climatique, (2) La croissance future des arbres pourrait être prédite par les relations -croissance-climat obtenues à partir d'un site local donné, lorsqu'on considère l'effet des contraintes génétiques ou le délai de la réponse génétique au climat sur la croissance. Ces deux types de modèles ont été utilisés pour prédire les variations de croissance radiale des quatre espèces entre 2010 et 2099 suivant plusieurs scénarios de changements climatiques dont les données ont été générées par GCMs et CRCM3. Les simulations de croissance obtenues à partir de ces deux modèles pourraient constituer deux bases théoriques pour les futures variations de croissance radiale de ces espèces au niveau de la forêt boréale de l'est du Canada au cours du 21$^{\text{ème}}$ siècle. Les prédictions indiquent que les peuplements localisés au nord auront une meilleure croissance en raison des conditions climatiques favorables prévues pour la saison de croissance, alors que les peuplements localisés au sud pourraient montrer de faibles variations ou bien même une réduction de croissance du fait de l'augmentation du stress hydrique. Parmi les quatre espèces, *le pin gris* pourrait être le plus avantagé par le réchauffement climatique pour ce qui est de la possibilité d'accroître la croissance radiale le long du gradient au cours du 21$^{\text{ème}}$ siècle.

Au chapitre 4, l'étude anatomique du bois a montré que du sud au nord, la date de début de formation des cellules du xylème de l'épinette noire au niveau des trois sites a respectivement été détectée le 20 mai (±3), le 24 (±3) mai et le 24 (±4) mai 2005 d'une part et le 12 (±4) mai, le 14 (±3) mai et le 20 (±3) mai 2006 d'autre part. La date de l'arrêt de formation de nouvelles cellules de bois tardif du xylème a été respectivement observée le 11 (±4) août, le 7 (±3) août et le 7 (±4) août 2005 d'une part et le 8 (±4) août, le 4 (±4) août et le 4 (±4) août 2006 d'autre part. Comparée à 2005, la température élevée de mai a été responsable de la formation précoce de cellules du xylème en 2006. Toutefois, les températures basses de juin-août ont entraîné l'arrêt précoce de la formation de cellules du xylème en 2006. Les arbres des sites situés au sud ont débuté plus précocement la formation de cellules du xylème que les arbres situés dans les deux autres sites nordiques en raison d'un printemps plus précoce au sud comparativement au nord.

Notre étude supporte l'idée générale selon laquelle les peuplements nordiques verraient leur croissance radiale accroître au cours d'un réchauffement climatique. Ainsi, dans le futur, les feuillus seraient en mesure de se développer au niveau des forêts conifériennes boréales pures du nord.

ABSTRACT

To address the central question of how climate change influences growth of trees and forests within the context of global warming, we used dendrochronological approach to systematically investigate the responses of four dominant boreal tree species – *Populus tremuloides*, *Betula papyrifera*, *Picea mariana*, and *Pinus banksiana* – to climatic variations in the past and future along a broad latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest. Tree-ring chronologies from 34 forested stands distributed at a one-degree interval were built over the gradient. In addition, we also used the wood anatomical approach to better understand the intra-annual xylem formation of *P. mariana* during today's climate (2005 and 2006 growing seasons) along a gradient from approximately 47.5°N to 50°N in eastern Canada.

Since the studied *P. tremuloides* and *B. papyrifera* stands are frequently defoliated by insects like the forest tent caterpillar (*Malacosoma disstria* Hubner) in the studied region, we first identified periods of severe insects defoliation based on the observed white/narrow tree rings as well as host and nonhost species comparisons in the Chapter I. Some major outbreaks occurred in relatively close synchrony at the regional scale, but the initiation year, the intensity and extent of the outbreaks varied spatially. For example, the 1950s outbreaks were observed from 1951-52 at 46°N, 1953-54 at 47°N, and 1954-56 at 48°N. Other major outbreaks like the 1964 and 1980 outbreaks were fairly well-synchronized at northern latitudes. The observed outbreaks in aspen stands at latitude 54°N also provided clear evidence that severe insect defoliation occurs much further north than the currently reported range limit, i.e., between 49 and 51°N, of the most important aspen defoliator, the forest tent caterpillar. Ring-width values of the identified severe outbreak years were further corrected to remove insect outbreaks noise and highlight climate signals for further climate-growth studies.

In Chapter II, the corrected 16 broadleaf ring-width chronologies together with 18 coniferous ring-width chronoliges were all transformed into principal components (PCs), and analyzed through bootstrapped correlation analysis over the period 1950–2003 to identify climate factors limiting the radial growth and the detailed radial growth-climate association along the gradient. All species taken together, previous summer temperature (negative influences), and current January and March-April temperatures (positive influences) showed the most consistent relationships with radial growth across the gradient. Combined with the identified species/site-specific climate factors, our study suggested that moisture conditions during the year prior to radial growth played a dominant role in positively regulating *P. tremuloides* growth, whereas January temperature and growing season moisture conditions positively impacted growth of *B. papyrifera*. Both *P. mariana* and *P. banksiana* were positively

affected by the current-year winter and spring or whole growing season temperatures over the entire range of our corridor. Owing to the impacts of different climate factors on growth, these boreal species showed inconsistent responsiveness to recent warming at the transition zone, where *B. papyrifera, P. mariana* and *P. banksiana* would be the most responsive species, whereas *P. tremuloides* might be the least.

In Chapter III, based on the established empirical calibration models, the dynamic models and the local models were, respectively, constructed according to the following two assumptions: (1) future growth of the stands at northern latitude may be forecasted by the growth-climate equations established for the stands currently growing at southern latitudes, given that tree growth conditions would be changing with climate warming over time; (2) future tree growth might be maximally predicted by the growth-climate equations obtained from the given local site, when considering the genetic constraints effect or the lagged effect of genetic response to climate on growth. The constructed two types of models were employed to predict radial growth change of the four species from 2010 to 2099 based on several climate change scenarios data generated from GCMs and CRCM3. The dynamic model- and the local model-based growth simulations may constitute two theoretical baselines for future radial growth change of these species in eastern Canada during the 21st century. The northern stands were predicted to show large growth increase due to future favourable growing season climate conditions, whereas the southern stands would show minor growth change or growth decline because of increased drought stress. Of the four species, *P. banksiana* would be the most beneficial species from climate warming to enhance radial growth over the whole gradient during the 21st century.

In Chapter IV, the wood anatomical study revealed that from south to north, the onset date of the xylem cell production of *P. mariana* at the three sites (Angliers, Collines Chicobi, and Collines Muskuchii) was detected on May 20 (±3), May 24 (±3), and May 24 (±4) in 2005, and on May 12 (±4), May 14 (±3), and May 20 (±3) in 2006, respectively. The termination date of the xylem latewood new cell production was observed on August 11 (±4), August 7 (±3), and August 7 (±4) in 2005, and on August 8 (±4), August 4 (±4), and August 4 (±4) in 2006, respectively. Compared with 2005, warm May temperature was responsible for early onset of xylem cell production in 2006. However, cold June-August temperatures resulted in early termination of xylem cell production in 2006. Trees at the southern site often started the onset of xylem cell production earlier than trees at the two northern sites because of earlier starting of spring in the south than in the north.

Our study supports the general concern that under climate warming, the northern stands would be greatly increasing the radial growth. As a consequence, the broadleaf species may be able to develop into the northern pure coniferous boreal forest in the future.

GENERAL INTRODUCTION

0.1. CONTEXT

0.1.1 Climate Change

Climate change at the hemispheric scale

Since the mid-nineteenth century, an increase in temperature has been widely observed in the Northern Hemisphere (Mann *et al.*, 1999; IPCC, 2007). This climate warming is mostly attributed to the effects of anthropogenic forcing (fossil fuel and biomass burning, and deforestation) and natural forcing (solar variation and volcanic aerosols) (Benestad, 1999; Shindell *et al.*, 2001; IPCC, 2007). The anthropogenic-induced increases of emissions of greenhouse gases such as $CO_{2,}$ CH_4, N_2O, HFCs, PFCs, and SF_6 (Swart *et al.*, 2004) and the enhancements of volcanic aerosols are generally believed to be responsible for the 20th-century climate warming. The human-induced buildup of atmospheric CO_2 concentrations has increased from 280 ppm in 1850 to 380 ppm in 2005 (IPCC, 2007). This buildup, coupled with increased concentration of other greenhouse gases together have resulted in an increase of 0.74°C in global mean surface temperature from 1906 to 2005 (IPCC, 2007). In the Northern Hemisphere, the greatest warming was observed during winter (December to February) and spring (March to May). Climate observations suggest that between 1950 and 1993, the average daily minimum air temperatures have often increased at a greater rate (0.2°C per decade) than average daily maximum air temperatures (0.1°C per decade) (Nicholls *et al.*, 1996). The trend analyses of temperature show a very likely ($0.01<p<0.1$) decrease in the frequency of extreme low temperatures but a smaller increase in the frequency of extreme high temperatures (IPCC, 2001). Associated with increased mean global surface temperature, precipitation has increased by 0.5 to 1% per decade in the 20th century over most mid and high latitudes of the Northern Hemisphere (IPCC, 2007), particularly with a 2 to 4%

increase in frequency of heavy or extreme precipitation events over these regions (Nicholls *et al.*, 1996; IPCC, 2001).

Climate change at regional scale

Based on recently updated and adjusted weather station data, the analyses of trends in temperature and precipitation suggest that in Canada (south of 60°N), annual mean temperature and annual total precipitation from 1900 to 1998 have increased between 0.5 °C and 1.5°C, and from 5% to 35%, respectively (Zhang *et al.*, 2000). In the trends of daily temperature, there was a relatively smaller increase in daily maximum temperature and a larger increase in daily minimum temperature. This resulted in a decrease in diurnal temperature range by 0.5°C to 2.0°C in the last century (Zhang *et al.*, 2000). For seasonal precipitation, the analysis of Canadian daily precipitation time series shows that between 1948 and 1995, autumn demonstrates the greatest increase in total precipitation and snowfall, while spring has the largest rain increase (Mekis and Hogg, 1999).

Climate change in the 21st century

Following the Intergovernmental Panel on Climate Change, atmospheric CO_2 concentration is also expected to rise to 700 ppm by the end of the current century. Consequently, this may lead to an additional 1.1°C - 6.4°C increase in global mean surface temperature by 2100, with rapid warming at mid to high northern latitudes (IPCC, 2007). Global model simulations suggest that possibly nearly all land areas will warm more rapidly than the global average in the 21st century, especially those at northern high latitudes in the cold season (IPCC, 2007). They also show that global average vapour concentration and precipitation will increase in the 21st century, and a likely increase in precipitation during the last half of the 21st century will be over northern mid- to high latitudes and Antarctica in winter (IPCC, 2007).

By 2100, in Canada (south of 60°N), it is expected that mean annual temperature in the eastern Canadian boreal forests (Quebec province) may be about 3.5°C higher than today, even 5°C higher during winter, and accompanied by increased precipitation by 10-25% (Plummer *et al.*, 2006).

0.1.2 Effects of climate change on growth of trees and forests at mid and high latitudes of the Northern Hemisphere

Global climate change may have profound impacts on growth of trees and forests through the direct CO_2 fertilization effect (See Appendix I Huang *et al.*, 2007) and indirect effect of increased atmospheric CO_2 concentration on growth. The direct CO_2 fertilization effect is that the rising atmospheric CO_2 might have a positive effect on the above/below-ground biomass by enhancing plant photosynthesis and water use efficiency in a CO_2-enriched world (Körner, 2006; Huang *et al.*, 2007). The indirect effect of increased atmospheric CO_2 concentration on growth is that as a result of greenhouse gases (mostly CO_2) -induced climate change (warming), increased temperature as well as the correspondingly increased precipitation over northern mid- to high latitudes could enhance growth of plants and change forest ecosystems.

Direct CO_2 fertilization effect on growth

Atmospheric carbon dioxide (CO_2) is a substrate for plant photosynthesis. Increased atmospheric CO_2 concentration is believed to, therefore, increase photosynthesis rate by increasing CO_2 intake directly (Arp, 1991; Long and Drake, 1992; Koch and Mooney, 1996; Curtis, 1996; Mooney *et al.*, 1999; Norby *et al.*, 1999). Increased atmospheric CO_2 might induce a partial closure of stomata, reducing water loss by transpiration, which results in an increase in the ratio of carbon gain to water loss, i.e. water use efficiency (Farquhar *et al.*, 1989; Bowes, 1993; Field *et al.*, 1995; Drake *et al.*, 1997; Farquhar, 1997; Körner, 2000). As a result, this effect can lengthen the duration of growing seasons in seasonally dry ecosystems, thus probably stimulating biomass accumulation (Ceulemans and Mousseau, 1994; Saxe *et al.*, 1998), and enhancing ecosystem net primary productivity (Amthor, 1995; Loehle, 1995). This CO_2-induced enhancement in primary productivity and water use efficiency is commonly referred to the direct 'fertilization effect' (Beedlow *et al.*, 2004).

Increased photosynthesis

CO_2 partial pressure is an important limiting factor for photosynthesis (Aranjuelo *et al.*, 2005). Net CO_2 assimilation rate per unit area of C_3 plants is affected by the ratio of atmospheric CO_2 concentration and O_2 concentration since they compete at the active site of the enzyme Rubisco for the primary acceptor, ribulose-1,5-bisphosphate (RuBP). Rubisco catalyses both carboxylation and oxygenation of RuBP. Oxygenation results in respiratory loss of CO_2, and carboxylation results in carbon fixation through the photosynthetic carbon reduction cycle (Morison and Lawlor, 1999). Higher CO_2 level hence increases the leaf internal CO_2 concentration and the CO_2:O_2 ratio at the Rubisco site, which favours carboxylation rather than oxygenation of RuBP (Andrews and Lorimer, 1987; Jensen, 2000), and thus suppresses respiration and enhances photosynthesis, consequently increasing net photosynthesis (Eamus, 1991; Stitt, 1991; Arp, 1991; Long and Drake, 1992; Saxe *et al.*, 1998).

Körner (2006) summarized that stimulation of leaf photosynthesis was evidenced unequivocally in experiments when plants were exposed to enriched CO_2. However, increases in the rates of photosynthesis varied with the duration of the experiment, the maturity stage of the trees, the plant N status, and the experimental exposure technique (Saxe *et al.*, 1998; Ainsworth and Long, 2005). It also varied within canopy, seasonally or between species (Norby *et al.*, 1999). Norby *et al.* (1999) reported that photosynthesis was stimulated by 40-80% in most of the experiments with the exception of greater enhancement in several cases under enriched-CO_2 environment. A meta-analytical review of free-air CO_2 enrichment (FACE) experiments found that trees were more responsive than other function types to elevated CO_2 (Ainsworth and Long, 2005). In a review of short-term CO_2-enriched experiments (less than one season), Ceulemans and Mousseau (1994) found that photosynthesis of deciduous species was more sensitive to elevated CO_2 than that of conifers. However, evidence from long-term studies (more than one season) suggested that photosynthesis stimulation enhanced by elevated CO_2 was similar in unstressed conifers and deciduous trees, ranging from 50-60% (Norby *et al*., 1999). Gunderson and Wullschleger (1994) did not observe a significant difference in photosynthesis response under elevated CO_2 between conifers and deciduous trees.

Increased water use efficiency

Increased atmospheric CO_2 concentration will increase the ratio of CO_2 to O_2 in the substomatal cavity. This will decrease carbon losses due to photorespiration. Drought induces stomatal closure and decreases partial pressure of CO_2 in the leaf. Increased CO_2 concentration may induce stomatal closure and could result in an increase in the ratio of carbon gain to water loss, i.e. water use efficiency, at the leaf and whole stand level, and higher plant biomass (Farquhar *et al*., 1989; Field *et al*., 1995; Picon *et al*., 1996; Drake *et al*., 1997; Centritto *et al*., 1999; Körner, 2000; Wullschleger *et al*., 2002; Morgan *et al*., 2004). Also increased allocation of carbon to root growth (e.g. increased fine roots, root surface area and volume) and osmotic adjustment in plants exposed to enriched CO_2 may, for example, enable plants to exploit soil water in a deeper and larger range of soil (Wullschleger *et al*., 2002). In addition, altering developmental processes including root and shoot architecture (Berntson and Woodward, 1992; Miao *et al*., 1992) and leaf morphology (Thomas and Harvey, 1983) under enriched CO_2 concentration might affect water relations and plant response to drought. Consequently, these responses could increase water uptake and improve water balance in plants, hence ameliorating the negative effects of water stress and better adapting to a water-limited environment (Wullschleger *et al*., 2002;

Morgan *et al*., 2004). A review article pointed out that although the cause and effect relationships between growth, gas exchange, anatomy and plant water relations were rarely established in many conducted experimental CO_2-enriched studies, it would be probable that plants could benefit from increased root-shoot ratio or fine-root proliferation to better adapt to a water-limited environment (Wullschleger *et al*., 2002). In a FACE experiment on a closed-canopy, deciduous sweetgum forest, Norby *et al*. (2004) observed the CO_2-induced increase in fine-root standing crop (total length of root visible) in summer, which might be an important mechanism for conferring increased resistance to late-season drought. Morgan *et al*. (2004) suggested that the effect of enriched-CO_2 induced increases in water use efficiency and thus plant biomass enhancement might be especially important in drier ecosystems.

Above-ground growth

Elevated CO_2 persistently increases leaf area index, leaf number, branches, thus positively changing canopy structure under optimal conditions (e.g. Idso and Kimball, 1994; Norby *et al*., 1995; Griffin *et al*., 1995; Epron *et al*., 1995; Ceulemans *et al*., 1996; Tingey *et al*., 1996; Tissue *et al*., 1997; Arp *et al*., 1998). Open-top chamber experiments usually showed an increase in leaf area of seedlings and saplings with CO_2 enrichment (Norby *et al*., 1999). For example, Tissue *et al*. (1997) reported a 217, 80, 58, and 41% increase in leaf area of loblolly pine (*Pinus taeda* L.) growing in elevated CO_2 environment for subsequent four growing seasons when compared to ambient CO_2, respectively. A meta-analysis found that trees had a 21% increase in leaf area index compared to less response of herbaceous C_3 grasses (Ainsworth and Long, 2005). Increase in leaf area of *Quercus alba* L. saplings in elevated CO_2 also can be ascribed to increased leaf number, leaf size and, more or less, changed leaf shape (Gregory, 1996). By modifying leaf area, number and size, as well as tree height, elevated CO_2 concentration could influence branching patterns

(Gunderson and Wullschleger, 1994) and, consequently, change canopy structure (Saxe *et al*., 1998). Past studies on *Liriodendron tulipifera* L. (Murray and Ceulemans, 1996), *P. taeda* (Tissue *et al*., 1997), and *Alnus glutinosa* L., *Fraxinus angustifolia* Vahl. and *Q. robur* L. (Bucher *et al*., 1997) found that elevated CO_2 significantly increased the number of branches (Saxe *et al*., 1998), which resulted in changes in crown size and structure (Bazzaz *et al*., 1993). A 25% increase in branch number summarized from six species at three FACE sites was reported (Ainsworth and Long, 2005).

Elevated CO_2 concentration generally increases stem biomass (Curtis *et al*., 1996; Saxe *et al*., 1998; Ainsworth and Long, 2005). An increase in seedling dry matter production of *P. radiata* D. and *P. virginiana* Mill. was observed under low nutrient conditions exposed in CO_2 enrichment for 22 and 16 weeks, respectively (Conroy *et al*., 1986; Luxmoore *et al*., 1986). Idso and Kimball (1992) found that *C. aurantium* trees had approximately 160% more trunk and branch volume under CO_2 enrichment than trees under ambient CO_2. Saxe *et al*. (1998) reviewed the short-term CO_2-enriched experiments and summarized that, on average, elevated atmospheric CO_2 significantly enhanced tree biomass with increasing exposure time. Under the mean exposure duration of 338 days, conifers increased their biomass by 130%, whereas deciduous trees exposed during 329 days increased by only 49%. Based on meta-analysis on the FACE experiments, Ainsworth and Long (2005) reported that elevated CO_2 resulted in taller plants with larger stem diameter, and plant height enhancement in the third growing season was greater than in the first and second. They further pointed out that shrubs and trees showed more height increases than C_3 crops, and trees exhibited the largest response (28%) in dry matter production. Norby *et al*. (2005) observed a growth increase of 23% in a synthesis analysis of four FACE studies on dominant trees in multi-species forests. Wang (2007) quantitatively evaluated the responses of above-ground biomass of woody species to enriched CO_2

by meta-analysis and observed an increase of 31% and 23% at the population and community levels, respectively. In addition, other reviews (e.g. Ceulemans and Mousseau, 1994; Lloyd and Farquhar, 1996; Curtis and Wang, 1998; Norby *et al*., 1999) showed an increase in stem growth and dry biomass, although the increased rates of growth were different among the studies. Norby *et al*. (1999) ascribed these differences to the growth rate or growth potential of different species, effects of environmental interactions, or differences in experimental protocol.

Elevated CO_2 might also affect phenology such as sprouting, periodicity of leafing, flowering, and fruiting through changes in tree biochemistry and physiology (Jach and Ceulemans, 1999), and through warming effect. Changes in starch or hormonal concentrations may alter dormancy status and growth patterns by shifting timing and duration of the vegetative season (Saxe *et al*., 1998; Norby *et al*., 1999). In a two-year open-top chamber experiment on three-year-old *P. sylvestris* L., elevated CO_2 significantly advanced date of bud burst in both first and second years of the experiment (Jach and Ceulemans, 1999). Repo *et al*. (1996) observed that dehardening in *P. sylvestris* seedlings grown at increased temperatures proceeded significantly faster if concurrently exposed to elevated CO_2 concentration. Saxe *et al*. (1998) reported that, if the leaf development is hastened under elevated CO_2 in the spring, trees could potentially benefit from an earlier onset of carbon assimilation at the start of growing seasons. They further pointed out that this could be an important factor to influence expansion of tree populations into areas currently too cold for their growth. Since most of the work is done with immature plants (seedlings and young trees), little is known about the CO_2 effect on flowering and fruiting (Saxe *et al*., 1998). LaDeau and Clark (2001) have done an experiment study exposing 19-year-old *P. taeda* to 4 years of CO_2 enrichment in an intact forest of North Carolina, and found that trees were twice as likely to be reproductively mature and produced three times as many cones and seeds as trees at ambient CO_2 concentration. This indicates that a higher carbon allocation to reproduction under enriched CO_2 results in trees reaching maturity sooner and at a smaller size (LaDeau and Clark, 2001). Further study demonstrated that seed weight increased by 91% in elevated CO_2 and seeds germinated much earlier, with more than three times germination success compared to the ambient seed source (Hussain *et al.*, 2001). A CO_2-enriched study on reproduction of hardwood trees (*Q. myrtifolia* Willd., *Q. chapmanii* Sarg., and *Q. geminate* Small) in a natural scrub-oak forest of Florida suggested that the number of acorns produced under elevated CO_2 was significantly higher than in ambient CO_2 (Stiling *et al*., 2004).

Below-ground growth

The responses of roots to CO_2 are dependent on experimental conditions (Ceulemans and Mousseau, 1994). Low nutrition and water availability tend to increase the ratio of root to shoot in response to CO_2 enhancement (Stulen and den Hertog, 1993; Saxe *et al*., 1998), allowing plants growing on poor and dry sites to explore a greater soil volume to acquire water and nutrients (Day *et al*., 1996; Norby *et al*., 2004; Phillips *et al*., 2006; Norby and Iversen, 2006). Earlier studies on responses of potted tree seedlings growing in low nutrient conditions generally concluded that the ratio of root mass to shoot mass increased in elevated CO_2 condition (Oechel and Strain, 1985). By reviewing plant root and rhizosphere response to elevated CO_2, Rogers *et al*. (1994) found that root dry weight increased in all studies under elevated CO_2. However, a few destructive harvest multi-year studies of trees in elevated CO_2 showed no significant effect on root-to-shoot ratio in *L. tulipifera* (Norby *et al*., 1992), *Q. alba* (Norby *et al*., 1995), *Betula pendula* Roth. (Rey and Jarvis, 1997), *P. taeda* (Tissue *et al*., 1997), *P. ponderosa* Dougl. (Walker *et al*., 1997), or *F. excelsior* L., *Q. petraea* Liebl. and *P. sylvestris* (Crookshanks *et al*., 1998). In a FACE experiment of *P. taeda* forest of North Carolina, Allen *et al*. (2000) found that elevated CO_2 caused significant increases in loblolly pine fine root increment after two growing seasons. Lukac *et al*. (2003) revealed that elevated CO_2 increased belowground allocation of biomass in three *populus* species investigated (*P. alba* L., *P. nigra* L., and *P. x euramericana* Dode (Guinier)), and standing root biomass enhanced by 47-76% as a result of FACE treatment. Norby *et al*. (2004) reported that annual production of fine roots was more than doubled in plots with 550 ppm CO_2 compared with plots in ambient CO_2 in a FACE experiment on a closed-canopy, deciduous sweetgum forest.

Impacts of changing temperature and precipitation on tree growth

As a result of climate warming, changes in temperature primarily determine biome area responses for the temperate deciduous forest, tundra, polar desert, and boreal forest vegetation types (Higgins and Vellinga, 2004). Located at high latitudes of the Northern Hemisphere, the circumboreal forests are expected to be among the first eco-regions to respond significantly to global warming over the 21^{st} century (IPCC, 2001). Climate warming influences tree growth and forest dynamics in different ways by altering ecophysiology (Prentice *et al.*, 1996), water availability (Bazzaz *et al.*, 1996; Heal *et al.*, 1996), forest disturbance regimes such as forest fires and insect outbreaks (Bergeron, 1998; Volney and Fleming, 2000), as well as ecosystem processes such as soil nutrient regimes by affecting organic matter mineralization dynamics (Running and Nemani, 1991; He *et al.*, 1999).

Phenology change

Climate warming has resulted in changes in tree phenology and extended growing season because of early spring and late autumn (IPCC, 2007). Long-term surface phenological observations from Europe indicate approximately 11-day lengthening of the growing season from 1959 to 1993 (Menzel and Fabian, 1999). Recent satellite remote sensing measurements also consistently show an extension of 12±5 days in North America from 1981 to 1999 (Zhou *et al.*, 2001) and of 12 days in vegetation area north of 45ºN from 1981 to 1994 (Shabanov *et al.*, 2002). Correspondingly, plant phenological observations demonstrated early leafing, flowering, and fruiting in 78% of 542 plant species in spring/summer, as well as late leaf coloring in 52% of those species in autumn recorded across Europe from 1971 to 2000 (Menzel *et al.*, 2006). Similar plant phenological responses to warming were also extensively observed in many empirical and experimental studies in North America (Beaubien and Freeland, 2000; Chuine and Beaubien, 2001; Root *et al.*, 2003; Sherry *et al.*, 2007). In the boreal forest of Canada, previous studies showed that warm winter could generate early bud in spring for white spruce in Quebec (Colombo, 1998) and for trembling aspen in Albert (Beaubien and Freeland, 2000). Positive effects of extended growing season on tree growth have also been observed in other studies in the southern mixed and coniferous boreal forest (Archambault and Bergeron, 1992; Tardif and Bergeron, 1993; 1997b; Hofgaard *et al.*, 1999; Girardin and Tardif, 2005).

Effect of temperature on tree radial growth of the northern boreal forest

Tree growth in the northern limit of the boreal forest is generally controlled by temperature (Fritts 1976; Jacoby and Cook, 1981; Jacoby and D'Arrigo, 1989; D'Arrigo and Jacoby, 1993; Earle *et al.*, 1994; Briffa *et al.*, 1995). Hence an increased temperature might have significant effects on tree growth in the northern tree line. Past studies showed that increasing temperature has led to enhanced tree growth at the northern tree limit in the 20th century compared to the Little Ice Age (Lavoie and Payette, 1992; Lloyd and Fastie, 2002; Gamache and Payette, 2004). While beyond a certain threshold rising temperature could induce drought stress and reduce tree growth at the northern tree limit (D'Arrigo *et al.*, 2008). With the slightly decreasing of the latitude, several studies demonstrated that increased temperature had negative effects on tree growth at the northern boreal forest. Dang and Lieffers (1989) reported that growth in black spruce (*Picea mariana* (Miller) BSP) at the northern boreal forest of Albert peatlands was negatively correlated with summer temperature, but positively related to summer precipitation. Brook *et al.* (1998) found that increased temperature negatively affected annual growth of *P. mariana*, whereas precipitation tended to have a positive effect on growth at the northern and southern limit of the boreal forest in central Canada. In addition, increased winter precipitation in northern areas as a result of recent climate warming (IPCC, 2001) can cause delayed snowmelt and shortened growing seasons, hence altering the response of tree growth to the rising temperature (Vaganov *et al.*, 1999; Kirdyanov *et al.* 2003).

Effect of synoptic climate factors (temperature, precipitation, and drought) on the southern boreal forest

In the southern boreal forest, precipitation often plays a more important role in regulating tree growth than temperature. Tardif and Bergeron (1993) reported that the radial growth of a flooding-influenced species of *Fraxinus Nigra* Marsh. at Lac Duparquet was negatively influenced by April-June precipitation of the prior year and positively affected by April-May temperature of the prior year and April temperature and June precipitation of the current year. Tardif *et al.* (2001a) studied the climate-growth relationships of the three tree species (eastern hemlock *Tsuga canadensis* (L), sugar maple *Acer saccharum* Marsh, and American beech *Fagus grandifolia* Ehrh.) in southwestern Montreal and found that their radial growth positively correlated with precipitation and negatively correlated with temperatures during the early summer months of the current growth year. Tardif *et al.* (2001b) also suggested that radial growth of *Betula papyrifera* Marsh. was mainly correlated to June precipitation, whereas six other conifer species (*Abies balsamea* L. (Mill.)*; Thuja occidentalis* L.*; Picea glauca* (Moench.) Voss*; P. mariana; Pinus banksiana* Lamb.*; Pinus resinosa* Sol. ex Aiton) were positively correlated to warm April and to cool-wet July of the current growth year at Lac Duparquet of northwestern Quebec. Girardin *et al.* (2004a) reconstructed the July Canadian Drought Code (CDC: a daily numerical rating of the average moisture content of deep organic layers) using tree rings of *P. mariana, P.*

banksiana, Thuja occidentalis, B. papyrifera and Fraxinus nigra in Abitibi Plains of eastern Canada. In the boreal plains of Manitoba, Girardin and Tardif (2005) found that the stronger factor influencing growth of *B. papyrifera, Populus tremuloides* Michx., *Populus balsamifera* L., *P. glauca, P. mariana; P. banksiana; and A. balsamea* was the summer drought stress. Similar moisture stress limiting tree growth was also reported in other studies in the southern boreal forest of Canada (Hogg, 1994; Chhin *et al.*, 2004).

Effect of changing temperature on other aspects of the boreal forest

Rapid warming in surface air temperature at mid to high northern latitudes has also led to increased soil temperature and soil freeze-thaw in both permafrost and non-permafrost regions (Osterkamp and Romanovsky, 1999). As a result, the decomposition rates of soil organic matter are accelerated (Davidson *et al.*, 2000), thereby resulting in more readily mineralized nutrients available to plants, particularly of the most common limiting nutrient, nitrogen (Luo *et al.*, 2004). In addition, climate warming might have direct effects on forest dynamics in the boreal forest. In the southern boreal forests of Quebec, a decrease in fire frequency has been observed due to increased precipitation after the Little Ice Age (Bergeron, 1991; Bergeron and Archambault, 1993). Under the simulation of a 2X CO_2 scenario, a decrease in fire frequency accompanied by a reduction of drought periods may continue during the 21st century (Bergeron and Flannigan, 1995). Furthermore, climate warming might also increase the frequency and amplitude of forest insect outbreaks (Volney and Fleming, 2000; IPCC, 2007) in the future.

All these impacts together might be leading to changes in growth of trees and forests. Consequently in the long run it will result in a shift in species composition and community structure (Weltzin *et al.*, 2003), and ultimately causing substantial change that varies with vegetation type in the boreal biome (Goetz *et al.*, 2005). Within the context of sustainable forest development, it is critical to better understand the responses of boreal tree species to climate variability and change, and increase our capacity to predict potential changes in forest composition and structure in this biome in the future.

0.2. STUDY METHODS AND RATIONALITY

Ecological gradient analysis is often used to identify the interactions between plant species and their spatial distributions in relation to eco-environmental factors (Ohmann and Spies, 1998). The landscape-scale species distribution and abundance patterns are generally believed to be controlled by climate, i.e. temperature and soil moisture (Gosz, 1992) and to be influenced by the spatial and temporal patterns of natural or human-caused disturbances (Bekker and Taylor, 2001). In western Quebec, under the shift in air mass dominance as well as the impacts of natural or human-induced disturbances such as forest fires (Bergeron, 2004) and insect outbreaks (Volney and Fleming, 2000), forest composition gradually changes from the deciduous-dominated temperate forest in the south to the coniferous-dominated boreal forest in the north (ESWG, 1996). A vegetation transition zone between the mixedwood and the coniferous-dominated boreal forest occurs at approximately 49ºN (Gauthier *et al.*, 2000).

To predict radial growth response of the dominant boreal tree species to future climate in the eastern Canadian boreal forest, this study was based on the assumption that the effect of future climate warming on tree and forest growth could be resembled by a broad-spatial-scale gradient study on the effect of past climate on tree growth. That is, we assume that tree growth response to climate at the temporal scale may be resembled by tree growth response to climate at the spatial scale, i.e., tree growth response to climate along a broad latitudinal gradient from south to north may constitute an analogue of tree growth response to future climate warming over time.

The main approach used in this study is dendrochronology (Fritts, 1976). That is, stem radial growth for any given year is often believed to integrate the effects of the previous and current year's climate (Fritts, 1976). Hence tree rings have long been used as a valid tool to explore the long-term growth reactions to the historical climate variations (e.g., Huang and Zhang, 2007) and to further assess the impacts of future climate warming on tree growth and forest ecosystems. In this study, dendroecology approach has also been used to investigate forest dynamics such as insect outbreaks, i.e., Chapter I (Huang *et al.*, 2008).

In addition, recent developed novel approach, micro-sampling-based intra-annual growth study (Deslauriers *et al.*, 2003a, 2003b; Rossi *et al.*, 2003; Zhai *et al.*, to be submitted), was also employed to investigate the major meteorological factors determining intra-annual radial growth (formation of the xylem) of black spruce during the growing seasons along a latitudinal gradient in western Quebec (see Chapter IV for more details).

0.3. GENRERAL QUESTIONS AND HYPOTHESES

It is hypothesized that (1) the present vegetation pattern in the boreal region is mainly controlled by the climatic response of deciduous species; (2) a decrease in the length of the growing seasons or a change in the general conditions towards the north would be responsible for a decrease in the abundance of the deciduous components of the boreal forest; (3) future climate will favour an extension of the mixedwoods into the conifers-dominated boreal forest. Under the predicted climate warming of the current century, however, to achieve the goal of sustainable forestry development, it is necessary to answer the following two general questions:

(1) How does the climate control the radial growth of the dominant boreal tree species along the gradient?

(2) How will future climate warming affect their radial growth along the

gradient?

0.4. STUDY AREA

Our study area is located at the Quebec-Ontario border along a latitudinal gradient ranging south from Petawawa (approximately 46°N) to Radisson (approximately 54°N) in the north (Figure 0.1), including the Ottawa River Valley, the southern Laurentians, the Abitibi Plains, the James Bay area, and the Radisson Plains (ESWG, 1996). The topography along the gradient is generally flat and uniform with low-elevation hills and rock outcrops (300-400 m a.s.l.).

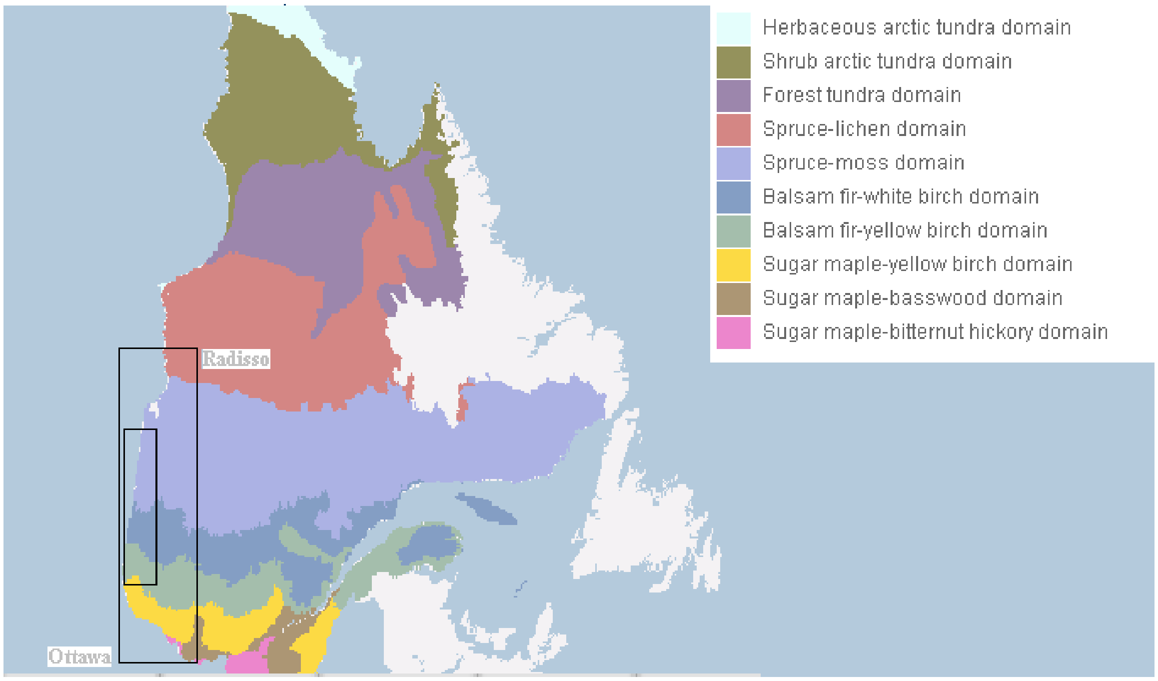

Figure 0. 1 Map showing our study region in the eastern Canadian boreal forest. Smaller square is our monitoring area of tree growth (approximate 47.5°N-50°N) and larger square is our broad-latitudinal gradient study region in the eastern Canadian boreal forest (approximate 46°N-54°N).

The climate of the region is dominated by dry polar and moderate polar air masses during the winter, and by moist maritime and moist tropical air masses during the summer (See Figure 2.1 in the Chapter II). Dry moderate air masses also often occur after an air mass has been advected far from its source region and has thus been modified considerably (Sheridan, 2002). A climate gradient is also enclosed within the studied latitudinal gradient. Averaged climate data generated from the ANUSPLIN model (see climate data section of Chapter II) for the reference period 1950-2003 showed a linear decrease in mean annual maximum temperature (R^2adj= 0.96, P<0.0001), mean annual temperature (R^2adj= 0.91, P<0.0001), mean annual minimum temperature (R^2adj= 0.85, P=0.0002), and mean annual total precipitation (R^2adj= 0.82, P=0.0005) against the latitude from south to north, i.e., from 10.39°C, 4.52°C, -1.35°C, and 893 mm at 46° N to 1.93°C, -2.84°C, -8.20°C, and 644 mm at 54° N, respectively. The growing degree-days (>5°) also declined from 1 868°C at 46° N to 862°C at 54° N across the latitude (R^2adj= 0.90, P<0.0001). Climate normals from 1971 to 2000 showed a clear decreasing trend in mean annual temperature (Environment Canada, 2002) (Figure 0.2), mean annual total precipitation (Figure 0.3), and mean growing season length (Figure 0.4) along the south-north latitudinal gradient. In the study area, a significant warming trend in growing seasonal average temperatures (April-September) from 1950 to 2003 was observed at each site (See Figure 2.1 in the Chapter II). Similar trends were also found in climatic data sets of the Climate Research Unit (CRU 2.1 data; Mitchell and Jones, 2005).

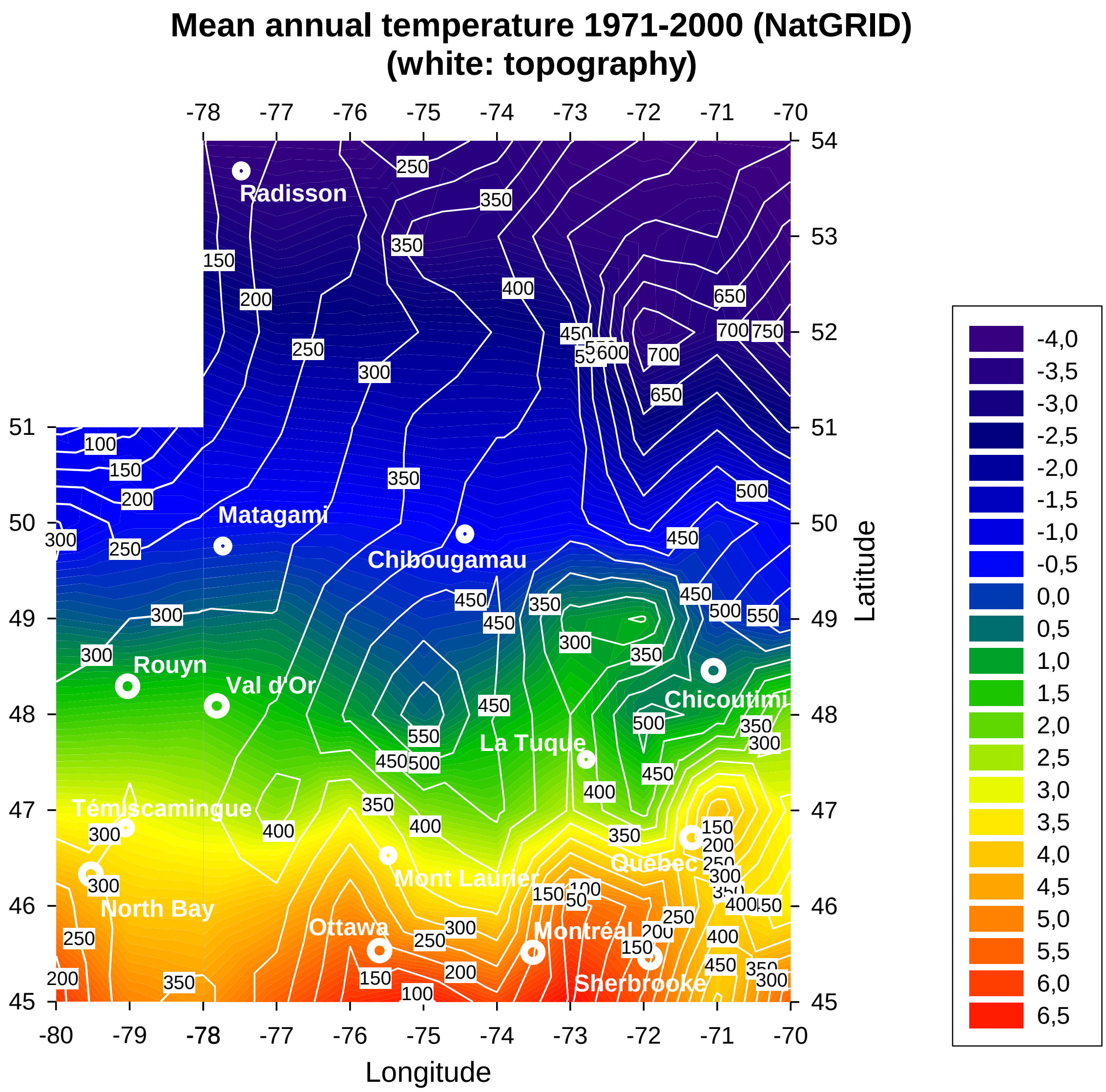

Figure 0. 2 Mean annual temperature from 1971 to 2000 along the latitudinal gradient in eastern Canada.

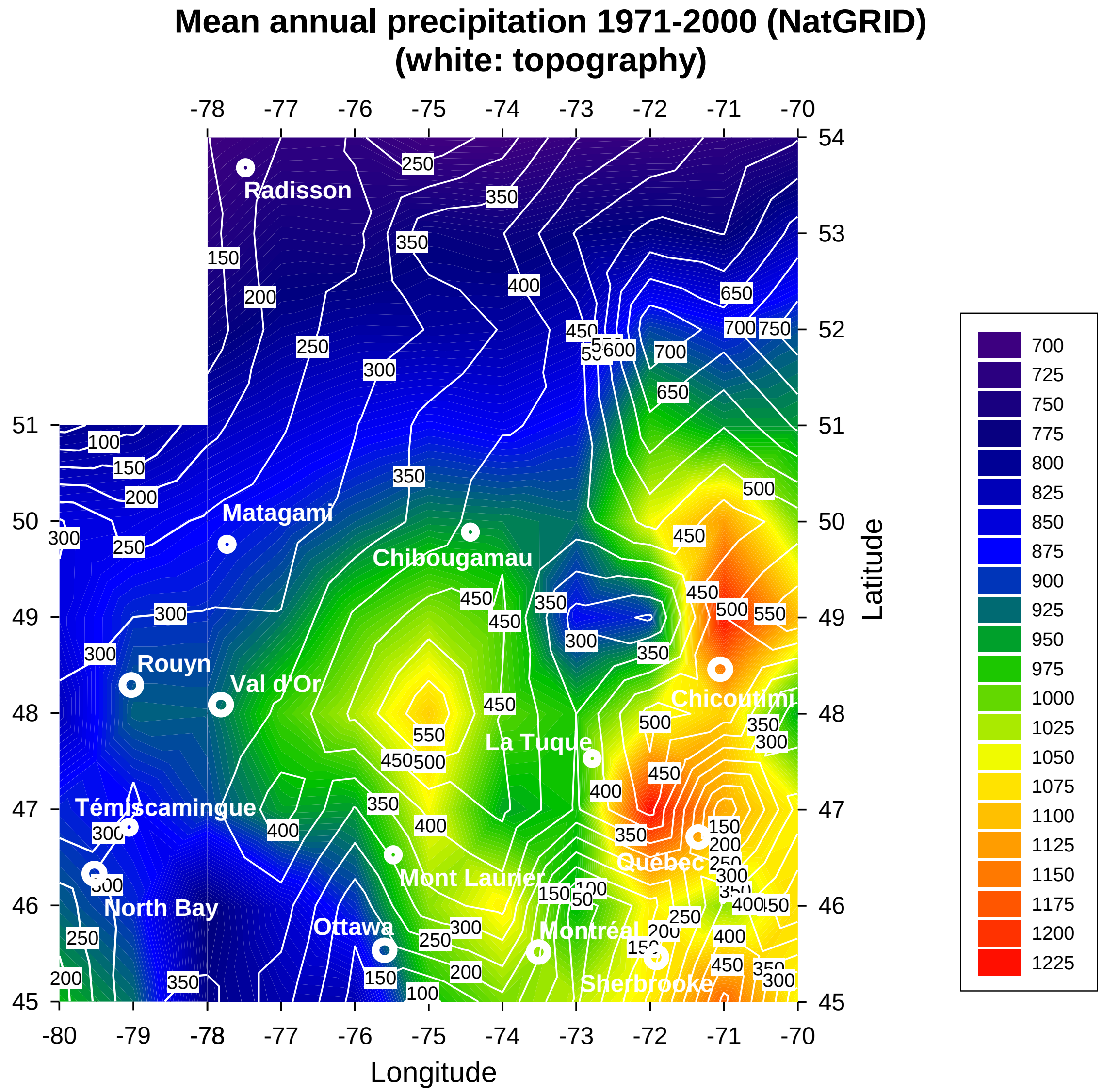

Figure 0. 3 Mean annual total precipitation from 1971 to 2000 along the latitudinal gradient in eastern Canada.

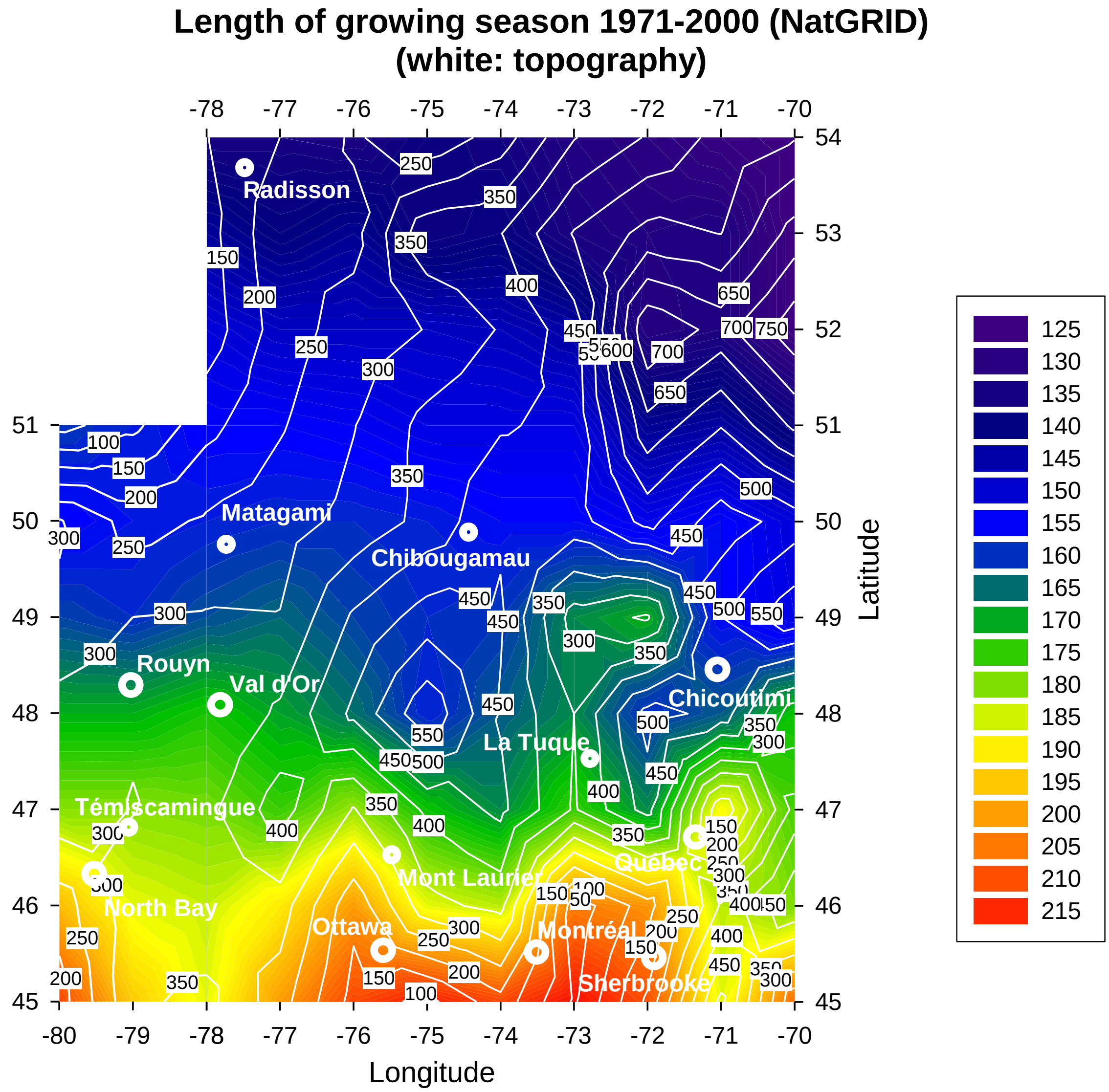

Figure 0. 4 Mean growing season length from 1971 to 2000 along the latitudinal gradient in eastern Canada.

Three bioclimatic zones encompass the study area from south to north (Figure 0.1), including 1) sugar maple-yellow birch domain, which is dominated by sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton); 2) balsam fir-yellow birch, and balsam fir-paper birch climax zone, which is dominated by balsam fir, yellow birch, paper birch with post-fire stands of jack pine and trembling aspen on the driest sites; and balsam fir-paper birch bioclimatic domain, 3) black spruce-lichen, and black spruce-moss climax zone, which is characterized by the dominant black spruce stands with post-fire stands such as trembling aspen, paper birch, and jack pine (ESWG, 1996). Along the south-north gradient, common boreal tree species including trembling aspen, paper birch, black spruce, and jack pine occur but their abundance changes from south to north (Gauthier *et al.*, 2000). The studied gradient crosses the southern boreal forest region where both black spruce and jack pine approach their southern distributional limit of regional dominance (Burns and Honkala, 1990) and where trembling aspen approximately approaches its northern distributional limit, i.e., in the Hudson Bay region (Little, 1971).

0.5. SPECIFIC OBJECTIVES AND THE RELATIONS BETWEEN CHAPTERS

In this study, we conducted a dendroclimatic investigation on four major boreal tree species along a broad latitudinal gradient spanning from 46ºN to 54ºN and covering the vegetation transition zone in the eastern Canadian boreal forest. We also used the wood anatomical approach to investigate the intra-annual xylem formation of the boreal species during the two growing seasons along the gradient from approximately 47.5 to 50ºN in western Quebec. The studied tree species were: trembling aspen, paper birch, black spruce, and jack pine.

The specific studied objectives were:

1) The Chapter I aimed to identify the major insect outbreaks years that occurred in trembling aspen stands along the gradient based on the observed white/narrow rings and the host/nonhost species comparisons in western Quebec.
2) The Chapter II aimed to establish and investigate the climate-radial growth associations of two broadleaf species (*P. tremuloides*, and *B. papyrifera*) and two coniferous species (*P. mariana*, and *P. banksiana*) along a latitudinal

gradient (46°N-54°N) covering the transition zone from the temperate to the boreal forest, and further explore the systematic changes in their climate-growth relationships along the gradient in the eastern Canadian boreal forest.

3) The Chapter III mainly focused on predicting future radial growth of these four dominant boreal tree species along the latitudinal gradient through the dynamic model and the local model constructed in the study based on several climate change scenarios data generated from different general climate models (GCMs) and Canadian Regional Climate Model (CRCM) in the eastern Canadian boreal forest.
4) The Chapter IV monitored the intra-annual radial growth (formation of the xylem) of black spruce and the meteorological conditions along the latitudinal gradient from 47.5°N to 50°N, and tried to identify the critical timings of the xylem formation process during a growing season from May to September as well as potential relation with the meteorological conditions along the gradient.

The relations between chapters are: since trembling aspen and paper birch are often defoliated by insect outbreaks in our study region (Bergeron and Charron, 1994; Cooke *et al.*, 2006), the Chapter I aimed to identify the major insect outbreak years in our studied broadleaf stands in western Quebec (See details in the Chapter I). The results of the Chapter I would serve as a basis for the Chapter II. That is, the identified severe insect outbreak years had to be removed from the residual ring-width chronologies of trembling aspen and, to some degree, of paper birch to reduce ‘noise’ in the chronologies, and the resulting corrected chronologies would be used for further climate-growth analysis in the Chapter II. Based on the calibrated climate-growth models in the Chapter II, the Chapter III would predict radial growth of these four dominant boreal tree species along the gradient using a novel concept (see details in the Chapter III) based on eight climate change scenarios data generated from

GCMs and CRCM in eastern Canada. To precisely understand how trees are reacting to climate warming, the Chapter IV tried to use a novel approach (weekly micro-sampling) to determine the major meteorological factors affecting intra-annual xylem formation of black spruce along a latitudinal gradient during the 2005 and 2006 growing seasons. The expected results of the Chapter IV may allow us to better understand the climate-growth associations established from the Chapters II and III.

My Ph.D study is the basis for our NSERC Strategic Project that was conducted from 2004 to 2010: Climate Change and Forest Productivity (PI: Dr. Yves Bergeron). The tree-ring raw data and chronologies established for the four species in this project are the basis for other studies which focus on predicting forest growth and productivity of these species along the gradient in western Quebec using mixed or hybrid modeling (Lapointe-Garant et al., 2009), or ecophysiological modelling or the process-based modelling. The corresponding results obtained from the Chapters I-IV could be used by other studies and compared with the results obtained from other studies of the whole strategic project.

Note: This thesis is written in the form of a collection of articles published or submitted to scientific journals. Hence there are a few repetitions in the texts between the General Introduction, General Conclusion and the Chapters papers as well as the Appendix I paper.

CHAPTER I

TREE-RING EVIDENCE EXTENDS THE HISTORIC NORTHERN RANGE LIMIT OF SEVERE DEFOLIATION BY INSECTS IN THE ASPEN STANDS OF WESTERN QUÉBEC, CANADA

Jian-Guo Huang, Jacques Tardif,
Bernhard Denneler, Yves Bergeron, and Frank Berninger

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1.1. RÉSUMÉ

Une reconstitution dendrochronologique des épidémies d’insectes a été réalisée le long d’un gradient allant de 46°N à 54°N dans la forêt boréale de l’ouest du Québec, au Canada. Les chronologies de l’espèce hôte, le peuplier faux-tremble, ont été construites de manière à identifier les périodes de défoliation sévère et des comparaisons ont été effectuées avec les chronologies d’espèces non hôtes. De plus, la fréquence des cernes pâles et étroits a été utilisée pour valider l’occurrence des épidémies d’insecte à ces latitudes. Quelques épidémies majeures sont survenues avec une synchronicité relativement étroite à l’échelle régionale mais l’année du début, l’intensité et l’étendue des épidémies variaient dans l’espace. Par exemple, les épidémies des années 1950 ont été observées de 1951 à 1952 au 46°N, de 1953 à 1954 au 47°N et de 1954 à 1956 au 48°N. D’autres épidémies importantes comme celles de 1964 et 1980 étaient assez bien synchronisées aux latitudes nordiques. Les épidémies observées dans les peuplements de peuplier faux-tremble à la latitude 54°N fournissent des preuves manifestes que des défoliations sévères causées par les insectes surviennent beaucoup plus au nord que la limite de l’aire de répartition couramment rapportée, soit entre 49°N et 51°N, dans le cas du plus important défoliateur du peuplier, la livrée des forêts. Notre étude montre que l’identification minutieuse des cernes pâles chez l’espèce hôte peut fournir une information valide qui permet d’élargir la base de données de l’inventaire des insectes forestiers tant à l’échelle temporelle que spatiale.

1.2. ABSTRACT

A dendrochronological reconstruction of insect outbreaks was conducted along a latitudinal gradient between 46 and 54°N in the boreal forest of western Quebec, Canada. Tree-ring chronologies of the host species, trembling aspen, were constructed to identify periods of severe defoliation and comparisons were made with those of non-host species. In addition, the frequency of white and narrow rings was used to further confirm the occurrence of insect outbreaks at these latitudes. Some major outbreaks occurred in relatively close synchrony at the regional scale, but the initiation year, the intensity and extent of the outbreaks varied spatially. For example, the 1950s outbreaks were observed from 1951-52 at 46°N, 1953-54 at 47°N, and 1954-56 at 48°N. Other major outbreaks like the 1964 and 1980 outbreaks were fairly well-synchronized at northern latitudes. The observed outbreaks in aspen stands at latitude 54°N also provided clear evidence that severe insect defoliation occurs much further north than the currently reported range limit, i.e., between 49 and 51°N, of the most important aspen defoliator, the forest tent caterpillar. Our study demonstrated that careful identification of white rings in host species can provide valid information allowing the expansion of the forestry insect inventory database both at the temporal and spatial scales.

1.3. INTRODUCTION

The forest tent caterpillar (*Malacosoma disstria* Hubner) (FTC) constitutes one of the major insects causing disturbances in the boreal forest of North America (Witter, 1979). Severe FTC defoliation can significantly reduce tree growth and increase both mortality and crown dieback of the host species (Batzer *et al.*, 1954; Hildahl and Reeks, 1960), consequently decreasing forest productivity (Bergeron and Charron, 1994; Hogg and Schwarz, 1999). In the boreal zone, trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.) are the preferred FTC host species (Peterson and Peterson, 1992; Hogg *et al.*, 2002a). Forest tent caterpillars feed during early-spring (Robison and Raffa, 1997) as soon as their eggs hatch during this period in synchrony with the budding of young, nutritious leaves of the host species (Fitzgerald, 1995). Recent studies regarding trembling aspen, balsam poplar, and paper birch have shown that light-coloured rings, i.e., 'white rings', may develop following severe FTC defoliation early in the growing season (Hogg and Schwarz, 1999; Sutton and Tardif, 2005). A recent experimental study simulating severe FTC defoliation by manually removing 98-100% of aspen leaves early in the growing season confirmed that white rings were produced as a consequence of severe defoliation (Hogg *et al.*, 2002b). Jones *et al.* (2004) have also shown that both reduced aspen radial growth and earlier growth cessation resulted from artificial defoliation.

In the boreal forest, the large aspen tortrix (LAT) (*Choristoneura conflictana* Walker) is another major defoliator of trembling aspen as well as of the secondary host species which include balsam poplar, paper birch, and willow (*Salix spp.*) (Cerezke, 1992). During early spring (May), bud and leaf tissue may be destroyed prior to aspen bud expansion as young LAT larvae mine into aspen buds. Later stages of larvae continue to feed within rolled leaves or within two or more leaves pulled together and secured with silken webbing until mid-June when feeding is completed (Cerezke, 1992). The feeding may cause partial or complete defoliation of trees, thus resulting in reduction of tree vigor and stem growth (Cerezke, 1992). Previous studies have documented aspen growth reduction caused by the LAT outbreaks across the Canadian boreal forest including the Quebec province (Martineau, 1985; Hogg and Wein, 2005). The severe LAT outbreaks could also occasionally lead to the formation of white rings. Hogg and Wein (2005) observed the occurrence of a distinct white ring in aspen stands in 1968 near Whitehorse, Yukon, which they attributed to LAT outbreaks. The documented severe LAT outbreaks in 2000-01 also led to fairly frequent white ring formation in aspen trees in north-western Alberta and adjacent north-eastern British Columbia (E.H. Hogg, unpublished data).

Large aspen tortrix outbreaks generally occur earlier and cause less defoliation when compared to FTC outbreaks (Frey *et al.*, 2004). However, since white rings occasionally form after severe LAT defoliation and frequently form after severe FTC defoliation in aspen, they could be used as indicators of past severe insect defoliation in boreal aspen stands. Studies regarding aspen wood anatomy also found that white rings were characterized by smaller diameter fibres, with reduced cell wall thickening and a higher proportion of lumen area, and an overall decreased wood density compared to normal rings (Sutton and Tardif, 2005). In addition to white ring formation, growth suppression was also observed in host trees during severe outbreak years (Hogg and Schwarz, 1999; Sutton and Tardif, 2007). Due to these distinguished characteristics associated with aspen defoliation, both white rings and growth suppression were used in past studies as reliable indicators to reconstruct severe insect outbreaks, particularly of FTC outbreaks (Cooke, 2001; Sutton and Tardif, 2007).

The northern limit of FTC distribution in northern Quebec was previously determined from forest inventory data as illustrated in Figure 1.1. Fitzgerald (1995) reported that the northern limit of FTC distribution in Quebec corresponded to the 47ºN latitude whereas Cooke and Lorenzetti (2006) set this limit between the 49-51ºN latitude. Given the wide distribution of both trembling aspen and paper birch in Quebec and their occurrence as far north as the Hudson Bay region near the 54-55ºN latitude (Little, 1971), this present study aims to address whether insect outbreaks could be observed as far north as the distributional limit of both host species. We hypothesized that insect outbreaks would occur as far north as the distribution of their host species and thus at more northern latitude than currently reported.

The present study was conducted along the latitudinal gradient between 46ºN and 54ºN in western Quebec, Canada. Our objectives were 1) to reconstruct past major insect outbreaks along this latitudinal gradient by using both the presence of white rings/growth suppression and a dendrochronological comparison of host and non-host species, 2) to explore possible systematic changes in the spatial distribution of insect outbreaks in the study area, and 3) to assess its northern limit in western Quebec, Canada.

1.4. MATERIALS AND METHODS

1.4.1. Study area

The study area is located in western Quebec along a latitudinal gradient ranging south from Petawawa (located in Ontario but very close to Quebec, around 46°N) to Radisson (around 54°N) in the north (Figure 1.1). The topography along the gradient is generally flat and uniform with low elevation hills and rock outcrops (300-400 m a.s.l.). The area is affected by cold and dry arctic air from the north during the winter, and by warm and moist air originating from the south during the summer. A climate gradient is also enclosed within the latitudinal gradient. The climate normals for the period 1971-2000 showed a decrease in mean annual temperature (4.73°C to -3.14°C), in annual total precipitation (868 to 684 mm), and in growing degree-days

(>5°) (1 868°C to 862°C) from the southern most meteorological station (Sheenboro, Lat. 45° 58’N, Long. 77° 15’W) to the northern most station (La Grande Rivière, Lat. 53°38’N, Long. 77°42’W) (Environment Canada, 2002). The common boreal tree species including trembling aspen, paper birch, black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), and balsam fir (*Abies balsamea* (L.) P. Mill) occur in the study area but their abundances change from south to north (ESWG, 1996). The vegetation transition zone between the mixedwood forests (means both broadleaf and conifer) and the conifer dominated boreal forests occurs approximately at the latitude 49°N (Hofgaard *et al.*, 1999).

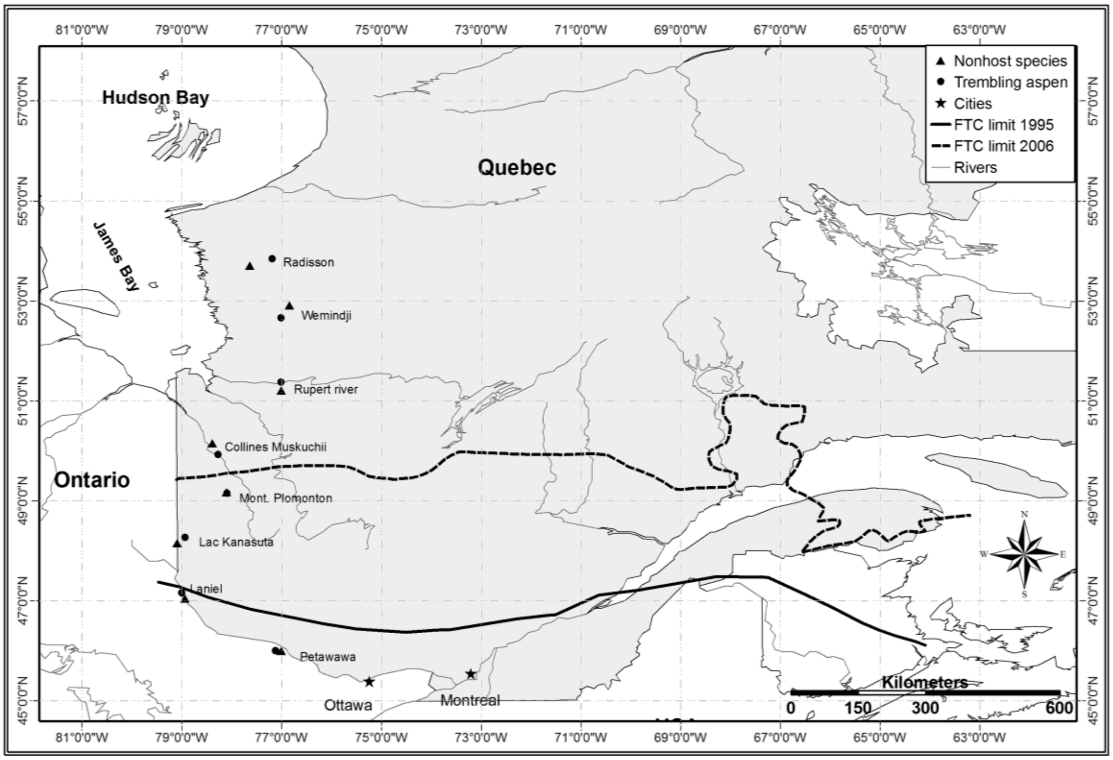


Figure 1. 1 Map showing sampling sites and the northern limit of FTC distribution along the latitudinal gradient from 46°N to 54°N in western Quebec, Canada. The heavy dark line represents the northern limit of FTC distribution in Quebec reported by Fitzgerald (1995). The dashed line represents the northern limit of FTC

distribution in Quebec identified by Cooke and Lorenzetti (2006).

1.4.2. Sampling and chronology development

We collected tree-ring samples from trembling aspen stands (host species), as well as from black spruce and jack pine stands (non-host species) along the latitudinal gradient from 46ºN to 54ºN at about 1º intervals in western Quebec (Figure 1.1). At 48°N latitude, the existing black spruce chronology developed by Hofgaard *et al.* (1999) was included into our analysis as a non-host species. Towards the northern end of the gradient, available old aspen stands were fairly rare and only two stands were sampled for the latitudes 52-54ºN. In total, eight aspen sites with corresponding non-host sites were established at intervals along the latitudinal gradient (Figure 1.1). In each stand, at least 20 old and healthy trees of each species were cored or transversely cut.

In the laboratory, all samples were dried, polished, and then visually crossdated under a binocular microscope. Most dated samples were carefully measured using a Velmex Measuring system inferfaced with Time Series Analysis Program (TSAP) (Frank Rinntech, Heidelberg, Germany) to a precision of 1/1000 mm. Some spruce and pine discs were scanned using program WinDENDRO™ 2005 to obtain ring-width values. The visual crossdating was further validated using the program COFECHA (Holmes, 1983). In order to identify possible insect outbreaks, occurrences of white/narrow rings were recorded for all aspen samples. An independent validation regarding the occurrence of white/narrow rings was also conducted at the Centre for Forest Interdisciplinary Research of the University of Winnipeg by an experienced technician to assure accuracy.

Each measured series was standardized using a 60-year spline function which preserved about 99% of the variation within individual series at a wavelength of 19 years (Cook and Peters, 1981). Standardization involved transforming ring-width measurements into dimensionless indices by dividing the observed ring-width measurements by those estimated via the spline function (Fritts, 1976). These growth indices contain a relatively stable mean and variance through time (Cook and Kairiustis, 1990). This procedure retained high-frequency variations (interannual to decadal) and filtered out medium to low-frequency trends such as trends in growth due to age/size, biological persistence, and long-term stand dynamics (Fritts, 1976; Cook and Kairiustis, 1990). Autoregressive modelling was also performed on each standardized series to remove temporal autocorrelation and to enhance the common signal. In order to further eliminate the effect of endogenous stand disturbances and to enhance the common signal, all residual series were averaged by site using a biweight robust mean, which reduced the effect of outlier values. Chronology construction utilized the program ARSTAN (ARSTAN Windows 4.0a) (Cook, 1985).

1.4.3. Insect outbreaks and spatial pattern

Trembling aspen (host) residual chronologies were compared with non-host species residual chronologies to determine periods of insect outbreaks using the program OUTBREAK (Swetnam *et al.*, 1985; Holmes and Swetnam, 1996). To eliminate the climate signal at each latitude in the residual host chronology, the non-host species chronology best correlated to the host species chronology (Swetnam *et al.*, 1985) was used for subsequent comparison. Dendroclimatic analyses also demonstrated that these host and non-host species responded to climate similarly (J.G. Huang, *unpublished data*). The OUTBREAK program eliminates the common signal (presumably climatic) by subtracting the non-host chronology from the host chronology (Holmes and Swetnam, 1996). After exploratory analyses, we selected the same criteria as those used by Sutton and Tardif (2007) to identify possible insect outbreaks at aspen sites along the latitudinal gradient. A potential insect outbreak was identified when three or more consecutive years of negative growth departure (in standard deviations SD) occurred in the host series including one or more years with a maximum growth departure of at least -1.28 SD. A fractional power of 0.1 was used to raise the index value of the non-host chronology to the selected power, thus avoiding false identification of outbreaks when high growth values were observed in the non-host species (Holmes and Swetnam, 1996). The frequency of white and/or narrow rings was also used as a key indicator for identifying outbreak periods. The potential periods of insect outbreaks identified were then compared with those reported by Cooke and Lorenzetti (2006) and other related studies. Based on the identified insect outbreak years and growth reduction years of aspen residual chronologies, comparisons among the latitudes were made to explore possible systematic changes in the spatial distribution of insect outbreaks across the study area.

1.5. RESULTS

1.5.1. Insect outbreaks reconstructed along the latitudinal gradient in western Quebec

A total eight host residual chronologies and seven non-host residual chronologies (Table 1.1) corresponding to each degree of latitude were developed, including the black spruce chronology at 48°N from Hofgaard *et al.* (1999) (Figure 1.2). The aspen chronologies varied from 78 years to 143 years in duration, with the longest aspen chronology dating back to 1862 at 53°N. The non-host chronologies ranged from 80-248 years. Growth pattern comparisons of host chronologies revealed high similarity at interannual scales, particularly for some growth reduction years (Figure 1.2).

Table 1. 1 Characteristics of the host and non-host chronologies along a latitude gradient between 46°N and 54°N in western Quebec, Canada. The site names are: Petawawa (46°N), Laniel (47°N), Lac Kanasuta (48°N), Mont. Plomonton (49°N),

Collines Muskuchii (50°N), Rupert river (51°N), Wemindji (53°N), and Radisson (54°N).

Sites	Latitude	Longitude	Elev.(asl)	Tree Species	Chr. Length
46°N	45°59.687	77°31.707'	184 m	Trembling Aspen (host)	1911-2004
46°N	46°00.419	77°25.092'	160 m	Jack Pine (non-host)	1925-2004
47°N	47°09.539	79°25.341'	210 m	Trembling Aspen (host)	1894-2004
47°N	47°02.517	79°20.746'	258 m	Jack Pine (non-host)	1883-2004
48°N	48°14.189	79°21.822'	285 m	Trembling Aspen (host)	1908-2004
48°N	48°09.203	79°30.065'	330 m	Black Spruce (non-host)	1690-1993*
49°N	49°09.592	78°32.885'	341 m	Trembling Aspen (host)	1864-2004
49°N	49°08.905	78°32.038'	440 m	Black Spruce (non-host)	1917-2004
50°N	49°56.754	78°42.881'	292 m	Trembling Aspen (host)	1870-2004
50°N	50°08.674	78°48.804'	245 m	Jack Pine (non-host)	1915-2004
51°N	51°20.957	77°25.343'	172 m	Trembling Aspen (host)	1925-2004
51°N	51°11.775	77°27.184'	215 m	Black Spruce (non-host)	1761-2004
53°N	52°39.180	77°24.019'	237 m	Trembling Aspen (host)	1862-2004
53°N	52°53.953	77°15.704'	226 m	Black Spruce (non-host)	1757-2004
54°N	53°48.402	77°35.785'	36 m	Trembling Aspen (host)	1927-2004
54°N	53°42.028	78°04.350'	125 m	Black Spruce (non-host)	1869-2004

Note: Elev. (asl), Elevation (above sea level); Chr. Length, Chronology Length. * Black spruce chronology at 48°N from Hofgaard *et al.* (1999).

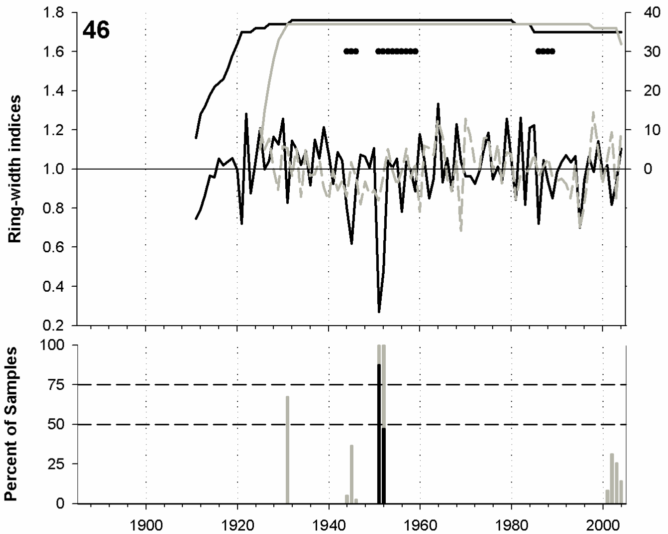
Periods of growth suppression were identified by OUTBREAK, as listed in Table 1.2. Among those periods, growth suppression in the 1950s appears to be common at almost all latitudes despite differences in the initial year, duration, and ending year (Table 1.2). The consistent recent periods of suppressed growth were identified at southern latitudes, i.e., 2001-04 at 47°N, 2000-04 at 48°N, and 2001-04 at 49°N. At northern latitudes, recent periods with depressed growth were also very similar, i.e., 1997-99 at 50°N, 1998-2004 at 51°N, 1998-2000 at 53°N, and 1994-2002 at 54°N. Other periods of suppressed growth were identified at local or regional scales (Table 1.2). White-ring years were also observed along the latitudinal gradient, as shown in

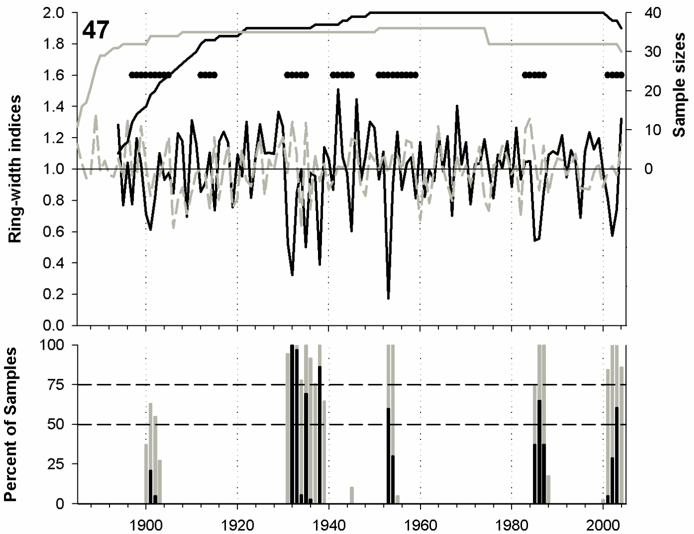
Table 1.2 and Figure 1.2. It is interesting to note that only two years with white rings were observed at 46°N, i.e. 1951-52. In contrast, white ring years occurred frequently at the 47°N, 53°N, and 54°N latitudes. In southwestern Quebec, similar periods with white rings were observed in 2001-03 at 47°N, 2001-02 at 48°N, and 2001-02 at 49°N. In northwestern Quebec, the 1964 and 1980 white ring years were commonly found at most northern latitudes. In spite of low sample replications in 1878 (4 samples), 1879 (2 samples), and 1869 (6 samples) at the 49°N, 50°N, and 53°N latitudes, respectively, white rings were observed in these years in all samples at these latitudes (Table 1.2, not shown in Figure 1.2). These white ring years generally corresponded to narrow annual growth increments. Severe insect defoliation was classified as those years where more than half of the samples showed white rings or where more than three-quarters of the samples showed both white and/or narrow rings. Otherwise isolated white ring years were considered indicative of insect defoliation. When associating white/narrow ring years with periods of abrupt growth suppression as identified by OUTBREAK (Table 1.2 and Figure 1.2), the severe insect outbreaks were determined along the latitudinal gradient in western Quebec (Table 1.2).

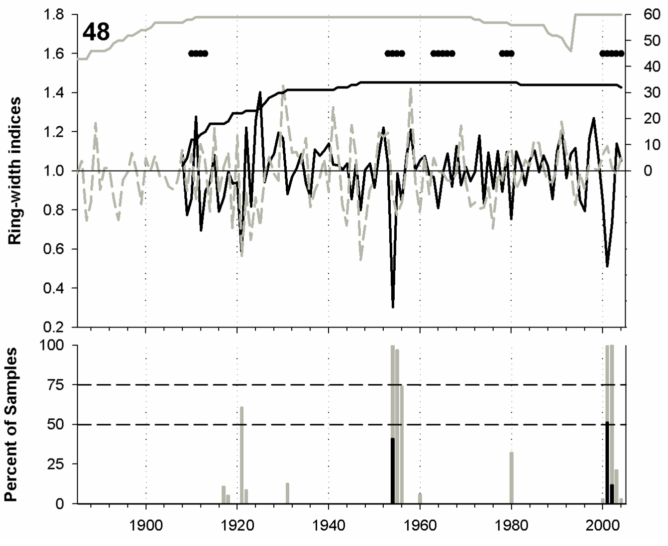
Overall, it appears that some major outbreaks reconstructed in western Quebec occurred in relatively close synchrony at the regional scale, but the initiation year, the intensity and extent of the outbreaks varied spatially. For example, the 1950s outbreaks were observed from 1951-52 at 46°N, 1953-54 at 47°N, and 1954-56 at 48°N. Other major outbreaks were fairly well-synchronized at the northern latitudes. As shown in Table 1.2 and Figure 1.2, the 1964 and 1980 outbreaks were identified in most aspen stands at latitude 48-54°N. In addition, several severe insect outbreaks and insect defoliation periods were found prior to 1938. For instance, severe insect outbreaks were observed in 1931-38 for the latitude 47°N. Insect defoliation periods were identified in 1901-02 at 47°N, in 1915, 1921-22, and 1937 at 53°N, and in 1937 at 54°N. Among the latitudes, only one severe insect outbreak was identified for aspen stands at 46°N in the past, i.e., 1951-52. However, frequent severe insect outbreaks were observed in aspen stands at the latitudes 53°N and 54°N (Table 1.2).

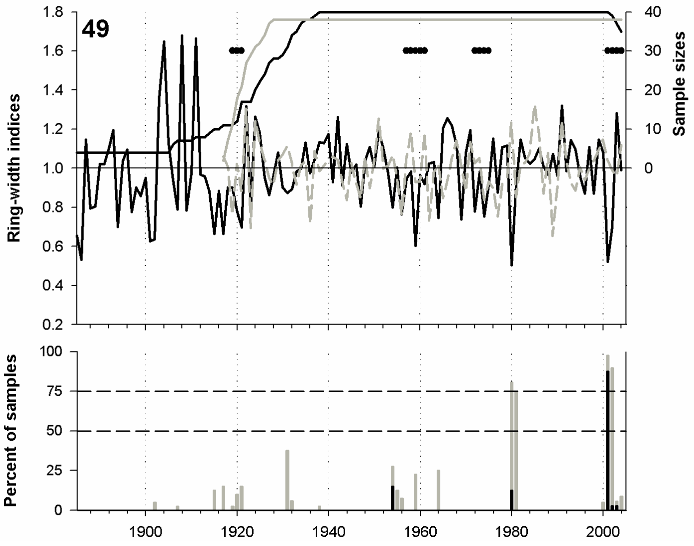
Table 1. 2 Periods of growth suppression identified by OUTBREAK, white rings years observed from the samples, and severe insect defoliation years determined along the latitudinal gradient from 46 to 54°N, western Quebec, Canada.

Latitude	Periods of growth suppression identified by OUTBREAK	Observed white rings	Severe insect defoliation
46°N	1944-46, 1951-59, 1986-89	1951-52	1951-52
47°N	1897-1905, 1912-15, 1931-35, 1941-45, 1951-59, 1983-87, 2001-04	1901, 1932-35, 1938, 1953-54, 1985-87, 2001-03	1931-38, 1953-54, 1985-87, 2001-04
48°N	1910-13, 1953-56, 1963-67, 1978-80, 2000-04	1954, 2001-02	1954-56, 2001-02
49°N	1919-21, 1957-61, 1972-75, 2001-04	1878, 1954, 1980, 2001-02	1980-81, 2001-02
50°N	1919-23, 1927-32, 1945-48, 1961-64, 1977-82, 1989-92, 1997-99	1879, 1980	1956, 1964, 1980, 1999-2000
51°N	1959-61, 1969-75, 1998-2004	1964, 1973, 1980	1964, 1973-74, 1980
53°N	1913-22, 1948-50, 1953-58, 1978-82, 1990-92, 1998-2000	1869, 1915, 1921, 1937, 1950, 1954, 1964, 1980, 1982, 1986	1950, 1954, 1964, 1980, 1982, 1986, 1990, 1998-2000
54°N	1945-54, 1994-2002	1937, 1946-51, 1961, 1964, 1974, 1982, 1990, 1998-2000	1946-52, 1964, 1974, 1982, 1990, 1998-2000


46
Ring-width indices
Sample sizes
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
40
30
20
10
0
Percent of Samples
100
75
50
25
0
1900
1920
1940
1960
1980
2000


47
Ring-width indices
Sample sizes
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
40
30
20
10
0
Percent of Samples
100
75
50
25
0
1900
1920
1940
1960
1980
2000


48
Ring-width indices
Sample sizes
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
60
50
40
30
20
10
0
Percent of Samples
100
75
50
25
0
1900
1920
1940
1960
1980
2000


49
Ring-width indices
Sample sizes
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
40
30
20
10
0
Percent of samples
100
75
50
25
0
1900
1920
1940
1960
1980
2000

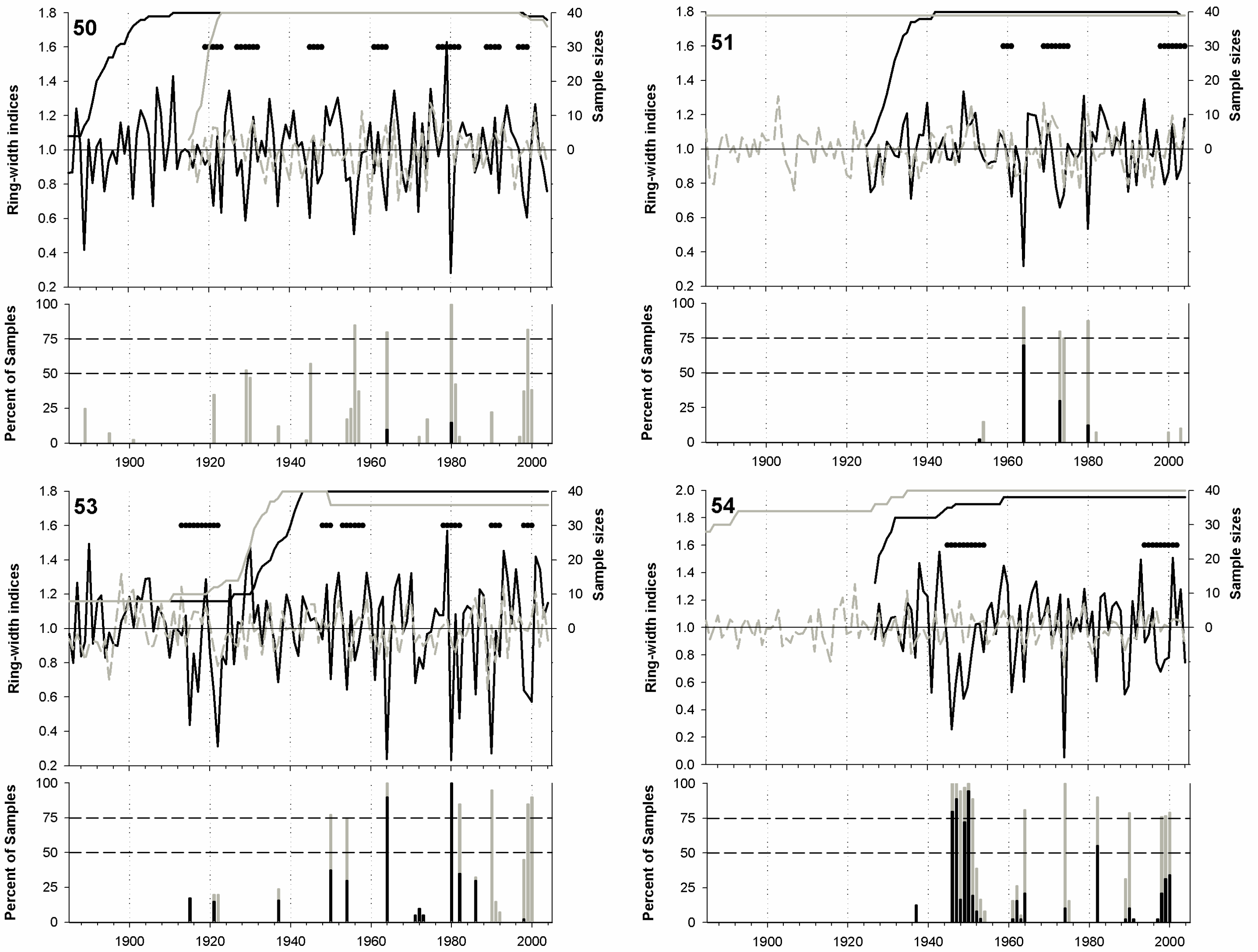

50
51
53
54
Ring-width indices
Sample sizes
Percent of Samples
1900
1920
1940
1960
1980
2000

Figure 1. 2 Insect outbreaks identified along the latitudinal gradient from 46 to 54°N in western Quebec, Canada. The bold line represents the trembling aspen residual chronology (host species) and the light dashed line corresponds to the non-host species residual chronology. Periods identified by the program OUTBREAK as possible insect outbreaks are indicated by a solid bar above the chronologies. Stacked bar chart showing the percent of samples with white rings (heavy dark bar) and narrow rings (light gray bar). The dashed lines in the lower panel indicate 50% and 75% criteria for severe insect defoliation.

1.6. DISCUSSION

Owing to less forest harvesting activities in north Quebec, long aspen chronologies established at northern latitudes provided a unique opportunity to confirm major insect outbreaks documented in forest insect databases and to identify possible insect outbreaks before 1938. Cooke and Lorenzetti (2006) have found that the 1950s (from 1951-54, with most extensive outbreak years of 1952-53) outbreaks were exceptionally extensive and covered more than 95% of the identified outbreak range in Quebec. This observation corresponds with severe insect outbreaks during the 1950s reconstructed at many of our sites. Bergeron and Charron (1994) and Cooke and Roland (2007) also reported the 1950s outbreaks at Lac Duparquet of northwestern Quebec, and Ontario. In the Abitibi-Temiscamingue region (around 47-49.5°N) of western Quebec, Cooke and Lorenzetti (2006) found the most recent FTC outbreaks to peak in 2001 and this observation supports the severe insect outbreaks reconstructed for latitudes 47 to 49°N. The reconstructed recent outbreaks at latitudes 47 to 49°N also correspond to a severe FTC outbreak in 1999-2002 in neighbouring province of Ontario (Cooke and Roland, 2007). The outbreaks peaking in 1988 in the Temiscamingue region (Cooke and Lorenzetti, 2006) also coincided to the 1985-87 outbreaks found in the same area as our study (our study site at 47°N). Cooke and Roland (2007) showed FTC outbreaks from 1989 to 1991 in Ontario as well. In addition, Cooke and Lorenzetti (2006) observed a period of 1960-90, characterized by less severe and less extensive defoliation cycles in Abitibi region. These findings are very consistent with insect outbreaks we reconstructed in this region (48-49°N) with the exception of the 1980 outbreak at latitude 49°N. Differences in timing and duration of the outbreaks among different sites could be ascribed to multiple factors such as topography, forest structures, insect populations, insectivores, and climate factors (Roland and Taylor, 1997; Cooke and Lorenzetti, 2006). For example, topography was suggested to be an important factor limiting the frequency and duration of outbreaks in Quebec (Cooke and Lorenzetti, 2006).

Cooke and Lorenzetti (2006) partitioned the Quebec province into nine areas with substantial regional-scale coherence in the spatiotemporal pattern of the FTC occurrence. After detailed comparisons among those clusters, they revealed that 1963 was a year of decline in insect populations across most of Quebec except Outaouais region. This decline in FTC activity was attributed to the following factors: 1) the FTC eggs at high altitudes in western Canada failed to hatch in the spring of 1963 (Gautreau, 1964); and 2) the hatchling died in May 1963 due to a late spring frost (Forest Insect and Disease Survey, 1963, p.51). In our study region, we did not observe severe outbreaks in 1963 in terms of white rings and is consistent with their conclusion. However, the 1964 and 1980 outbreaks were extensively observed in the north of Abitibi-Temiscamingue region of western Quebec, as shown in Table 1.2 and Figure 1.2, well above the northern limit of distribution of FTC as identified by Cooke and Lorenzetti (2006). This suggests that during the past aerial surveys these two severe outbreaks were not reported in the north either because aspen distribution in the north is sporadic or because the region was not traditionally surveyed since these areas were beyond the previously reported limit of FTC distribution. Sutton and Tardif (2007) have also observed FTC activities unreported by aerial survey.

Owing to limited available forest inventory data (1938-2002), Cooke and Lorenzetti (2006) did not reveal other possible outbreaks prior to 1938. However, based on white/narrow rings we reconstructed severe and persistent outbreaks in 1931-38 for the latitude 47°N. In addition, the observed white rings in 1878, 1879, and 1869 at latitude 49°N, 50°N, and 53°N, respectively, might also indicate severe insect defoliation in study region in the past. This is very consistent with the suspected broad-scale outbreaks during the 1870s in western Manitoba (Sutton and Tardif, 2007). Other outbreaks that are not recorded in forest insect inventory databases such as 1901-02 at 47°N, 1915, 1921-22, and 1937 at 53°N, and 1937 at 54°N provided additional insect outbreak evidence for better understanding of insect disturbances and dynamics in the past in western Quebec. It also illustrates that white/narrow rings are valid parameters to explore insect outbreak history prior to available insect inventory data.

1.6.1. Systematic changes in the spatial distribution of insect outbreaks across the landscape

As illustrated in Table 1.2 and Figure 1.2, along the south-north latitudinal gradient the relatively close-synchronized 1950s outbreaks at southern latitudes could indicate that the insect outbreaks were spread from south to north and occurred at a large-spatial scale in this region. The fairly well-synchronized outbreaks of 1964 and 1980 at 48-54°N might suggest that the severe but short insect outbreaks in these two years occurred at a broad spatial scale in the north. These two major outbreaks were also widely observed across large areas of Saskatchewan and Alberta (Simpson and Coy, 1999; Hogg *et al.*, 2005). The close-synchronized and well synchronized outbreaks at the regional scale might be related to regional environmental factors (e.g. regional climate), forest structures, population dispersal rate, and insect population density regulation (Fleming and Volney, 1995; Cooke and Roland, 2007). However these factors require further investigation to be validated. Other important outbreak years such as 1974 and 1990 at northern latitudes, and 2001-02 at southern latitudes (47-49°N) indicate that outbreaks in those years also generally occurred at the regional scale in western Quebec (Table 1.2 and Figure 1.2). Cooke and Roland (2007) reported severe FTC outbreaks in 1951-53, 1963-66, 1976-78, 1989-1991, and 1999-2002 in both northeast and northwest Ontario, indicating that those large-spatial/regional-scale insect outbreaks observed in northwest Quebec and southwest Quebec in our study best relate to nearby Ontario province. In spite of no white rings observed in 1921 and 1945, the consistently significant growth suppression during this period may indicate insect defoliation at the regional or local scale (Figure 1.2). The potential factors causing growth reduction in those years such as drought or moisture stress were excluded because drought-induced growth reductions in aspen ring widths were often observed in climatically dry areas such as the aspen parklands of western Canada, where annual total precipitation is around 350-450 mm (Hogg *et al.*, 2005). However, in our study region annual total precipitation in those growth reduction years was ample, ranging from 650-1000 mm. Cooke and Roland (2007) suggested that ring widths of trembling aspen growing in northeastern and northwestern Ontario where annual precipitation is around 535.6 mm and 656.5 mm, respectively, appear to be far less sensitive to drought or moisture stress than annual defoliation by aspen defoliators, mostly FTC.

It is also interesting to note that more insect outbreaks occurred at northern latitudes 53°N and 54°N than at southern latitudes (Figure 1.2). This might be due to increased forest fragmentation (small aspen stands in continuous forest dominated by non-host tree species) in the northern boreal area. Roland (1993) pointed out that higher forest fragmentation significantly increased the duration of insect outbreaks like FTC. Other modelling or empirical studies (Hastings, 1990; Hassell *et al.*, 1991) also support this conclusion. Fragmented boreal forest may limit dispersal of natural enemies like parasitoids and/or transmission of pathogens of tent caterpillar, thus leading to slower suppression of local severe outbreaks (Kareiva, 1987; Reeve, 1988). As a consequence, these local outbreaks in high host density would act as local sources of dispersing moths, either allowing fast increase during the early phase of an outbreak or keeping mean density high when populations in continuous forests are declining (Roland, 1993). In continuous boreal forest dominated by non-host tree species in the north, small aspen stands could also increase the duration of the outbreaks through isolating caterpillar populations and limiting movement of natural enemies (Roland, 1993). In the long run, this may translate into more rapid population cycling (Cobbold *et al.*, 2005).

1.6.2. Northern range limit of severe defoliation by insects in western Quebec

In contrast to the currently reported range limit of the most important aspen defoliator, the FTC (Fitzgerald, 1995; Cooke and Lorenzetti, 2006), our study showed that insect outbreaks could occur much further north than reported. For example, we reconstructed severe insect outbreaks occurring at latitude 54ºN in western Quebec. This roughly corresponds to the distributional limit of the host species. Observations in Manitoba (56-57°N) also suggest that white rings and corresponding growth suppression that might be related to insect outbreaks occurred close to the actual northern limit of aspen distribution in Manitoba (F. Conciatori, unpublished data). Furthermore, the differences in northern range limit of severe defoliation by insects may result from the different data sources. Both Fitzgerald (1995) and Cooke and Lorenzetti (2006) used the forestry insect inventory data whereas we reconstructed insect outbreaks using dendrochronological techniques. Our results clearly demonstrate the limitations of the forestry insect inventory databases. In general, forest ecosystem characteristics (e.g., forest type, forest structure and condition, stand age, soil drainage class, and site index) in forestry insect inventory data varies greatly from location to location, hence leading to incomplete assessment of insect disturbances and dynamics (Cooke and Roland, 2007). In addition, standards of data collection and processing during aerial surveys by subjective and imprecise aerial sketch mapping techniques differ across survey areas (NFDP, 2005). Studies have shown that defoliated estimates are frequently exaggerated during sketch mapping (Harris and Dawson, 1979). In addition, in areas with moderate to severe defoliation, the extent and severity of insect outbreaks were usually overestimated as a consequence of including small non-forested regions, roads, cultivated areas, small lakes, or burned areas, as well as homogenizing defoliation severity. The overestimation of insect outbreaks may also be caused by including areas or species that were defoliated by multiple agents. For example, the mortality of some aspen stands could be caused by both the LAT outbreaks before aspen bud expansion and subsequently by the FTC defoliation during the early-growing season (Hogg *et al.*, 2005). Finally, some areas of defoliation may have been missed in surveys due to limited road access, or due to the omission of local observers (For more information, please see Generic Forest Health Surveys Guidebook 2002). In remote and less-populated areas of northern Quebec, our results indicated that severe outbreaks failed to be identified for various reasons and hence demonstrated that dendrochronological techniques constitute a valid method to reconstruct the history of severe outbreaks occurring in remote areas yet missed during the insect surveys. The dendroecological approach used to reconstruct several severe FTC outbreaks that were not detected by aerial surveys in Ontario was also successfully (Cook and Roland, 2007). Sutton and Tardif (2007) also formulated similar conclusions.

1.7. CONCLUSION

Precise prediction of boreal insect dynamics is very critical for Canada’s sustainable forest development, yet this requires a large database to better understand insect dynamics. Forest insect surveys provide very valuable data for investigating insect dynamics, however they also demonstrate some inherent shortcomings such as limited available data, and some outbreaks and areas missed during past air surveys.

In this study, we used dendrochronological comparison of host and non-host species as well as white/narrow rings as key indicators to reconstruct the history of severe insect outbreaks along a latitudinal gradient from 46ºN to 54ºN in western Quebec. We found additional severe insect outbreaks that were not reported in previous studies and that occurred prior to available forest insect inventory data. Our findings indicated that analysis of white/narrow rings may extend forestry insect inventory data to a larger spatial scale (e.g., remote areas or survey-missed areas) and to a longer temporal scale (e.g., insect outbreaks prior to forest insect inventory surveys). The identification of severe insect outbreaks at 54°N latitude clearly indicated that the northern limit of defoliating insects is substantially further north than reported in the documentary records. Improved understanding of the historical, distributional limits of defoliating insects provides critical baseline information needed to monitor the impacts of environmental change.

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CHAPTER II

RADIAL GROWTH RESPONSE OF FOUR DOMINANT BOREAL TREE SPECIES TO CLIMATE ALONG A LATITUDINAL GRADIENT IN THE EASTERN CANADIAN BOREAL FOREST

Jian-Guo Huang, Jacques C. Tardif, Yves Bergeron,

Bernhard Denneler, Frank Berninger, and Martin P. Girardin

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2.1. RÉSUMÉ

Afin de comprendre comment les changements climatiques influencent la croissance des arbres dans le contexte du réchauffement global, nous avons utilisé une analyse dendroclimatique pour comprendre les réactions de quatre espèces d'arbres importantes de la forêt boréale - *Populus tremuloides, Betula papyrifera, Picea mariana* et *Pinus banksiana* – aux variations climatiques le long d'un large gradient latitudinal s'étendant de 46 à 54ºN à l'est de la forêt boréale canadienne. Des courbes dendrochronologiques provenant de 34 peuplements forestiers distribués à 1º d'intervalle ont été construites, transformées en composantes principales (CP), et analysées par analyse de corrélation 'bootstrapped' au cours de la période 1950-2003 pour identifier les facteurs climatiques restreignant la croissance radiale et l'association croissance radiale-climat le long du gradient. Toutes espèces confondues, ce sont les températures estivales passées (influence négative) et les températures actuelles en janvier et en mars-avril (influences positives) qui ont démontré les relations avec la croissance radiale les plus consistantes le long du gradient. Combinée aux facteurs climatiques identifiés spécifiques aux espèces ou aux sites, notre étude suggère que les conditions hydriques durant l'année précédant la croissance radiale jouent un rôle dominant dans la régulation positive de la croissance de *P. tremuloides*, tandis que la température en janvier et les conditions hydriques de la saison de croissance ont un impact positif sur la croissance de *B. papyrifera*. *P. mariana* et *P banksiana* étaient toutes deux positivement affectées par l'hiver et le printemps de l'année en cours, ou par les températures de l'entière saison de croissance, à travers toute l'étendue de notre corridor. Dû aux impacts des divers facteurs climatiques sur la croissance, ces espèces boréales ont été inconsistantes dans leur réponse au réchauffement récent dans la zone de transition, où *B. papyrifera, P. mariana* et *P. banksinana* seraient les espèces les plus sensibles, alors que *P. tremuloides* serait la moins sensible. Avec un réchauffement continu, les peuplements de *B. papyrifera* situés au nord du 49ºN, ceux de *P. tremuloides* situés à des latitudes nordiques, et ceux de *P. mariana* et de *P. banksiana* situés au nord du 47ºN pourraient profiter du réchauffement de la température en hiver et au printemps pour amplifier leur croissance radiale au cours des prochaines décennies, tandis que les peuplements plus au sud pourraient avoir une croissance radiale réduite.

2.2. ABSTRACT

To address the central question of how climate change influences tree growth within the context of global warming, we used dendroclimatological analysis to understand the reactions of four major boreal tree species – *Populus tremuloides*, *Betula papyrifera*, *Picea mariana*, and *Pinus banksiana* – to climatic variations along a broad latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest. Tree-ring chronologies from 34 forested stands distributed at a one-degree interval were built, transformed into principal components (PCs), and analyzed through bootstrapped correlation analysis over the period 1950–2003 to identify climate factors limiting the radial growth and the detailed radial growth-climate association along the gradient. All species taken together, previous summer temperature (negative influences), and current January and March-April temperatures (positive influences) showed the most consistent relationships with radial growth across the gradient. Combined with the identified species/site-specific climate factors, our study suggested that moisture conditions during the year prior to radial growth played a dominant role in positively regulating *P. tremuloides* growth, whereas January temperature and growing season moisture conditions positively impacted growth of *B. papyrifera*. Both *P. mariana* and *P. banksiana* were positively affected by the current-year winter and spring or whole growing season temperatures over the entire range of our corridor. Owing to the impacts of different climate factors on growth, these boreal species showed inconsistent responsiveness to recent warming at the transition zone, where *B. papyrifera*, *P. mariana* and *P. banksiana* would be the most responsive species, whereas *P. tremuloides* might be the least. Under continued warming, *B. papyrifera* stands located north of 49°N, *P. tremuloides* at northern latitudes, and *P. mariana* and *P. banksiana* stands located north of 47°N might benefit from warming winter and spring temperatures to enhance their radial growth in the coming decades, whereas other southern stands might be decreasing in radial growth.

2.3. INTRODUCTION

The human-induced buildup of atmospheric CO_2 concentrations from 280 ppm in 1850 to 380 ppm in 2005 and of other greenhouse gases has resulted in an increase of 0.74°C in global mean surface temperature from 1906 to 2005 (IPCC, 2007). In the Northern Hemisphere, the greatest warming was observed during winter (December to February) and spring (March to May). Atmospheric CO_2 concentration is also expected to rise to 700 ppm by the end of the current century. Consequently, this may lead to an additional 1.1°C - 6.4°C increase in global mean surface temperature by 2100, with rapid warming at mid to high northern latitudes (IPCC, 2007). In Canada, south of 60°N, mean annual temperature and annual total precipitation from 1900 to 1998 have increased between 0.5°C and 1.5°C, and from 5% to 35%, respectively (Zhang *et al.,* 2000). By 2100, it is expected that mean annual temperature in the eastern Canadian boreal forests (Quebec province) may be about 3.5°C higher than today, even 5°C higher during winter, and accompanied by increased precipitation by 10-25% (Plummer *et al.,* 2006).

Climate warming could have profound impacts on the temperature and nutrient-limited circumboreal forests at mid to high latitudes in the Northern Hemisphere (Oechel *et al.,* 1993). Long-term surface phenological observations from Europe (Menzel and Fabian, 1999) and recent satellite remote sensing measurements from North America (Zhou *et al.,* 2001) have respectively indicated approximately an 11-day lengthening of the growing season from 1959 to 1993 and 12±5 days extension from 1981 to 1999 as a consequence of recent warming. Correspondingly, plant phenological observations demonstrated early leafing, flowering, and fruiting in spring/summer, as well as late leaf coloring in autumn recorded across Europe (Menzel *et al.,* 2006) and North America (Chuine and Beaubien, 2001). Rapid warming in surface air temperature at mid to high northern latitudes has also led to increased soil temperature and soil freeze-thaw in both permafrost and non-permafrost regions (Osterkamp and Romanovsky, 1999). As a result, the decomposition rates of soil organic matter are accelerated (Davidson *et al.*, 2000), thereby resulting in more readily mineralized nutrients available to plants, particularly of the most common limiting nutrient, nitrogen (Luo *et al.*, 2004). In addition, the rising atmospheric CO_2 might have a positive effect on the above/below-ground biomass by enhancing plant photosynthesis and water use efficiency in a CO_2-enriched world (Körner, 2006), i.e., the direct CO_2 fertilization effect (Huang *et al.*, 2007). All these impacts together might be leading to a shift in species composition and community structure (Weltzin *et al.*, 2003), and ultimately causing substantial change that varies with vegetation type in the boreal biome (Goetz *et al.*, 2005). Within the context of sustainable forest development, it is critical to better understand the responses of boreal tree species to climate variability and change, and increase our capacity to predict potential changes in forest composition and structure in this biome.

Ecological gradient analysis is often used to identify the interactions between plant species and their spatial distributions in relation to eco-environmental factors (Ohmann and Spies, 1998). The landscape-scale species distribution and abundance patterns are generally believed to be controlled by climate, i.e. temperature and soil moisture (Gosz, 1992) and to be influenced by the spatial and temporal patterns of natural or human-caused disturbances (Bekker and Taylor, 2001). In western Quebec, under the shift in air mass dominance as well as the impacts of natural or human-induced disturbances such as forest fires (Bergeron, 2000) and insect outbreaks (Volney and Fleming, 2000), forest composition gradually changes from the deciduous-dominated temperate forest in the south to the coniferous-dominated boreal forest in the north (ESWG, 1996). A vegetation transition zone between the mixedwood and the coniferous-dominated boreal forest occurs at approximately 49ºN (Gauthier *et al.*, 2000).

A recent study has revealed that the current forest situation and the limits of the vegetation zone in the mixedwood boreal forest of Quebec may not have reached a balance with the present climate conditions (Bergeron *et al.,* 2004). A warming climate and a possible decreasing abundance of fires due to climate change and fire suppression (Bergeron, 2000) may favor an extension of the mixedwood into the coniferous forest. Bergeron (2000) reported an increased abundance of northern white cedar (*Thuja occidentalis* L.) in the landscape since 1850 as a consequence of a decrease in fire frequency. Tardif and Bergeron (1999) observed a movement of black ash (*Fraxinus nigra* Marsh.) populations from low flood plain sites to more elevated sites along the flooding gradient in the southeastern Quebec boreal forest. They attributed this movement to an increase in frequency and height of spring water levels associated with increasing snowfall and warmer spring temperatures.

Stem radial growth for any given year often integrates the effects of the previous and current year’s climate (Fritts, 1976). Hence tree rings have long been used as a valid tool to explore the long-term growth reactions to the historical climate variations and to further assess the impacts of future climate warming on tree growth and forest ecosystems. In the eastern Canadian boreal forest, a dendroclimatic investigation on black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) along a latitudinal gradient (48°N-50°N) indicated that the present vegetation situation was not in equilibrium and that detailed knowledge of species-specific growth responses to changes in a wide range of climate variables was needed (Hofgaard *et al.,* 1999). In this study, we conducted a dendroclimatic investigation on four major boreal tree species along a broad latitudinal gradient spanning from 46ºN to 54ºN and covering the vegetation transition zone in the eastern Canadian boreal forest. These species were: trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), black spruce, and jack pine. The objectives of our study were to 1) explore growth responses of the common boreal tree species to a wide range of climate variables along the latitudinal gradient from 46ºN to 54ºN in western Quebec, 2) investigate changes in their radial growth-climate associations along the gradient, and 3) assess future potential changes in tree growth in the eastern boreal forest of Canada. We hypothesized that with increasing latitude, temperature may play a more important role in affecting the radial growth of the studied species, whereas synergistic factors (temperature, precipitation, drought) regulating the radial growth could be significant in the south.

2.4. MATERIALS AND METHODS

2.4.1. Study area

Our study area is located at the Quebec-Ontario border along a latitudinal gradient ranging south from Petawawa (approximately 46°N) to Radisson (approximately 54°N) in the north (Figure 2.1), including the southern Laurentians, the Abitibi Plains, the James Bay area, and the Radisson Plains (ESWG, 1996). The topography along the gradient is generally flat and uniform with low-elevation hills and rock outcrops (300-400 m a.s.l.).

The climate of the region is dominated by dry polar and moderate polar air masses during the winter, and by moist maritime and moist tropical air masses during the summer (Figure 2.1). Dry moderate air masses also often occur after an air mass has been advected far from its source region and has thus been modified considerably (Sheridan, 2002). A climate gradient is also enclosed within the studied latitudinal gradient. Averaged climate data generated from the ANUSPLIN model (see climate data section) for the reference period 1950-2003 showed a linear decrease in mean annual maximum temperature (R^2adj= 0.96, P<0.0001), mean annual temperature (R^2adj= 0.91, P<0.0001), mean annual minimum temperature (R^2adj= 0.85, P=0.0002), and mean annual total precipitation (R^2adj= 0.82, P=0.0005) against the latitude from south to north, i.e., from 10.39°C, 4.52°C, -1.35°C, and 893 mm at 46° N to 1.93°C, -2.84°C, -8.20°C, and 644 mm at 54° N, respectively (Figure 2.2). The growing degree-days (>5°) also declined from 1 868°C at 46° N to 862°C at 54° N across the latitude (R^2adj= 0.90, $P<0.0001$). In the study area, a significant warming trend in growing seasonal average temperatures (April-September) from 1950 to 2003 was observed at each site (Figure 2.1). Similar trends were also found in climatic data sets of the Climate Research Unit (CRU 2.1 data; Mitchell and Jones, 2005).

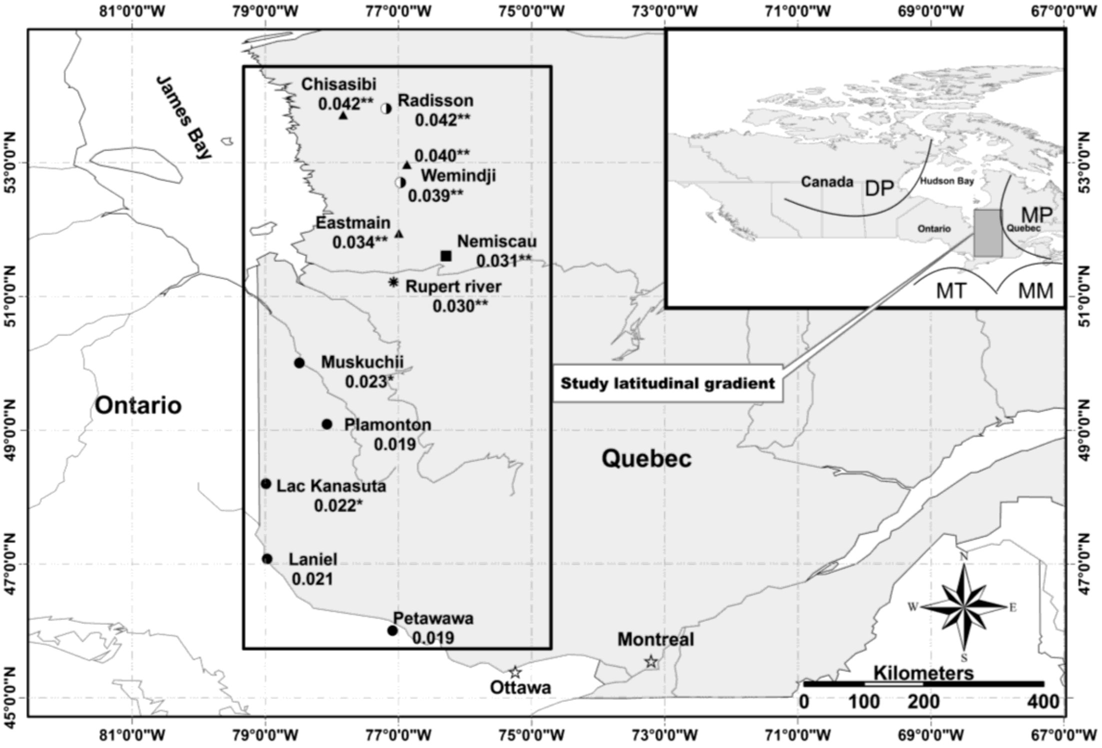

Figure 2. 1 Map showing the sampling sites for trembling aspen, paper birch, black spruce and jack pine and the climate data sites in the eastern Canadian boreal forest. Five solid circles indicate that all four species were sampled per site; Three triangles indicate that only two conifers were sampled per site; Two half-solid circles indicate that only two deciduous species were sampled per site; An asterisk indicates that

trembling aspen, black spruce and jack pine were sampled at the site; A square indicates the paper birch sampling site at 51°N; In total, 12 sets of the climate data were used in the current study. The number associated with each site refers to the slope (°C per year) of the regression line conducted on the growing season average temperature (April-September) for the period 1950–2003; 95% (*) and 99.99% (**) significant levels are indicated. The origins of major air mass types affecting the climate of the region are also indicated: dry polar (DP), moist polar (MP), moderate moist (MM), and moist tropical (MT) (based on Sheridan, 2002).

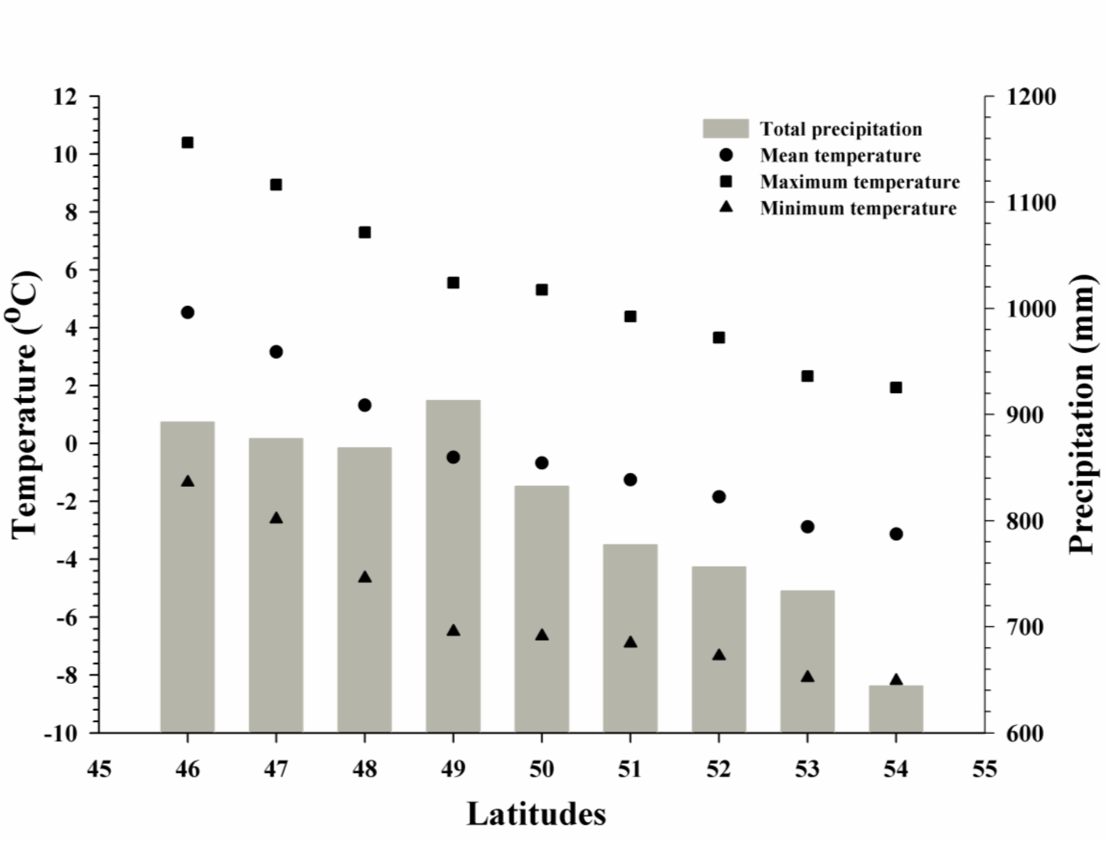

Figure 2. 2 Annual maximum, mean, and minimum temperatures, and mean annual total precipitation from 1950 to 2003 along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest.

Three bioclimatic zones encompass the study area from south to north, including 1) sugar maple-yellow birch domain, which is dominated by sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton) with some other species such as paper birch and trembling aspen; 2) balsam fir-yellow birch, and balsam fir-paper birch climax zone, which is dominated by balsam fir (*Abies balsamea* (L.) Mill.), yellow birch, paper birch with post-fire stands of jack pine and trembling aspen on the driest sites; and 3) black spruce-lichen, and black spruce-moss climax zone, which is characterized by the dominant black spruce stands with post-fire stands such as trembling aspen, paper birch, and jack pine (ESWG, 1996). Along the south-north gradient, common boreal tree species including trembling aspen, paper birch, black spruce, and jack pine occur but their abundance changes from south to north (Gauthier *et al.,* 2000). The studied gradient crosses the southern boreal forest region where both black spruce and jack pine approach their southern distributional limit of regional dominance (Burns and Honkala, 1990) and where trembling aspen approximately approaches its northern distributional limit, i.e., in the Hudson Bay region (Little, 1971).

2.4.2. Field sampling and laboratory chronology construction

Thirty-four forested stands were sampled in 2005 for the purposes of this study. To minimize the site effect on tree growth and to be representative of the majority of the forests, all stands were chosen from typical mesic or submesic conditions along the gradient (see Appendix II. 2.1). Tree-ring samples were collected from two deciduous species (trembling aspen and paper birch), as well as from two coniferous species (black spruce and jack pine) along the latitudinal gradient ranging from 46ºN to 54ºN. Sampling was conducted at approximately 1º intervals (Figure 2.1). At 48°N, tree-ring increment cores were collected to update the existing black spruce chronology developed by Hofgaard *et al.* (1999). Towards the northern end of the gradient, available old trembling aspen and paper birch stands were fairly rare and only two stands were sampled for each species between 52ºN and 54ºN. Given the numerous incomplete rings or missing rings in some hardwood boreal species like paper birch (Tardif *et al.*, 2001a), tree cross sections were collected for exact crossdating when tree cutting was permitted. In each stand, at least 20 old and healthy trees were cored or cut transversely at 1.3 m height (see Appendix II. 2.1). In total, 668 trees (340 cross sections and 655 cores) were sampled from south to north.

In the laboratory, all tree-ring samples were dried and carefully polished with successively finer grits of sandpaper. Visual crossdating for each sample was conducted under a binocular microscope. The dated samples were carefully measured using a Velmex measuring system interfaced with the ‘Time Series Analysis Program’ (TSAP; Frank Rinntech, Heidelberg, Germany) to a precision of 0.001 mm. Some black spruce and jack pine discs were scanned using WinDENDRO to obtain ring-width values. Visual crossdating was verified using COFECHA (Holmes, 1983) in which the Spearman rank correlation option was selected to diminish the influence of sharp growth reductions caused by insect outbreaks. In addition, the white/narrow rings that were associated with insect outbreaks and observed in trembling aspen and paper birch stands were validated by an independent and experienced technician at the University of Winnipeg.

Standardization was carried out to remove the age and size related trends in tree growth and to make the younger, faster growing portion of the tree more comparable to the older, slower growing portion of the tree (Fritts, 1976). This was done using a 60-year cubic spline with a 50% frequency response, which preserved approximately 99% of the variation within individual series at a wavelength of 19 years (Cook and Peters, 1981). When the first standardization did not perform well, the stiffness of the spline was modified to more flexible spline functions. Standardization involved transforming the ring-width measurements into dimensionless indices by dividing the observed ring-width measurements by those estimated using the spline function (Fritts, 1976). These growth indices contained a relatively stable mean and variance over time. This procedure retained high-frequency variations (interannual to decadal) and filtered out medium- to low-frequency trends such as trends in growth due to age/size, biological persistence and long-term stand dynamics (Cook, 1990). Because the standardized tree-ring indices are auto-correlated over time, the autoregressive model (AR) was also performed on each standardized series to remove temporal autocorrelation and enhance the common signal. The minimum Akaike Information Criterion (AIC) (Akaike, 1974) was used to choose the best AR models. The first-order autoregressive model was found to well describe the autocorrelation structure. The residual tree-ring series were then averaged using residuals from AR modeling of the standardized measurement series (Cook, 1985). This procedure provided time-series with first-order autocorrelation values (AR1) approximating values (zero) observed in climate data over our region. To further eliminate the effect of endogenous stand disturbances and enhance the common signal, all residual series were averaged by site using a biweight robust mean, which reduced the effect of outlier values. Chronology construction was carried out using ARSTAN (version 4.0a) (Cook, 1985). In total, 34 residual ring-width chronologies were constructed for four species at nine latitudes.

In western Quebec, studies have shown that both trembling aspen and paper birch stands undergo defoliation by insects such as the forest tent caterpillar (*Malacosoma disstria* Hubner) and (or) large aspen tortrix (*Choristoneura conflictana* Walker) (Bergeron and Charron, 1994; Huang *et al.*, 2008). In the study area, Huang *et al.* (2008) have identified severe insect outbreaks in the host species based on the occurrence of white/narrow rings as well as the host (trembling aspen) and nonhost (black spruce or jack pine) species comparison using OUTBREAK (Swetnam *et al.*, 1985) (For more method details, please see Huang *et al.*, 2008). To maximally eliminate the non-climatic noise associated with insect outbreaks in trembling aspen chronologies and, to a certain degree, in paper birch chronologies and at each latitude, the years identified as severe insect outbreak ones in Huang *et al.* (2008) were first removed from the residual chronologies of host species. Second, corrected chronology indices for the removed years were estimated through regressing the host residual chronology against the corresponding non-host residual chronology at each latitude. The final corrected trembling aspen and paper birch residual chronologies were used in all subsequent dendroclimatological analyses presented in this study.

2.4.3. Climate data

Owing to limited climate observational data in northwestern Quebec, the climate data that were used in our dendroclimatic analyses were generated from ANUSPLIN (version 4.3) (Hutchinson, 2004) by the Great Lakes Forestry Centre of the Canadian Forest Service. ANUSPLIN employs thin plate-smoothing splines to develop elevation-dependent spatially continuous climate surfaces from sparse weather station data (McKenney *et al.,* 2006). Based on the existing climate station data, it has the potential to generate monthly climate data for the period 1901 to 2003 (Hutchinson, 2004). However, given the lower reliability of the climate data in the north due to fewer climate observations available prior to 1950 and also to the short time span of some chronologies, only the climate data generated for the period 1950-2003 were used. In addition, at each latitude when the distance between sampling sites was less than 30 km, the same set of climate data was used for all study sites nearby. Otherwise, another independent set of climate data was generated from ANUSPLIN and used for dendroclimatic analysis. According to this criterion, in total 12 climate data sets were used for the dendroclimatological analyses involving four tree species and nine latitudes (Figure 2.1). The climate variables included monthly maximum temperature (Tmax), monthly mean temperature (T), monthly minimum temperature (Tmin), monthly total precipitation, start date of the growing season (daily mean temperature ≥ 5°C for five consective days after March 1st), end date of the growing season (daily minimum temperature reached -2°C or less after August 1st), growing season length (GSL), and growing degree-days (GDD, > 5°) (McKenney *et al.*, 2006). In addition, the Monthly Drought Code (MDC) from May to October was also calculated as described by Girardin and Wotton (2009) from monthly Tmax and precipitation data generated by ANUSPLIN, and it was used to investigate if soil moisture variability had any impact on tree growth in the region. The MDC is a numerical parameter representing the average moisture content of deep and compact organic layers (Turner, 1972) and was previously shown to correlate well with growth in boreal tree species (Girardin *et al.*, 2006).

2.4.4. Comparison of chronologies and their relationships to climate

To quantify the common variance among species and site residual chronologies along the gradient and to better synthesize changes in the radial growth-climate associations across the latitude, a Principal Components Analysis (PCA) was used. All the data were standardized to have zero mean and unit standard deviation prior to using PCA. The PCA was performed on all residual chronologies from the four species and for the common interval 1950-2003. Through standard PCA techniques in CANOCO (version 4.52; ter Braak and Smilauer, 2003), the 34 residual chronologies were transformed into principal components. A correlation matrix where the 34 site chronologies were considered as variables and the years as observations was used. The loadings of the PCs were utilized for analysis of common and species-specific patterns over the latitude. The eigenvalue-one criterion (Kaiser, 1960) and the criterion that any PC accounts for at least 5% of the total variance were used to determine the meaningful PCs to be retained for interpretation (Legendre and Legendre, 1998).

Given that our less reliable precipitation data predicted from ANUSPLIN could influence the results of growth-climate associations calculated by response function, the bootstrapped correlation analysis was used in our study. To identify the common climate factors limiting the radial growth of all four species along the gradient, bootstrapped correlations between the retained meaningful PCs and monthly climate data (variables described above) were calculated using DENDROCLIM2002 (Biondi and Waikul, 2004). This program uses a bootstrapping method to test the significance of correlation coefficients at the 0.05 level. The bootstrap method provides a test of significance of the stability of the correlation coefficients within a specific time period by repeated, random sampling of the data (Guiot, 1992). All correlations were calculated on a 16-month basis from May of the year prior to ring formation to August of the year of ring formation and for the period 1950-2003. Correlations between the residual ring-width chronologies and climate variables over various multimonth periods were also explored.

To assess potential changes in the radial growth-climate associations across the gradient, a PCA was conducted on bootstrapped correlation coefficients obtained from the radial growth-climate analysis for each species along the gradient (Tardif *et al.*, 2003). This could allow us to constrain the PCA on tree growth responses to climate only and thus extract the common variance among the radial growth-climate associations of a given species along the gradient. In this procedure, the correlation coefficients that were calculated between the climatic variables and residual chronologies using the bootstrap method were screened and climate variables showing a significant correlation at least once were retained. Through standard PCA techniques in CANOCO (version 4.52; ter Braak and Smilauer, 2003), correlation coefficients of the radial growth-climate associations of each species at nine latitudes were then transformed into new sets of orthogonal variables (Tardif *et al.,* 2003). The loadings of the PCs were utilized for analysis of common and site-specific growth response to climate over the latitude. The first two PCs were retained for further interpretation since they account for a high proportion of the total variance (at least 15%). The equilibrium circle of descriptors in the biplot was displayed to help us judge whether the contribution of each climate variable to the reduced space is greater or smaller. The climate variables located outside the circle account for more of the explained variation than those located inside the circle (Legendre and Legendre, 1998).

2.5. RESULTS

2.5.1. Chronologies and general statistics

The length of the trembling aspen chronologies varied from 78 to 143 years, with the longest chronology dating back to 1862 at 53°N (Table 2.1). The paper birch chronologies spanned from 76 to 176 years in length. Besides the black spruce chronology at 48°N from Hofgaard *et al.* (1999), black spruce and jack pine chronologies developed in our study ranged from 63 to 248 years and from 69 to 179 years, respectively (Table 2.2). As listed in Table 2.2, chronological statistics of both conifers were in general similar along the gradient, suggesting that these two species contained a similar number of the common signals from south to north. The similar characteristic was also observed for both hardwoods (Table 2.1). Of the four species, trembling aspen showed the fastest radial growth whereas black spruce had the slowest radial growth. Both deciduous species had greater mean sensitivity and standard deviations than the two conifers. High EPS (Wigley *et al.,* 1984) and all series correlation within a population, which are the primary tools in evaluating tree-ring chronology quality, indicated a strong common signal in uneven-aged populations along the gradient (Tables 2.1 and 2.2).

Table 2. 1 Statistical characteristics of the trembling aspen and paper birch residual chronologies along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest.

Species	Trembling aspen**								Paper birch**							
Sites	46°N	47°N	48°N	49°N	50°N	51°N	53°N	54°N	46°N	47°N	48°N	49°N	50°N	51°N	53°N	54°N
Chronology length	1911-2004	1894-2004	1908-2004	1864-2004	1870-2004	1925-2004	1862-2004	1927-2004	1903-2004	1829-2004	1899-2004	1911-2004	1893-2004	1907-2004	1879-2004	1929-2004
Number of trees (radii)	20(38)	20(40)	19(34)	20(40)	21(40)	20(40)	20(40)	20(38)	18(36)	18(36)	21(38)	20(39)	20(40)	20(38)	20(38)	17(33)
Mean ring width (mm)	2.37	1.83	2.91	1.86	1.48	1.77	1.61	1.60	1.27	0.96	1.92	0.92	1.56	0.78	1.23	1.44
Mean sensitivity	0.19	0.29	0.20	0.24	0.25	0.19	0.31	0.33	0.20	0.30	0.22	0.31	0.23	0.24	0.21	0.22
Standard deviation (mm)	0.19	0.24	0.17	0.22	0.22	0.18	0.26	0.29	0.17	0.24	0.21	0.27	0.19	0.22	0.20	0.21
1st order autocorrelation*	0.36	0.66	0.34	0.44	0.33	0.51	0.36	0.60	0.54	0.59	0.46	0.27	0.46	0.52	0.47	0.69
Common interval analysis for the period 1950-2004																
Number of trees (radii)	18(35)	19(36)	18(32)	18(35)	21(38)	20(39)	20(40)	19(36)	15(27)	10(16)	18(27)	13(16)	19(38)	15(27)	20(36)	11(20)
Variance in PC1 (%)	41.45	51.04	40.34	41.77	51.78	44.09	63.77	60.06	31.32	47.75	36.18	52.00	27.84	25.46	47.99	49.91
EPS	0.92	0.95	0.91	0.92	0.95	0.95	0.97	0.96	0.84	0.88	0.86	0.89	0.86	0.85	0.94	0.90
All series correlation	0.39	0.49	0.38	0.39	0.50	0.42	0.63	0.58	0.27	0.43	0.33	0.48	0.25	0.21	0.46	0.46

*Calculated from standard chronology; ** All chronological statistics were obtained prior to removal of insect outbreak years; EPS, expressed population signal; Common interval analysis for paper birch at 51°N from 1951 to 2000.

Table 2. 2 Statistical characteristics of black spruce and jack pine residual chronologies along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest.

Species	Black spruce									Jack pine								
Sites	46°N	47°N	48°N	49°N	50°N	51°N	52°N	53°N	54°N	46°N	47°N	48°N	49°N	50°N	51°N	52°N	53°N	54°N
Chronology length	1942-2004	1889-2004	1690-2004	1917-2004	1831-2004	1761-2004	1822-2004	1757-2004	1869-2004	1925-2004	1883-2004	1915-2004	1910-2004	1915-2004	1921-2004	1936-2004	1826-2004	1916-2004
Number of trees (radii)	19(38)	19(37)	36(72)	19(38)	20(39)	20(39)	20(38)	20(40)	20(40)	19(37)	18(36)	20(39)	20(39)	20(40)	17(29)	20(40)	18(31)	20(40)
Mean ring width (mm)	1.38	1.02	0.68	1.20	0.67	0.41	0.55	0.93	0.84	1.88	1.26	1.62	1.21	1.59	1.63	1.49	0.62	1.13
Mean sensitivity	0.17	0.17	0.17	0.16	0.19	0.16	0.14	0.13	0.12	0.14	0.18	0.17	0.21	0.15	0.15	0.13	0.16	0.16
Standard deviation (mm)	0.15	0.15	0.15	0.13	0.15	0.14	0.13	0.11	0.11	0.13	0.15	0.14	0.18	0.12	0.14	0.12	0.15	0.15
1st order autocorrelation*	0.63	0.50	0.76	0.24	0.27	0.47	0.59	0.54	0.50	0.67	0.36	0.52	0.52	0.58	0.71	0.81	0.68	0.72
Common interval analysis for the period 1950-2004																		
Number of trees (radii)	17(33)	17(32)	23(46)	19(38)	20(38)	20(39)	20(38)	18(36)	20(40)	17(32)	17(30)	18(35)	19(33)	18(36)	17(29)	19(38)	14(23)	16(32)
Variance in PC1 (%)	49.78	35.91	40.67	38.14	41.39	32.93	39.72	42.81	32.85	35.95	33.54	47.96	48.71	42.58	42.03	38.76	32.87	40.43
EPS	0.94	0.88	0.90	0.92	0.92	0.90	0.92	0.92	0.90	0.89	0.88	0.94	0.92	0.92	0.91	0.91	0.85	0.90
All series correlation	0.48	0.31	0.38	0.35	0.38	0.30	0.37	0.40	0.30	0.33	0.31	0.46	0.46	0.40	0.39	0.36	0.29	0.37

* Calculated from standard chronology; EPS, expressed population signal.

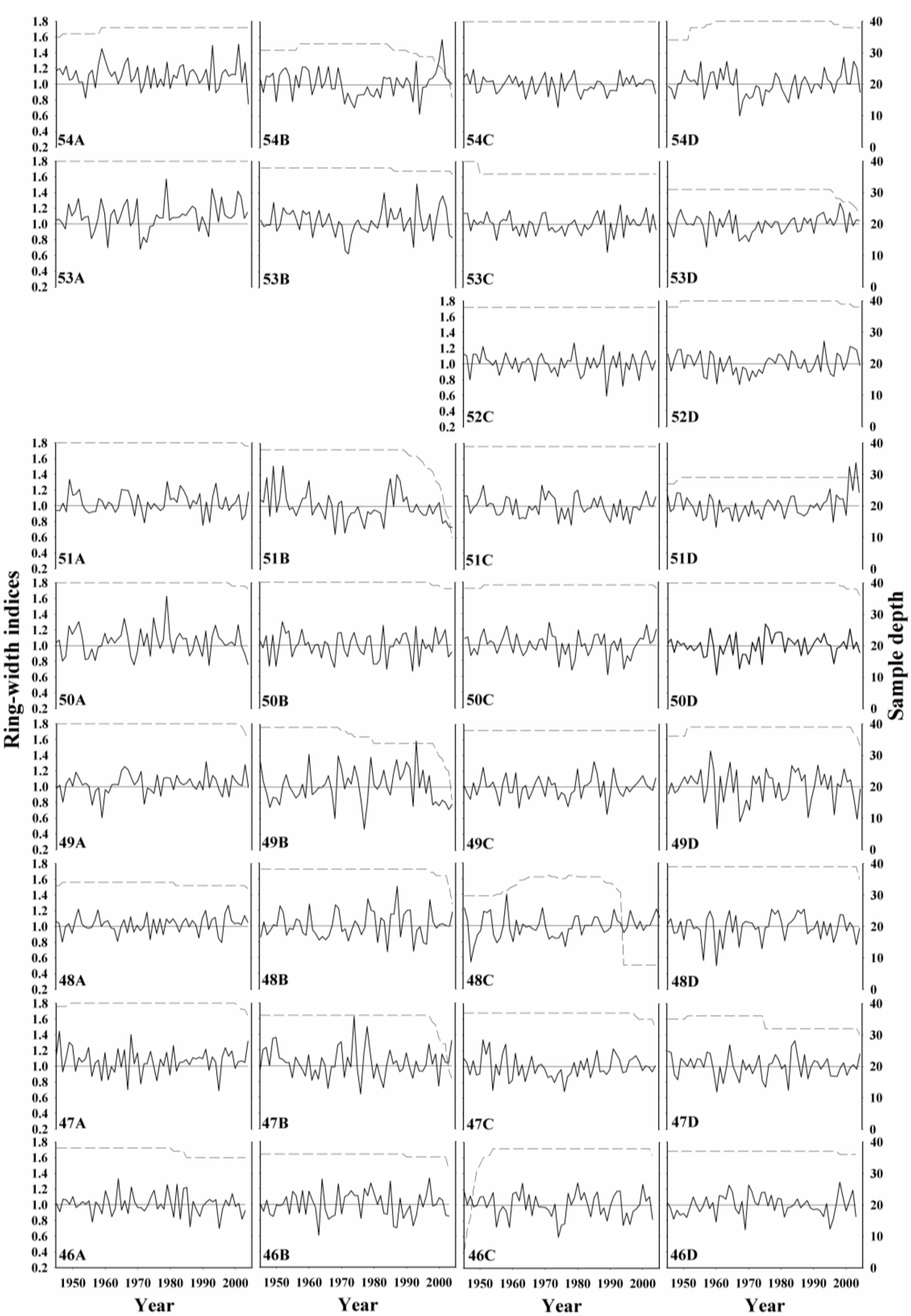
Ring-width indices
Sample depth
Year
54A
54B
54C
54D
53A
53B
53C
53D
52C
52D
51A
51B
51C
51D
50A
50B
50C
50D
49A
49B
49C
49D
48A
48B
48C
48D
47A
47B
47C
47D
46A
46B
46C
46D
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
0
10
20
30
40
1950
1960
1970
1980
1990
2000

Figure 2. 3 Ring-width residual chronologies for the period 1945-2004 constructed for trembling aspen (A), paper birch (B), black spruce (C) and jack pine (D) along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest. The dashed lines indicate the number of tree-ring series.

Both deciduous species also showed higher inter-annual fluctuations in ring-width indices in the residual chronologies than the two conifers (Figure 2.3), indicating that hardwood species may be more sensitive to inter-annual variations in climate than coniferous species. The residual chronologies for a given species in general demonstrated similar inter-annual growth variations between nearby sites (Figure 2.3).

2.5.2. Growth variations among sites/species and their relation to the common climate

As shown in Figure 2.4, PCA conducted on all the residual chronologies showed that the first four PCs (PCI, PCII, PCIII, and PCIV) were meaningful according to the criteria used in the study, and they in turn accounted for 20.7%, 11.1%, 8.6%, and 7.5% of the total variance of all the chronologies. The PCI describes the environmental signals (e.g. climate) that were held in common by all sites and species. Along the gradient, trembling aspen at 48°N-54°N, paper birch at 50°N-54°N, black spruce at 46°N-54°N, and jack pine at 47°N -54°N had significant contributions to the PCI, as indicated by their significant higher loadings than the expected values provided by the dashed line. Linear regression of the loadings of each species on the PCI against the latitude demonstrated a significant increasing linear trend for trembling aspen and paper birch towards northern latitudes (R^2adj=0.41, P=0.05, and R^2adj=0.83, P=0.001, respectively), yet an insignificant linear trend for both conifers. This less significant linear trend in trembling aspen indicated that trembling aspen at most latitudes may contain a similar number of environmental signals. Among the four species, both conifers had more contributions to the PCI than the hardwoods along the gradient. The contribution of both hardwoods to the PCI at 50°N-54°N and that of both conifers at 48°N-54°N were in general similar, respectively. In contrast, trembling aspen at 46°N-47°N, paper birch at 46°N-49°N, and jack pine at 46°N had low contributions to the PCI, as shown by their lower actual loadings than the ones shown by the dashed line in Figure 2.4.

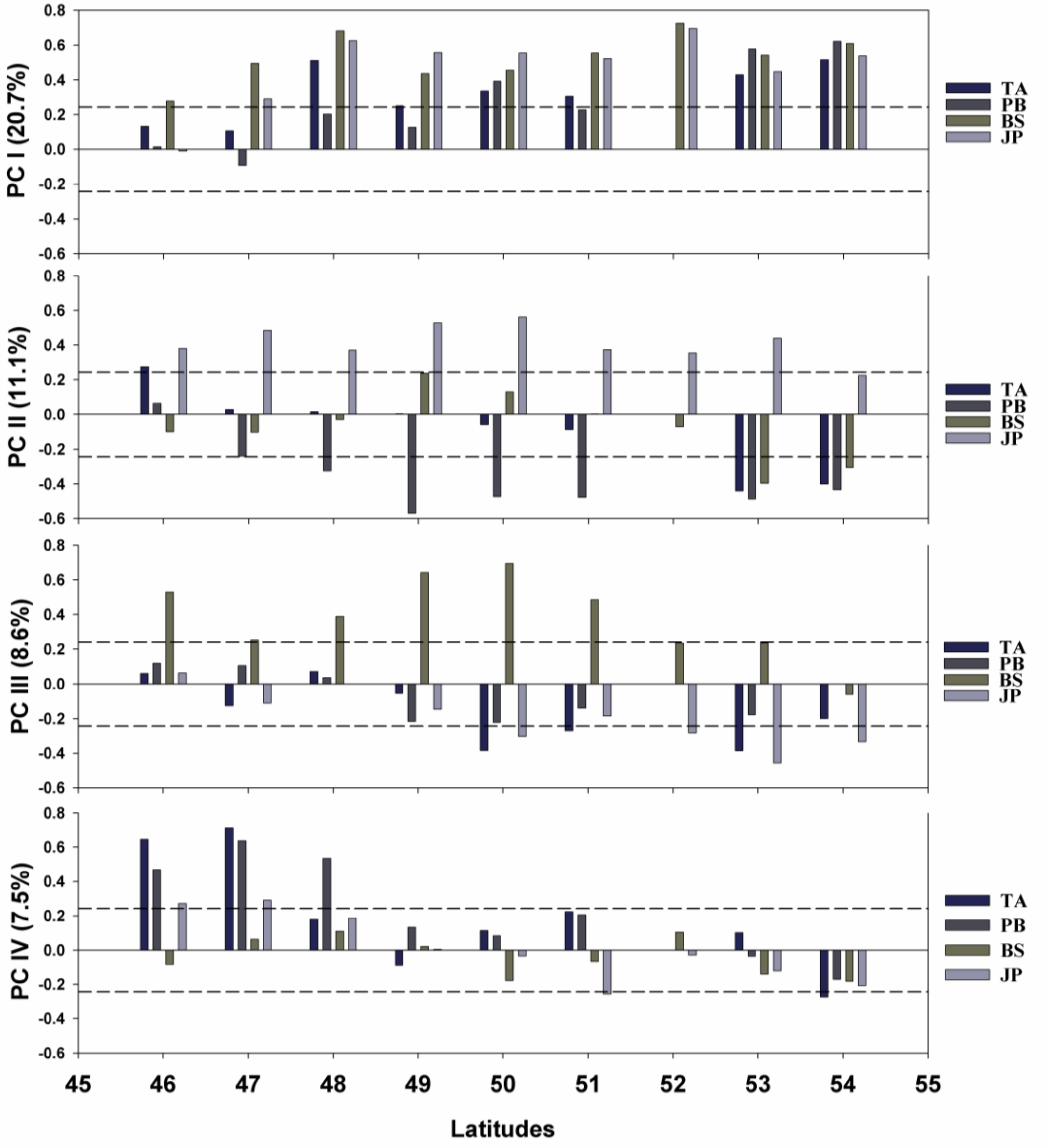

Figure 2. 4 Principal component analysis of the residual chronologies of trembling aspen (TA), paper birch (PB), black spruce (BS) and jack pine (JP) for the period 1950-2003. The dashed line represents the equilibrium circle of the biplot that enables us to judge whether the contribution of each residual chronology to the reduced space is greater or smaller than expected under the hypothesis of an equal contribution to all principal components (Legendre and Legendre, 1998). The residual chronologies that are clearly shorter than the value of their respective equilibrium contributions contribute little to the formation of the reduced space.

The PCII, PCIII, and PCIV encompass variables specific to differences among species. The PCII is mainly a jack pine-paper birch related axis with a few trembling aspen and black spruce northern sites, in which jack pine had high positive loadings, whereas the other three species had negative loadings. The PCIII is mainly a black spruce-other three species related axis, in which black spruce had high positive loadings, yet others had negative ones. Both PCII and PCIII together clearly separated these four species into different groups. The PCIV mostly reflects variables for trembling aspen at 46°N-47°N and paper birch at 46°N-48°N, as suggested by their high loadings compared with low loadings of other stands. Correlation conducted between the PCI and the climate variables (Appendix II. 2.2) showed that all four species or most of the species were correlated negatively with previous summer temperatures (June-August), positively with January and March-April temperatures and previous June precipitation. Since positive PCII and PCIII implied positive conifer growth and negative hardwood growth (refer to Figure 2.4), correlation for PCII suggested that jack pine was reacting positively to November temperatures and current March precipitation, and negatively to October precipitation, whereas an inverse relationship was found for paper birch. Correlation for the PCIII indicated that black spruce was responding negatively to the current June-July temperatures and current May precipitation, yet an adverse relationship occurred for trembling aspen at northern latitudes. Since PCIV only highlighted trembling aspen and paper birch stands at 46°N-48°N, correlation for the PCIV reflected that these southern hardwoods were positively responding to current June precipitation, and negatively to current summer MDC (June-August). These common climate factors observed among species/sites were consistent with the ones shown in Figs. 2.5 and 2.6.

2.5.3. Detailed radial growth-climate associations at different latitudes

In addition to a common growth response to climate along a broad spatial scale in the eastern boreal forest of Canada described above, species/site-specific growth responses to climate were also found, as illustrated by both Figure 2.5 and Figure 2.6. Trembling aspen's radial growth north of 47°N was negatively influenced by autumn temperatures of the previous year (September-November), with most significantly negative correlations to previous autumn Tmax. Especially for northern latitudes, this negative effect was confirmed by significantly negative correlations between residual chronologies and the previous summer and early autumn MDC (Figs. 2.5 and 2.6). Trembling aspen radial growth, as a whole, was also positively correlated with the growing season temperatures, with a weak change in significant correlations from March-April at southern latitudes to June-July at northern latitudes. In contrast, only a few positive correlations were found between trembling aspen growth and precipitation along the gradient, such as positive correlations between previous June precipitation and the radial growth of stands at 49°N-51°N. Trembling aspen radial growth was also found to be positively correlated with the GSL along the south-north gradient, with most significant correlations at 48°N-51°N. However, a few significant correlations were found for stands at 46°N.

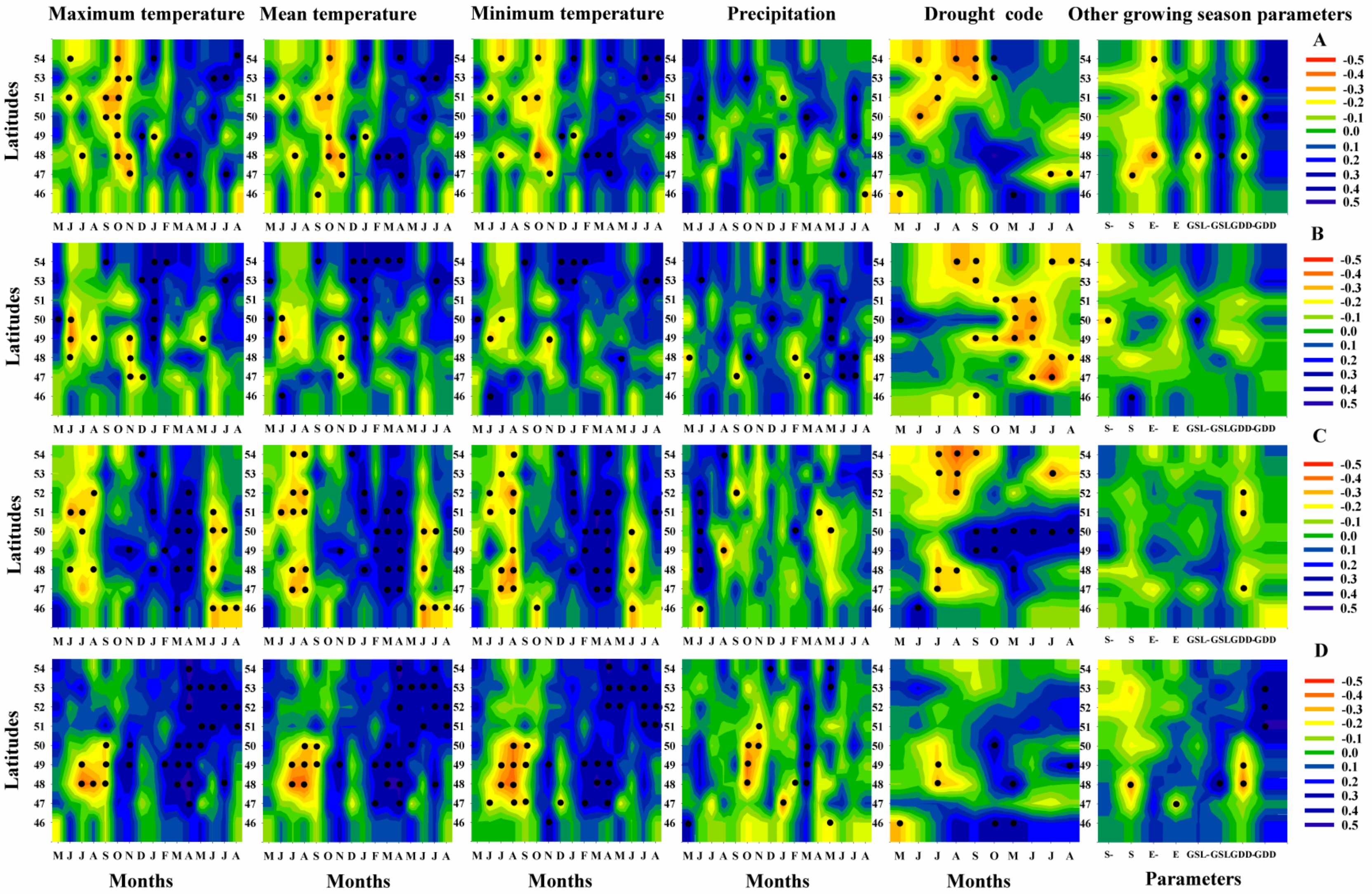
Maximum temperature
Mean temperature
Minimum temperature
Precipitation
Drought code
Other growing season parameters
A
B
C
D
Latitudes
54
53
52
51
50
49
48
47
46
M J J A S O N D J F M A M J J A
M J J A S O M J J A
S- S E- E GSL- GSL GDD- GDD
-0.5
-0.4
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
0.5
Months
Parameters

Figure 2. 5 Bootstrapped correlation coefficients between trembling aspen (A), paper birch (B), black spruce (C) and jack pine (D) residual tree-ring chronologies and the monthly climate variables (monthly maximum, mean, and minimum temperatures, monthly total precipitation, monthly drought code, and other growing season parameters) for the period 1950-2003 along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest. Other growing season parameters include the start date of the growing season in the previous year (S-) and the current year (S), end date of the growing season in the previous year (E-) and the current year (E), growing season length in the previous year (GSL-) and the current year (GSL), as well as growing degree-days in the previous year (GDD-) and the current year (GDD). The black dots indicate significant correlations at $P \leq 0.05$ level.

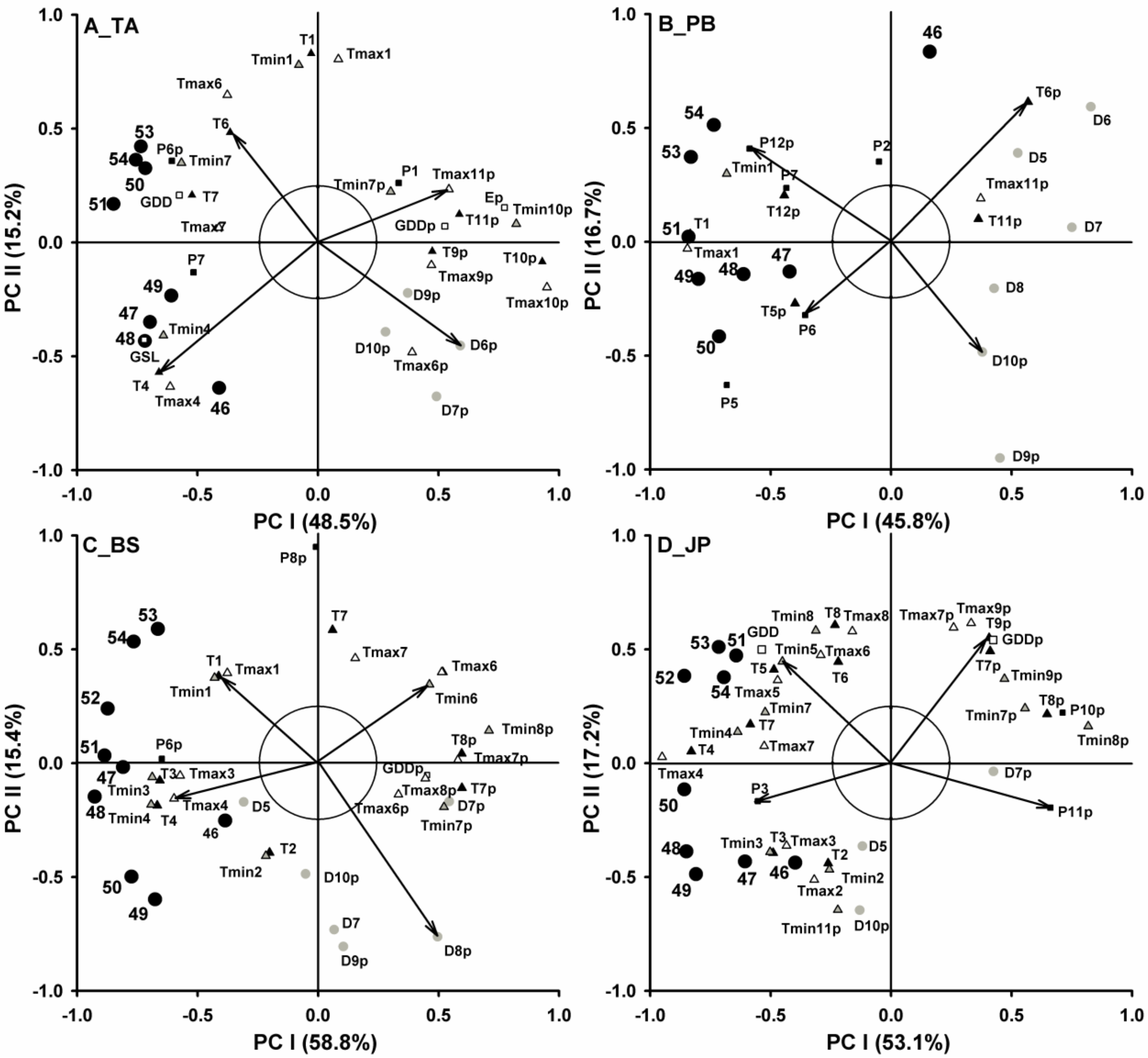
A_TA
PC I (48.5%)
PC II (15.2%)
T1
Tmin1
Tmax1
Tmax6
T6
53
54
50
51
P6p
Tmin7
GDD
T7
Tmax7
P7
49
47
48
GSL
Tmin4
T4
Tmax4
46
Tmin7p
P1
Tmax11p
Ep
Tmin10p
GDDp
T11p
T9p
Tmax9p
T10p
Tmax10p
D9p
D10p
D6p
Tmax6p
D7p
B_PB
PC I (45.8%)
PC II (16.7%)
46
54
53
P12p
Tmin1
P7
T12p
P2
T6p
D6
D5
Tmax11p
T11p
D7
51
T1
Tmax1
49
48
47
T5p
P6
50
P5
D8
D10p
D9p
C_BS
PC I (58.8%)
PC II (15.4%)
P8p
T7
53
54
T1
Tmax1
Tmin1
Tmax7
Tmax6
Tmin6
52
51
P6p
47
T3
Tmax3
Tmin3
48
Tmin4
T4
Tmax4
D5
46
T2
Tmin2
D10p
50
49
D7
D9p
D8p
T8p
Tmin8p
Tmax7p
GDDp
Tmax8p
T7p
Tmax6p
D7p
Tmin7p
D_JP
PC I (53.1%)
PC II (17.2%)
Tmin8
T8
Tmax8
Tmax7p
Tmax9p
T9p
GDDp
53
51
GDD
Tmin5
Tmax6
T5
T6
T7p
Tmin9p
52
54
Tmax5
Tmin7
Tmin4
T7
T4
Tmax7
Tmax4
50
P3
Tmin7p
T8p
P10p
Tmin8p
D7p
P11p
48
49
Tmin3
T3
Tmax3
47
46
T2
D5
Tmin2
Tmax2
Tmin11p
D10p
-1.0
-0.5
0.0
0.5
1.0

Figure 2. 6 Principal component analysis of correlation coefficients of the radial growth-climate associations of each of the four species, trembling aspen (A: TA), paper birch (B: PB), black spruce (C: BS) and jack pine (D: JP), along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest. Black dots represent our study sites at different latitudes. The equilibrium circle of the biplot enables us to judge whether the contribution of each climate variable to the reduced space is greater or smaller than expected under the hypothesis of an equal contribution to all principal components (Legendre and Legendre, 1998). Climate variables that are clearly shorter than the value of their respective equilibrium contributions were not shown in the biplot. For clarity, arrows pointing from the origin to the climate variables were only, as an example, selectively drawn with black arrows. The climate variables are positioned in the biplot based on their correlations with the canonical axes. In addition, the biplot also approximates the correlation coefficient among descriptors and climate variables. Climate variables and latitudes at sharp angles are positively correlated (cos 0° = 1.0, i.e., perfect correlation). Conversely, obtuse angles indicate negative correlation (cos 180° = -1.0, i.e., perfect correlation). Climate variable abbreviations are for monthly maximum temperature (Tmax, white ▲), monthly mean temperature (T, black ▲), monthly minimum temperature (Tmin, gray ▲), monthly total precipitation (P, black ■), monthly drought code (D, gray ●), and other growing season parameters (white ■) including start (S) and end (E) date of the growing season, growing season length (GSL), as well as growing degree-days (GDD). Climate variables in the previous year are indicated with a ‘p’. For example, monthly maximum, mean, and minimum temperature in the previous August and current August were indicated by Tmax8p, T8p, Tmin8p, and Tmax8, T8, and Tmin8, respectively; Monthly drought code in the previous May and current May were indicated by D5p, and D5, respectively.

Paper birch radial growth was positively correlated with the January temperature at most of our sites along the gradient, with significant correlations for Tmax and T at 49°N-54°N (Figure 2.5). In particular, its radial growth at 53°N-54°N was positively correlated to whole winter temperatures (Figure 2.5). In addition, paper birch radial growth was also negatively correlated with previous summer and autumn temperatures in the south, with most significant correlations for Tmax at 47°N-50°N (Figs. 2.5 and 2.6). Compared with trembling aspen, paper birch was found to be positively correlated with precipitation during the current May-July along the gradient, particularly for the latitudes 47°N-51°N where significant positive correlations were found. This positive precipitation effect was also reflected by its high sensitivity to MDC, where significantly negative correlations between radial growth and the current May-August MDC were observed at most of our sites. Paper birch growth did not show significant associations with other growing season parameters. Like trembling aspen at 46°N, a few significant correlations were found for paper birch at 46°N.

The radial growth-climate associations of black spruce indicated that the previous summer temperature (June-August) and the current June temperature were negatively associated with their radial growth at most of the latitudes, with most significant variables found for T and Tmin (Figs. 2.5 and 2.6). This negative effect was also confirmed by negative correlations between radial growth and the previous summer MDC. In addition, temperatures during the winter and early-growing season (December-April) showed positive correlations with black spruce growth along the gradient. In particular, these positive effects were more significant for T and Tmin for the stands at 47°N-52°N. Stands at 46°N were found to be different from the others and showed significant negative correlations with Tmax and T of the current June-August. Precipitation and other growing season parameters did not show any systematic associations with radial growth along the gradient, with the exception of positive correlations with the previous June precipitation. In addition, responses of black spruce at individual sites to MDC were also found. For example, black spruce stands at 46°N were positively correlated with the previous June MDC, and those at 49°N and 50°N were positively associated with the previous autumn (September-October) and the current May-August MDC.

Correlation functions for jack pine showed that growing season temperatures were positively correlated with their radial growth from south to north, with a seasonal shift from February-April south of 50°N to April-August north of 50°N (Figs. 2.5 and 2.6). Tmax and T showed more significant climate variables than Tmin. In addition, previous July-September temperature (Tmin) was found to be more negatively correlated to radial growth of jack pine at 47°N-50°N. In contrast, stands at 46°N seemed to be different from others, as suggested by a few significant correlations with climate variables. Precipitation and other growing season parameters generally did not exhibit any systematic impacts on the radial growth along the gradient, except for some individual sites.

2.5.4. Changes in the radial growth-climate associations along the gradient

As shown in Figure 2.6, PCA conducted on the bootstrapped correlation coefficients of the radial growth-climate associations for each of the four species along the gradient showed that the PCI accounted for 48.5%, 45.8%, 58.8%, and 53.1% of the variance for trembling aspen, paper birch, black spruce, and jack pine, respectively. Subsequently, the PCII explained respectively 15.2%, 16.7%, 15.4%, and 17.2% of the variance. Along the south-north gradient, the PCA well separated the radial growth-climate associations of each species into two parts on a broad spatial scale. All trembling aspen stands were separated into the southern latitudes (46°N-49°N) and northern latitudes (50°N-54°N) along the latitude 49°N whereas the other three species were set in the southern part (46°N-50°N, except for paper birch at 46°N) and the northern part (51°N-54°N) along the latitude 50°N. In addition, the PCA results also showed that stands at closer sites/latitudes in general had similar radial growth-climate associations.

2.6. DISCUSSION

The partitioning of the variance in the PCA indicated that all species responded to some common environmental signals. The PCI reflected that there were common climate signals across four species from south to north. Higher loadings at northern latitudes suggested that all species in the north were reacting to the same climate factors, whereas low loadings in the south reflected that either all species were reacting to different climate factors or that they were less climate-sensitive in the south. Of the four species, both black spruce and jack pine contained a similar number of common climate signals across most of the latitudes, suggesting that these species responded to climate similarly from south to north. This is consistent with previous large-spatial-scale studies of tree species across their distributional range. For example, Cook and Cole (1991) reported that eastern hemlock (*Tsuga canadensis* L.) was positively correlated to March temperatures throughout its range in eastern Northern America. Frank and Esper (2005) also reported that *Picea abies* (L.) H. Karst., *Larix decidua* Mill., and *Pinus cembra* L. tend to show most similar responses to climate across their wide distribution in the European Alps. However the reactions of both trembling aspen and paper birch to climate were more similar to the conifers in the north than in the south, as indicated by significant increasing loadings of their site chronologies on the PCI towards northern latitudes. This is inconsistent with the above-cited studies that reported similar growth response to climate across a large-spatial scale for the studied species. The inconsistency might be due to the following reasons: 1) these southern deciduous stands were less sensitive to climate, 2) insect outbreaks might reduce or affect their sensitivity to climate, 3) insect outbreak noise might still remain in the residual chronologies of these deciduous stands, and 4) these stands were influenced by the local climate and/or other factors such as species competition. In addition to common climate signals shared by all four species along the broad gradient, the variance explained by the PCII-PCIV suggested some other common climate signals shared within certain species and/or certain studied sites.

2.6.1. Common climate factors with consistent growth limiting effect among species

All our PCA and bootstrapped correlation analysis results together indicated that the previous summer temperature and moisture budget as well as current March-April temperatures were the common factors affecting radial growth of all four species though these factors were not found at all the sites. For example, previous summer temperatures were shown to negatively affect radial growth of trembling aspen at most latitudes, of paper birch at 48°N-50°N, of black spruce at almost all the latitudes, and of jack pine at 47°N-50°N. Hot previous summer temperatures could enhance stand respiration and evapotranspiration, thereby resulting in increased water deficits. This water-stress effect was also confirmed by positive correlation to previous June precipitation and negative correlation to previous summer MDC at many latitudes. Climate conditions in late summer generally influence the size of the buds and the number of leaf primordials produced within them for the growth of pre-determined boreal conifers in the previous year (Kozlowski *et al.*, 1991). The size of the dormant bud then affects the amount of leaf area for the most photosynthetically efficient class of leaves and needles produced in the current year of bud expansion and ring formation. On the other hand, a proper moisture budget allows optimal tree growth and assimilation of the carbohydrates for the next year's growth if soil moisture is sufficient to maintain foliage water potential and minimize vapor pressure deficits (Dang *et al.*, 1998). Trembling aspen as a typical upper canopy species has been widely shown to be moisture limited due to summer drought in the aspen parkland of western Canada (Brandt *et al.*, 2003; Hogg *et al.*, 2005) as well as in the United States (Worrall *et al.*, 2008). Using a conceptual model, Frey *et al.* (2004)

demonstrated how drought can either operate directly to cause rapid trembling aspen dieback through xylem cavitation or indirectly in combination with pathogens and other factors to cause long-term growth decline through decreased photosynthesis and a gradual exhaustion of carbohydrate reserves. In contrast, paper birch is a more shade-tolerant, sub-canopy species (Strong and La Roi, 1983) and thus exhibits moderate previous summer water-stress effect. Negative summer temperature effect observed only for paper birch at middle latitudes might be attributed to regional strong evapotranspiration during hot summers in those latitudes compared with the others. The summer water deficits were also reported in other hardwood species in the mixed boreal forest of Canada such as black ash (*Fraxinus nigra* Marsh.) (Tardif and Bergeron, 1993), sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) (Tardif *et al.,* 2001b) as well as white oak (*Quercus alba* L.) and red oak (*Quercus rubra* L.) (Tardif *et al.,* 2006).

Our black spruce showed strong previous summer moisture stress along the gradient. This trend agreed with previous black spruce studies such as Dang and Lieffers (1989) and Hofgaard *et al.* (1999) who also observed negative summer temperature effects on radial growth in the boreal forest. Negative correlation with previous summer temperature and positive correlation with previous June precipitation might also be explained by a climatic driven floral induction in masting trees like spruce, because these climatic factors were found to be critical for predicting seed production of Norway spruce (*Picea abies* (L.) Karst.) in southern Norway (Selås *et al.*, 2002). In contrast to black spruce, this previous summer water-stress effect was only observed for jack pine stands in the south. The discrepancy observed for both conifers might be ascribed to differences in species/sites. Jack pine is one of the least shade-tolerant evergreen species and usually grows on the sandy soils in the boreal forest, hence demonstrating better drought resistance than black spruce. However, during hot summers in the south, stands growing at high elevations or on slopes such as our jack pine stands at 48°N-50°N would show certain water deficits due to high evapotranspiration but low soil water reserves. Hofgaard *et al.* (1999) also documented a negative effect of previous summer temperature on radial growth of jack pine between 48°N and 50°N in the mixed boreal forest of western Quebec. Chhin *et al.* (2008) found negative effects of previous summer temperatures on the growth of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in the Rocky Mountains of western Canada as well. Our multi-species results were consistent with Girardin and Tardif (2005) who also documented negative previous summer temperature effects on radial growth of several hardwoods and conifers in Manitoba.

Current March-April temperatures were found to positively influence radial growth of trembling aspen at southern latitudes, of paper birch at 54°N, and of both black spruce and jack pine at almost all the latitudes. Warmer spring temperatures could favor leaf emergence or budburst earlier, thus resulting in better growth in a prolonged growing season. Graumlich (1993) observed that warm temperatures in April may favor conifer species owing to their evergreen foliage, which allows them to take advantage of early growing season warmth. Suni *et al.* (2003) revealed the significance of air temperature triggering the onset of photosynthesis of boreal conifers in spring. Based on field investigations on photosynthesis in balsam fir in New Brunswick, Canada, Goodine *et al.* (2008) further pointed out that spring air temperature might be particularly important for tree species whose root systems extend below the frost line to trigger the onset of photosynthesis. As for tree species whose root systems grow in frozen soils, the onset of photosynthesis may be triggered by soil thawing (Goodine *et al.* 2008). Warm spring air temperature might accelerate soil thawing, resulting in the availability of unfrozen soil water that is necessary for the photosynthetic onset. Subsequent recovery of full photosynthetic capacity (i.e., the photosynthetic rate of well-watered foliage at a reference temperature and saturating irradiance) may be also favored by warm air temperature (Goodine *et al.*, 2008). Our results were also supported by many previous studies that observed positive spring temperature effect on radial growth of both hardwoods and conifers in the eastern Canadian boreal forest (Tardif *et al.,* 2001a; Girardin *et al.,* 2006).

In addition, our results indicated that January temperature was the common factor for positively affecting radial growth of trembling aspen at 54°N, paper birch at most of the latitudes, and black spruce at northern latitudes. Warmer winter temperatures would protect tree tissues (e.g., buds and roots) from being damaged by severe winter freezing (Miller-Rushing and Primack, 2008). Adversely, a cold winter could cause root damage of shallow-rooted species when there is no snow pack (Cox and Zhu, 2003), which in turn results in low root pressure and low ability to transport water to buds. Wind and snow abrasion during cold winters can also damage tree crowns, leading to foliage loss (Grier, 1988). In addition, a cold winter could cause freezing-induced cavitation, which may delay flowering or leaf out by delaying the flow of water to buds in the spring (Wang *et al.,* 1992). Our results agreed with the findings of winter temperature effect on radial growth in previous studies (e.g., Tardif *et al.,* 2001a; Pederson *et al.,* 2004). For instance, Pederson *et al.* (2004) observed that January temperature was the most limiting factor for radial growth of six northern range margin tree species in the Hudson River Valley. Additionally, we also found that current summer precipitation or ample moisture was the major common factor influencing radial growth of both hardwoods in the south. With leaf expansion during a hot summer, sufficient precipitation may mitigate water stress for favoring radial growth of the southern hardwoods.

2.6.2. Common climate factors with inverse growth limiting effect among species

In addition to the common climate factors with consistent growth limiting effect found among species as discussed above, the common climate factors with inverse limiting effects on radial growth of our studied species were also observed. For instance, jack pine/paper birch and trembling aspen stands at some southern latitudes were mainly responding positively/negatively to November temperatures and current March precipitation, and negatively/positively to October precipitation, respectively. This is an indication of a regional climate signal. In autumn, paper birch might be damaged by the combination of dry (snow-free) conditions in October followed by severe cold in November, which may lead to deep soil frost. In contrast, jack pine might be favored by warm, dry (sunny) conditions to continue photosynthesis. Sufficient March snow may meet the water demands of jack pine stands during an early growing season, but it could postpone the start of the growing season for hardwood stands in the south. Our results were consistent with the previous studies. For example, Hofgaard *et al.* (1999) also observed a positive November effect on jack pine growth in western Quebec. Savva *et al.* (2008) found significantly positive growth responses of jack pine to precipitation during March in the nearby province of Ontario.

Our results also indicated that current hot summer (June-July) temperatures may increase water stress for limiting radial growth of black spruce south of 51°N, but provide sufficient warmth for favoring radial growth of the other three species at northern latitudes. Levanič and Eggertsson (2008) also documented positive relations between paper birch radial growth and the current summer temperatures in northern Iceland. In addition, during the growing season ample May precipitation may provide the required water supply for enhancing radial growth of paper birch at 49°N-51°N and of jack pine at 53°N-54°N, yet limit radial growth of black spruce at middle latitudes. Compared with the positive growing season precipitation effect on radial growth of both black spruce and jack pine reported by Tardif *et al.* (2001a), a few positive precipitation effects on their radial growth revealed in our study might be ascribed to less accuracy of the modeled precipitation data from the ANUSPLIN model (McKenney *et al.,* 2006). Other growing season parameters such as start and end date of the growing season, GSL, and GDD were found to play a minor role in regulating radial growth of all four species except for some individual sites.

2.6.3. Species/site-specific climate response

Our results revealed that previous autumn temperature (mostly October Tmax) was also a critical factor that negatively affected the radial growth of trembling aspen across the latitudes. Hot autumn temperatures might enhance stand respiration, thus increasing consumption of the carbohydrates that are reserved for the current year’s growth. In addition, trembling aspen may be able to benefit from a prolonged GSL to enhance growth, as reflected by its positive correlation to GSL. Taking both common and specific climate responses together, our results suggested that the previous year’s moisture condition was the most important factor affecting trembling aspen growth in the current year. Similar findings were also reported in other studies (e.g., Hogg *et al.*, 2005; Leonelli *et al.*, 2008). A recent wood anatomical study conducted in western Quebec found that trembling aspen could produce 3-5% new xylem cells before leaf emergence during the early growing season (Lihong Zhai, *unpublished data*), indicating that the carbohydrate reserves in the previous year might play a critical role in producing some new xylem cells.

Paper birch at most of the latitudes was demonstrated to be strongly water limited during the growing season, as suggested by positive correlation to summer precipitation and negative correlation to current summer MDC. This agreed with Tardif *et al.* (2001a) who also observed a positive relationship between paper birch and June precipitation and a negative one with current summer MDC in western Quebec. Ample precipitation would result in improved water conditions and thus favor the formation of carbohydrates during the growing season (Tardif *et al.*, 2001a). Stands at 46°N showed different climate responses from the others and appeared to be able to enhance growth through warm previous early summer temperatures and an early start of the growing season. Combined with the common limiting factor January temperature, our study as a whole indicated that the current year's climate conditions would play a more important role in controlling paper birch radial growth than the previous year's conditions across the latitudes. A recent wood anatomical study conducted in western Quebec also found that new cells of the xylem were not observed when paper birch leaves unfolded after one week (Lihong Zhai, *unpublished data*).

In addition to the common climate factors shared with other species, black spruce stands at 49°N-50°N demonstrated significantly positive correlation to the current summer MDC. This might be ascribed to the effect of local climate on radial growth or an unknown reason. Jack pine stands north of 50°N were also found to be significantly positively correlated to the current GDD. In addition, jack pine response to the growing season temperatures along the gradient showed a seasonal shift from February-April in the south to April-August in the north, suggesting that trees in the south could react to early spring temperatures earlier than those in the north. This corresponds to empirical and modelling phenology observations (Girardin *et al.*, 2008). Altogether, our study suggested that the current-year winter and spring or whole growing season temperatures were particularly important factors for positively affecting radial growth of both conifers across our broad gradient.

2.6.4. Changes in growth-climate associations from south to north

Common variances in the radial growth-climate associations across the latitudes explained by the first two PCs were similar among the four species (ranging from 62.5% to 74.2%), suggesting that the radial growth-climate associations of these four species changed in a similar manner across the latitudes. High variance represented by the PCI indicated that stands from south to north shared similar radial growth-climate associations except for stands at 46°N that contained less common but more local climate effects. Along the broad gradient, PCII clearly separated the radial growth-climate associations of each species into two parts, i.e., southern and northern, indicating that these stands were influenced by different air masses in the south and in the north, respectively. In western Quebec, on the regional scale, the southern area is affected by warm, moist air originating from the south during summer, whereas the northern area is influenced by cold, dry polar air during winter (Figure 2.1) (Sheridan, 2002). The balance between, and the position of, these main air masses undulates over the landscape between years and throughout all seasons. This large-scale climate pattern has given the boreal forest and its ecotones their positions and shapes through time (Bryson, 1966). Although stands are influenced by different air masses in the south and north across the gradient, no sharp climate boundary existing between south and north was revealed (Sheridan, 2002). Rather, the climate transition gradually changes from south to north between 48°N and 50°N, as indirectly evidenced by previous studies (Hofgaard *et al.*, 1999; Bergeron *et al.*, 2004). In addition, similar radial growth-climate associations within nearby sites/latitudes indicated a regional climate effect.

Along the vegetation transition zone (approximately 49°N) (Bergeron *et al.*, 2004), it is generally believed that the forests south of 49°N are mostly controlled by warm, moist air masses from the south, and forests north of 49°N are mainly shaped by cold, dry polar air. However, paper birch, black spruce and jack pine stands at 50°N were set in the south, as revealed by the PCA, indicating that they were also influenced by the southern climate, not by the northern climate. This could provide evidence to support the previous speculation that the warm, moist air masses and the cold, dry polar air masses might have been advancing and retreating northwards, respectively, due to recent warming at the transition zone (Hofgaard *et al.*, 1999; Girardin *et al.*, 2006). In contrast, PCA suggested that trembling aspen at 50°N was affected by the northern climate. This contrasting result might suggest that at the transition zone these boreal species have been responding to recent climate warming in different ways. Schulze and Mooney (1994) pointed out that species would respond to climate change individually rather than as a cohesive biome. Based on our analyses, paper birch, black spruce and jack pine would be more likely to respond positively to climate warming, whereas trembling aspen might be less responsive to warming. The positive responsiveness of paper birch, black spruce and jack pine to warming could be explained by the warming winter and growing season temperatures observed in the study region from 1950 to 2003, because these climate factors were the most important factors for positively affecting their radial growth across the latitudes, but less important for trembling aspen.

2.6.5. Potential changes in tree growth along the gradient

Since climate warming has been resulting in a warmer winter and spring in the Northern Hemisphere (IPCC, 2007), our study may allow us to assess potential changes in tree growth along the gradient based on the above understanding of their growth responses to climate. Over broad spatial scale, both black spruce and jack pine north of 47°N, paper birch north of 49°N as well as trembling aspen at northern latitudes (e.g., 53°N and 54°N) might be able to benefit from warming winter and spring temperatures to enhance their radial growth in the coming decades. Several jack pine provenance tests in Canada and Europe also reported that the northern seed sources were currently growing at temperatures below the optimum and would benefit from future increased temperatures (Savva *et al.*, 2007). Reich and Oleksyn (2008) observed that warming might alleviate the limited effects of cold temperatures on tree growth such as cold conditions and effects of cold on soil resource supply, hence leading to enhanced growth and survival of Scots pine (*Pinus sylvestris* L.) in the far north across Europe. Our mixed modelling analysis also showed moderate growth increases in trembling aspen at northern sites (M.-P. Lapointe-Garant, *unpublished data*). In contrast, paper birch south of 49°N and trembling aspen along most of other latitudes might be decreasing in their growth owing to high evapotranspiration and moisture stress in hot summer and autumn seasons as well as increased insect outbreaks (Volney and Fleming, 2000) and other factors such as species competition (Bergeron *et al.,* 2004). Through investigations from two contrasting deciduous forest ecosystems in the boreal and temperate regions of central Canada, Barr *et al.* (2002) reported that the warm spring of 1998 caused early leaf out and increased photosynthesis but had little effect on respiration in the boreal forest ecosystem, whereas in the temperate ecosystem the same warming spring not only caused early leaf out but also enhanced respiration and drought stress. However, our analysis may not be sensitive to longer-term processes associated with climatic variation, e.g., lags in growth responses caused by 1) slow, climate-related changes in soil nutrient regimes, 2) depletion of stored carbohydrates in the roots, 3) depletion of soil water in the rooting zone; and lags in growth responses induced by climate-related increases in damage by insects and disease, or species-specific ecophysiological processes such as leaf longevity, flowering, cone production and seed development. In addition, future impacts of climate change on tree growth would be strongly influenced by future changes in damage by insects and diseases and by the stand-level dynamics (e.g., mortality and subsequent growth releases of survivors) that are not easy to determine from tree-ring analysis of living trees. Despite this, taken together, our results support the general concern that with climate warming, deciduous species might be able to enhance their growth in the north and then gradually develop into a pure coniferous boreal forest in the future.

2.7. CONCLUSIONS

To examine the potential impact of climate change on forest growth, our study investigated radial growth response of four dominant tree species to climate along the broad latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest. We found that the moisture conditions in the previous year played a dominant role in positively affecting radial growth of trembling aspen over the gradient, whereas January temperature and growing season moisture conditions were major factors for positively affecting radial growth of paper birch. Both black spruce and jack pine were primarily positively impacted by the current-year winter and spring or whole growing season temperatures along the gradient. Since different climate factors limited radial growth, the growth responsiveness of these four species to recent warming was inconsistent at the vegetation transition zone, where paper birch, black spruce and jack pine would be the most positively responsive species, whereas trembling aspen might be the least. With continued warming, both black spruce and jack pine north of 47°N might be able to benefit from warming winter and spring temperatures to enhance radial growth. Paper birch north of 49°N and trembling aspen at northern latitudes such as 53°N and 54°N could also increase their growth during favorable growing season conditions, whereas paper birch stands at southern latitudes and trembling aspen at most of other latitudes might be decreasing in radial growth. Foresters should take into account that some hardwoods might be favored by the future climate and thus they could make more room for hardwood and mixedwood management in the eastern Canadian boreal forest. In addition, these potential growth changes in different boreal species might also cause substantial changes in carbon sinks in the boreal forest. Hence it is of great importance to take our multiple species and broad spatial-scale study as a template for exploring the effects of climate warming on growth of different tree species in other boreal regions of the Northern Hemisphere. This could aid us to quantitatively assess potential changes in tree growth and forest composition across the mid-high latitudes of the Northern Hemisphere, which in turn may be used in the long-term planning of sustainable forest management and the assessment of the role of boreal forests in global carbon equilibrium.

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CHAPTER III

IMPACT OF FUTURE CLIMATE ON RADIAL GROWTH OF FOUR DOMINANT BOREAL TREE SPECIES ALONG A LATITUDINAL GRADIENT IN THE EASTERN CANADIAN BOREAL FOREST

Jian-Guo Huang, Yves Bergeron, Frank Berninger,
Lihong Zhai, Jacques C. Tardif, and Bernhard Denneler

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3.1. RÉSUMÉ

Les conditions futures de croissance des arbres pourraient changer avec le réchauffement climatique au cours du temps, ce qui entraîne une incertitude importante dans la prévision de croissance au cours du 21ème siècle. Dans cet article, les modèles dynamiques et les modèles locaux sont construits à partir des deux hypothèses suivantes: (1) la croissance future des peuplements au niveau des latitudes nordiques pourrait être prédite par les relations croissance-climat établies pour les peuplements actuellement localisés au niveau des latitudes sud, étant donné que les conditions de croissance des arbres pourraient changer au cours du temps avec le réchauffement climatique, (2) la croissance future des arbres pourrait être prédite par les relations -croissance-climat obtenues à partir d'un site local donné, lorsqu'on considère l'effet des contraintes génétiques ou le délai de la réponse génétique au climat sur la croissance. Ces deux types de modèles ont été utilisés pour prédire les variations de croissance radiale de quatre espèces (*peuplier faux-tremble*, *bouleau blanc*, é*pinette noire*, et *pin gris*) entre 2010 et 2099 suivant plusieurs scénarios de changements climatiques dont les données ont été générées par GCMs et CRCM3. Les simulations de croissance obtenues à partir de ces deux modèles pourraient constituer deux bases théoriques pour les variations futures de croissance radiale de ces espèces au niveau de la forêt boréale de l'est du Canada au cours du 21ème siècle. Les prédictions indiquent que les peuplements localisés au nord auront une meilleure croissance en raison des conditions climatiques favorables prévues pour la saison de croissance, alors que les peuplements localisés au sud pourraient montrer de faibles variations ou bien même une réduction de croissance du fait de l'augmentation du stress hydrique. Parmi les quatre espèces, le *pin gris* pourrait être le plus avantagé par le réchauffement climatique pour ce qui est de la possibilité d'accroître la croissance radiale le long du gradient au cours du 21ème siècle.

3.2. ABSTRACT

Future tree growth conditions could change with climate warming over time, thereby resulting in large uncertainty in growth prediction during the 21st century. In this paper, the dynamic models and the local models were, respectively, constructed according to the following two assumptions: (1) future growth of the stands at northern latitude may be forecasted by the growth-climate equations established for the stands currently growing at southern latitudes, given that tree growth conditions might change with climate warming over time; (2) future tree growth might be maximally predicted by the growth-climate equations obtained from the given local site, when considering the genetic constraints effect or the lagged effect of genetic response to climate on growth. The constructed two types of models were employed to predict radial growth change of four dominant boreal tree species *Populus tremuloides*, *Betula papyrifera*, *Picea mariana*, and *Pinus banksiana* from 2010 to 2099 based on several climate change scenarios data generated from GCMs and CRCM3. The northern stands were predicted to show large growth increase due to future favourable growing season climate conditions, whereas the southern stands would show minor growth change or growth decline because of increased drought stress. Of the four species, *P. banksiana* would be the most beneficial species from climate warming to enhance radial growth over the whole gradient during the 21st century. These simulation results could be only considered as one possible scenario of future growth in eastern Canada under climate warming. The dynamic model and the local model-based growth simulations may constitute two theoretical baselines for future radial growth change of these species in the eastern Canadian boreal forest during the 21st century.

3.3. INTRODUCTION

Climate warming is likely to result in changes in growth, structure, and composition in the temperature and nutrient-limited circumboreal forests at mid to high latitudes (Oechel *et al.*, 1993; IPCC, 2007). This potential growth change in boreal species might necessitate not only moderate adjustment of the current boreal forest ecosystem management, but it may also cause substantial changes in boreal carbon balance. The changes in boreal carbon balance could in turn result in reassessment of the carbon pool of boreal forest and consequently, modification of global carbon cycle model, since the boreal forest stores approximately 40% of the total carbon in the terrestrial ecosystems (Kasischke, 2000). It is, therefore, of great importance to quantitatively assess potential growth response of the dominant tree species to future climate warming in the boreal biome.

Previous modelling studies have attempted to quantitatively predict potential changes in tree growth, net primary productivity, and forest productivity under increased greenhouse gases emissions scenarios (mostly 2 X CO_2 concentrations) using either the empirical statistical model (e.g., Rathgeber *et al.*, 2000; Girardin *et al.*, 2008; Lapointe-Garant et al., 2009) or process-based model (e.g., Running and Coughlan, 1988; Friend *et al.*, 1993; Berninger and Nikinmaa, 1997; Cramer *et al.*, 2001; Nabuurs *et al.*, 2002; Morales *et al.*, 2005). For example, Chhin *et al.* (2008) based on the established empirical regression model at a given site, reported negative impact of future climate warming on forest productivity of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in Alberta. Girardin *et al.* (2008) used both the empirical regression model and process-based model to forecast radial growth of boreal tree species jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), and black spruce (*Picea mariana (Mill.) BSP*) in the Duck Mountain Provincial Forest of Manitoba, Canada. They observed a possible decrease in forest productivity in the study region under future changing climate. A common feature among previous studies is that their growth predictions were made based on the assumption that future growth conditions would be the same as the current growth conditions. However, tree growth conditions might be changing with a warming climate over time, coupled with future potential changes in disturbance regimes such as forest fires and insect outbreaks (IPCC, 2007). Hence previous studies only provided probably a dubious scenario for future potential changes in growth and productivity of trees and forests, which might have limited applicability over time (probably only during the coming decades).

In this paper, we compared two different assumptions that may constitute two theoretical baselines for predicting potential growth change of trees and forests under future different climate change scenarios. Given that tree growth conditions might be changing with a warming climate over time, our first assumption (AP1) is that tree growth response to climate at the temporal scale may be resembled by tree growth response to climate at the spatial scale. That is, tree growth response to climate along a broad latitudinal gradient from south to north may constitute an analogue of tree growth response to future climate warming over time. For instance, with climate warming, during future certain time period the conditions at a northern latitude where trees currently grow would be similar to the current conditions of a more southern latitude. Therefore, growth of those northern stands during future time period could be predicted using the climate-growth equations obtained from the currently more southern stands (growth lower limit).

However, a 25-year jack pine provenance study in the boreal forest of Canada found that northern populations transferred to a southern latitude did not benefit from a warmer climate (Savva *et al.*, 2007). Conversely, the northern populations were observed to be more conservative in their growth cycle phenology than the local populations (Savva *et al.*, 2007), hence an inherent early onset of growth cessation resulted in a lower radial growth in those northern populations. This might indicate a genetic constraints effect on growth or a lagged effect in genetic response to climate (Rehfeldt *et al.*, 2002) since the onset of bud and growth cessation is a genetically-constrained photoperiodic response (Beaulieu and Rainville, 2005; Jackson, 2009). Therefore, future tree growth at northern latitudes might not be completely resembled by the stands at southern latitudes under the AP1 if the photoperiod difference between these two latitudes is large. In this case, we assume that future tree growth might be maximally predicted by the climate-growth equations obtained from the given site (growth upper limit) when taking the genetic constraints effect or genetic lagged effect on growth into account, i.e., the second assumption (AP2). Taken both assumptions together, we propose that future potential changes in tree growth at a given site would be very likely to be set between these two predictions.

Huang *et al.* (2010) have conducted a study covering a broad latitudinal gradient spanning from 46°N to 54°N to investigate the growth response of four dominant boreal tree species, trembling aspen, paper birch (*Betula papyrifera* Marsh.), black spruce, and jack pine to recent climate warming in the eastern Canadian boreal forest. This broad latitudinal gradient may constitute an analogue of future climate warming given that the northern growth conditions might be changing to the southern growth conditions with climate warming during the 21st century. In the current study we attempted to first establish the calibrated climate-growth models for each species at different latitudes, and then further assess if there is any large difference in the predicted mean growth change among different models/scenarios/latitudes. This may allow us to further determine the most appropriate model for predicting future radial growth at a given latitude over time. In addition, we, based on different IPCC SRES scenarios data generated from the three General Circulation Models (GCMs) and Canadian Regional Climate Model (CRCM), further forecasted potential changes in radial growth of each species for a given latitude from 2010 to 2099 using (1) the above selected calibrated climate-growth models at more southern latitudes (growth lower limit), and (2) the model at the given site (growth upper limit), respectively.

Both growth predictions were further compared and discussed to assess their rationale and future implications. Our study would open a window of simulating future growth of trees and forests in a new way that needs to be taken into account in future forest simulations and management under a changing climate.

3.4. MATERIALS AND METHODS

3.4.1. Study area

Our study area is located at the Quebec-Ontario border along a latitudinal gradient ranging south from Petawawa (approximately 46°N) to Radisson (approximately 54°N) in the north (Figure 3.1), including the Ontario river valley, the southern Laurentians, the Abitibi Plains, the James Bay area, and the Radisson Plains (ESWG, 1996; Huang *et al.*, 2010). The topography along the gradient is generally flat and uniform with low-elevation hills and rock outcrops.

The climate of the region is dominated by dry polar and moderate polar air masses during the winter, and by moist maritime and moist tropical air masses during the summer (Sheridan, 2002) (Figure 3.1). A climate gradient is also enclosed within the studied latitudinal gradient, as described in details in Huang *et al.* (2009). In the study area, a significant warming trend in growing seasonal average temperatures (April-September) from 1950 to 2003 was observed at each site. Similar trends were also found in climatic data sets of the Climate Research Unit (CRU 2.1 data; Mitchell and Jones, 2005).

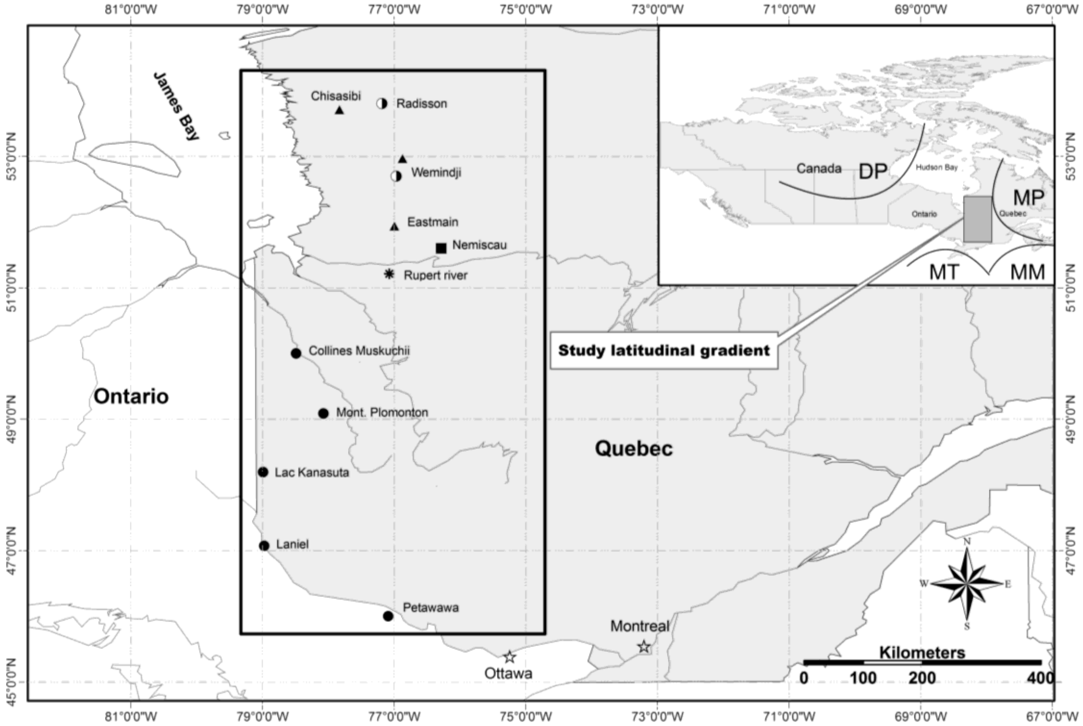

Figure 3. 1 Map showing the sampling sites for trembling aspen, paper birch, black spruce and jack pine and the climate data sites in the eastern Canadian boreal forest. Five solid circles indicate that all four species were sampled per site; three triangles indicate that only two conifers were sampled per site; two half-solid circles indicate that only two deciduous species were sampled per site; an asterisk indicates that trembling aspen, black spruce and jack pine were sampled at the site; a square indicates the paper birch sampling site at 51°N; in total, 12 sets of the ANUSPLIN climate data and the corresponding climate change scenarios data were used in the current study. The origins of major air mass types affecting the climate of the region are also indicated: dry polar (DP), moist polar (MP), moderate moist (MM), and moist tropical (MT) (based on Sheridan, 2002). (Map adapted from Huang *et al.*, 2010).

Along the south-north gradient in the eastern Canadian boreal forest, common boreal tree species including trembling aspen, paper birch, black spruce and jack pine occur but their abundance changes from south to north, i.e., the abundance of the conifers, in particular black spruce, increase but broadleaf species decrease (Gauthier *et al.*, 2000). In phytogeographical terms the area goes from the southern boreal forest to the taiga (Burns and Honkala, 1990), where trembling aspen approximately approaches its northern distributional limit, i.e., in the Hudson Bay region (Little, 1971). The treeline is about 500 km north of the northernmost sites.

3.4.2. Tree-ring growth increment data

Our tree-ring width data sets of trembling aspen, paper birch, black spruce and jack pine have been described by Huang *et al.* (2010), who used it to identify and calibrate response functions. All tree-ring series were developed according to the standard techniques such as crossdating, standardization, and calculation of residual ring-width chronologies, as documented in Huang *et al.* (2010). In addition, since our trembling aspen and paper birch stands were defoliated by insects such as the forest tent caterpillar (*Malacosoma disstria* Hubner) and (or) large aspen tortrix (*Choristoneura conflictana* Walker), the ring-width values in severe insect outbreak years were further corrected to maximally eliminate the insect noise. The detailed approach was documented in Huang *et al.* (2008; 2010). In total, 8 corrected trembling aspen and 8 paper birch residual chronologies as well as 9 black spruce and 9 jack pine residual chronologies were used in the current climate-growth modelling study. The expressed population signal (EPS), which is the primary tool to evaluate the most reliable period of the chronology of all the residual chronologies was above the generally accepted cutoff value of 0.85 (Wigley *et al.*, 1984).

3.4.3. Climate data for the model calibration

Owing to limited climate observational data in northwestern Quebec, in total 12 climate data sets were generated from ANUSPLIN (version 4.3) (Hutchinson, 2004) for the period 1901 to 2003 by the Great Lakes Forestry Centre of the Canadian Forest Service, as reported in Huang *et al.* (2010), and used for the current climate-growth model calibration analyses involving four tree species and nine latitudes (Figure 3.1). Climate variables used in the model calibration analysis included monthly maximum temperature (Tmax), monthly minimum temperature (Tmin), and monthly total precipitation (McKenney *et al.,* 2006). In addition, the monthly Canadian Drought Code (CDC) from May to October was also calculated for each climate data set, as described by Girardin and Wotton (2009), from monthly Tmax and precipitation data generated by ANUSPLIN. The CDC was used to investigate if soil moisture variability had any impact on tree growth in the region. The CDC is a numerical parameter representing the average moisture content of deep and compact organic layers (Turner, 1972) and was previously shown to correlate well with growth in boreal tree species (Girardin *et al.,* 2006, Huang *et al*., 2010).

3.4.4. Climate change scenarios data

The corresponding 12 sets of climate change scenarios data were produced from climate models and used for future growth simulation over the gradient. For each of the 12 sets of climate change scenarios data, eight extra climate change scenarios data were generated from three GCMs and the CRCM3 for future growth simulation of a given species at each site/latitude. These eight climate change scenarios data included three scenarios data generated from the Canadian third-generation coupled global climate model (CGCM3) under A1B, A2, and B1 scenarios (Flato *et al.,* 2000), two scenarios data generated from UK Hadley Centre HadCM3 under A2 and B2 scenarios (Collins *et al.,* 2001), and two scenarios data generated from Max Planck Institut für Meteorologie ECHAM4 under A2 and B2 scenarios (Roeckner *et al.,* 1996), as well as one scenario data generated from CRCM3 under A2 scenario. They were correspondingly referred to CA1B, CA2, CB1, HA2, HB2, EA2, EB2 and MA2 in the following texts.

Future climate change scenarios are built based on the effects of various concentrations of greenhouse gases and other pollutants within the atmosphere on the Earth-atmosphere system (IPCC, 2007). The CGCM3 covers the subset domain grid cell dimensions of 3.75° longitude x 3.71° latitude. The HadCM3 covers the subset domain grid cell dimensions of 3.75° longitude x 2.25° latitude. The ECHAM4 covers the subset domain grid cell dimensions of 2.8° longitude x 2.8° latitude. The historical baseline statistics for pre-climate change weather conditions were 1900-2000 for the CGCM3, 1950-2000 for HadCM3, and 1961-2000 for ECHAM4.

The CRCM3 was developed using the same physical principles as GCMs through the commonly termed approach of dynamical downscaling. It allows production of simulations at higher spatial resolution. The two simulations (CRCM 4.1.1 ACU; CRCM4.1.1 ADC) (Music and Caya, 2007; Brochu and Laprise, 2007) were carried out for a domain centred over Quebec and covering an area of approximately 5,050 km by 4,000 km with a horizontal grid-size mesh of 45 km (true at 60 degrees north latitude) for the period 1961-2100. Daily maximum and minimum temperature, and precipitation time series from these two simulations at each climate data set were further averaged together for the given climate data site along the gradient. Based on the above daily climate scenarios data generated from three GCMs and the CRCM3, the monthly mean maximum, minimum temperatures and monthly total precipitation under each scenario were further calculated at each climate data site for final simulation use.

Differences in means between the ANUSPLIN climate data and simulated monthly climate change scenarios data over 1961–1990 were tested ($p(t\text{-test}) < 0.05$)) and, when necessary, adjustments were applied to all simulated climate scenarios data; variance between observed and simulated data was not significantly different (for most variables $p(F\text{-test}) > 0.05$) and thus was not adjusted (Girardin *et al.*, 2008; Lapointe-Garant *et al.*, 2009). The adjusted monthly maximum temperature and precipitation data were also used to calculate the CDC from May to October for each climate data set according to Girardin and Wotton (2009). The common period 1961-2099 climate scenarios data among different GCMs were used for future growth simulations.

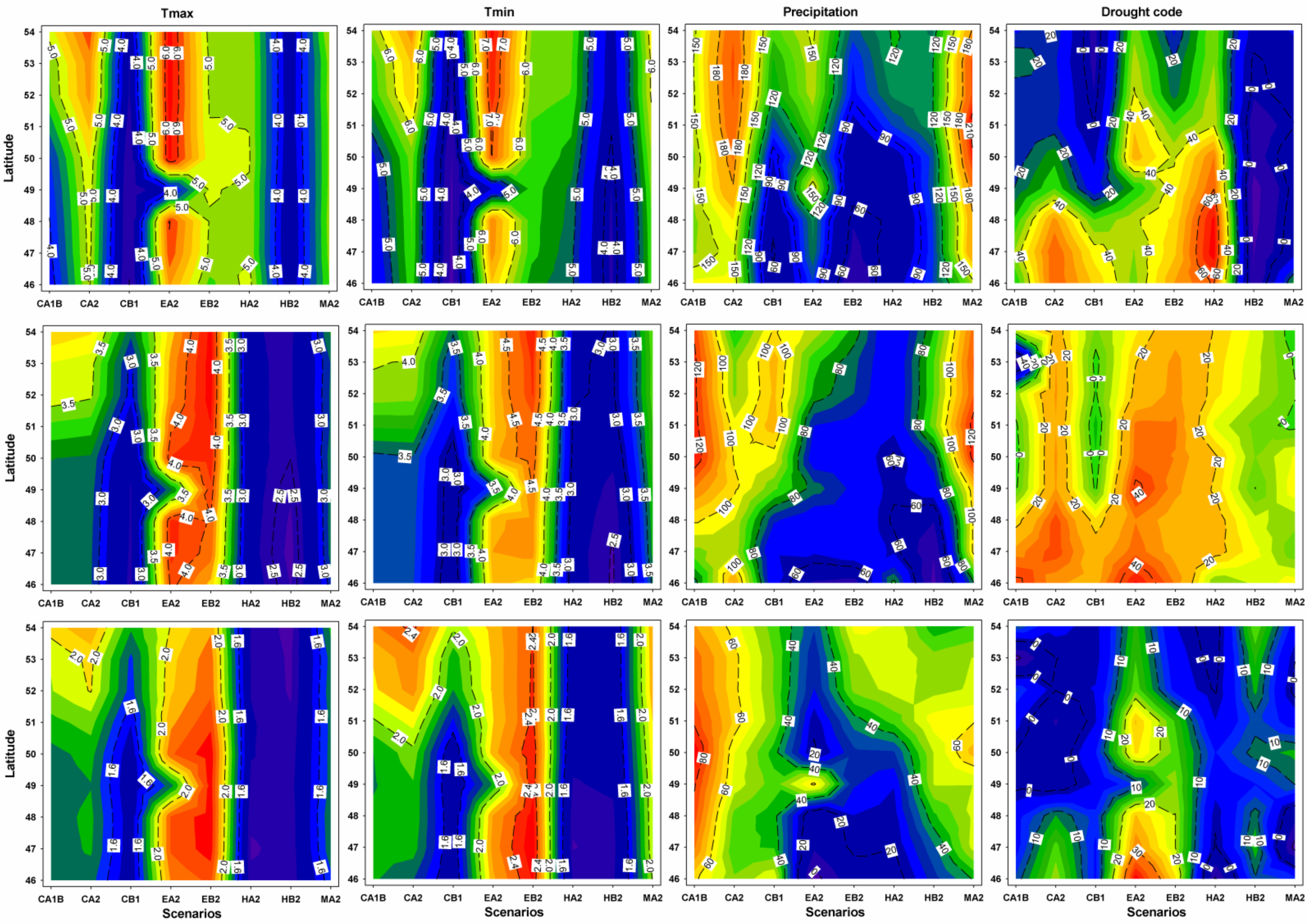
Tmax
Tmin
Precipitation
Drought code
Latitude
Latitude
Latitude
46
47
48
49
50
51
52
53
54
CA1B
CA2
CB1
EA2
EB2
HA2
HB2
MA2
Scenarios
Scenarios
Scenarios
Scenarios

Figure 3. 2 Climate anomalies of future three subperiods 2010-2039 (lower panel), 2040-2069 (middle panel), and 2070-2099 (upper panel) relative to mean climate during the period 1961-1990 along the gradient in the eastern Canadian boreal forest. Abbreviations: Tmax, anomalies for mean maximum temperature during each subperiod; Tmin, anomalies for mean minimum temperature during each subperiod; precipitation, anomalies for mean total precipitation during each subperiod; drought code, anomalies for mean drought code during each subperiod. See definition for scenarios abbreviations in the text. The thermal lines are shown on the figure.

As shown by positive climate anomalies of future three subperiods in relative to mean climate during 1961-1990 in Figure 3.2, the largest positive temperature anomalies were simulated by the ECHAM4 (EA2 and EB2), whereas the smallest positive anomalies were simulated by the HadCM3 (HA2 and HB2). The higher precipitation anomalies were predicted by the CGCM (CA1B, CA2, and CB1) and CRCM3 (MA2) than that predicted by the ECHAM4 and HadCM3. Severe drought anomalies were predicted by ECHAM4 (EA2 and EB2) than other models during 2010-2039. Except for CB1, HB2 and MA2, intensified drought anomalies were forecasted by the other climate change scenarios over the gradient during 2040-2069. Over the period 2070-2099, severe drought anomalies in the south were simulated by most of the models, except for HB2 and MA2.

3.4.5. Empirical models of tree-ring growth increments

Least-squares stepwise multiple regression employing a backward selection was used to establish the empirical climate-growth models. The stepwise multiple regression function was given as following:

$$\mathrm{Y}j = b0 + b1\mathrm{X}1j + b2\mathrm{X}2j + b3\mathrm{X}3j + .. + bm\mathrm{X}mj + \varepsilon j$$

Where:

$\mathrm{Y}j$: the annual value of tree-ring growth increment;

Xj : the climate data;

b : the regression coefficients;

ε : the error.

The period of analysis involved May of the year prior to tree-ring formation to September of the year of tree-ring formation. Hence 62 predictor variables were first involved in the initial starting model, including 17 monthly maximum temperatures, 17 monthly minimum temperatures, 17 monthly total precipitations, and 11 monthly CDC at each site/species. Maximum common period of the ANUSPLIN climate data and the residual chronology for each site/species was involved in the model calibration process to produce a reliable calibration model for future growth simulation.

Each calibrated model was established according to the following two steps. (1) Backward stepwise regression analysis trial was conducted to reduce the monthly climate predictor variables from the full starting stepwise model involving 62 monthly climate variables. At this step, minimum tolerance for entry into the models was set at a less strict level 0.1 to avoid omitting some secondary important monthly climate factors in the model. The minimum Akaike Information Criterion (AIC) (Akaike, 1974) was used to choose the best calibration model for each species/site. After this step, only statistically important monthly climate variables (around 20-30 monthly variables, $p<0.1$) were retained. (2) Based on the above retained monthly climate variables, mean values (temperature and CDC) or total sums (precipitation) of multi-months combination of climate variables were calculated to further reduce the number of the predictors and the multicollinearity among monthly climate variables. Backward stepwise regression analysis was again conducted between each residual chronology and the mean values of combined climate variables calculated above to establish the final best calibrated model of tree-ring growth increment. At this step, minimum tolerance for entry into the models was set at 0.05. The minimum AIC was again used to choose the best final calibration model for each species/site. Variance inflation factor (VIF) was also calculated for detecting multicollinearity. After this step, there were generally less than 10 combined climate variables involved in final calibration model (See Appendix II. 3.1).

The stability of each regression model was cross-validated using a split sample calibration–verification scheme (Cook and Kairiukstis, 1990). First, maximum time period of climate data that was used to generate the above full calibration model was split into two subperiods by the year of 1965, i.e., an independent calibration subperiod and an independent verification subperiod. Second, based on the combined multiple-monthly climate variables, once estimated for the calibration subperiod, the regression coefficients were applied to those combined multi-months climate variables over the verification periods to produce a series of tree-ring growth increment estimates. For example, if the full time period of a tree-ring chronology was 1902-2003, the period was first split into two subperiods 1902-1965 and 1966-2003. When the first subperiod 1902-1965 was used for model calibration, then the subsequent subperiod 1966-2003 was used for model verification. Thereafter, the regression coefficients obtained from the subperiod 1902-1965 calibration model were applied to the combined multi-months climate variables over the verification periods 1966-2003 to produce a series of tree-ring growth increment estimates. The above modelling processes were repeated when using reverse subperiod for model calibration (1966-2003) and model verification (1902-1965).

The strength of the relationship between tree-ring growth increment estimates and observations was measured using the Pearson R^2, the reduction of error (RE), the product means test (PM), and the sign test (ST) (Fritts, 1976; Cook *et al.*, 1994). The RE statistic is a measure of the explained variance in the verification period. A positive value between zero and one indicates that the model has some skills in predicting growth. This statistic is highly sensitive to the presence of trends in the data or to a few bad estimates. The PM test calculates the products of the deviations and collects the positive and negative products in two separate groups based on their signs. The values of the products in each group are summed, and the means computed. The difference between the absolute values of the two means can be tested for significance using the *t* statistics. A significant PM test result indicates that the magnitude and the direction of these changes are statistically significant. The ST is a nonparametric method based upon the number of agreements and disagreements in sign of departure from the mean in the observed and reconstructed series (Cook *et al.*, 1994). As a general rule, if the number of agreement exceeds the number of disagreements by greater than expected by chance alone, the reconstruction passes. When the number (N) of observations in the verification period is >50, the number of agreements required for the test to indicate significance at the 95% confidence level is $(N - 1 - 1.96\sqrt{N}) / 2$. For $N > 50$, the normal distribution is used to derive significance. When $N < 50$, the cumulative distribution tables for the binomial distribution can be used instead to test significance. A significance table is detailed by Fritts (1976). Stepwise multiple regressions were conducted using the software SAS 10 (SAS Corporation, Cary, North Carolina, USA). The program VFY (Holmes, 1999) was used for calculation of the RE, PM and ST verification statistics.

3.4.6. Potential mean growth change

Based on the above full period calibration model obtained for each species/site (Appendix II. 3.1), the yearly ring-width index for a given species at a site from 1962 to 2099 was simulated using each of the 8 monthly climate change scenario data generated from those three GCMs and the CRCM3. To better assess future radial growth trend over time, the percentage of potential growth change (GC) in ring-width index was also calculated through the following equation:

$$GC = ((STRI_i - MTRI) / MTRI) \times 100$$

in which $STRI_i$ indicates the simulated ring-width index of the given species at a site in the year *i*, 1962≤ *i* ≤2099; MTRI indicates mean of the simulated ring-width index from 1962 to 2001 for the given species/site.

3.4.7. Assessment of difference in mean GC among different scenarios/functions/ latitudes

To assess if the predicted GCs of a given species at different latitudes differ among different climate change scenarios using different functions (models), mean growth change of each species per latitude was calculated using all the calibration models of the given species (8 models for trembling aspen, 7 models for paper birch, 9 models for black spruce, and 9 models for jack pine) under eight climate change scenarios data. Partition of variance in mean GC was further made through ANOVAs (Sokal and Rohlf, 1995) to test the importance of different factors (sites, models, and scenarios) for the predictions. In ANOVAs, the dependent variable was mean GC, and the independent variables were scenarios, functions, and latitudes, and their interactive effects. The variance explained by the errors was considered as the variance explained by climate variability.

3.4.8. Model structure under the AP1 and AP2, respectively

To determine the best calibrated models from the southern latitudes for predicting mean GC of a given species at a northern latitude under climate warming (i.e., AP1), the time period 2010-2099 was first split into three subperiods 2010-2039, 2040-2069, and 2070-2099, and a 30-year mean annual temperature for each subperiod was then calculated based on the eight climate change scenarios data generated from GCMs and CRCM3 at each latitude (Table 3.3). Second, the 1961-1990 mean annual temperature was also calculated based on climate data that were generated from ANUSPLIN and used for model calibration at each latitude (Table 3.3). Third, comparisons between mean annual temperature of future three subperiods and the 1961-1990 ANUSPLIN mean annual temperature at different latitudes was made to identify the best match of growth conditions between future three subperiods and the appropriate southern latitudes. That is, we assume that growth condition at a given latitude/site during future subperiod would be similar to the growth condition at a southern latitude where the 1961-1990 ANUSPLIN mean temperature was close to the mean temperature of future subperiod at the given latitude/site. Last, since tree growth condition might be gradually changing from the given latitude to the best southern latitude with climate warming over time, the calibrated models of a given species established from the given latitude and the identified best southern latitude as well as their intermediate latitudes were all involved for future growth simulation of the given site.

We defined the model constructed under the AP1 as the dynamic model. The model structure is shown by a flow chart in Figure 3.3, in which, as an example, calculation of average mean growth change of stands at 54°N during 2010-2039 is shown. Average mean growth change of the stands at other latitudes during each of three future subperiods was calculated according to the similar flow based on the equations identified for each site and each subperiod in Table 3.3.

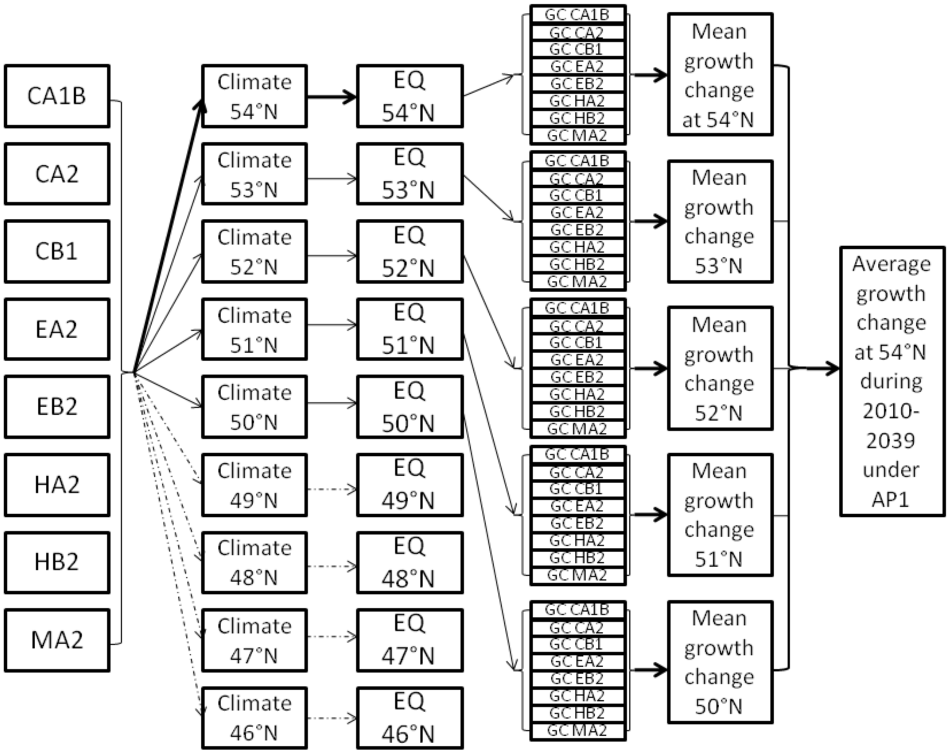

Figure 3. 3 Flow chart of the dynamic model (i.e., under the AP1). To be clear, we took stands at 54°N during 2010-2039 as an example to explain how the flow chart works (solid arrows). From left colum to right colum, eight climate change scenarios (CA1B, CA2, CB1, EA2, EB2, HA2, HB2, and MA2) at each of the nine climate data sets (from 46 to 54°N), nine established empirical climate-growth equations (EQ) from 46 to 54°N, growth change (GC) during 2010-2039 predicted for each of eight scenarios data using each of the equations eastablished from 54, 53, 52, 51 and 50°N (solid arrows), mean growth change during 2010-2039 for each latitude, as well as average growth change during 2010-2039 obtained from mean growth change calculated from the previous step.

We defined the model constructed under the AP2 as the local model. The model structure is shown by a flow chart in Figure 3.4, in which calculation of mean growth change of stands at a given latitude during 2010-2099 was shown.

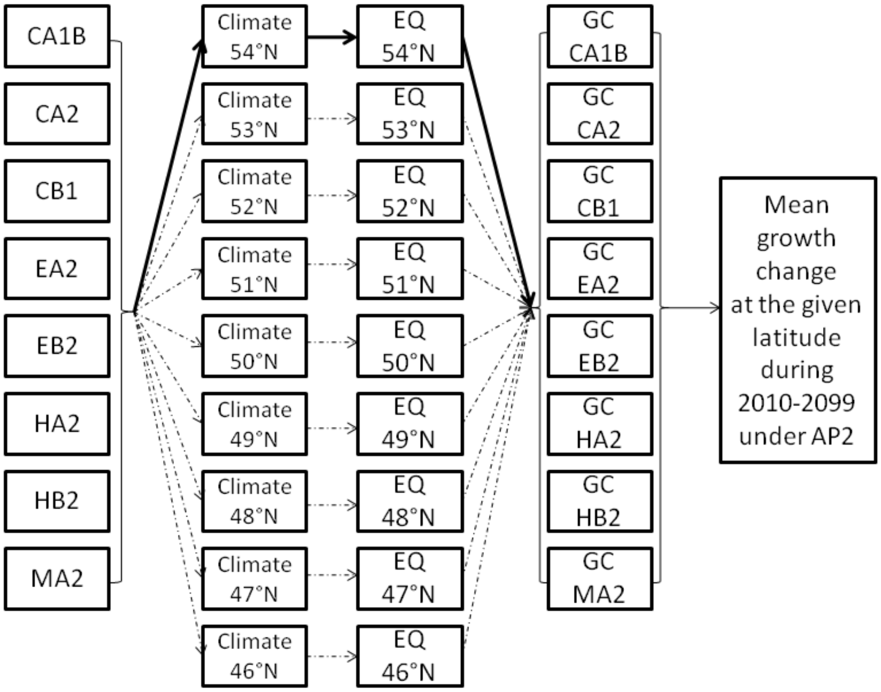

Figure 3. 4 Flow chart of the local model (i.e., under the AP2). From left colum to right colum, eight climate change scenarios (CA1B, CA2, CB1, EA2, EB2, HA2, HB2, and MA2) at each of the nine climate data sets (from 46 to 54°N), nine established empirical climate-growth equations (EQ) from 46 to 54°N, growth change (GC) during 2010-2099 predicted for each of eight scenarios data using each equation eastablished at given latitude, mean growth change for given latitude during 2010-2099. The soild arrow shows the flow of mean growth change calculated for 54°N.

3.4.9. Potential mean GC of the four species from 2010 to 2099 along the gradient

We used the dynamic model (under the AP1) to calculate average growth change of a given species at a northern site/latitude over each of future three subperiods according to the following steps. (a) Since several models were involved for growth simulation at a given northern latitude during a future subperiod as listed in Table 3.3, each of the involved models was first used to predict eight GCs when using eight climate change scenarios data at the latitude where this involved model was established (as shown in Fig. 3.3). Second, mean value of these eight GCs was further obtained as the final mean GC of this involved latitude. (b) The above first and second steps were conducted for each of the involved several models, thus resulting in several final mean GCs. (c) The least squares mean was further calculated based on the several final mean GCs calculated in (b). Finally, this is the predicted average GC of the given species at the given northern latitude during the given future subperiod. The 95% confidence interval was also built. Partition of variance in average GC during each subperiod was further assessed by ANOVAs. In ANOVA, the independent variable is average GC, and the dependent variables are scenarios, functions, and scenarios* functions. The variance explained by the errors was considered as the variance explained by climate variability. The proportion of the variance in average GC explained by the above factors in three subperiods was further summarized as the total proportion of the variance in average GC explained by those factors during the period 2010-2099.

We used the local model to calculate (under the AP2) future mean growth change of a given species at a site over time period 2010-2099 according to the steps: (1) only the calibrated model obtained at the given site was involved for simulation based on each of eight climate scenarios data generated from three GCMs and CRCM3. (2) The least square mean in growth change of the given species was further calculated based on eight GCs calculated above, and the 95% confidence interval was also built. Previous empirical tree-ring modelling studies often used the local models to simulate future tree growth under different climate change scenarios (Laroque and Smith, 2003; Chhin *et al.* 2008; Girardin *et al.*, 2008). Partition of variance in mean GC was further made through ANOVAs. In ANOVA, the independent variable is mean GC, and the dependent variable is scenarios. The variance in mean GC explained by the errors was considered as the variance explained by climate variability.

To clearly compare and assess future potential changes in mean GC of the four species predicted by two types of models at the spatiotemporal scales, the least square mean of average GC of each species/site during each of three subperiods was also calculated based on the above yearly average GC of each species/site simulated under each assumption. All analysis was done by SAS 10 (SAS Corporation, Cary, NC, USA).

3.5. RESULTS

3.5.1. Empirical climate-growth calibration models

Along the gradient, we were able to establish the satisfying empirical climate-growth calibration models for 33 of 34 stands involving all four species (Appendix II. 3.1). We failed to establish a satisfactory climate-growth calibration model for paper birch stands at 47ºN ($adjR^2 < 0.10$, $p>0.05$), which might be affected and biased by insect outbreak noise still remaining in these stands. As listed in Tables 3.1 and 3.2, the amount of variance ($adjR^2$) in observed ring-width index explained by climate variables ranged from 16% to 32% for trembling aspen, from 15% to 35% for paper birch, from 19% to 26% for black spruce, and from 20% to 46% for jack pine along the gradient. Of the four species, jack pine had the highest growth variance explained by the climate. The other three species had more or less similar growth variations explained by the climate along the gradient. The variation inflation factors were all much lower than the generally accepted threshold value of 10 (Belsley *et al.*, 1980) (data not shown).

The fidelity of the calibrated empirical climate-growth models was evaluated with the correlation (r), RE, PM, and ST verification statistics using a cross-validation split scheme (Tables 3.1 and 3.2). The significant and positive RE values (indications of predictive model skill), reveal that the models are reasonably robust over the full length of the calibration period. The positive but insignificant values reveal that the model has some predictive skills. Both the PM and ST results suggest significant predictive skills to reproduce the magnitude and direction of year-to-year changes. Among four species, higher R^2 and RE values in most of jack pine stands along the gradient indicate that jack pine models are much more robust than that of the other three species, and may have high fidelity to predict radial growth.

Table 3. 1 Statistics of the model calibration and verification for trembling aspen (TA) and paper birch (PB) along the gradient. Significant level is at $p<0.5$ if $R^2 > 0.10$.

Latitude	Calibration_TA				Verification_TA					Calibration_PB				Verification_PB				
(ºN)	Period	R^2	adjR^2	SE	Period	r	RE	PM	ST	Period	R^2	adjR^2	SE	Period	r	RE	PM	ST
46	1912-1965	0.22	0.14	.09	1966-2003	0.29	*0.04*	1.70	21/17	1905-1965	0.27	0.22	.07	1966-2003	0.26	*0.03*	1.89	23/15
	1966-2003	0.21	0.13	.08	1912-1965	0.27	*0.04*	2.03	28/26	1966-2003	0.20	0.15	.09	1905-1965	0.49	0.21	4.09	36/25
	1912-2003	0.21	0.16	.08						1905-2003	0.18	0.15	.08					
47	1902-1965	0.32	0.25	.06	1966-2003	0.36	*0.05*	4.63	25/13									
	1966-2003	0.31	0.25	.08	1902-1965	0.15	0.19	1.29	35/29									
	1902-2003	0.27	0.23	.09														
48	1910-1965	0.20	0.16	.08	1966-2003	0.46	0.17	5.72	27/11	1907-1965	0.24	0.21	.08	1966-2003	0.22	*0.02*	2.05	20/18
	1966-2003	0.40	0.36	.07	1910-1965	0.29	0.05	2.82	35/21	1966-2003	0.16	0.13	.06	1907-1965	0.46	0.21	6.99	41/18
	1910-2003	0.33	0.29	.08						1907-2003	0.20	0.17	.07					
49	1915-1965	0.29	0.23	.08	1966-2003	0.26	0.25	7.36	30/8	1912-1965	0.17	0.14	.07	1966-2003	0.53	0.28	6.32	28/10
	1966-2003	0.14	0.12	.06	1915-1965	0.46	0.29	10.33	38/13	1966-2003	0.29	0.21	.06	1912-1965	0.40	0.16	5.12	33/21
	1915-2003	0.26	0.22	.08						1912-2003	0.21	0.18	.05					
50	1902-1965	0.15	0.11	.09	1966-2003	0.60	0.29	7.15	26/12	1928-1965	0.36	0.30	.06	1966-2003	0.59	0.24	8.40	32/6
	1966-2003	0.42	0.37	.07	1902-1965	0.29	0.13	2.61	41/23	1966-2003	0.31	0.27	.06	1928-1965	0.50	0.20	4.83	20/18
	1902-2003	0.23	0.20	.09						1928-2003	0.33	0.31	.07					
51	1929-1965	0.18	0.15	.06	1966-2003	0.62	0.36	8.29	26/12	1909-1965	0.47	0.39	.07	1966-2003	0.31	0.11	3.01	22/16
	1966-2003	0.36	0.30	.07	1929-1965	0.32	*0.01*	3.01	24/13	1966-2003	0.25	0.20	.05	1909-1965	0.38	*0.03*	2.51	31/26
	1929-2003	0.29	0.25	.07						1909-2003	0.32	0.26	.06					
53	1926-1965	0.52	0.46	.07	1966-2003	0.29	*0.05*	3.18	21/17	1933-1965	0.47	0.38	.04	1966-2003	0.55	0.26	7.26	23/15
	1966-2003	0.32	0.24	.08	1926-1965	0.51	0.32	8.45	26/14	1966-2003	0.50	0.43	.05	1933-1965	0.58	0.50	4.81	22/11
	1926-2003	0.38	0.32	.08						1933-2003	0.40	0.35	.05					
54	1927-1965	0.37	0.30	.07	1966-2003	0.46	*0.03*	3.48	24/14	1931-1965	0.21	0.18	.05	1966-2003	0.59	0.33	9.22	28/10
	1966-2003	0.38	0.35	.08	1927-1965	0.34	0.12	4.43	25/14	1966-2003	0.40	0.37	.05	1931-1965	0.30	*0.03*	2.47	21/14
	1927-2003	0.34	0.30	.08						1927-2003	0.24	0.22	.04					

Note: r: correlation coefficient; R^2: explained variance; adjR^2: square of the multiple correlation coefficients following adjustment for loss of degrees of freedom; SE: standard error of the estimate; RE: reduction of error statistic, which is a measure of shared variance between the actual and modelled series, but is usually lower than the calibration R^2. A positive value signifies that the regression model has some skill (Cook and Kairiukstis, 1990). PM: product means test (Fritts, 1991); ST: sign test (Fritts, 1976). The italic texts indicate insignificant values.

Table 3. 2 Statistics of the model calibration and verification for black spruce (BS) and jack pine (JP) along the gradient. Significant level is at p<0.5 if R^2 >0.10.

Latitude		Calibration_BS					Verification_BS					Calibration_JP					Verification_JP	
(ºN)	Period	R^2	adjR^2	SE	Period	r	RE	PM	ST	Period	R^2	adjR^2	SE	Period	r	RE	PM	ST
46	1946-1965	0.22	0.18	.05	1966-2003	0.32	0.07	2.20	24/14	1926-1965	0.36	0.27	.04	1966-2003	0.48	0.21	7.65	27/11
	1966-2003	0.26	0.20	.06	1946-1965	0.50	0.26	7.00	13/7	1966-2003	0.32	0.25	.04	1926-1965	0.41	0.65	3.00	28/12
	1946-2003	0.26	0.22	.06						1926-2003	0.30	0.24	.03					
47	1902-1965	0.31	0.25	.07	1966-2003	0.37	*0.01*	3.15	26/12	1902-1965	0.33	0.30	.04	1966-2003	0.42	0.11	5.93	25/13
	1966-2003	0.20	0.15	.08	1902-1965	0.41	0.12	3.00	45/19	1966-2003	0.31	0.23	.05	1902-1965	0.43	0.16	4.13	42/22
	1902-2003	0.26	0.22	.03						1902-2003	0.38	0.34	.03					
48	1902-1965	0.30	0.23	.06	1966-2003	0.48	0.17	5.34	25/13	1920-1965	0.40	0.37	.03	1966-2003	0.55	0.22	5.62	26/12
	1966-2003	0.24	0.17	.05	1902-1965	0.43	0.16	3.25	39/25	1966-2003	0.57	0.52	.03	1920-1965	0.55	0.26	10.43	30/16
	1902-2003	0.26	0.21	.05						1920-2003	0.50	0.46	.02					
49	1919-1965	0.25	0.17	.04	1966-2003	0.41	0.16	4.23	24/14	1913-1965	0.45	0.39	.03	1966-2003	0.59	0.33	9.08	25/13
	1966-2003	0.44	0.36	.03	1919-1965	0.35	0.14	2.68	28/19	1966-2003	0.38	0.33	.03	1913-1965	0.57	0.20	5.94	38/15
	1919-2003	0.33	0.26	.03						1913-2003	0.40	0.36	.02					
50	1902-1965	0.22	0.17	.05	1966-2003	0.34	0.11	3.24	23/15	1917-1965	0.30	0.26	.01	1966-2003	0.53	0.26	6.97	23/15
	1966-2003	0.23	0.19	.05	1902-1965	0.42	0.18	5.51	42/22	1966-2003	0.51	0.47	.02	1917-1965	0.38	0.08	3.58	30/19
	1902-2003	0.23	0.19	.03						1917-2003	0.38	0.35	.01					
51	1902-1965	0.23	0.19	.06	1966-2003	0.42	0.15	3.48	24/14	1938-1965	0.48	0.41	.02	1966-2003	0.37	0.09	3.68	24/14
	1966-2003	0.26	0.20	.05	1902-1965	0.44	*0.02*	4.54	37/27	1966-2003	0.24	0.20	.02	1938-1965	0.57	0.32	8.55	22/6
	1902-2003	0.27	0.23	.05						1938-2003	0.32	0.27	.01					
52	1902-1965	0.22	0.18	.04	1966-2003	0.43	0.14	4.13	29/9	1938-1965	0.30	0.28	.03	1966-2003	0.42	0.09	3.06	23/15
	1966-2003	0.19	0.15	.05	1902-1965	0.34	*0.02*	3.06	37/27	1966-2003	0.40	0.33	.02	1938-1965	0.54	*0.06*	3.19	18/10
	1902-2003	0.24	0.21	.03						1938-2003	0.34	0.30	.02					
53	1911-1965	0.26	0.21	.04	1966-2003	0.52	0.20	4.75	25/13	1902-1965	0.47	0.44	.03	1966-2003	0.55	0.23	5.37	28/10
	1966-2003	0.29	0.23	.04	1911-1965	0.48	0.06	4.56	31/24	1966-2003	0.48	0.46	.04	1902-1965	0.26	0.29	1.99	38/26
	1911-2003	0.25	0.22	.03						1902-2003	0.42	0.39	.03					
54	1902-1965	0.24	0.17	.04	1966-2003	0.46	0.20	4.22	27/11	1918-1965	0.24	0.16	.04	1966-2003	0.49	0.19	7.04	24/14
	1966-2003	0.27	0.16	.05	1902-1965	0.35	0.09	3.78	44/20	1966-2003	0.39	0.35	.03	1918-1965	0.32	0.25	3.19	18/10
	1902-2003	0.23	0.19	.03						1918-2003	0.24	0.20	.02					

Note: see definitions for the parameters in Table 1.

3.5.2. Difference in mean GC among scenarios/functions/latitudes and partition of variance

As shown in Figure 3.5 A, the partition of variance results showed that the northern functions of two broadleaf species and jack pine generally predict large growth increase, whereas their southern functions may predict minor growth change (either increases or decreases). The functions of black spruce mostly show moderate growth increase across the latitudes except for the southernmost function and northernmost function. Correspondingly, high variability in mean GC was observed among different functions, ranging from -5.62% to 19.17% for trembling aspen, from -3.81% to 20.90% for paper birch, from -11.30% to 14.05% for black spruce, and from 0.76% to 28.42% for jack pine. In contrast, relatively less variability in mean GC was found among different scenarios, varying from 2.65% in HB2 scenario to 10.45% in MA2 for trembling aspen, from 5.62% in HA2 to 7.51% in MA2 for paper birch, from 1.84% in HA2 to 4.66% in EB2 for black spruce, and from 7.52% in CB1 to 11.63% in EB2 for jack pine, respectively (Figure 3.5 B). Within each climate model, A2 scenario would generally predict better growth in trembling aspen and jack pine than B2 scenario. However, no such difference was found for other two species. Relatively less variability in mean GC was also revealed among different latitudes, in which higher growth increase was predicted at northern latitudes, whereas lower growth would occur at southern latitudes (Figure 3.5 C). Along the latitudinal gradient, mean growth change increased towards north. The increases were from 5.05% to 10.59% for trembling aspen, from 3.95% to 8.55% for paper birch, from -0.15% to 7.67% for black spruce, and from 7.03% to 13.55% for jack pine, respectively.

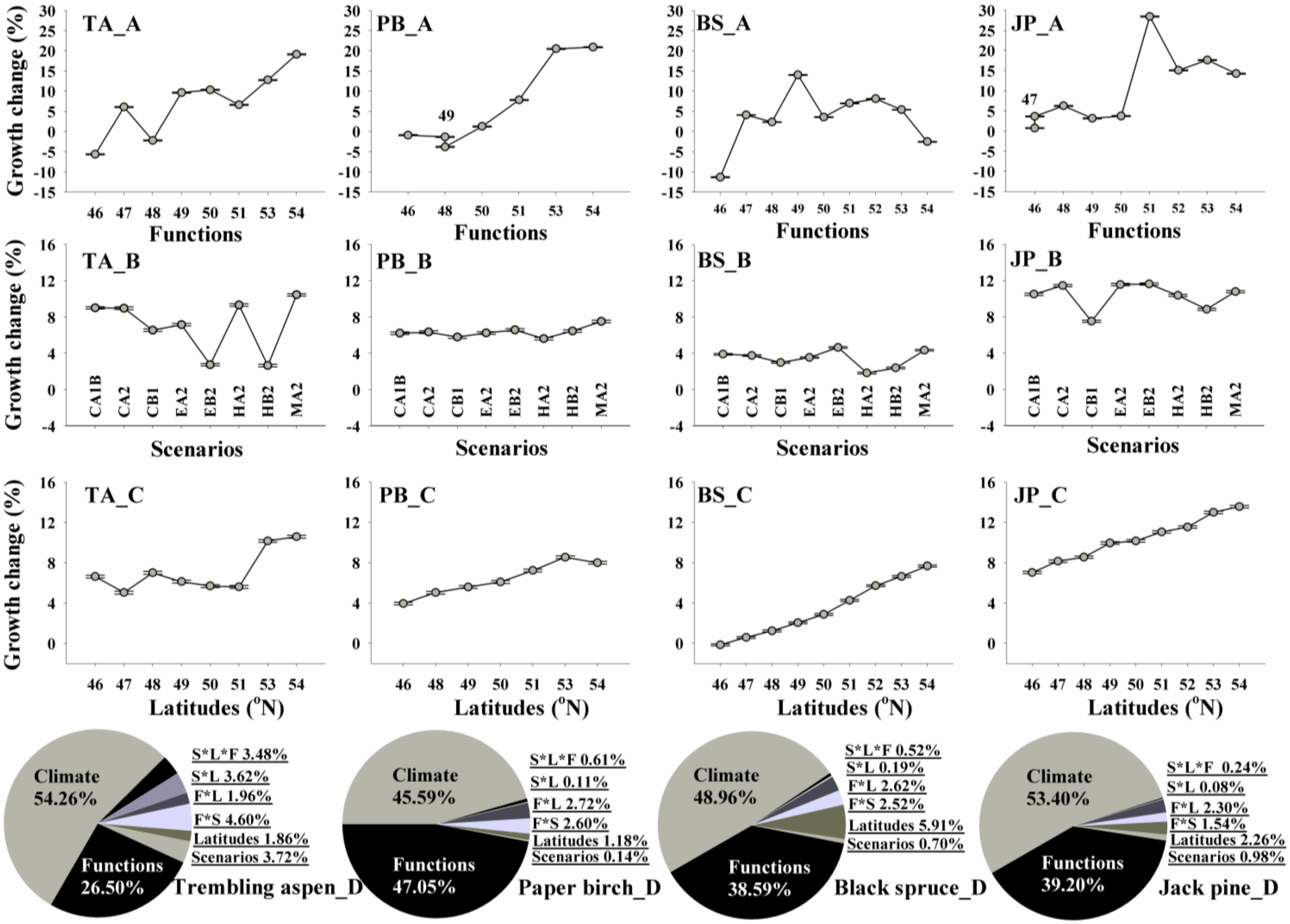
TA_A
PB_A
BS_A
JP_A
Growth change (%)
Functions
49
47
TA_B
PB_B
BS_B
JP_B
CA1B CA2 CB1 EA2 EB2 HA2 HB2 MA2
Scenarios
TA_C
PB_C
BS_C
JP_C
Latitudes (°N)
Climate 54.26%
Functions 26.50%
S*L*F 3.48%
S*L 3.62%
F*L 1.96%
F*S 4.60%
Latitudes 1.86%
Scenarios 3.72%
Trembling aspen_D
Climate 45.59%
Functions 47.05%
S*L*F 0.61%
S*L 0.11%
F*L 2.72%
F*S 2.60%
Latitudes 1.18%
Scenarios 0.14%
Paper birch_D
Climate 48.96%
Functions 38.59%
S*L*F 0.52%
S*L 0.19%
F*L 2.62%
F*S 2.52%
Latitudes 5.91%
Scenarios 0.70%
Black spruce_D
Climate 53.40%
Functions 39.20%
S*L*F 0.24%
S*L 0.08%
F*L 2.30%
F*S 1.54%
Latitudes 2.26%
Scenarios 0.98%
Jack pine_D

Figure 3. 5 Partition of variance in mean growth change of trembling aspen (TA), paper birch (PB), black spruce (BS), and jack pine (JP) along the latitudinal gradient from 46°N to 54°N. The factors included functions, scenarios, latitudes, and interactive effects of the above three factors. The variance explained by the errors is considered as the variance explained by the climate. The proportion of variance in mean growth change per species explained by functions (F), scenarios (S), latitudes (L), and the interactive effects of the above three factors, as well as climate was shown in the pie plot. The grey dots are the least square means of growth change of each species predicted from 2010 to 2099. The standard error of the means is shown by grey short lines.

As shown in Figure 3.5 D, the results of partition of variance showed that the yearly climate variability explains approximate half of the variance in mean GC of the four species (ranging from 45.59% for paper birch to 54.26% for trembling aspen). The choice of the respective growth functions explains about one third to half of the variance (ranging from 26.50% for trembling aspen to 47.05% for paper birch). The scenarios together with its interactive effects explain only a small portion of the variance, ranging from 2.84% for jack pine to 15.42% for trembling aspen. The rest of the variance in mean GC could be explained by the latitude and its interactive effect with the function.

3.5.3. Calibration models selection

The appropriate calibration models during each subperiod were selected for each latitude and listed in Table 3.3. In many cases, when the 1961-1990 ANUSPLIN mean temperatures of several southern latitudes fall within the range of 30-year mean temperatures of each future subperiod, the calibration models from these several southern latitudes were all involved. For instance, during future subperiod 2010-2039, we assume that the growing conditions of trembling aspen at 54°N might be gradually changing from its current conditions at 54°N (upper limit) to the growing conditions at a more southern latitude (e.g., 50°N) if future 2010-2039 mean temperature at 54°N will be approximate to the 1961-1990 mean temperatures of a southern latitude such as 50°N (lower limit). In this case, the calibration models from 54, 53, 52, 51 and 50°N were all selected for growth simulations of stands at 54°N during 2010-2039. With time (e.g., 2040-2069), growth conditions at the lower limit mentioned above (e.g., 50°N) was considered as the upper limit, and growth conditions at a more southern latitude than 52°N was considered as the lower limit. The calibrated models spanning from the upper limit to the lower limit were all involved for growth simulation during next subperiod. The same principle was applied into each of all the latitudes over future subperiods. However, the selected calibration models to predict mean GC during 2070-2099 at 48°N were incomplete because the 2070-2099 mean temperature (5.67°C) is beyond the temperature range we investigated along the gradient. Hence caution needs to be taken during future interpretation of the results. The appropriate calibration functions at 46°N and 47°N were not determined since future 30-year mean temperatures will be warmer (2010-2039 mean temperature is 4.47°C at 47°N and 5.83°C at 46°N) than the 1961-1990 mean temperature of the southernmost latitude we investigated (1961-1990 mean temperature is 4.25°C at 46°N) (Table 3.3).

Table 3. 3 The 30-year mean annual temperatures for the period 1961-1990 calculated on climate data generated from ANUSPLIN, and for the period 2010-2039, 2040-2069, and 2070-2099 averaged from eight climate change scenarios data generated from different GCMs and CGCM3 at each site along the latitudinal gradient from 46°N to 54°N. The corresponding functions applied at each latitude from 48°N to 54°N were determined based on comparisons of future 30-year mean temperatures at each period per latitude with the 1961-1990 mean temperatures at different latitudes. Functions at 46°N and 47°N were not determined since future mean temperatures will be warmer than the temperature gradient we investigated. The

italic text indicates the growth change predicted with uncertainties. The value in the bracket is the standard deviation (SD) of each mean.

Latitude (°N)		Time Period			
		1961-1990	2010-2039	2040-2069	2070-2099
46	T (°C)	4.25 (0.65)	5.83 (0.81)	7.31 (0.96)	8.75 (1.14)
	Functions				
47	T (°C)	3.02 (0.75)	4.47 (0.84)	5.97 (0.98)	7.45 (1.20)
	Functions				
48	T (°C)	1.14 (0.78)	2.66 (0.84)	4.18 (0.97)	5.67 (1.21)
	Functions		L48-L47	L48-L46	*L47-L46*
49	T (°C)	-0.63 (0.80)	0.82 (0.82)	2.36 (0.96)	3.88 (1.22)
	Functions		L49-L48	L48-L47	L48-L46
50	T (°C)	-0.89 (0.85)	0.67 (0.85)	2.24 (0.97)	3.79 (1.25)
	Functions		L50-L48	L49-L47	L48-L46
51	T (°C)	-1.54 (0.92)	0.13 (0.85)	1.73 (0.94)	3.32 (1.23)
	Functions		L51-L48	L49-L47	L48-L46
52	T (°C)	-3.06 (1.00)	-1.28 (0.89)	0.38 (0.97)	2.02 (1.27)
	Functions		L52-L50	L51-L48	L49-L47
53	T (°C)	-3.21 (1.01)	-1.42 (0.90)	0.23 (0.98)	1.89 (1.28)
	Functions		L53-L50	L51-L48	L49-L47
54	T (°C)	-3.18 (1.07)	-1.35 (0.94)	0.34 (1.02)	2.03 (1.32)
	Functions		L54-L50	L51-L48	L49-L47

3.5.4. Predicted mean GC of the four species along the gradient under the AP1

The dynamic mode was used to predict mean growth change of a given species during the period 2010-2099 along the gradient from 48 to 54°N. As an example, mean growth changes at 48, 51 and 54°N were shown in Figure 3.6, and the others were shown in Appendix II. 3.2. The results showed that trembling aspen stands at 53°N and 54°N would have a positive mean GC (i.e., less than 15% growth increase) during the whole period 2010-2099. Stands at 50°N and 51°N would show moderate growth increase (less than 10%) from 2010s to 2060s, yet moderate growth decrease (less than 10%) during 2070s-2090s. However, stands at 49°N would demonstrate moderate growth increase (less than 8%) from 2010s to 2040s, followed by growth increase/decrease fluctuations during 2050s-2060s and by growth decrease (less than

10%) after 2070s. Stands at 48°N might show low growth increase (less than 5%) during next one or two decades, followed by gradual growth decrease during the rest of the 21st century, with a large 95% confidence interval. The results of partition of variance showed that the variance in mean GC explained by yearly climate variability increased from south to north, ranging from 53.51% to 73.42%, whereas that explained by the functions decreased from south to north, ranging from 40.86% to 18.38%. Both yearly climate variability and functions together accounted for most proportion of the variance in mean GC in trembling aspen along the gradient, yet other factors like scenarios and scenarios*functions explained only very little variance in mean GC.

Paper birch stands at 53 and 54°N would show moderate growth increases (less than 20%) during the first half of the 21st century, followed by gradual growth decrease (less than 20%) in the last half of the 21st century (Figure 3.6 and Appendix II. 3.2). Stands at 51°N would demonstrate weak growth increase (less than 10%) from 2010s to 2040s, followed by gradual growth decrease from 2050s to 2090s. Stands at 48-50°N would demonstrate moderate growth decrease (less than 10%) from 2010s to 2090s. Partition of variance demonstrated that variance in mean GC explained by the yearly climate variability for stands at 48-51°N (ranging from 84.19% to 96.10%) was higher than that for stands at 53 and 54°N (from 61.54% to 63.91%), whereas that explained by the functions for stands at 48-51°N (0.02% to 5.90%) was lower than that for stands at 53 and 54°N (26.26% to 27.58%). In addition, other factors such as scenarios and scenarios*functions explained only very little variance in mean GC from south to north.

Along the gradient, black spruce stands at 52-54°N would show obvious growth increase (up to about 20%) during the 21st century (Figure 3.6 and Appendix II. 3.2). In contrast, stands at 49-51°N would demonstrate growth increase (less than 15%) from 2010s to 2060s, followed by moderate growth decrease during 2070s-2090s, with a large 95% confidence interval. Stands at 48°N would show weak growth increase (less than 6%) during the coming decade, followed by gradual growth decrease during the rest of the current century. The results of partition of variance showed that the variance in mean GC explained by the yearly climate variability increased (from 45.17% to 74.13%), and by the functions decreased (from 47.71% to 15.53%), from south to north, respectively. This trend was similar to the ones found for trembling aspen along the gradient. As expected, other factors such as scenarios and scenarios*functions explained only very little variance in mean GC along the gradient.

In contrast to the previous three species, jack pine stands at all the latitudes would show consistent growth increase during the entire 21st century, as shown in Figure 3.6 and Appendix II. 3.2. Of these latitudes, up to 20% growth increase would be expected for stands at 52-54°N, and up to 10% growth increase would be predicted for stands at 48-51°N. Partition of variance showed that along the south-north gradient the variance in mean GC explained by the yearly climate variability would decrease from 92.01% to 35.17%, and the variance explained by the functions would increase from 2.69% to 59.26%. As found in other three species, other factors such as scenarios and scenarios*functions also accounted for only very little variance in mean GC.

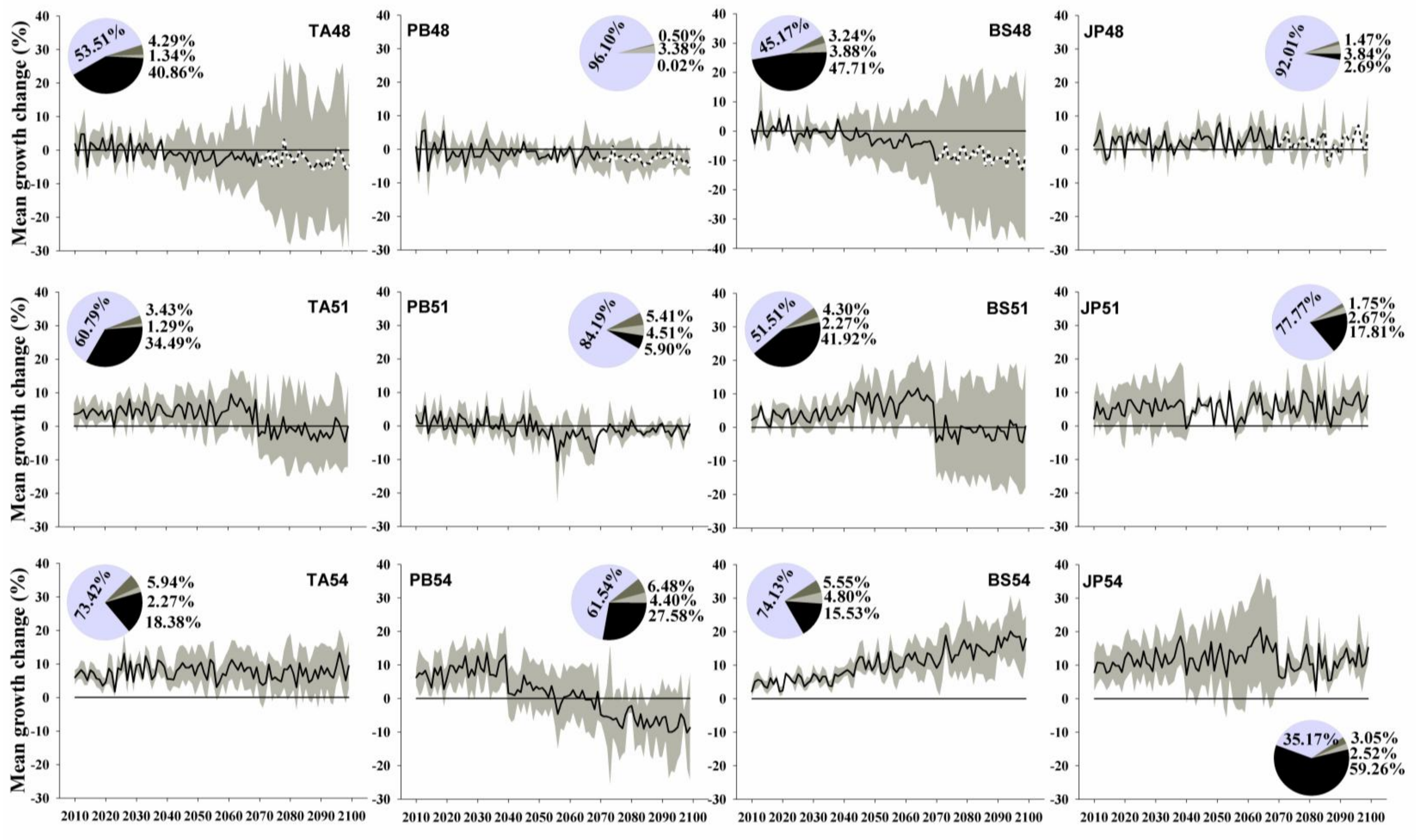
Mean growth change (%)
TA48
53.51%
4.29%
1.34%
40.86%
PB48
96.10%
0.50%
3.38%
0.02%
BS48
45.17%
3.24%
3.88%
47.71%
JP48
92.01%
1.47%
3.84%
2.69%
TA51
60.79%
3.43%
1.29%
34.49%
PB51
84.19%
5.41%
4.51%
5.90%
BS51
51.51%
4.30%
2.27%
41.92%
JP51
77.77%
1.75%
2.67%
17.81%
TA54
73.42%
5.94%
2.27%
18.38%
PB54
61.54%
6.48%
4.40%
27.58%
BS54
74.13%
5.55%
4.80%
15.53%
JP54
35.17%
3.05%
2.52%
59.26%
40
30
20
10
0
-10
-20
-30
-40
2010
2020
2030
2040
2050
2060
2070
2080
2090
2100

Figure 3. 6 Mean growth change of trembling aspen (TA), paper birch (PB), black spruce (BS) and jack pine (JP) from 2010 to 2099 predicted by the dynamic model for latitudes 48, 51, and 54°N in the study gradient. The pie plots indicate the proportion of variance in mean growth change explained by, counter clock wise, functions (dark), scenarios (grey), functions * scenarios (darker grey), and climate (blue). The grey zones are 95% confidence interval. White dashed lines indicate the estimation of mean growth change with uncertainties because the 2070-2099 mean temperature at 48°N will be warmer than the temperature range covered by our latitudinal gradient.

3.5.5. Predicted mean GC of the four species along the gradient under the AP2

When considering the genetic constraint effect or lagged effects on growth, the local model-based simulation results, as illustrated in Figure 3.7 and Appendix II. 3.3, showed that except for 46 and 48°N trembling aspen stands at most of the latitudes would show moderate growth increase during 2010-2099, with highest growth increase rate (up to 40%) at northern latitudes such as 53 and 54°N. In contrast, stands at 46°N and 48°N would only show gradual growth decrease during the entire 21st century. Variance in mean GC was explained mostly by yearly climate variability (92.09% to 97.59%), yet less by the scenarios.

Paper birch stands at 51-54°N would show growth increase during the whole current century, whereas stands at other southern latitudes such as at 46-50°N might show growth decrease during most of the current century. Like trembling aspen stands, the fastest growth increase rate (up to 40-50% growth increase) was found for paper birch stands at northern latitudes such as 53 and 54°N. Variance in mean GC was also explained mostly by yearly climate variability (ranging from 89.37% to 97.91%), yet less by the scenarios (Figure 3.7 and Appendix II. 3.3).

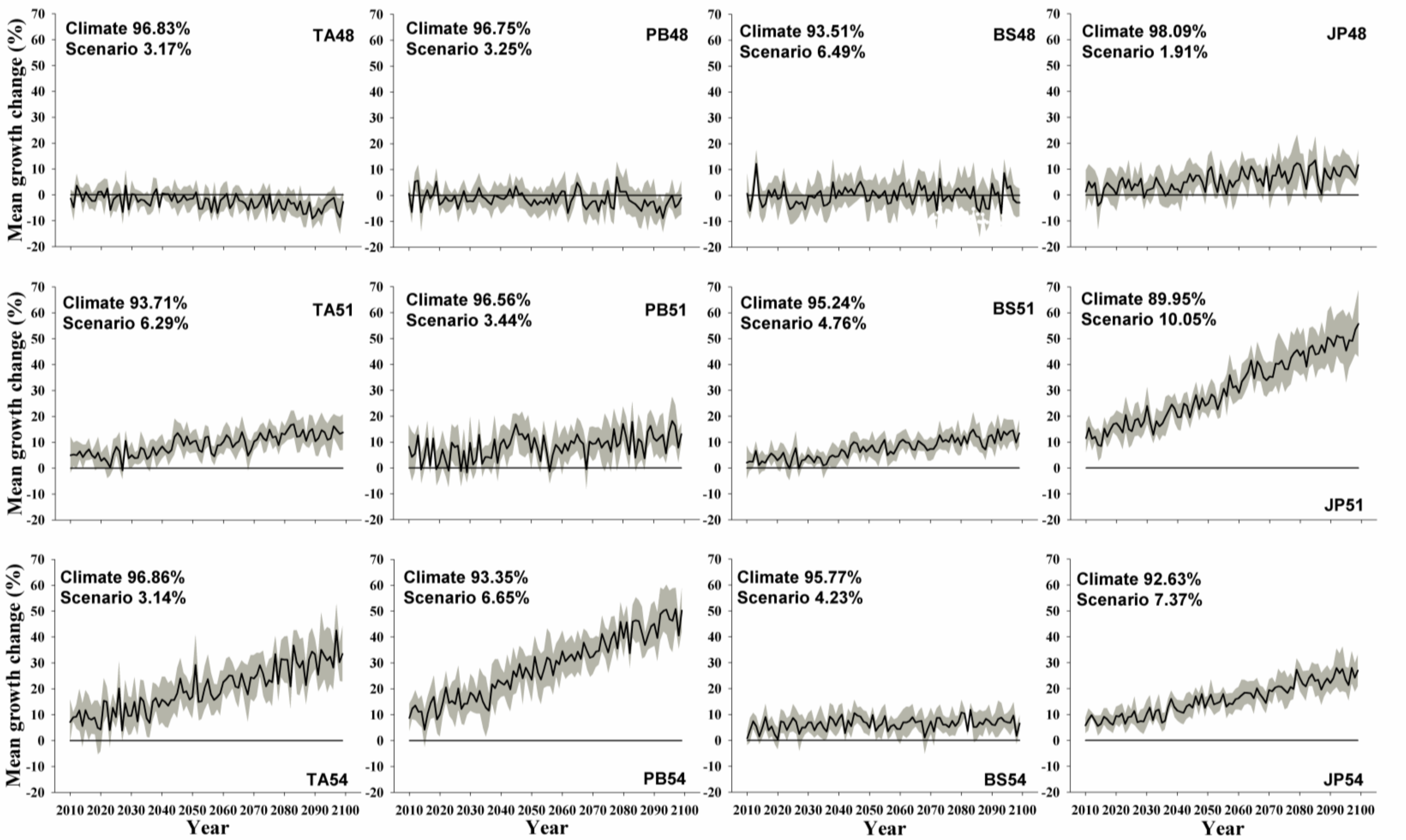
Mean growth change (%)
Year
Climate 96.83%
Scenario 3.17%
TA48
Climate 96.75%
Scenario 3.25%
PB48
Climate 93.51%
Scenario 6.49%
BS48
Climate 98.09%
Scenario 1.91%
JP48
Climate 93.71%
Scenario 6.29%
TA51
Climate 96.56%
Scenario 3.44%
PB51
Climate 95.24%
Scenario 4.76%
BS51
Climate 89.95%
Scenario 10.05%
JP51
Climate 96.86%
Scenario 3.14%
TA54
Climate 93.35%
Scenario 6.65%
PB54
Climate 95.77%
Scenario 4.23%
BS54
Climate 92.63%
Scenario 7.37%
JP54
70
60
50
40
30
20
10
0
-10
-20
2010 2020 2030 2040 2050 2060 2070 2080 2090 2100

Figure 3. 7 Mean growth change of trembling aspen (TA), paper birch (PB), black spruce (BS) and jack pine (JP) from 2010 to 2099 predicted by the local model at latitudes 48, 51 and 54°N in the study gradient. The proportion of variance in mean growth change explained by the climate and scenarios was indicated. The grey zones are 95% confidence interval.

Black spruce stands at north of 48°N would show moderate growth increase from 2010 to 2099 (Figure 3.7 and Appendix II. 3.3). In contrast, stands at 47-48°N might show relatively low annual growth increase/decrease fluctuations over the current century, and stands at 46°N would show up to 30% linear growth decrease from 2010 to 2099. Variance in mean GC was also explained mostly by yearly climate variability (ranging from 88.39% to 95.77%), and less by the scenarios.

Jack pine stands at 51-54°N showed significant linear growth increase (up to 60% increase) by the end of the current century (Figure 3.7 and Appendix II. 3.3). Stands at 48-50°N would demonstrate moderate growth increase (10% growth increase) over time. However, stands at 46- 47°N might show weak growth increase, with certain yearly growth increase/decrease fluctuations in mean GC over time. Like other three species, variance in mean GC in jack pine was also explained mostly by yearly climate variability (ranging from 89.95% to 98.09%), and less by the scenarios (Figure 3.7).

3.5.6. Comparisons of the mean GC of four species simulated under the two assumptions at the spatiotemporal scales

As shown in Figure 3.8, comparisons of predicted mean GC between the two assumptions showed that during the whole 21st century moderate future growth change (either increases or decreases) was predicted by the dynamic model, whereas significant future growth change (either increases or decreases) was forecasted by the local model. Across the gradient, both consistent and inverse growth change (either increases or decreases) were predicted between the two assumptions over time, and the fastest growth increase was always predicted for stands at northern latitudes. Under both assumptions, consistent growth increase was predicted for trembling aspen stands at north of 49°N from 2010 to 2060s and at 53-54°N from 2070s to 2090s, as well as for paper birch stands at 51-54°N during the period 2010-2030s and at 53-54°N during the period 2040s-2060s. Black spruce stands at 49-54°N during the period 2010-2060s and at 52-54°N during the period 2070s-2090s would also consistently demonstrate growth increase under both assumptions. As for jack pine stands, consistent growth enhancement was forecasted across all the latitudes from 48 to 54°N during the whole 21st century. In contrast, consistent growth decrease was predicted under both assumptions for trembling aspen stands at 48°N during 2040s-2090s, and for paper birch stands at 48-49°N during the period 2010s-2090s and at 50°N during 2010s-2030s and 2070s-2090s, as well as for black spruce stands at 48°N during the period 2070s-2090s.

Comparisons between two simulations also showed that inverse growth change would occur for trembling aspen stands at 49-51°N from 2070s to 2090s, i.e., growth decrease under the AP1 VS growth increase under the AP2, as well as for stands at 48°N from 2010-2030s, i.e., growth increase under the AP1 VS growth decrease under the AP2 (Figure 3.8). Adverse growth change was also found for paper birch stands at 50-51°N during 2040s-2060s and stands at 51-54°N for the period 2070s-2090s, i.e., growth decrease under the AP1 VS growth increase under the AP2. In addition, black spruce stands at 48°N was also forecasted to show inverse growth change during certain periods, i.e., growth increase under the AP1 VS growth decrease under the AP2 during the period 2010-2030s, as well as growth decrease under the AP1 VS growth increase under the AP2 during the period 2040s-2060s. Moreover, inverse growth change was found for black spruce stands at 49-51°N during the period 2070s-2090s as well, i.e., growth decrease under the AP1 VS growth increase under the AP2.

Growth predictions for stands at 46 and 47°N were made only under the AP2, and the results showed that during the whole 21st century trembling aspen, paper birch and black spruce stands at 46°N would show consistent growth decrease, whereas trembling aspen, black spruce, and jack pine stands (no paper birch) at 47°N would show consistent growth increase. At 46°N, jack pine stands were predicted to decrease growth from 2010 to 2030s and increase growth from 2040s to 2090s (Figure 3.8).

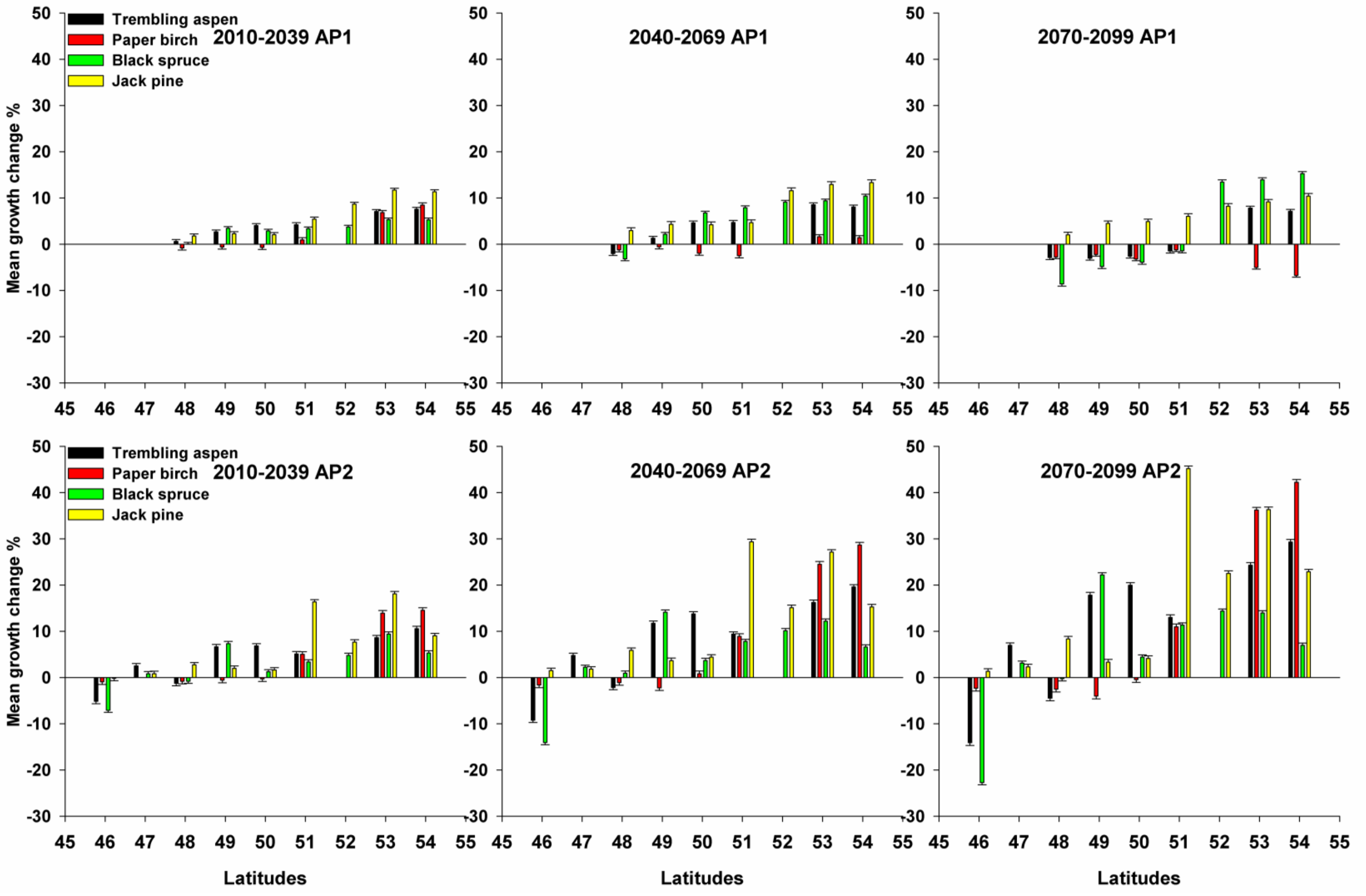
Trembling aspen
Paper birch
Black spruce
Jack pine
2010-2039 AP1
2040-2069 AP1
2070-2099 AP1
2010-2039 AP2
2040-2069 AP2
2070-2099 AP2
Mean growth change %
50
40
30
20
10
0
-10
-20
-30
45
46
47
48
49
50
51
52
53
54
55
Latitudes

Figure 3. 8 Comparison between the least square means in average GC of trembling aspen (TA), paper birch (PB), black spruce (BS) and jack pine (JP) predicted by the dynamic model (under the AP1), and that predicted by the local model (under the AP2) at each latitude from 48°N to 54°N over time slices 2010-2039, 2040-2069, and 2070-2099 in the eastern Canadian boreal forest. The error bars were shown by the short dashed lines.

3.6. DISCUSSION

3.6.1. Spatiotemporal comparisons among the two assumptions

We attributed the consistent growth increase found in the northern stands under both assumptions to positive effect of future increased winter and/or growing season temperatures and/or precipitation on growth, as reflected by their limiting climate variables involved in the calibrated models in Appendix II. 3.1. Warming might alleviate limited effects of cold temperatures on tree growth such as cold conditions and effects of cold on soil resource supply, hence leading to enhanced growth in the northern stands that are growth-limited and cold-stressed (Chapin *et al.*, 1993). Tree growth enhancement in northern regions of the Northern Hemisphere was frequently predicted in past studies (e.g., Nabuurs *et al.*, 2002; Reich and Oleksyn, 2008). Compared with other three species, the consistent growth increase predicted for southern jack pine stands from 2010 to 2099 might indicate that the southern jack pine stands would be greatly favoured by climate warming due to its better drought-tolerance than other three species.

We ascribed the consistent growth decrease observed in the southern stands under both assumptions to future increased drought stress induced by climate warming. Theoretical models of forest decline indicate that under climate warming severe weather events such as droughts are important predisposing and inciting factors resulting in growth decline and tree mortality (Manion, 1991). Empirical evidence also showed the importance of drought resulting in growth decline in the dominant boreal species (Frey *et al.*, 2004; Hogg *et al.*, 2005; Reich and Oleksyn, 2008; Huang *et al.*, 2009).

Inverse growth change in the predicted mean GC under both assumptions for stands mentioned in the results section could be due to different models involved in final predictions. When taking trembling aspen as an example, as listed in Table 3.3, we observed that mean GC for trembling aspen stands at 51°N from 2070s-2090s under the AP1 was predicted using three models obtained at 48-46°N, whereas under the AP2 it was forecasted through the single model obtained at 51°N. The latter assumed an unchanging growth condition in the future and highlighted the most limiting climate factors such as temperature in the models. Obviously, this assumption is less realistic under a much warmer future climate during 2070s-2090s. Therefore future radial growth of trembling aspen at 51°N during 2070s-2090s would be more likely to change between the two predictions. The same inference could be made for other stands showing inverse growth change predicted under both assumptions, as discussed above.

3.6.2. Established empirical models and major climate factors affecting radial growth

In the study, we used the climate variables of multimonths combination as the predictors to build the final empirical growth models. We found that all models are robust and reliable over time, as suggested by those statistical parameters listed in Tables 3.1-3.2. The values of adjR^2 (ranging from 0.15 to 0.46) in our study were generally lower than the ones reported in the monthly climate factors-based modelling studies (adjR^2 generally ranging from 0.40 to 0.60, Laroque and Smith, 2003; Girardin *et al.*, 2008), but were similar to the ones reported in the seasonal factors-based modelling study (Chhin *et al.*, 2008). This might indicate that the multicollinearity has been well overcome in the seasonal factors-based study, as also suggested by low VIF.

As listed in Appendix II. 3.1, those climate factors involved in the final model generally reflected the critical climate conditions during the current growing season and climate conditions in the previous summer and/or autumn and/or current winter. They were generally consistent with Huang *et al.* (2009) who found that moisture conditions in the previous and/or current growing season played a dominant role in positively regulating *P. tremuloides* and *B. papyrifera* growth, whereas the current-year winter and spring or whole growing season temperatures were critical for positively affecting growth of both *P. mariana* and *P. banksiana* over the entire range of our corridor. Hofgaard *et al.* (1999) also reported positive effect of growing season temperature on radial growth of black spruce and jack pine in western Quebec. Similar conclusions were also drawn in other boreal tree-ring studies (Graumlich, 1993; Girardin *et al.*, 2006; Goodine *et al.*, 2008).

Our results show that the northern models predict large growth increase, whereas the southern models may predict minor growth changes (either increases or decreases). This trend somehow follows the principle of the limiting factors hypothesis along the gradient reported by previous studies (Fritts, 1976; Huang *et al.* 2009), i.e., with increasing latitude, temperature may play a more important role in affecting the radial growth of the studied species, whereas synergistic factors (temperature, precipitation, drought) regulating the radial growth could be significant in the south. Hence with climate warming the northern stands would become temperature limitations relax, leading to large growth increase due to extension of the growing season and early phenology; whereas the southern stands would become drought limited, thus tending to show minor growth increases or decreases. It is generally believed that the northern boreal forest ecosystems would be one of the most responsive ecosystems that may be able to benefit from climate warming to greatly enhance growth (IPCC, 2007).

Morin *et al.* (2009), based on the process-based models of leaf unfolding of 22 North America tree species, predicted a greater advance in leaf unfolding date with increased latitude during the 21st century. Through projecting the forest resources from 2000 to 2100 for 15 European countries under a broad range of climate scenarios using the European Forest Information Model (EFISCEN), Eggers *et al.* (2008) observed significantly future increased forest growth in northern Europe, but minor growth change in southern Europe. They further attributed this pronounced growth increase and minor growth change to the effect of climate warming on the length of the growing season in boreal forests, and to the mitigation of summer drought effect from higher spring precipitation and the simulated increased water use efficiency in response to increased atmospheric CO_2 concentration, respectively.

3.6.3. Effects of scenarios and functions on future growth prediction

Previous studies reported large prediction differences resulting from different climate scenarios (Morin *et al.*, 2009). For example, through scaling up the impacts as assessed by the ecological model TEM (terrestrial ecosystem model), Joyce and Nungasser (2000) reported that net primary productivity for a certain forest type in USA increased from 2.3 to 48.3%, varying by climate scenarios. In Europe, Eggers *et al.* (2008) found large variability between the four SRES scenarios they conducted (a1fi, a2, b1 and b2), yet small variability between the four climate models they compared (CGCM2, HadCM3, CSIRO2, and PCM). In contrast, we found that there is less variability in predicted MGC among different climate change scenarios and among the four climate models, as shown in Figure 3.5. This might indicate only minor uncertainty in MGC due to scenarios differences and climate model differences in our study. However, we are unclear what factors causing this difference between our study and the previous studies. Despite this, the contrasting result might allow us to propose that the effects of scenarios difference on growth simulation might be relatively less important than previously thought, at least as shown in our case study.

In addition, 45.59%-54.26% variance in mean GC explained by yearly climate variability, as indicated by ANOVAs, suggests that future predicted mean GC cannot be attributed to future yearly climate variability alone, but to other factors such as model differences and scenarios differences etc. In our case study, model differences could account for almost one third to half of variance in mean GC except for yearly climate variability. However, most of the previous studies did not attempt to clarify the contribution of possible factors to future growth simulations using ANOVAs (Rathgeber *et al.*, 2000; Laroque and Smith, 2003; Chhin *et al.*, 2008). Their final predicted results that were mostly attributed to climate change (warming) and variability are thus questionable. Hence we suggest that future growth/ productivity simulations need to be further clarified using the detailed ANOVAs to make the uncertainties quantatively understandable, as shown in our paper.

3.6.4. Rationale of predicted future mean GC of the four species under the two assumptions

Under the AP1, the predicted results showed that trembling aspen, paper birch and black spruce stands along the gradient from 48 to 54°N would show different time periods of increasing/decreasing growth across the latitudes over time. Here, we called this 'different time periods of growth increase/decrease' as 'Stair Pattern' growth change over the period 2010-2099. More specifically, in the coming one or two decades all the stands along the gradient may benefit from warming climate to enhance the radial growth. With time, the northern stands may be able to continue to benefit from warming climate to enhance growth, whereas the southern stands might gradually decrease the radial growth. For example, trembling aspen stands at 49°N was predicted to increase the radial growth till 2030s and to decrease growth thereafter, whereas stands at 50°N and 51°N could enhance growth up to 2060s, and stands at 53°N and 54°N would increase growth till the end of the current century.

Our predicted mean GC for a given site/species under the AP1was moderate rather than an abrupt linear growth change in the 21st century, indicating that it is likely to be realistic and rationality, since 1) the optimum growth of trees often occurs in an intermediate climate condition (Fritts, 1976; Kramer and Kozlowski, 1979). Therefore trees might not continuously enhance growth with the rising temperature during the latter period of the 21st century when their optimal growth reaches. 2) Under climate warming, the favoured future growth enhancement might be inhibited by other factors such as nutrients-deficiency (e.g., nitrogen) at the study site since the boreal forest is commonly limited by nitrogen (Näsholm *et al.*, 1998). 3) With warming, the site condition might be changing from its current state to a southern site where other climate variables such as precipitation and drought might also become critical for growth, except for temperature. Therefore, future decreased precipitation or increased drought-stress would have negative effect on growth during future certain periods. In this case, mean GC during future subperiods simulated by the southern models, which highlight precipitation and/or drought, could compromise growth increase predicted only by the northern models during the whole 21st century, resulting in moderate growth change. 4) Future changing disturbance regimes also controlled by climate such as insect outbreaks and forest fires might also have negative effect on growth. 5) Mean GC calculated through means of growth estimates obtained by several linear models from different latitudes might be equivalent to the mean GC estimated by the nonlinear model, which often integrates both climate and non-climate factors into the model and finally predicts modest growth change rather than abrupt growth change during future warming (e.g., Lapointe-Garant *et al.*, 2009). However, to what extent the nonlinear model could be resembled by the means of several linear models cannot be quantified, thus it needs to be further clarified in the future.

In contrast, our predicted mean GC under the AP2 showed high variability and large range of growth increase/decrease across species/sites. This might suggest that the final predicted mean GC was very sensitive to the calibrated full-period model used for final prediction for a given site/species. Different calibrated models that were established for a given site/species by different experts (different experience) may, more or less, highlight different climate factors, resulting in different future growth simulations. In addition, the simulated larger growth change under the AP2 was also completely based on the assumption that future growth conditions would be the same as the current growth conditions. In fact, this would be possible only during the coming decades and it will be very likely to shift to the southern site condition with climate warming, i.e., that is the growth simulation under the AP1.

Although growth conditions will be changing with warming climate in the future, stands would not be able to adapt to the new growth conditions immediately because the adaptiveness of trees is largely dependent on their genetic response to climate (Rehfeldt *et al.*, 2002). However this response is a very long evolutional process, and cannot be achieved in a single generation with intense selection (Rehfeldt *et al.*, 2001). For example, as many as twelve generations of *Pinus contorta* Douglas ex Louden may be required to accommodate global warming (Rehfeldt *et al.*, 2002). The lag in genetic response of *Pinus sylvestris* L. to climate warming could be more than 1500 years (Rehfeldt *et al.*, 2002). Therefore, during future 100 years, stands would not be capable to adapt to the new climate and change their response to climate. In other words, growth response to climate is genetically controlled at least in next 100 years. Hence growth function established at a given site under the present climate would be still useful for predicting future 100-year growth. Furthermore, given that the current populations established after a long evolution process are close to the optimal growth (suboptimal growth) (Rehfeldt *et al.*, 1999), climate warming might positively affect the northern populations inhabiting severe climates, yet negatively influence the southern populations that currently inhabit mild climates (Rehfeldt *et al.*, 2002). Thus under the AP2 the northern growth functions would underestimate future growth of the northern stands, whereas the southern functions would overestimate future growth of the southern stands. However, future tree growth might be also negatively affected by nutrients deficiency and forest disturbances (e.g., insect outbreaks and fires), as well as other unknown factors (e.g., species competition). Therefore, we ascertain that under the AP2 the single model established at a given site would overestimate future radial growth change of the southern stands, or might maximally simulate growth of the northern stands. Altogether, we infer that under climate warming, potential mean GC in boreal tree species in the future might be set between the simulations obtained by the dynamic model and the local model, respectively.

3.6.5. Uncertainties and implications

Our calibration models might be somehow affected by the ANUSPLIN climate data we used during calibration process because climate data during early decades in the 20th century are less reliable due to less climate measurements available during that period, especially in the northern latitudes (north of 49°N). In addition, our future growth predictions might be influenced by other external factors that were not involved in the models, such as insect herbivory (Hogg *et al.*, 2005), fire disturbances (Girardin and Wotton, 2009), intra- and inter-species competition (Bergeron *et al.*, 2004), as well as potential direct CO_2 fertilization effect (Huang *et al.*, 2007). Furthermore, since our study focused on the residual chronologies, it indicates that even if growth increase is higher in the north, it does not mean that the absolute growth will not remain higher in the south. Last, we assume that the sampled stands will survive during the 21st century in the study. However, they will definitely die in the next few decades due to the fact that their longevity are generally not long enough, especially jack pine and trembling aspen. Hence their new generations will replace the current stands and might not have the same response to climate as the ones we modelled. Nevertheless, our study provides a new way to simulate growth of trees and forests under future warming, i.e., tree growth response to climate at the temporal scale may be resembled by tree growth response to climate at the spatial scale. The simulation results only could be considered as one of the possible scenarios of future growth change in the eastern Canadian boreal forest under climate warming.

3.7. CONCLUSIONS

Our study opens a new window for predicting future growth of trees and forests using the empirical models when considering the potential effect of both climate warming and genetic constraints on tree growth. The dynamic model-based simulation of future growth change (under the AP1) was modest across the gradient, and might indicate the lower limit of future tree growth. In contrast, the local model-based prediction of growth change (under the AP2) was abrupt, and might indicate the upper limit of future tree growth. Taken together, our study might provide two baselines for potential future growth change across the gradient in the eastern Canadian boreal forest. Hence we propose that future potential growth change of a given stands over the studied gradient would be very likely to be set between these two simulations. Overall, our simulations indicate that with climate warming all northern stands might enhance the radial growth during the 21st century. Of the four species, jack pine might be the most beneficial species from climate warming to extensively increase growth across the gradient in the eastern Canadian boreal forest. These potential growth changes of individual species at spatiotemporal scales would result in shift in compositions and structure of the boreal forests, consequently leading to substantial changes in carbon redistribution in the boreal biome during the 21st century.

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CHAPTER IV

VARIATIONS IN INTRA-ANNUAL RADIAL GROWTH (FORMATION OF THE XYLEM) OF BLACK SPRUCE ALONG A LATITUDINAL GRADIENT IN WESTERN QUEBEC

Jian-Guo Huang, Yves Bergeron, Lihong Zhai,
and Bernhard Denneler

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4.1. RÉSUMÉ

Afin de comprendre comment les arbres réagiront au réchauffement climatique durant une saison de croissance, nous avons utilisé une approche de micro-échantillonnage dans laquelle nous nous sommes intéressés à la formation intra-annuelle de cellules du xylème du épinette noire dans trois sites le long d'un gradient latitudinal approximativement de 47,5 à 50°N dans l'ouest du Québec durant les saisons de croissance 2005 et 2006. La date critique de formation de cellules du xylème a été comparée entre les trois sites durant ces deux saisons de croissance à l'aide d'une ANOVA. Le lien potentiel entre la formation de cellules du xylème et les conditions météorologiques a aussi été discuté. La date de début de formation du xylème pour un site donné a respectivement été détectée le 20 mai (±3), le 24 (±3) mai et le 24 (±4) mai 2005 d'une part et le 12 (±4) mai, le 14 (±3) mai et le 20 (±3) mai 2006 d'autre part. La date de l'arrêt de formation de nouvelles cellules de bois tardif du xylème a été respectivement observée le 11 (±4) août, le 7 (±3) août et le 7 (±4) août 2005 d'une part et le 8 (±4) août, le 4 (±4) août et le 4 (±4) août 2006 d'autre part. Comparée à 2005, la température élevée aurait pu être responsable de la formation précoce de cellules du xylème en 2006. Toutefois, les températures basses de juin-août auraient pu entraîner l'arrêt de la formation de cellules du xylème le long du gradient en 2006. L'effet positif de la température élevée sur la formation de xylème a aussi été observé dans les trois sites, dans lesquels les arbres situés plus au sud ont entamé plus précocement la production de cellules du xylème que les arbres situés plus au nord, en raison notamment d'un printemps plus précoce dans le sud. Une telle différence n'a pas été notée entre les deux sites situés au nord. Cela aurait pu être lié à la similarité des conditions climatiques prévalant dans ces deux sites nordique proches ou bien même à des conditions locales de sites ou de vigueurs d'arbres similaires entre ces deux sites.

4.2. ABSTRACT

To improve our understanding of how trees are reacting to a warming climate during a growing season, we used the micro-sampling approach to investigate the intra-annual xylem cell formation of *Picea mariana* at three sites along a latitudinal gradient from approximately 47.5 to 50ºN in western Quebec during the growing seasons 2005 and 2006. The critical timings of the xylem cell formation were compared among the three sites during these two growing seasons using ANOVAs. Potential relation of xylem cell formation with the meteorological conditions was also discussed. From south to north, the onset date of the xylem cell production at the corresponding site was detected on May 20 (±3), May 24 (±3), and May 24 (±4) in 2005, and on May 12 (±4), May 14 (±3), and May 20 (±3) in 2006, respectively. The termination date of the xylem latewood new cell production was observed on August 11 (±4), August 7 (±3), and August 7 (±4) in 2005, and on August 8 (±4), August 4 (±4), and August 4 (±4) in 2006, respectively. Compared with 2005, warm May temperature might be responsible for early onset of xylem cell production in 2006. However, cold June-August temperatures may result in early termination of xylem cell production across the gradient in 2006. The positive effect of warm temperature on xylem formation was also observed across the three sites, where trees at the southern site often started the onset of xylem cell production earlier than trees at the two northern sites due to earlier starting of spring in the south. Such difference was not found between the two northern sites. This might be due to the same climate dominance at these two nearby northern sites or similar local site conditions and tree vigour.

4.3. INTRODUCTION

Climate warming has led to early spring and late autumn, thus prolonging the length of the growing season (IPCC, 2007). As a consequence, trees might have reacted to this extended growing season length, correspondingly changing the starting and ending date of phenology and stem xylem growth. Phenology is often easily monitored and has been well investigated (Menzel and Fabian, 1999; Zhou *et al.*, 2001; Chuine and Beaubien, 2001; Menzel *et al.*, 2006). For example, in Canada, Beaubien and Freeland (2000) collected data on the first flowering date of trembling aspen (*Populus tremuloides* Michx.) and found a 26-day shift to earlier blooming from 1900 to 1997. They also found an 8-day advancement in the first flowering date over the period 1936-1996 through analyzing the spring flowering index (mean of the first flowering dates of *P. tremuloides*, *Amelanchier alnefolia* Nutt., and *Prunus virginiana* L.).

In contrast, intra-annual stem xylem growth is less understood since cell production of the xylem is difficult to be monitored during the growing season. Recent developed micro-sampling approach provided a feasible way to monitor dynamic process of the stem xylem formation from the first cell to the last cell during a growing season (Deslauriers *et al.*, 2003b; Ko Heinrichs *et al.*, 2007; Dufour and Morin, 2007; Rossi *et al.*, 2007). It may also allow refining our understanding of how the meteorological factors regulate the formation of the xylem from May to September since the number of tracheids produced by the cambium, their outer sizes, and the thickness of cell walls are limited by environmental factors such as climate (Richards, 1959; Antonova *et al.*, 1995; Schmitt *et al.*, 2004). Deslauriers *et al.*, (2008), based on an intra-annual investigation of *Pinus leucodermis* Ant. in southern Italy, found that hot climate conditions in 2003 may result in an increased duration of xylogenesis of about 23 days in comparison with 2004. Zhai *et al.* (to be submitted) used micro-sampling approach to quantify the relationship of climate-intra-annual growth of the xylem of three boreal tree species during the 2007 growing season in western Quebec. They found that trembling aspen and paper birch (*Betula papyrifera* Marsh.) were positively impacted by growing season precipitation, and jack pine (*Pinus banksiana* Lamb.) was positively regulated by growing season temperature.

It is also noted that the effects of climate warming on growth of trees and forests become more significant towards northern latitudes and high elevations, and vary across species (Huang *et al.*, 2009). Therefore, an investigation on intra-annual growth over a large latitudinal gradient may allow demonstrating a systematic change in starting and ending date of the xylem formation during a growing season over the gradient. It may thus provide valuable information to assess and simulate potential future changes in intra-annual growth of the given northern trees with climate warming over time if we assume that the growth conditions of the northern trees during future period would be similar to growth conditions of the trees currently growing in the south (Huang *et al.*, to be submitted).

In the boreal forest, black spruce (*Picea mariana* Mill.) is one of the widely distributed coniferous species over broad spatial scale, and plays an important role in sustaining Canadian forest ecosystems and productivity (Harvey *et al.*, 2002). Hence under the frame of sustainable forest development, it is critical to improve our understanding of how intra-annual formation of the xylem of black spruce stands is responding to the warming climate during a growing season. This will help us to further assess potential impacts of future warming on growth and productivity of black spruce in the Canadian boreal forest in combination with other growth data.

In this paper, an investigation on intra-annual xylem formation of black spruce was conducted along a latitudinal gradient from approximately 47.5 to 50ºN in western Quebec during the two growing seasons 2005 and 2006. The purposes of the study were to (1) quantify the critical timings (the onset of the xylem cell production, termination of the earlywood new cell production, termination of the latewood new cell production) of the xylem formation of black spruce over the gradient during these two growing seasons; (2) compare the xylem formation at the three sites with the meteorological conditions during two different growing seasons. Since growing season temperatures positively affect spruce radial growth over the gradient in western Quebec (Huang *et al.*, 2010), it is hypothesized that the northern spruce stands may start the xylem growth later than the southern stands, but terminate the xylem growth earlier than the southern stands.

4.4. MATERIALS AND METHODS

4.4.1. Study area

Our study area is located in western Quebec along a latitudinal gradient ranging from Angliers (approximately 47.5°N) in the south to Muskuchii (approximately 50°N) in the north (Figure 4.1). The topography along the gradient is generally flat and uniform with low-elevation hills and rock outcrops (300-400 m a.s.l.). The region just covers the climate transition zone, where its northern part is dominated by dry polar and moderate polar air masses during the winter, and its southern part is affected by moist maritime and moist tropical air masses during the summer (Sheridan, 2002). A climate gradient is also enclosed within the studied latitudinal gradient, as described in Huang *et al.* (2009). Under the shape of this climate, a vegetation transition zone covers the boreal forest of western Quebec from 48 to 50°N (Hofgaard *et al.*, 1999; Bergeron *et al.*, 2004). The common boreal tree species including trembling aspen, paper birch, black spruce, and jack pine occur across the gradient but their abundance changes from south to north, i.e., increased abundance for conifers yet decreased abundance for broadleaf species (Gauthier *et al.*, 2000).

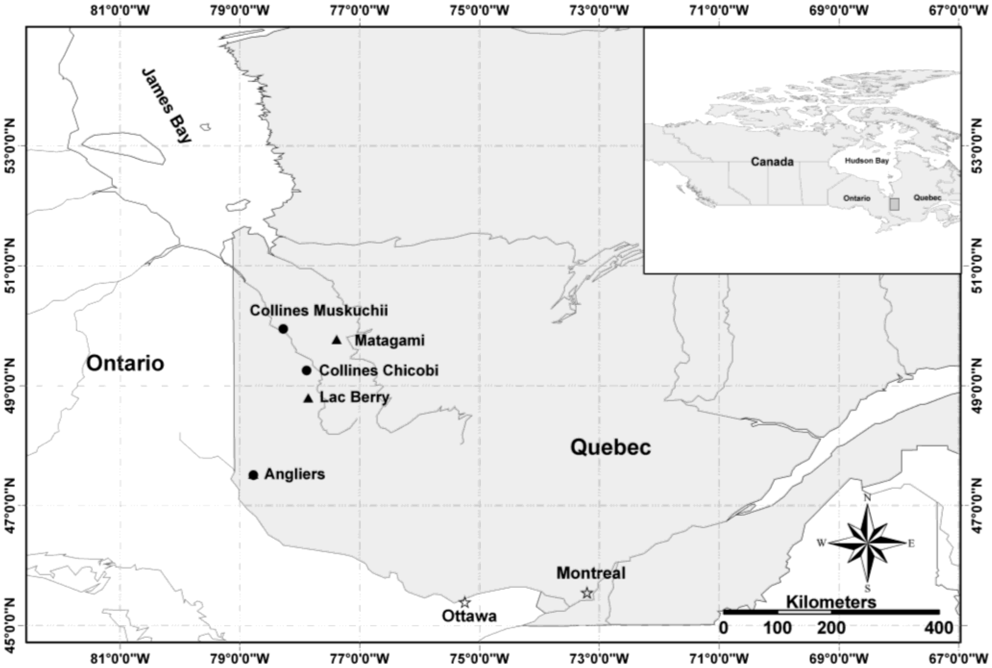

Figure 4. 1 Map showing the studied three sites at Angliers, Collines Chicobi and Collines Mushuchii (solid circles) and the corresponding nearby climate data sites Angliers, Lac Berry, and Matagami (solid triangles) along the latitudinal gradient in western Quebec.

4.4.2. Climate data, field sampling, and laboratory preparation

Three mesic sites along the latitudinal gradient between 47.5°N and 50°N, including Angliers (47°32.60’N, 79°13.60’N), Collines Chicobi (49°16.96’N, 78°19.11’W), and Collines Muskuchii (49°56.75’N, 78°42.88’N) (Figure 4.1), were chosen to monitor the intra-annual radial growth (formation of the xylem) of black spruce from May to September. At each site a micro-weather station (3 m height) was installed to monitor the hourly meteorological conditions throughout the years of 2005-2006. A soil temperature sensor was installed to measure the hourly soil temperature at the depth of 10cm below ground. In total, the measured meteorological parameters that were used to explore the relations with the xylem formation in our study include hourly maximum, mean, and minimum air temperature, hourly precipitation, hourly maximum, mean, and minimum soil temperature at the depth of 10cm below ground. Since the three installed meteorological stations did not work well to measure daily weather conditions through the whole two growing seasons (daily temperature and precipitation data available only till August), we compared the monitored weather data of each site with the data obtained from the nearby climate station, and found they matched well (Figure 4.2). Therefore daily weather data from the stations Angliers, Lac Berry, and Matagami were correspondingly used in the studied three sites along the south-north gradient (Figure 4.2).

As shown in Figure 4.3, climate data during the growing seasons showed that across the three sites, monthly temperatures from June to August in the year of 2005 were higher than that in the year of 2006. However, May temperature in 2005 was lower than in 2006. Along the gradient, the southern site Angliers was hotter than the other two northern sites. July temperature in 2005 and 2006 was 20.27ºC and 19.36 ºC at Angliers, respectively, whereas it was correspondingly 17.49 ºC and 17.37 ºC at Collines Chicobi, and 17.33 ºC and 16.94 ºC at Collines Muskuchii, respectively. As listed in Table 4.3, growing degree days (≥5ºC) from May to August 31st in 2005 was higher than that in 2006 for three sites. However, GDD (≥5ºC) at the onset date of the first xylem cell production in 2005 was generally lower than in 2006. Weekly mean air temperature prior to the onset date of the first xylem cell production across the three sites during the two growing seasons varied from 7.8 ºC to 11.8 ºC. Weekly mean soil temperature prior to the onset date of the first xylem cell production across three sites during the two growing seasons varied from 4.3 ºC to 7.1 ºC. Within a site, weekly mean air temperature prior to the onset date of the first xylem cell production in 2005 was lower than that in 2006.

Five healthy black spruce trees per site were chosen as our monitored trees. The selected stands at Angliers grow on a dense and moist slope, co-occurring with jack pine stands. Their mean age measured in 2006 was 65±6 years, and the DBH was 17.65±2.32 cm. The selected stands at Collines Chicobi grow on a flat and fertile soil, co-occurring with jack pine, trembling aspen and paper birch stands (Hamel *et al*. 2004). Their mean age measured in 2006 was 50±6 years, and the DBH was 23.45±4.24 cm. The selected stands at Collines Muskuchii grow also on a flat and fertile soil, co-occurring with jack pine, white birch, and balsam fir stands. Their mean age measured in 2006 was 98±14 years, and the DBH was 25.25±2.35 cm.

The sampling work was conducted throughout the two growing seasons from May to September in 2005 and 2006. To monitor the cambial activity and xylem growth (Forster *et al.*, 2000), the micro-cores (2.5 mm in diameter and 20-25 mm in length) were weekly taken from the stem of each tree at 1.3m DBH using Trephor (Rossi *et al.*, 2006a). To avoid any disturbance from injury wood (Forster *et al.*, 2000), the distance between adjacent sampling locations was at least 20-30 mm. Each micro-core was stored immediately in a microtube with 50% aqueous ethanol and stored at 5°C to avoid tissue deterioration.

In the laboratory, the micro-cores were prepared according to the following steps (Schweingruber, 1978; Deslauriers *et al.*, 2003a): (1) each micro-core was fixed in paraffin with certain angle (45-60°); (2) 12-20 µm thick cross-sections were obtained from each micro-core through cutting with a rotating microtome (Leica); (3) all cross-sections were stained with safranin (1% in water) and permanently fixed on slices.

Each prepared slice was further used to obtain a series of cell parameters for final analysis. The main procedures included (1) five radial files per slice were randomly (resin ducts avoided) chosen; (2) cell number along each of the selected five radial files were obtained using an image analysis system and the software WinCELL^{TM} (Régent Instruments, Inc. 2007).

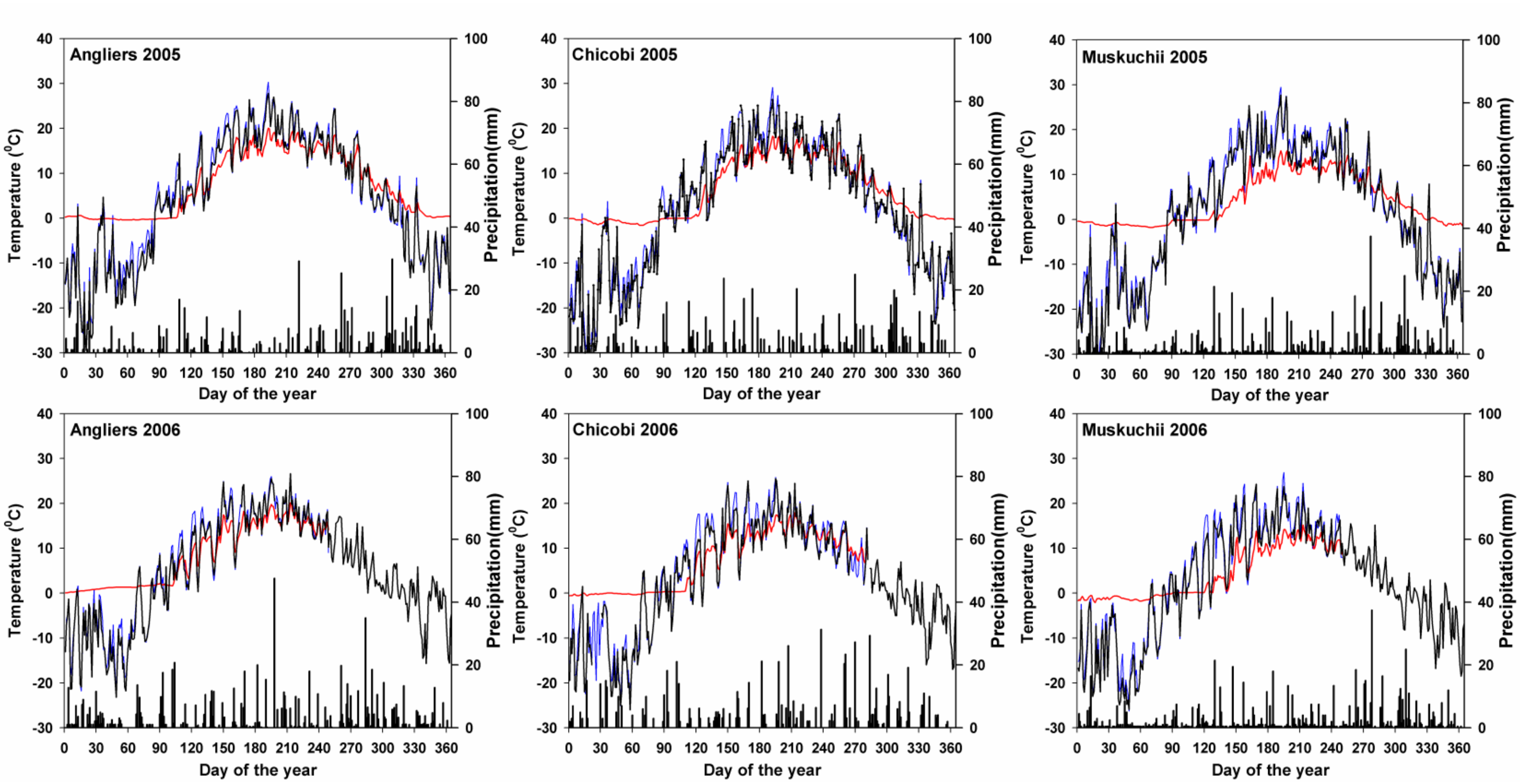

Figure 4. 2 The daily mean temperature monitored by our weather stations (blue curves) and the daily mean temperature (black curves) and total precipitation (vertical bars) obtained from the nearby climate stations along the gradient during the growing seasons 2005 and 2006. The red curves represent the daily soil temperature monitored by our weather stations.

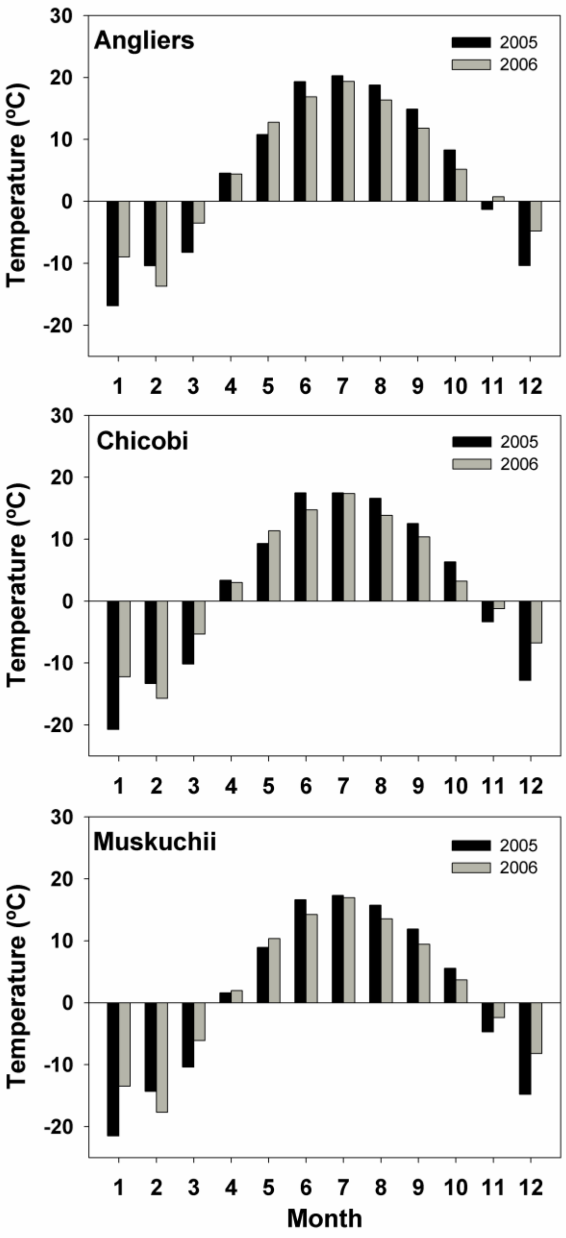

Figure 4. 3 Monthly mean temperatures at the studied three sites Angliers, Collines Chicobi, and Collines Muskuchii along the gradient during the years of 2005 and 2006.

4.4.3. Standardization

Due to eccentric growth, tree ring-width varies greatly along the circumference of tree trunk and along the stem. Correspondingly, cell number of each prepared slice varies among different samples and trees (Schmitt *et al.*, 2004). Therefore a procedure called ‘Standardization’ (Vagnov *et al.*, 1990) was conducted to obtain a series of unbiased cell numbers. Standardization has been often used in previous wood anatomy studies (Deslauriers *et al.*, 2003a; Rossi *et al.*, 2006b; Zhai *et al.*, to be submitted). It is calculated according to the following steps (Rossi *et al.*, 2003): (1) the number of cells of the three previous years was counted on each of the five radial files per sample; in our case, cell numbers in 2002-2004, and 2003-2005 were counted for standardization of cell measurements in 2005, and 2006, respectively; (2) 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; (3) the number of xylem cells in each xylem formation phase (i.e., cell enlargement, cell wall thickening, and mature cell, see Appendix II. 4.1) was then multiplied by the ratio to standardize the measured data according to the sample's relative position on the stem (Deslauriers *et al.*, 2003a; 2003b). According to the relative position of the sample, the standardized number of cells in each j-sample and i-phase (ncij) 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.

4.4.4. Curve fitting through the Gompertz function

To appropriately describe growth curve of the xylem formation during a growing season, the Gompertz function was employed to fit the raw measurements of each xylem growth time series (Cheng and Gordon, 2000). The Gompertz function is described by Cheng and Gordon (2000) as follows:

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

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 the Gompertz function, the critical points of intra-annual xylem development such as the onset date of xylem cell formation, termination date of xylem earlywood cell production, and termination date of xylem latewood new cell production were determined. The curve fitting was done by the software SigmaPlot 10 (Sigma Plot Version 10, Systat Software Inc). To test the difference among sites and between the growing seasons, the identified critical dates were compared through ANOVAs with the software SAS 10 (SAS Corporation, Cary, NC, USA).

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

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

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.*, 2003a, b).

4.4.5. Growth relations to climate

We compared the weekly cell increment, the onset date of the xylem cell production, termination date of the earlywood new cell production, and termination date of the latewood new cell production with climate (the meteorological conditions) for two growing seasons 2005 and 2006 and among three sites along the gradient. Climate here is mainly referred to growing degree days (GDD ≥5ºC) prior to the onset date of the xylem cell production, mean air and soil temperatures during the week prior to the onset date of the xylem cell production, GDD (≥5ºC) from May to August 31st, and monthly mean temperatures.

4.5. RESULTS

4.5.1. Gompertz curve fit

The Gompertz curves were well fit to the weekly cell number increment of the stem xylem, as shown by high adjusted R^2 (Table 4.1) and well data points fit in Figure 4.4. The parameters of the Gompertz curves were listed in Table 4.1. Generally, across the three sites, stands produced more weekly xylem cells in the growing season 2005 than the growing season 2006 (Table 4.2). Along the gradient, stands at the southern site Angliers produced less weekly cells than the other two northern sites. Stands at the sites Collines Chicobi and Collines Muskuchii approximately produced similar weekly cells during each growing season.

Table 4. 1 Parameters of the Gompertz curve fit on the weekly cell number of the stem xylem of black spruce at the three sites Angliers, Collines Chicobi, and Collines Muskuchii during the growing seasons 2005 and 2006. SE: Standard error of the estimate.

Sites	Year	A	B	K	Γ	Adj. R^2	SE	P
Angliers	2005	33.39	5.32	0.029	0.24	0.98	1.53	<.0001
	2006	37.87	5.12	0.026	0.25	0.98	1.39	<.0001
Chicobi	2005	40.51	8.59	0.052	0.53	0.97	2.67	<.0001
	2006	33.37	8.12	0.049	0.41	0.98	1.75	<.0001
Muskuchii	2005	55.17	5.95	0.033	0.46	0.98	2.65	<.0001
	2006	44.01	6.09	0.034	0.37	0.98	1.83	<.0001

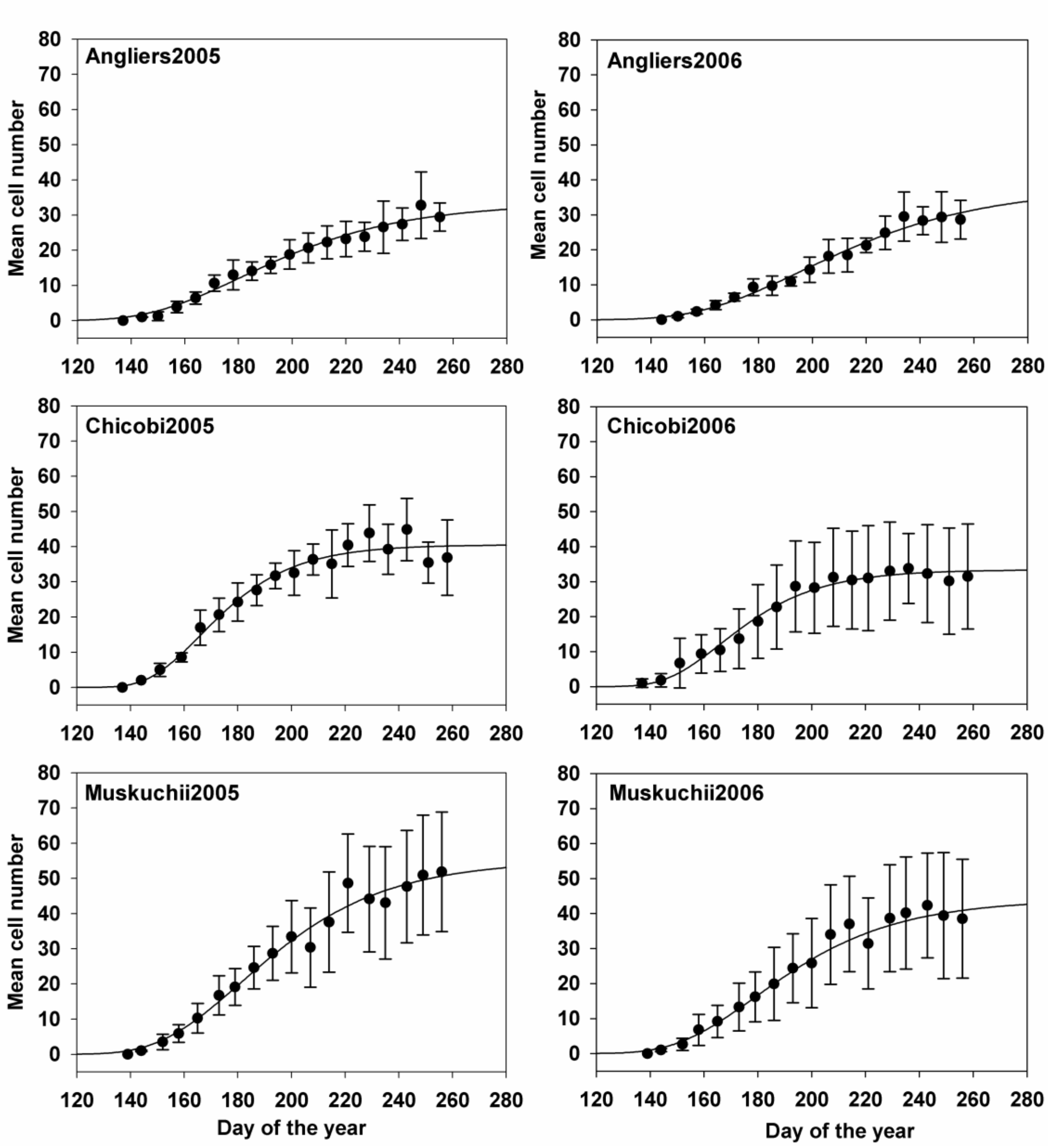

Figure 4. 3 Gompertz curve fit to mean cell number from May to September at the three sites during the two growing seasons 2005 and 2006. The error bars indicate the standard deviations (SD).

As listed in Table 4.2, generally there were more earlywood cells than latewood cells produced during a growing season at each site. Interestingly, higher ratio of latewood cells to the total cells was observed in 2006 than in 2005. Trees at Collines Muskuchii produced relatively highest total xylem cell number over the gradient.

Table 4. 2 Earlywood cell number, latewood cell number, total cell number and the ratio between earlywood, latewood and the total cell number at the three sites during two growing seasons.

Sites	Year	Earlywood cell	Latewood cell	Total	EW/Total	LW/Total
Angliers	2005	18.8	7.76	26.56	70.8%	29.2%
	2006	10.96	10.32	21.28	51.5%	48.5%
Chicobi	2005	31.72	8.72	40.44	78.4%	21.6%
	2006	22.72	8.52	31.24	72.7%	27.3%
Muskuchii	2005	28.72	18.92	48.64	59%	41%
	2006	19.88	14.12	34	58.5%	41.5%

4.5.2. Critical dates during the xylem formation

As listed in Table 4.3, it is generally observed that the onset date of the xylem cell production, termination date of the earlywood new cell production, and termination of the xylem latewood new cell production in 2005 were later than in 2006 at each of the three sites. Across the three sites, the onset of the xylem cell production and the termination date of the earlywood cell production at Angliers were one week earlier than the two northern sites during two growing seasons. However, the termination of the xylem cell production at Angliers was later than that observed at the two northern sites. No difference in the onset of the xylem cell production, termination date of the earlywood new cell production, and termination date of the xylem latewood new cell production were observed at two northern sites during two growing seasons, except for the onset date of the xylem cell production in 2006.

Table 4. 3 The onset date of the first xylem cell, growing degree days (GDD≥5ºC) at the onset date of the first xylem cell production, mean air temperature during the week prior to the xylem cell onset date (Tmean), mean soil temperature (below ground 10 cm) during the week prior to the onset of the xylem cell formation (Tsoil), and termination date of the earlywood new cell production (EW), termination date of the last latewood cell production, and GDD from May to August 31st for the studied three sites Angliers, Collines Chicobi, and Collines Muskuchii during the growing seasons 2005 and 2006.

Sites	Year	Onset date (±SD)	GDD (ºC) at the onset date	Tmean	Tsoil 10cm	EW ending date	Termination date (SD)	May-August GDD (ºC)
Angliers	2005	May 20 (3)	106.6	7.8	5.5	July 7 (3)	August 11 (4)	1547
	2006	May 12 (4)	130.1	11.3	6.8	June 30 (4)	August 8 (4)	1447
Chicobi	2005	May 24 (3)	101	9.4	6.4	July 9 (4)	August 7 (3)	1301
	2006	May 14 (3)	114	11.8	7.1	July 5 (3)	August 4 (4)	1196
Muskuchii	2005	May 24 (4)	77.9	8.91	4.3	July 9 (4)	August 7 (4)	1210
	2006	May 20 (3)	147.2	11.3	5.3	July 5 (3)	August 4 (4)	1137

Overall, as shown in Figure 4.5, it is clear that the duration of the xylem cell production at Angliers was the longest among three sites during two growing seasons. The duration of the xylem cell production at Chicobi and Muskuchii was similar in the studied two years. Within a site, the earlywood duration was longer than the latewood duration. Latewood duration at the northern sites was shorter than the southern site Angliers. ANOVAs results showed that some differences were detected among sites (growth reactions of southern trees better than the northern trees) and between years (growth reactions in 2005 better than 2006), but it was not statistically significant (data not shown).

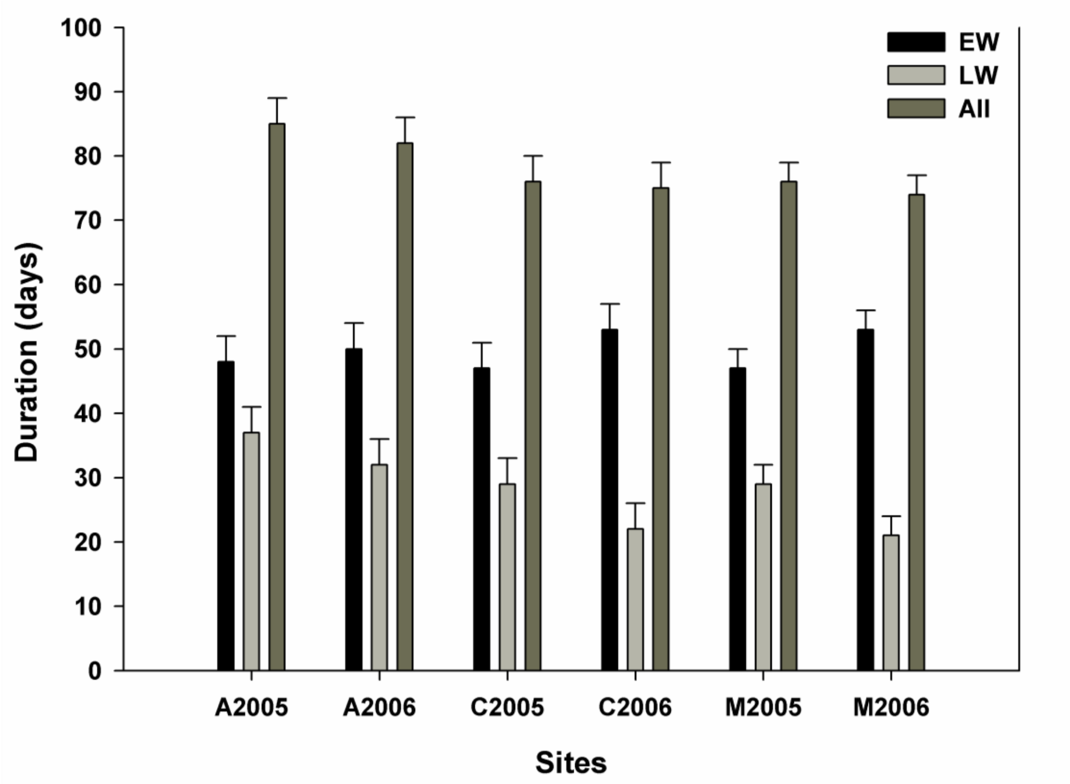

Figure 4. 4 Duration of earlywood (EW), latewood (LW) and whole cell production period (All) at Angliers (A), Chicobi (C), and Muskuchii (M) during the growing seasons 2005 and 2006. The error bars were shown.

4.6. DISCUSSION

4.6.1. Earlywood growth and climate

The onset date of the xylem cell production of black spruce was ranging from mid-May to the end of May during the two growing seasons. This agreed with recent intra-annual studies in western Quebec (Tardif *et al.*, 2001a; Ko Heinrichs *et al.*, 2007; Zhai *et al.*, to be submitted). For instance, Ko Heinrichs *et al.* (2007) observed the onset of xylem cells of several boreal species approximately from mid-May to May 22 at Lac Duparquet of western Quebec. Zhai *et al.* (to be submitted) reported the onset of xylem cell formation on May 7 for jack pine, May 28 for trembling aspen, and June 5 for paper birch at Lac Dances of northwestern Quebec. Similar dates for the onset of xylem cell formation of boreal tree species such as paper birch, black spruce and red pine were also documented in past studies (Fraser, 1952; Ahlgren, 1957; Forster *et al.*, 2000).

It is generally believed that the onset of xylem formation is controlled by photoperiod, temperature and water availability (Hänninen, 1995; Leinonen *et al.*, 1997) as well as auxin production (Wang *et al.*, 1997). In our study area, water availability in May is rarely found to limit black spruce growth because of sufficient winter snow and spring rainfall (Huang *et al.*, 2010). Hence the threshold temperature that is generally referred to above 5 ºC and varies across species (Grace, 1989; Körner, 1998; Schmitt *et al.*, 2004) might be the major climate factor for stimulating the onset of xylem growth in May in the studied region. In this study, mean air temperature during the week prior to the onset of the xylem cell production was ranging from 7.8 to 9.4 ºC in 2005, and from 11.3 to 11.8 ºC in 2006 across the three sites, respectively. Mean soil temperature during the week prior to the onset of the xylem cell production was ranging from 4.3 to 6.4 ºC in 2005, from 5.3 to 7.1 ºC in 2006 across the sites (Table 4.1). In the same region, Ko Heinrichs *et al.* (2007) also reported that the onset of the xylem cell production was at a time while both air and soil temperature were increasing on the studied site. Zhai *et al.* (to be submitted) observed that the onset of the xylem cell production was at 5.3 ºC for jack pine, and approximately at 8.2°C-10.4°C for trembling aspen and paper birch in the mixed boreal forest of northwestern Quebec as well. In other boreal region, the threshold temperature triggering the onset of cell production was also observed. 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.

Growing degree days (≥5°C) was reported to be a major climate factor controlling trembling aspen productivity at the spatial scale in western Quebec (Lapointe-Garant *et al.*, 2009). Across the three sites along the gradient, however, GDD at the onset date of the xylem cell production was found to vary largely across the three sites and two growing seasons, ranging from 77.9 to 147.2 °C. This indicates that GDD seems to play a less important role in triggering the onset of the xylem cell production than in controlling forest productivity in the studied gradient.

Black spruce trees were observed to start production of the xylem cells earlier in 2006 than in 2005 across the three sites. This may be directly attributed to warmer May temperature in 2006 than in 2005. Deslauriers *et al.* (2003a) also observed earlier onset of cell production of balsam fir in warmer 1999 than in 1998 and 2000 in northeastern Quebec. In eastern Italian Alps, Rossi *et al.* (2007) also reported the earliest cambial activity onset observed for the studied three species (*Larix deciduas* Mill., *Pinus cembra* L., and *Picea abies* (L.) Karst) in 2003 due to warmer April-May temperature in 2003 compared to 2002 and 2004. Along the south-north gradient, trees at the southern site Angliers initiated the onset of the xylem cell formation earlier than the two northern sites in both growing seasons, indicating that earlier warm spring temperature in the south may trigger earlier onset of phenology and xylem growth for trees in the south. Small difference in the onset of the xylem formation in two northern sites might be due to similar climate dominance (cold and dry climate from the arctic in winter (Sheridan, 2002)) at these two nearby sites or similar local site conditions and tree vigour in these two sites.

Earlywood new cell production terminated later in 2005 than in 2006 across three sites, suggesting that warmer June and July temperature in 2005 than 2006 might result in longer duration of earlywood production. As a result, higher percentage of earlywood cells was observed in 2005 across three sites. Deslauriers *et al.* (2003a) also observed that the duration of earlywood formation of balsam fir was about 6-7 weeks in the normal years 1998 and 2000, but was about 9-10 weeks in the warmer year 1999. Wang *et al.* (2002) documented that warmer years produced more earlywood cells for black spruce at tree line in northern Quebec. Along the gradient, trees at the southern sites relatively produced higher percentage of earlywood cells than the northern site Collines Muskuchii. This also indicates that warmer climate in the south may produce more earlywood. June is widely reported to be the critical month to produce earlywood cells (Deslauriers *et al.*, 2003a; 2003b; Mäkinen *et al.*, 2003; Rossi *et al.*, 2007; Zhai *et al.*, to be submitted).

4.6.2. Latewood growth and climate

The onset of spruce latewood cell production, i.e., termination date of earlywood cell production, was ranging from the end of June to early July across the three sites. This is consistent with Deslauriers *et al.* (2003a) who reported that the earlywood-latewood transition for balsam fir occurred from July 2 to July 19 in northeastern Quebec. Across the three sites, our studied black spruce trees terminated production of new xylem latewood cells during the former half of August. Zhai *et al.* (to be submitted) also observed that the ending date of new cell production of jack pine, trembling aspen, and white birch was on August 9th, 16th, and 16th, respectively, in northwestern Quebec. Vaganov *et al.* (2006) documented that at high latitude new cell production of tree species usually ceased in about mid-August. Therefore the duration of the latewood xylem new cell production was around three to five weeks across three sites during two growing seasons. Deslauriers *et al.* (2003a) also observed that the duration of latewood cell production for balsam fir was around 3-5 weeks in northeastern Quebec. After the termination of new latewood cell production, however, lignin deposition in latewood cells (i.e., lignifications) still persisted till the end of August to mid-September. Our results are consistent with the previous intra-annual growth studies that also observed the lignifications by the end of August to mid or late September (Deslauriers *et al.*, 2003a; Zhai *et al.*, to be submitted).

Higher ratio of latewood cells to total xylem cells produced in 2006 than in 2005 across the three sites might be due to cold July-August temperature in 2006 than in 2005. Cold summer temperature in 2006 resulted in earlier starting of the latewood cell production (i.e., termination of the xylem earlywood cell production) and earlier termination of latewood new cell production across three sites, thereby producing less total cells in cold year. Consequently, higher ratio of latewood cells to total cells was observed in narrow ring-width year 2006 rather than in wider ring-width year 2005. Wang *et al.* (2002) also found that less xylem cells and high latewood density of black spruce were observed in cold years than in hotter years in tree line of Quebec boreal forest.

Comparisons among sites showed that the northern trees terminated latewood new cell production earlier than the southern trees during each of the two growing seasons. This might be ascribed to colder summer temperatures in the north than in the south. This supports our hypothesis that trees terminated cell production earlier in the north than in the south. August temperature was reported to be strongly correlated with the maximum tree-ring wood density (D'Arrigo *et al.*, 1992; Schweingruber *et al.*, 1993).

Overall, we found that the duration of the xylem cell production for the southern trees was relatively one week longer than the northern trees across the sites. And trees in warm May in 2006 started the onset of xylem cell production earlier than trees in cold May in 2005, indicating that May temperature is critical for the onset of the xylem formation. However, cold June-August temperature in 2006 resulted in earlier termination of earlywood cell production and of latewood cell production, suggesting that June-August temperature played a particularly important role in regulating cell production process. Hence despite the expected occurrence of earlier phenology due to early spring climate warming, trees might not be certainly producing many xylem cells and thus wider ring-width if cold June-August temperatures would occur in the future. This may challenge the general thoughts that the boreal trees might be benefiting from climate warming to enhance growth. Therefore tree growth modelling should integrate the results of finer-scale intra-annual studies into future growth simulation.

4.7. CONCLUSIONS

Under climate warming, tree growth modelling needs to be improved through integrating the findings of finer-scale intra-annual tree growth studies. To attain this goal, we investigated the dynamics of intra-annual xylem formation of black spruce along a latitudinal gradient from approximately 47.5 to 50ºN during two growing seasons 2005 and 2006 in western Quebec. We found that warmer May in 2006 resulted in earlier onset of the xylem cell formation than in 2005. However, cold June-August temperature in 2006 caused earlier termination of the earlywood and latewood cell production than in 2005. Consequently higher ratio of latewood cells to the total xylem cells in 2006 was found across the three sites in comparison with 2005. Along the south-north gradient, warmer temperature in the south initiated earlier onset of xylem cell production of the southern black spruce than the northern stands. The identified onset date and termination date of the xylem cell formation of black spruce along the gradient and their associations with climate may be used to better understand how black spruce stands are responding to climate warming at different latitudes of the studied region. With different warming amplitudes in different seasons, warm summer might result in greater growth of the northern black spruce stands compared to the southern stands. However, cold summer temperature might lead to more latewood production, thus increasing wood density. Future more studies will be needed to improve our capability of modelling of black spruce growth and productivity in the eastern Canadian boreal forest.

4.8. ACKNOWLEDGEMENTS

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GENERAL CONCLUSION

Climate is one of the major forces to drive changes in terrestrial forest ecosystems. Recent strengthened climate warming has been resulting in significant changes in tree and forest growth, probably leading to profound shifts in forest composition and structure on the earth, when coupled with climate-induced changes in forest disturbances such as insect outbreaks (IPCC, 2007) and forest fires (Bergeron *et al.*, submitted). The temperate and boreal forests at mid and high latitudes of the Northern Hemisphere play a central role in sustaining the whole earth ecosystem and environment through providing forest ecosystems multiple social, economical and environmental functions. Therefore it is of great importance to better understand their growth responses to climate warming and to further predict their future potential growth changes with a warming climate during the 21st century.

In this thesis, a broad latitudinal gradient region spanning from 46 to 54ºN and covering the broadleaf and coniferous mixed boreal forest of eastern Canada was chosen as an example study region of the terrestrial boreal forest ecosystems to systematically investigate the climate-radial growth associations. Insect outbreaks that occurred in the studied host species trembling aspen stands along this broad spatial latitudinal gradient were first identified and assessed (Chapter I). Then after correcting the radial growth of the years that were contaminated by insect outbreaks reported in the previous chapter, the effects of recent climate change on radial growth of the four dominant boreal tree species trembling aspen, paper birch, black spruce, and jack pine were systematically investigated along this broad spatial latitudinal gradient in the eastern Canadian boreal forest (Chapter II). Furthermore, based on the previous paper, future radial growth of these four species was predicted under the multiple climate change scenarios during the 21st century using a novel concept, i.e., changes in tree and forest growth under future climate warming over time could be resembled by a broad spatial latitudinal gradient study (Chapter III). In addition, the intra-annual formation of the xylem of black spruce during the 2005-2006 growing seasons along a latitudinal gradient from approximately 47.5 to 50ºN was also monitored and assessed in order to provide some precise information of how the meteorological factors regulated tree intra-annual radial growth at different latitudes under a warming climate (Chapter IV). This study provides us very important results about dynamic changes in insect outbreaks at spatiotemporal scales in western Quebec, and the reactions of radial growth of these four species to past, current, and future climates along a broad spatial latitudinal gradient.

Insect outbreaks

In the Chapter I, the results showed that some major outbreaks occurred in relatively close synchrony at the regional scale, but the initiation year, the intensity and extent of the outbreaks varied spatially. For example, the 1950s outbreaks were observed from 1951-52 at 46°N, 1953-54 at 47°N, and 1954-56 at 48°N. Other major outbreaks like the 1964 and 1980 outbreaks were fairly well-synchronized at northern latitudes. We also found additional severe insect outbreaks that were not reported in previous studies and that occurred prior to available forest insect inventory data like severe insect outbreaks prior to 1938. The observed outbreaks in trembling aspen stands at latitude 54°N also provided clear evidence that severe insect defoliation occurs much further north than the currently reported range limit, i.e., between 49 and 51°N, of the most important aspen defoliator, the forest tent caterpillar. Our findings indicated that analysis of white/narrow rings may extend forestry insect inventory data to a larger spatial scale (e.g., remote areas or survey-missed areas) and to a longer temporal scale (e.g., insect outbreaks prior to forest insect inventory surveys).

As forecasted by IPCC (2007), accompanied with climate warming, extreme climate events are likely to increase during the current century, such as droughts. Consequently, these increased droughts will be favourable for strengthened insect activities, leading to rapid insects spread (increased amplitude) and more frequent outbreaks (increased frequency) in the forests (Volney and Fleming, 2000). Climate warming may also increase the abundance of the broadleaf species in the pure coniferous boreal forest, as predicted in the Chapters II and III. The increased broadleaf stands in the north may create favourable conditions (e.g., food and host trees) to allow insects spreading northwards. As a consequence, this might result in substantial changes in growth decline of the boreal host species and changes in forest composition and structure, even the whole boreal ecosystems. Hence a better understanding of past insect outbreaks at spatiotemporal scales using dendro-technique as shown in our study will be needed to better quantify future insect outbreaks and potential corresponding changes in forest productivity and ecosystems. As shown in our study of the Chapter I, improved understanding of the historical, distributional limits of defoliating insects may provide critical baseline information needed to monitor the impacts of environmental change.

Radial growth reactions to recent climate

In the Chapter II, our multiple-species and broad latitudinal gradient study demonstrates similar and dissimilar growth responses to climate at different latitudes among species in the eastern Canadian boreal forest. We found that the moisture conditions in the previous year played a dominant role in positively affecting radial growth of trembling aspen over the gradient, whereas January temperature and growing season moisture conditions were major factors for positively affecting radial growth of paper birch. Both black spruce and jack pine were primarily positively impacted by the current-year winter and spring or whole growing season temperatures along the gradient. Since different climate factors limited radial growth, the growth responsiveness of these four species to recent warming was inconsistent at the vegetation transition zone, where paper birch, black spruce and jack pine would be the most positively responsive species, whereas trembling aspen might be the least. In addition, along the broad gradient, PCA clearly separated the radial growth-climate associations of each species into two parts, i.e., southern and northern, indicating that these stands were influenced by different air masses in the south (i.e., warm, moist air originating from the south during summer) and in the north (i.e., cold, dry polar air during winter), respectively, (Sheridan, 2002). Recent studies also speculated that the warm, moist air masses and the cold, dry polar air masses might have been advancing and retreating northwards, respectively, due to recent warming at the transition zone (Hofgaard *et al.*, 1999; Girardin *et al.,* 2006). Therefore, different responsiveness of species to recent climate warming might allow us to assess the retreating speed of cold air masses or advancing speed of warm and moist air masses in western Quebec with global warming. Future such studies would be needed to further clarify it.

Future radial growth simulations with climate warming during the 21st century

Based on the Chapter II, the Chapter III tried to simulate future radial growth of these four species using multiple climate change scenarios data generated from three Global Climate Models and a Canadian Regional Climate Model through two different models. One model is the dynamic model, which was based on the assumption that tree growth response to climate at the temporal scale may be resembled by tree growth response to climate at the spatial scale, given that tree growth conditions might be changing with a warming climate over time. That is, tree growth response to climate along a broad latitudinal gradient from south to north may constitute an analogue of tree growth response to future climate warming over time. Therefore, through a broad latitudinal gradient study, growth of those northern stands during future time period could be predicted using the climate-growth equations obtained from the currently more southern stands. The other model is the local model, which was based on the assumption that future tree growth at northern latitudes might not be completely resembled by the stands at southern latitudes using the dynamic model if the photoperiod difference between these two latitudes is large, when considering a genetic constraints effect on growth or a lagged effect in genetic response to climate (Rehfeldt *et al.*, 2002). In this case, tree growth might be maximally simulated by growth model established at the local site, the one we called the local model.

Our study opens a new window for predicting future growth of trees and forests using the empirical models when considering the potential effect of both climate warming and genetic constraints on tree growth. The simulated future growth change using the dynamic model was modest across the gradient, and might indicate the lower limit of future tree growth. In contrast, the predicted growth change using the local model was abrupt, and might indicate the upper limit of future tree growth. Taken together, our study might provide two theoretical baselines for potential future growth change across the gradient in the eastern Canadian boreal forest. Hence we propose that future potential growth change of a given stands over the studied gradient would be very likely to be set between these two simulations. These potential growth changes of individual species at spatiotemporal scale would result in shift in compositions and structure of the boreal forests, consequently leading to substantial changes in carbon redistribution in the boreal biome during the 21st century.

Intra-annual xylem formation of black spruce

Better tree and forest growth modelling needs to incorporate the precise information of intra-annual growth of different species to climate. In the Chapter IV, we attempted to better understand the intra-annual xylem formation of black spruce along a latitudinal gradient from approximately 47.5 to 50ºN during two growing seasons 2005 and 2006 in western Quebec using recent developed micro-sampling approach. We found that early onset date of the xylem cell production of black spruce across the three sites was detected in 2006 than 2005, whereas early termination of the xylem latewood new cell production was observed in 2006 than in 2005. We attributed the former to warmer May temperature in 2006 than in 2005, and ascribed the latter to colder June-August temperature in 2006 than in 2005. Across the gradient, trees at the southern site initiated the onset of xylem cell formation earlier than trees at the two northern sites. The absence of such difference in the two northern sites might be due to similar climate dominance (cold and dry climate from the Arctic in winter (Sheridan, 2002)) at these two nearby northern sites, or similar site conditions and tree vigor at these two sites. Therefore trees might not be certainly able to benefit from earlier spring temperature to enhance growth if the critical summer season temperatures (June-August) would become cold. As well, the site conditions and tree vigor would be also important to affect the xylem cell production, as shown by the two northern sites. More intra-annual growth studies would be needed to improve our understanding of how the boreal trees are reacting to climate warming in the future.

Potential future changes in growth of trees and forests

Our systematic studies in this Ph.D project allow us to infer potential changes in future growth of trees and forests in the eastern Canadian boreal forest at spatiotemporal scales under climate warming in the Northern Hemisphere (IPCC, 2007). Our study clearly shows that, due to warmer winter and favourable growing seasons climate, of the four species, jack pine might be the most beneficial species from climate warming to extensively increase growth across the whole gradient of eastern Canada during the 21st century,whereas paper birch is the least species to benefit from climate warming due to increased droughts or species competition or insects outbreaks (IPCC, 2007); Black spruce and trembling aspen are intermediate species that might benefit from climate warming. Specifically, black spruce and trembling aspen at north of 51°N would increase their radial growth during the 21st century, whereas their stands at 49-51°N would increase growth from present to 2060s, and thereafter decrease growth. The southern black spruce and trembling aspen stands (south of 49°N) would reduce growth with warming climate because of increased droughts and/or other factors such as species competition and nutrient deficiency (Bergeron *et al.*, 2004). Across the studied gradient, our study only shows that paper birch at north of 51°N would enhance growth until 2060s, and thereafter decrease growth; paper birch stands at south of 51°N might decline growth with climate warming. These growth decreases might be mostly attributed to increased droughts or other factors such as increased insects or species competition induced by climate warming in the future (IPCC, 2007).

These potential growth changes in different boreal species over different spatiotemporal scales might also cause substantial changes in carbon redistributions in the boreal forest of eastern Canada. It also provides more promising options for future sustainable forest ecosystem management. That is, future increased growth and abundance of deciduous species would not only create more logging room, but also meet more social values (Christensen *et al.*, 1996; Harvey *et al.*, 2002). For example, more mixed wood forests would enhance biodiversity and forest resilience to cope with natural disturbances (Bergeron *et al.*, submitted) because ecosystem management recognizes that biodiversity and structural complexity at the temporal and spatial scales strengthen ecosystems against disturbances and supply the genetic resources necessary to adapt to long-term changes (Christensen *et al.*, 1996). Hence it is of great importance to take our multiple species and broad spatial-scale study as a template for exploring the effects of climate warming on growth of different tree species in other boreal regions of the Northern Hemisphere. This could aid us to quantitatively assess potential changes in tree growth and forest composition across the mid-high latitudes of the Northern Hemisphere, which in turn may be used in the long-term planning of sustainable forest management and the assessment of the role of boreal forests in global carbon equilibrium.

Altogether, to our knowledge, this Ph.D study is the first study 1) discovering the occurrence of insect outbreaks at the northern distributional limit of the host species in Canada’s boreal forest (Chapter I); 2) using a novel, sophisticated approach to systematically investigate the radial growth responses of multiple-species to climate at a broad spatial-scale gradient, and providing direct evidence of different responsiveness of different tree species to recent climate warming at the vegetation transition zone in the whole boreal forest of the Northern Hemisphere (Chapter II); 3) constructing two theoretical baselines for future radial growth simulation of the four dominant boreal tree species in the eastern Canadian boreal forest in the 21st century based on the dynamic model and the local model we defined (Chapter III); 4) investigating the intra-annual xylem formation of black spruce along a latitudinal gradient during the two growing seasons in western Quebec. Several novel approaches used in the study may be extensively used in other boreal regions of the Northern Hemisphere. The findings of the thesis would certainly contribute to better understanding of tree and forest growth to climate warming and to improve our simulation of future forest growth and productivity in the temperate and boreal forest. Future more similar studies will be needed to extensively understand how the whole boreal forests are responding to a changing climate and what substantial changes in forest compositions and structure may be caused by future warming climate. The expected results from future studies would be certainly integrated into global carbon cycle modelling, which will produce more precise simulation for better understanding of carbon sequestration on the earth.

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APPENDIX I

RESPONSE OF FOREST TREES TO INCREASED ATMOSPHERIC CO_2

Jian-Guo Huang, Yves Bergeron,
Bernhard Denneler, Frank Berninger, and Jacques Tardif

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A.1. ABSTRACT

The CO_2 fertilization hypothesis stipulates that rising atmospheric CO_2 has a positive effect on tree growth due to increasing availability of carbon. The objective of this paper is to compare the recent literature related to both field CO_2-enriched experiments with trees and empirical dendrochronological studies detecting CO_2 fertilization effect in tree rings in order to evaluate tree growth response to atmospheric CO_2 enrichment by combining evidence from both ecophysiology and tree-ring research. Based on considerable experimental evidence of direct CO_2 fertilization effect (increased photosynthesis, water use efficiency, and above- and below-ground biomass), and predications from the interactions of enriched CO_2 with temperature, nitrogen and drought, we propose that warm, moderately drought-stressed ecosystems with an ample nitrogen supply might be the most CO_2 responsive ecosystems. Empirical tree-ring studies took the following three viewpoints on detecting CO_2 fertilization effect in tree rings: 1) finding evidence of CO_2 fertilization effect in tree rings, 2) attributing growth enhancement to favourable climate rather than atmospheric CO_2 enrichment, and 3) considering that tree growth enhancement might be caused by synergistic effects of several factors such as favourable climate change, CO_2 fertilization, and anthropogenic atmospheric deposition (e.g. nitrogen). At temperature-limiting sites such as high elevations, non-findings of CO_2 fertilization evidence could be ascribed to the following possibilities: 1) cold temperatures, a short season of cambial division, and nitrogen deficiency that preclude a direct CO_2 response, 2) old trees past half of their maximum life expectancy and consequently only a small increase in biomass increment due to CO_2 fertilization effect might be diminished, 3) the elimination of age/size-related trends by statistical detrending of tree-ring series that might remove some long-term CO_2-related trends in tree rings, and 4) carbon partitioning and growth within a plant that is species-specific. Our review supports the atmospheric CO_2 fertilization effect hypothesis, at least in trees growing in semi-arid or arid conditions because the drought-stressed trees could benefit from increased water use efficiency to enhance growth.

Keywords CO_2 fertilization effect, CO_2 enrichment experiment, dendrochronology, ecophysiology, tree rings, water use efficiency.

A.2. INTRODUCTION

Atmospheric carbon dioxide (CO_2) is a substrate for plant photosynthesis. Increased atmospheric CO_2 concentration is believed to, therefore, increase photosynthesis rate by increasing CO_2 intake directly (Arp, 1991; Long and Drake, 1992; Koch and Mooney, 1996; Curtis, 1996; Mooney *et al*., 1999; Norby *et al*., 1999). Increased atmospheric CO_2 might induce a partial closure of stomata, reducing water loss by transpiration, which results in an increase in the ratio of carbon gain to water loss, i.e. water use efficiency (Farquhar *et al*., 1989; Bowes, 1993; Field *et al*., 1995; Drake *et al*., 1997; Farquhar, 1997; Körner, 2000). As a result, this effect can lengthen the duration of growing seasons in seasonally dry ecosystems, thus probably stimulating biomass accumulation (Ceulemans and Mousseau, 1994; Saxe *et al*., 1998), and enhancing ecosystem net primary productivity (Amthor, 1995; Loehle, 1995). This CO_2-induced enhancement in primary productivity and water use efficiency is commonly referred to the direct ‘fertilization effect’ (Beedlow *et al*., 2004).

As one of the greenhouse gases, CO_2 has been the most important factor associated with a rise in temperature during recent decades (IPCC, 2007). A new simulation study under a doubled CO_2 concentration suggested that the positive feedbacks of CO_2 and CH4 might be important, i.e. higher temperatures may lead to increased releases (or reduced uptake) of CO_2 and/or CH4 by the ocean, forests and soils (Torn and Harte, 2006; Scheffer *et al*., 2006). As a consequence, the greenhouse gases-induced temperature increases over the coming century might be able to reach 1.6-6.0°C (Torn and Harte, 2006) compared to 1.4-4.5°C predicted previously (IPCC, 2001). The increased temperature as well as the correspondingly increased precipitation over northern mid- to high latitudes could enhance growth of plants and change forest ecosystems. This is so-called indirect effect of atmospheric CO_2 enrichment on plants.

With continuously anthropogenic atmospheric CO_2 enrichment, it was hypothesized that CO_2 enhancement could enhance tree growth and change growth of forests through direct CO_2 fertilization effect (LaMarche *et al*., 1984; Hari and Arovaara, 1988; Kienast and Luxmoore, 1988; Graumlich, 1991; Graybill and Idso, 1993). Interestingly, many tree-ring studies have reported an increase in radial growth of trees with the rise of atmospheric CO_2 concentration (e.g. LaMarche *et al*., 1984; Payette *et al*., 1985, 1989; D'Arrigo *et al*., 1987; Hari and Arovaara, 1988; Kienast and Luxmoore, 1988; Archambault and Bergeron, 1992; Graybill and Idso, 1993; D'Arrigo and Jacoby, 1993; Becker *et al*., 1994; Nicolussi *et al*., 1995; Spiecker, 1996; Knapp *et al*., 2001; Zhang *et al*., 2003; Bunn *et al*., 2005; Wang *et al*., 2006; Huang and Zhang, 2007), although some other studies found no anomalous growth enhancement during recent decades (Schweingruber *et al*., 1993; Mielikäinen and Timonen, 1996; Mäkinen *et al*., 2000). However it is still unclear whether increased growth of trees observed is attributed to direct CO_2 fertilization effect or to indirect effect of enriched atmospheric CO_2 concentration.

The large size and long life spans of trees make it technically and economically challenging to measure and monitor their growth response to CO_2 enrichment. In practice, two kinds of approaches to detect the effects of atmospheric CO_2 enrichment on trees were used: 1) short-term field CO_2-enrichment experiments on seedlings or young trees and 2) empirical dendrochronological studies. During the past decades, CO_2 enrichment experiments were conducted over five continents and the results showed that elevated CO_2 concentration can have significant effects on growth of young trees or seedlings (e.g. Chidumayo, 1990; Sage, 1994; Amthor, 1995; Curtis, 1996; Eamus, 1996; Drake *et al*., 1997; Saxe *et al*., 1998; Curtis and Wang, 1998; Norby *et al*., 1999; Medlyn *et al*., 1999; Schlesinger and Lichter, 2001; Ainsworth and Long, 2005; Körner, 2006). In contrast, results from dendrochronological studies to detect atmospheric CO_2 fertilization effect in tree rings are controversial and still under debate (LaMarche *et al*., 1984; Hari and Arovaara, 1988; Kienast and

Luxmoore, 1988; Graumlich, 1991; Briffa, 1991; D'Arrigo and Jacoby, 1993; Graybill and Idso, 1993; Becker *et al*., 1994; Nicolussi *et al*., 1995; Spiecker, 1996; Rolland *et al*., 1998; Knapp *et al*., 2001; Bunn *et al*., 2005; Wang *et al*., 2006).

The objective of this paper is to compare the recent literature related to both field CO_2-enriched experiments with trees and empirical dendrochronological studies detecting CO_2 fertilization effect in tree rings in order to evaluate tree growth response to atmospheric CO_2 enrichment by combining congruent evidences from both ecophysiology and tree-ring research. Since some meta-analytical reviews on enriched-CO_2 experimental studies already exist (e.g. Curtis and Wang, 1998; Norby *et al*., 1999; Ainsworth and Long, 2005; Wang, 2007), we will synthesize the results from the literature reviews and empirical dendrochronological studies to assess whether CO_2 fertilization effect really occurs in tree rings in natural forests. The text is structured as follows: 1) empirical evidence from CO_2 enrichment experiments, 2) empirical dendrochronological studies testing CO_2 fertilization effect in tree rings, 3) evidence for CO_2 fertilization effect displayed in tree rings in natural forests, and 4) conclusions.

A.3. EMPIRICAL EVIDENCE FROM CO_2 ENRICHMENT EXPERIMENTS

Physiological Response to CO_2

The theoretical hypothesis suggests that plants growing in a higher temperature (Long, 1991; Drake *et al*., 1997), and higher nitrogen (N) availability environment (Luo *et al*., 2004; Norby and Iversen, 2006) with moderate drought (Beerling *et al*., 1996; Wullschleger *et al*., 2002; Morgan *et al*., 2004; Nowak *et al*., 2004) might have larger growth increases under atmospheric CO_2 enrichment. CO_2 and temperature dependencies of photosynthesis and temperature dependencies of dark respiration are metabolic pathways that produce ATP and reductants to meet energy demands for plant growth and maintenance (Berry and Björkman, 1980; Morison and Lawlor, 1999; Wang *et al.*, 2001). Plants exchange CO_2 and other gases with the atmosphere mainly through the leaf stomata. Within the leaf, CO_2 reacts with the enzyme Ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) during photosynthesis to form carbohydrates (carbon fixation) that are allocated to different parts of trees, such as leaves, twigs, branches, stems, and roots (Jensen, 2000; Beedlow *et al.*, 2004) (Figure 1). Concurrently, respiration that could oxidize the carbohydrate to CO_2 and O_2 in living cells, leaves, buds or shoots, branches, stems, and roots may consume some of the carbon and release it to the atmosphere as CO_2 (carbon release) (Norby *et al.*, 1999; Beedlow *et al.*, 2004) (Figure 1).

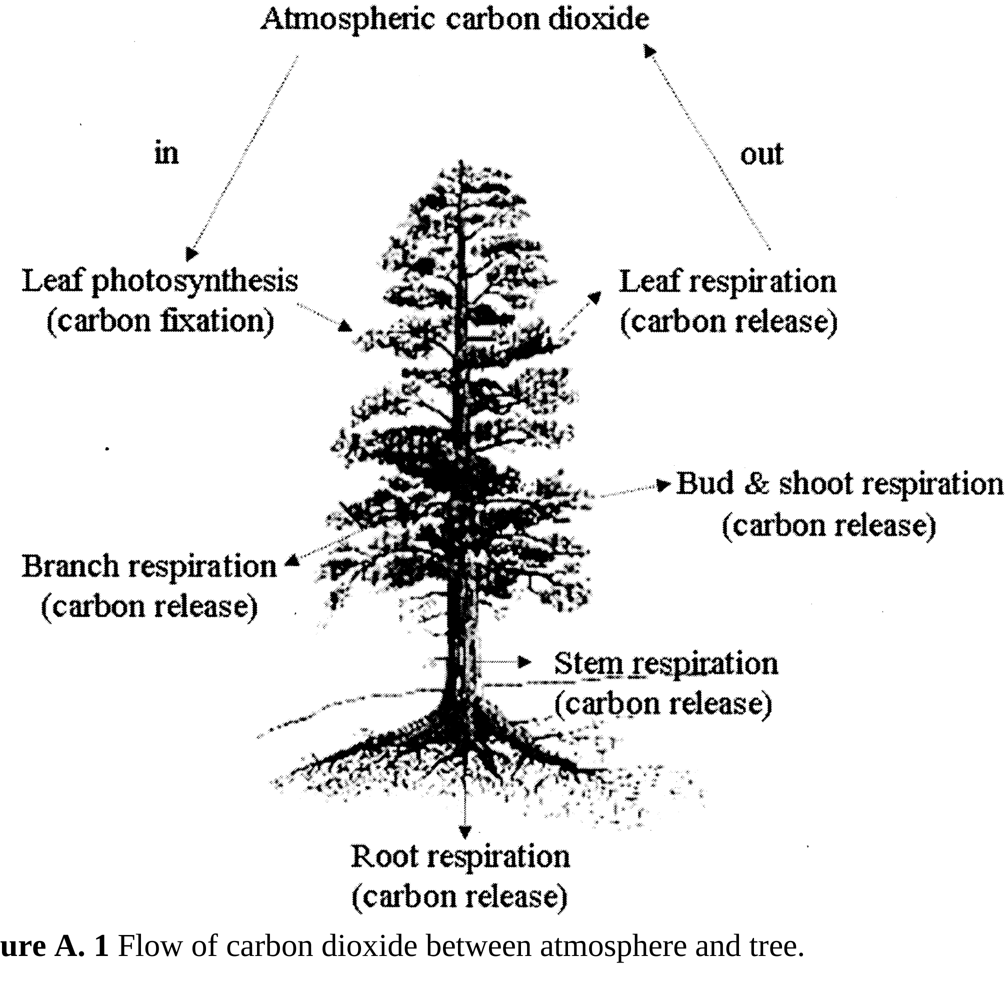

Figure A. 1 Flow of carbon dioxide between atmosphere and tree.

CO_2 partial pressure is an important limiting factor for photosynthesis (Aranjuelo *et al*., 2005). Net CO_2 assimilation rate per unit area of C_3 plants is affected by the ratio of atmospheric CO_2 concentration and O_2 concentration since they compete at the active site of the enzyme Rubisco for the primary acceptor, ribulose-1,5-bisphosphate (RuBP). Rubisco catalyses both carboxylation and oxygenation of RuBP. Oxygenation results in respiratory loss of CO_2, and carboxylation results in carbon fixation through the photosynthetic carbon reduction cycle (Morison and Lawlor, 1999). Higher CO_2 level hence increases the leaf internal CO_2 concentration and the CO_2:O_2 ratio at the Rubisco site, which favours carboxylation rather than oxygenation of RuBP (Andrews and Lorimer, 1987; Jensen, 2000), and thus suppresses respiration and enhances photosynthesis, consequently increasing net photosynthesis (Eamus, 1991; Stitt, 1991; Arp, 1991; Long and Drake, 1992; Saxe *et al*., 1998). The structure of the Rubisco-enzyme is highly conserved among plant groups (Yu *et al*., 2005) and plant physiologists expect that the behaviour of Rubisco under different environmental conditions is predictable. The ratio of carboxylation over oxygenation decreases with temperature (Long, 1991). Based on calculations of enzyme kinetics the enhancement of photosynthesis by increases of the ambient CO_2 concentration should be higher under warm conditions. Also, the ratio of carboxylation to oxygenation decreases with the CO_2 to O_2 ratio in the leaf. Drought also decreases the CO_2 concentration without affecting the O_2 concentration (Long, 1991). Increases in ambient CO_2 concentration would therefore enhance more the photosynthesis of drought-stressed plants.

Körner (2006) summarized that stimulation of leaf photosynthesis was evidenced unequivocally in experiments when plants were exposed to enriched CO_2. However, increases in the rates of photosynthesis varied with the duration of the experiment, the maturity stage of the trees, the plant N status, and the experimental exposure technique (Saxe *et al*., 1998; Ainsworth and Long, 2005). It also varied within canopy, seasonally or between species (Norby *et al*., 1999). Norby *et al*. (1999)

reported that photosynthesis was stimulated by 40-80% in most of the experiments with the exception of greater enhancement in several cases under enriched-CO_2 environment. A meta-analytical review of free-air CO_2 enrichment (FACE) experiments found that trees were more responsive than other function types to elevated CO_2 (Ainsworth and Long, 2005). In a review of short-term CO_2-enriched experiments (less than one season), Ceulemans and Mousseau (1994) found that photosynthesis of deciduous species was more sensitive to elevated CO_2 than that of conifers. However, evidence from long-term studies (more than one season) suggested that photosynthesis stimulation enhanced by elevated CO_2 was similar in unstressed conifers and deciduous trees, ranging from 50-60% (Norby *et al.*, 1999). Gunderson and Wullschleger (1994) did not observe a significant difference in photosynthesis response under elevated CO_2 between conifers and deciduous trees.

CO_2 and Temperature

When taking into account the interactive effects of increased CO_2 concentration and temperature, based on the strong dependence of the ratio of carboxylation rates to oxygenation rates on temperature from theoretical calculations, Long (1991) suggested that with increases in temperature, the proportion of potential carbon uptake, lost due to photorespiration, will increase. Higher substomatal CO_2 concentration will favour photosynthesis over photorespiration (Long, 1991). With the elevation of CO_2 concentration from 350 to 650 µmol mol^{-1}, Long (1991) predicted (based on the so-called Farquhar model of photosynthesis (Farquhar *et al*., 1980)), that CO_2 uptake (A_{sat} µmol $m^{-2}s^{-1}$) would increase by 14, 54, and 73% at leaf temperature of 10, 20 and 30ºC, respectively (Figure 2), which is similar to that in a study of three C_3 species (*Scrophularia desertorum* (Munz) R. Shaw, *Cardaria draba* Desv., *Populus fremontii* Wats.) (Sage and Sharkey, 1987). Long (1991) further pointed out that following from this interaction of CO_2 concentration and temperature, the temperature optimum (T_{opt}) of CO_2 uptake will increase, T_{opt}

increases by 3 °C at CO_2 concentration = 500 µmol mol^{-1} and 5 °C at CO_2 concentration = 650µmol mol^{-1} (Figure 2). Correspondingly, the predicted upper temperature at which positive CO_2 uptake may be maintained is also increased by 4 °C and 7 °C, respectively (Long, 1991).

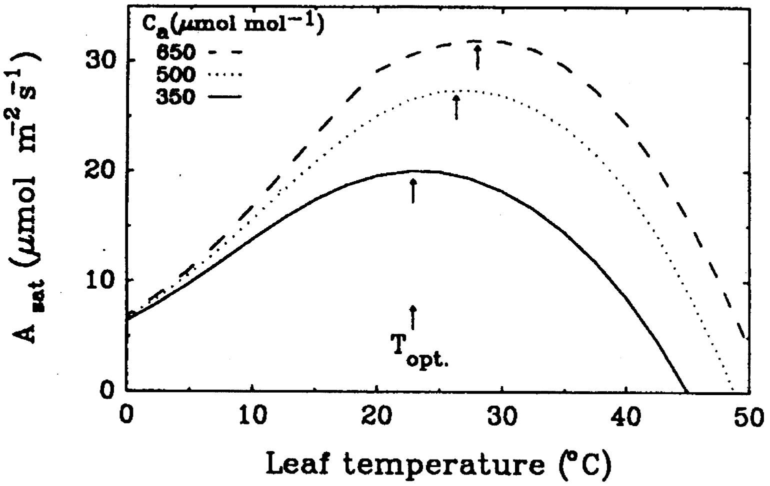

Figure A. 2 Predicted light-saturation rates of leaf CO_2 uptake (A_{sat}) with leaf temperature for three atmospheric CO_2 concentrations (C_a µmol mol^{-1} of CO_2 in air). Arrows indicate T_{opt}, i.e. the temperature at which A_{sat} is maximal for each value of C_a (after Long, 1991).

Idso *et al.* (1992) found that at a mean leaf temperature of 31, 35, and 42 °C, the additional 300 ppmv of CO_2 in the CO_2-enriched enclosures of sour orange trees (*Citrus aurantium* L.) increased net photosynthetic rates of leaves exposed to full sun by approximately 75, 100, and 200% over rates experienced by leaves in the ambient-air enclosures, respectively, demonstrating that the upper-limiting temperature for growth was raised 7 °C by the extra CO_2. The FACE experimental data showed that light-saturated CO_2 uptake of plants under elevated CO_2 concentration was enhanced by 19% for the FACE experiments conducted below 25 °C, and by 30% for those conducted above 25 °C, respectively (Ainsworth and Long, 2005). Response of plant growth to elevated CO_2 concentration cannot be readily predicted from the response of photosynthesis alone (Morison and Lawlor, 1999). It involves not only the photosynthetic responses of leaves but also whole-plant respiration (Gifford, 1992). Since dark respiration is a temperature dependent process, warmer temperatures hence increase the respiration rates of plants, which results in decreases of carbohydrate content in plants, and consequently limiting respiration and growth (Long, 1991; Rowland-Bamford *et al*., 1996). In a CO_2 enriched environment, additional carbohydrates as a result of increased photosynthesis could supply the demands of respiration on more energy at warmer condition (Long, 1991).

CO_2 and N

As a most critical component of many important structural, genetic, and metabolic compounds in plant cells (for instance N compounds comprise 40 to 50% of the dry matter of protoplasm, i.e. the living substance of plant cells), N is required in relatively large quantities in connection with all growth processes in plants (Stitt and Krapp, 1999; Johnson, 2006), especially for plants growing in a CO_2 enriched environment. When plants are exposed to a CO_2 enriched environment, an increase in biomass of plant or soil organic matter (carbon fixation) will increase the N demand in plants and enhance sequestration of N into long-lived plant biomass and soil organic matter pools (Luo *et al*., 2004). Consequently, more N would be sequestered in organic matter (van Groenigen and van Kessel, 2002) because formation of organic matter requires N and other nutrients in relatively fixed proportions with carbon (Luo *et al*., 2004; Norby and Iversen, 2006). Over a longer time, N availability will progressively decline unless compensated by additional N supplies or reduced losses. Finally, long-term responses of plants to CO_2 could be limited since ecosystem productivity would become N limited (Comins and McMurtrie, 1993; Luo *et al*., 2004; Norby and Iversen, 2006). Based on the physiological and biogeochemical theory deductions discussed above, Luo *et al*. (2004) proposed the Progressive

Nitrogen Limitation (PNL) hypothesis that ecosystems in a CO_2-enriched atmosphere will sequester carbon and N in long-lived biomass and soil organic pools, thereby limiting available N and constraining the continued response of net primary productivity to elevated CO_2 concentration. Recent studies have provided partial evidence for the PNL (Hungate *et al*., 2006), or despite no evidence observed for the PNL, they claimed that it still could be possible to occur through time (Finzi *et al*., 2006; Norby and Iversen, 2006). For example, Norby and Iversen (2006) did not find any evidence for the PNL in a six-year record of N dynamics of a deciduous sweetgum (*Liquidambar styraciflua* L) stand exposed to elevated CO_2 concentration in the FACE experiment at Oak Ridge, Tennessee, USA. However, the authors claimed that ‘we cannot, however, say that PNL will not start developing in this experimental forest sometime in the future’. They observed two indications of the increasing deficit of N return in leaf litter and the greater reliance of CO_2-enriched trees on uptake rather than retranslocation to meet their N requirements, which might suggest a change in the N economy (Norby and Iversen, 2006). They attributed this change in N economy to the fact that N supply in soil may be sufficient to meet an increasing demand for available N (Johnson *et al*., 2004), especially as roots of CO_2-enriched trees develop deeper in the soil profile (Norby *et al*., 2004). A recent meta-analysis of FACE experiments also supports that there are positive interactions between CO_2 and N (Ainsworth and Long, 2005). Reich *et al*. (2006) pointed out that N limitation might progressively suppress the positive response of plant biomass to elevated CO_2 in sites with low or moderate soil N availability, but such limitation of the CO_2 fertilization effect by insufficient N may be weak or absent in N-rich sites. At the population and community levels, N status in the soil can also influence relative responsiveness to elevated CO_2 (Wang, 2007).

CO_2 and Drought

Increased atmospheric CO_2 concentration will increase the ratio of CO_2 to O_2 in the substomatal cavity. This will decrease carbon losses due to photorespiration. Drought induces stomatal closure and decreases partial pressure of CO_2 in the leaf. Increased CO_2 concentration may induce stomatal closure and could result in an increase in the ratio of carbon gain to water loss, i.e. water use efficiency, at the leaf and whole stand level, and higher plant biomass (Farquhar *et al*., 1989; Field *et al*., 1995; Picon *et al*., 1996; Drake *et al*., 1997; Centritto *et al*., 1999; Körner, 2000; Wullschleger *et al*., 2002; Morgan *et al*., 2004). Also increased allocation of carbon to root growth (e.g. increased fine roots, root surface area and volume) and osmotic adjustment in plants exposed to enriched CO_2 may, for example, enable plants to exploit soil water in a deeper and larger range of soil (Wullschleger *et al*., 2002). In addition, altering developmental processes including root and shoot architecture (Berntson and Woodward, 1992; Miao *et al*., 1992) and leaf morphology (Thomas and Harvey, 1983) under enriched CO_2 concentration might affect water relations and plant response to drought. Consequently, these responses could increase water uptake and improve water balance in plants, hence ameliorating the negative effects of water stress and better adapting to a water-limited environment (Wullschleger *et al*., 2002; Morgan *et al*., 2004). A review article pointed out that although the cause and effect relationships between growth, gas exchange, anatomy and plant water relations were rarely established in many conducted experimental CO_2-enriched studies, it woud be probable that plants could benefit from increased root-shoot ratio or fine-root proliferation to better adapt to a water-limited environment (Wullschleger *et al*., 2002). In a FACE experiment on a closed-canopy, deciduous sweetgum forest, Norby *et al*. (2004) observed the CO_2-induced increase in fine-root standing crop (total length of root visible) in summer, which might be an important mechanism for conferring increased resistance to late-season drought. Morgan *et al*. (2004) suggested that the effect of enriched-CO_2 induced increases in water use efficiency and thus plant biomass enhancement might be especially important in drier ecosystems.

Downregulation

Long-term exposure to elevated CO_2 over periods of several weeks or longer often leads to a reduction of the photosynthetic capacity of plants (Arp, 1991; Gunderson and Wullschleger, 1994; Loehle, 1995; Ainsworth *et al*., 2004). Usually down-regulation is due to a reduction of the capacity of dark reactions to process CO_2 (Drake *et al*., 1997; Ainsworth *et al*., 2004). Decreased photosynthetic efficiency could be caused by 1) reduced light capture (PSII activity), which results from inhibition due to the accumulation of inactive PSII reaction centres and the decrease in light harvesting complexes, and/or 2) decreased carboxylation of RuBP catalysed by Rubisco (Long *et al*., 2004; Aranjuelo *et al*., 2005). Rubisco, which constitutes about 30% of the total protein in a plant leaf, is a major sink for plant N and is widely accepted as the ultimate rate-limiting step in photosynthetic carbon fixation (Jensen, 2000). Decreased efficiency of Rubisco might be due to a reduction of leaf N concentration and photosynthetic N-use efficiency (Stitt and Krapp, 1999; Medlyn *et al*., 1999; Nowak *et al*., 2004). Past studies frequently reported some down-regulation of photosynthesis and biomass (e.g. Eamus and Jarvis, 1989; Sage, 1994; Gunderson and Wullschleger, 1994; Vivin *et al*., 1995; Miglietta *et al*., 1998; Saurer *et al*., 2003; Ellsworth *et al*., 2004). In a meta-analysis that summarized effects of long-term CO_2 increase on photosynthetic model parameters obtained from 15 field-based elevated CO_2 experiments on European tree species, Medlyn *et al*. (1999) observed a 10-15% reduction in photosynthesis when measured at the same CO_2 concentration. Adam *et al*. (2004) found that after 14 years of exposure to elevated CO_2 concentration, CO_2-induced enhancement of photosynthesis has declined and this decline was strongly correlated with the decrease in the above-ground wood biomass enhancement ratio reported by Idso and Kimball (2001).

In addition, elevated CO_2 concentration could reduce the light compensation point for net photosynthesis and increase maximum quantum efficiency by reducing respiration, which is of significance for survival and growth of tree seedlings in deeper shade (Körner, 2006), with possible implications on interspecific competition and forest regeneration (Saxe *et al*., 1998). Reduced stomatal conductance, enhanced photosynthesis, or both factors combined could enhance leaf water use efficiency and, hence, improve drought tolerance of plants (Eamus, 1991; Saxe *et al*., 1998; Wullschleger *et al*., 2002; Morgan *et al*., 2004). Increases in both net photosynthesis and water use efficiency enhance assimilation of carbon available for growth of plants.

A.4. GOROWTH RESPONSE TO CO_2

Currently, there are four methods of exposing tree foliage to elevated CO_2 in the field or under semi-field conditions, including the following: 1) Free Air CO_2 Enrichment (FACE) (e.g. Hendrey *et al*., 1993; Ellsworth *et al*., 1995; Miglietta *et al*., 2001; Hättenschwiler *et al*., 2002; Pepin and Körner, 2002), 2) Open-top chamber experiments (e.g. Ashenden *et al*., 1992; Whitehead *et al*., 1995; Norby *et al*., 1997; Körner *et al.*, 2005), 3) Closed-top chamber experiments (e.g. Tingey *et al*., 1996; Beerling and Woodward, 1996), and 4) Branch-bag experiments (e.g. Barton *et al*., 1993). In spite of existing advantages and disadvantages in each technique (Saxe *et al*., 1998; Ainsworth and Long, 2005; Körner, 2006), a large body of field studies conducted in tropical, temperate, and boreal forests showed that elevated atmospheric CO_2 concentration could have significant impacts on the above- and below- ground growth of trees.

Above-ground Growth

Elevated CO_2 persistently increases leaf area index, leaf number, branches, thus positively changing canopy structure under optimal conditions (e.g. Idso and Kimball, 1994; Norby *et al*., 1995; Griffin *et al*., 1995; Epron *et al*., 1995; Ceulemans *et al*., 1996; Tingey *et al*., 1996; Tissue *et al*., 1997; Arp *et al*., 1998). Open-top chamber experiments usually showed an increase in leaf area of seedlings and saplings with CO_2 enrichment (Norby *et al*., 1999). For example, Tissue *et al*. (1997) reported a 217, 80, 58, and 41% increase in leaf area of loblolly pine (*Pinus taeda* L.) growing in elevated CO_2 environment for subsequent four growing seasons when compared to ambient CO_2, respectively. Ceulemans *et al*. (1995) observed 8-18% leaf area increases for *Populus* clones under CO_2 enrichment. A meta-analysis found that trees had a 21% increase in leaf area index compared to less response of herbaceous C_3 grasses (Ainsworth and Long, 2005). Increase in leaf area of *Quercus alba* L. saplings in elevated CO_2 also can be ascribed to increased leaf number, leaf size and, more or less, changed leaf shape (Gregory, 1996). By modifying leaf area, number and size, as well as tree height, elevated CO_2 concentration could influence branching patterns (Gunderson and Wullschleger, 1994) and, consequently, change canopy structure (Saxe *et al*., 1998). Past studies on *Liriodendron tulipifera* L. (Murray and Ceulemans, 1996), *P. taeda* (Tissue *et al*., 1997), and *Alnus glutinosa* L., *Fraxinus angustifolia* Vahl. and *Q. robur* L. (Bucher *et al*., 1997) found that elevated CO_2 significantly increased the number of branches (Saxe *et al*., 1998), which resulted in changes in crown size and structure (Bazzaz *et al*., 1993). A 25% increase in branch number summarized from six species at three FACE sites was reported (Ainsworth and Long, 2005).

Elevated CO_2 concentration generally increases stem biomass (Curtis *et al*., 1998; Saxe *et al*., 1998; Ainsworth and Long, 2005). An increase in seedling dry matter production of *P. radiata* D. and *P. virginiana* Mill. was observed under low nutrient conditions exposed in CO_2 enrichment for 22 and 16 weeks, respectively (Conroy *et al*., 1986; Luxmoore *et al*., 1986). Idso and Kimball (1992) found that *C. aurantium* trees had approximately 160% more trunk and branch volume under CO_2 enrichment than trees under ambient CO_2. Norby *et al*. (1992) showed that *L. tulipifera* trees grown in enriched CO_2 for 2.5 growing seasons had 27% more dry mass than trees grown in ambient CO_2. Saxe *et al*. (1998) reviewed the short-term CO_2-enriched experiments and summarized that, on average, elevated atmospheric CO_2 significantly enhanced tree biomass with increasing exposure time. Under the mean exposure duration of 338 days, conifers increased their biomass by 130%, whereas deciduous trees exposed during 329 days increased by only 49% (Figure 3, Saxe *et al.*, 1998). Based on meta-analysis on the FACE experiments, Ainsworth and Long (2005) reported that elevated CO_2 resulted in taller plants with larger stem diameter, and plant height enhancement in the third growing season was greater than in the first and second. They further pointed out that shrubs and trees showed more height increases than C_3 crops, and trees exhibited the largest response (28%) in dry matter production.

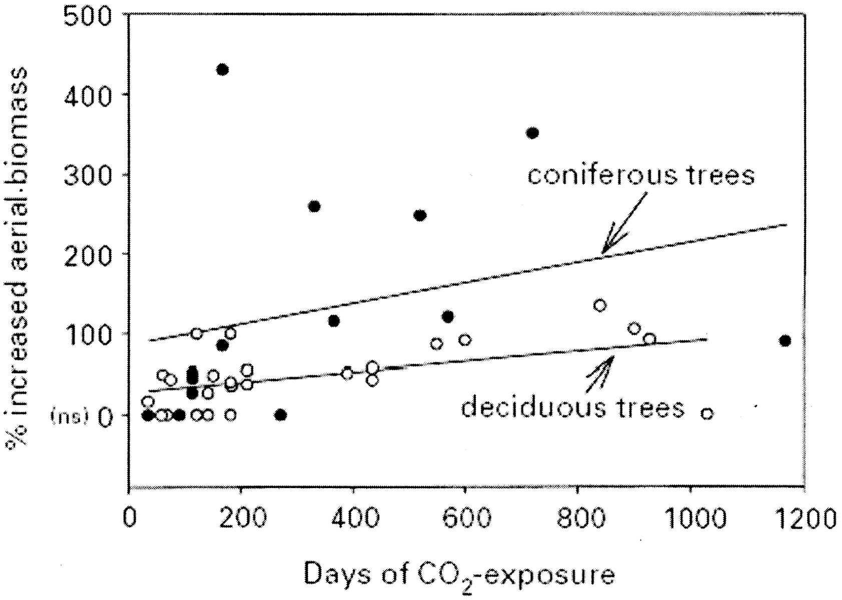

Figure A. 3 Biomass enhancement of trees (● coniferous; ○ deciduous) under elevated CO_2 in experiments of variable exposure duration (after Saxe *et al.*, 1998).

Norby *et al.* (2005) observed a growth increase of 23% in a synthesis analysis of four FACE studies on dominant trees in multi-species forests. Wang (2007) quantitatively evaluated the responses of above-ground biomass of woody species to enriched CO_2

by meta-analysis and observed an increase of 31% and 23% at the population and community levels, respectively. In addition, other reviews (e.g. Ceulemans and Mousseau, 1994; Lloyd and Farquhar, 1996; Curtis and Wang, 1998; Norby *et al*., 1999) showed an increase in stem growth and dry biomass, although the increased rates of growth were different among the studies. Norby *et al*. (1999) ascribed these differences to the growth rate or growth potential of different species, effects of environmental interactions, or differences in experimental protocol.

Elevated CO_2 might also affect phenology such as sprouting, periodicity of leafing, flowering, and fruiting through changes in tree biochemistry and physiology (Jach and Ceulemans, 1999), and through warming effect. Changes in starch or hormonal concentrations may alter dormancy status and growth patterns by shifting timing and duration of the vegetative season (Saxe *et al*., 1998; Norby *et al*., 1999). In a two-year open-top chamber experiment on three-year-old *P. sylvestris* L., elevated CO_2 significantly advanced date of bud burst in both first and second years of the experiment (Jach and Ceulemans, 1999). Repo *et al*. (1996) observed that dehardening in *P. sylvestris* seedlings grown at increased temperatures proceeded significantly faster if concurrently exposed to elevated CO_2 concentration. Saxe *et al*. (1998) reported that, if the leaf development is hastened under elevated CO_2 in the spring, trees could potentially benefit from an earlier onset of carbon assimilation at the start of growing seasons. They further pointed out that this could be an important factor to influence expansion of tree populations into areas currently too cold for their growth. Since most of the work is done with immature plants (seedlings and young trees), little is known about the CO_2 effect on flowering and fruiting (Saxe *et al*., 1998). LaDeau and Clark (2001) have done an experiment study exposing 19-year-old *P. taeda* to 4 years of CO_2 enrichment in an intact forest of North Carolina, and found that trees were twice as likely to be reproductively mature and produced three times as many cones and seeds as trees at ambient CO_2 concentration. This indicates that a higher carbon allocation to reproduction under enriched CO_2 results in trees reaching maturity sooner and at a smaller size (LaDeau and Clark, 2001). Further study demonstrated that seed weight increased by 91% in elevated CO_2 and seeds germinated much earlier, with more than three times germination success compared to the ambient seed source (Hussain *et al*., 2001). A CO_2-enriched study on reproduction of hardwood trees (*Q. myrtifolia* Willd., *Q. chapmanii* Sarg., and *Q. geminate* Small) in a natural scrub-oak forest of Florida suggested that the number of acorns produced under elevated CO_2 was significantly higher than in ambient CO_2 (Stiling *et al*., 2004).

Below-ground Growth

The responses of roots to CO_2 are depended on experimental conditions (Ceulemans and Mousseau, 1994). Low nutrition and water availability tend to increase the ratio of root to shoot in response to CO_2 enhancement (Stulen and den Hertog, 1993; Saxe *et al*., 1998), allowing plants growing on poor and dry sites to explore a greater soil volume to acquire water and nutrients (Day *et al*., 1996; Norby *et al*., 2004; Phillips *et al*., 2006; Norby and Iversen, 2006). Earlier studies on responses of potted tree seedlings growing in low nutrient conditions generally concluded that the ratio of root mass to shoot mass increased in elevated CO_2 condition (Oechel and Strain, 1985). By reviewing plant root and rhizosphere response to elevated CO_2, Rogers *et al*. (1994) found that root dry weight increased in all studies under elevated CO_2. However, a few destructive harvest multi-year studies of trees in elevated CO_2 showed no significant effect on root-to-shoot ratio in *L. tulipifera* (Norby *et al*., 1992), *Q. alba* (Norby *et al*., 1995), *Betula pendula* Roth. (Rey and Jarvis, 1997), *P. taeda* (Tissue *et al*., 1997), *P. ponderosa* Dougl. (Walker *et al*., 1997), or *F. excelsior* L., *Q. petraea* Liebl. and *P. sylvestris* (Crookshanks *et al*., 1998). In a FACE experiment of *P. taeda* forest of North Carolina, Allen *et al*. (2000) found that elevated CO_2 caused significant increases in loblolly pine fine root increment after two growing seasons. Lukac *et al*. (2003) revealed that elevated CO_2 increased belowground allocation of biomass in three *populus* species investigated (*P. alba* L., *P. nigra* L., and *P. x euramericana* Dode (Guinier)), and standing root biomass enhanced by 47-76% as a result of FACE treatment. Norby *et al*. (2004) reported that annual production of fine roots was more than doubled in plots with 550 ppm CO_2 compared with plots in ambient CO_2 in a FACE experiment on a closed-canopy, deciduous sweetgum forest.

Interactions with Other Environmental Factors

Körner (2006) proposed, based on a meta-analysis of FACE experiments, that CO_2 enrichment effects are only transitory in established ecosystems with closed nutrient cycles and fully developed canopies. Nutrient limitations are, according to Körner, strong enough to limit long-term increases in tree growth. Altogether, Körner (2006) claimed that there are only low long-term increases in growth and no increases in leaf area index. On the other hand Nowak *et al*. (2004) insisted that there are increases in growth which persist over time in most FACE experiments. The results confirmed that increases in below ground activity will be higher than above ground growth. Furthermore, the results confirmed that increases in soil fertility and N additions interact positively with CO_2. However, they did not confirm any positive interactions between drought and CO_2 enrichment. Forest ecosystems from areas with high precipitation had higher growth increases than dry ecosystems.

A.5. IMPLICATIONS FOR MATURE TREES IN THE FORESTS

Most field CO_2-enriched experiments showed that elevated CO_2 concentration directly enhanced growth of young trees or seedlings regardless of growth conditions (e.g. Ceulemans and Mousseau, 1994; Curtis and Wang, 1998; Norby *et al*., 1999, 2001; Ainsworth and Long, 2005; Körner, 2006), providing strong evidence to support the direct CO_2 fertilization effect. But those CO_2-enriched experiments were conducted in the field for only hours, weeks, or a few growing seasons. When exposed for longer time periods, photosynthesis and biomass accumulation could be lower than predicted from the initial growth response (Sage, 1994; Gunderson and Wullschleger, 1994; Vivin *et al*., 1995; Miglietta *et al*., 1998; Saurer *et al*., 2003; Ellsworth *et al*., 2004) because trees might adjust to development under elevated CO_2 with time (i.e. acclimation) (Loehle, 1995). Hypothetically, if down-regulation of photosynthesis does not occur, tree growth rate might still not increase proportionally with increase in photosynthesis (Norby *et al*., 1999; Hungate *et al*., 2003; Berninger *et al*., 2004). Because when trees are exposed to CO_2 enrichment, other limiting factors may become more important, thus limiting the ability of trees to increase their growth rates in response to further increases in CO_2 concentration, particularly in natural ecosystems (Norby *et al*., 1999; Körner, 2003; Hungate *et al*., 2003; Berninger *et al*., 2004). Investigating growth of *P. sylvestris* trees using a combination of process-based models and dendroecological approaches, Berninger *et al*. (2004) postulated that the growth rate of trees at the northern tree-line can not parallel the increase in photosynthesis although photosynthesis is enhanced under elevated CO_2 concentration. They ascribed this asynchrony to the reason that potential growth rate is limited directly by temperature. Using carbon isotopes Tardif *et al*. (in press) also showed that both tree-ring formation and carbon uptake in tree-ring cellulose were limited by cool summer temperature.

Seedlings or young trees usually grow much more rapidly than mature trees when exposed to increased CO_2 environment, thus magnifying the effect of rising CO_2 on growth of mature trees (Saxe *et al*., 1998; Norby *et al*., 1999; Körner, 2006; Wang, 2007). In addition, the response of experimental trees exposed to an abrupt increased CO_2 concentration (typical 600-700ppm) in experimental studies may be different from the response of trees under the much smaller natural increase (Wang *et al*., 2006). By comparing the ring-widths of five Mediterranean forest tree species (*Arbutus unedo* L., *F. ornus* L., *Q. cerris* L., *Q. ilex* L., and *Q. pubescens* Willd.) growing close to a natural source of CO_2 and a nearby control site in Tuscany, Italy, Tognetti *et al*. (2000) found that CO_2 enrichment did not lead to a significant enhancement of radial increment. They attributed the result to the counteracted effect from other resource limitations, such as low nutrient availability with the positive effect of elevated CO_2 under drought stress, or to the acclimation of trees to high CO_2.

Taken together, there is an ample body of evidence from short- to medium-term CO_2 enrichment studies to suggest that trees may be able to increase their photosynthesis and growth under elevated CO_2. Apart from a few long-term FACE studies (e.g. Hättenschwiler *et al*., 2002; Rasse *et al*., 2005; Handa *et al*., 2005; Asshoff *et al*., 2006), most studies are associated with the problems of a short duration of the experiments. Also, all chamber experiments alter the environment of trees. Another potential problem is the constancy of CO_2 values in chambers of FACE experiments that might potentially affect photosynthetic production and growth. Despite all these weaknesses enrichment experiments provide valuable information to allow prediction of which ecosystems might be most responsive to CO_2. We propose that warm, moderately drought-stressed ecosystems with an ample N supply might be the most CO_2 responsive ecosystems.

A.6. EMPIRICAL DENDROCHRONOLOGICAL STUDIES TESTING CO_2 FERTILIZATION EFFECT IN TREE RINGS

Trees provide long-term records of growth and, hence, are a natural archive for documenting environmental information. In dendrochronology, growth series for an individual tree can be translated into an aggregate of environmental factors from both human and natural origins that affected growth over time (Fritts, 1976; Schweingruber, 1996). Cook (1987) suggested that radial growth (ring width) in any one year (t) is a function of an aggregate of all factors. In order to understand environment impacting factors on trees, age/size-related growth detrending is required. However an obvious problem is that growth decline with age/size is difficult to model and the detrending processes commonly used in dendroclimatology might eliminate somehow high and/or low frequency variations in tree-ring time series. Traditional detrending assumes that ring growth can be decomposed into different effects as follows (Cook, 1987, 1990):

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_{CO2t} + e_t$$

in which:

R_t - the observed ring width in the year of t,

A_t - the age/size related growth trend due to normal physiological aging processes,

C_t - the climate effects that affected tree growth in the year of t,

$D1_t$ - the occurrence of disturbance factors within the forest stand (e.g. a blow down of trees),

$D2_t$ - the occurrence of disturbance factors from outside the forest stand (e.g. an insect outbreak that defoliates the trees),

E_{CO2t} - the CO_2 fertilization effect,

e_t - random processes not accounted by those above processes,

δ - either a ‘0’ for absence or ‘1’ for presence of the disturbance signal.

An additional problem is that this separation of different signals must be done in absence of detailed information of stand history, since our ability to infer past disturbances from scars, stumps or snags are limited, especially for disturbances occurred a long time ago or less obviously.

Empirical dendrochronological studies test CO_2 fertilization effects (E_{CO2t}) in tree rings through the removal of other factors in tree-ring growth. The trend of CO_2 fertilization effect could thus be detectable in residuals of the growth-climate models (e.g. Jacoby and D’Arrigo, 1989; Graumlich, 1991; D’Arrigo and Jacoby, 1993; Knapp *et al.*, 2001) (Table 1). By selecting of good sampling sites in which the influences of indigenous ($D1_t$) and exogenous ($D2_t$) factors were minimized (e.g. Nicolussi *et al*., 1995; Soulé and Knapp, 2006), CO_2 fertilization effect was assessed either by analyzing trends in basal area increment (BAI) or by comparing growth trends among age classes or between old trees and young trees or by computing the biotic growth factor (ß factor, which is a parameter used for comparing responses of various species to CO_2 enrichment (Bacastow and Keeling, 1973)) (Table 1). Because of discrepancies in site conditions (mesic, semi-arid, arid, subalpine, alpine, treeline etc.), tree species, data treatments among different studies (Table 1), the conclusions related to detecting CO_2 fertilization effect are various, although LaMarche *et al*. (1984) first claimed a possible CO_2 fertilization effect in tree rings. After an extensive survey of the pertinent literature, three viewpoints on detecting CO_2 fertilization effect in tree rings were found:

Finding evidence of CO_2 fertilization effect in tree rings

LaMarche *et al*. (1984) and Graybill (1987) first observed increased radial growth of *P. aristata* Engelm., *P. longaeva* Bailey, and *P. flexilis* James in semiarid region of western USA and claimed that it was an evidence of a possible CO_2 fertilization effect in subalpine tree rings. After modeling of the growth-climate relationships in regression analysis and comparison with other dendroclimatic reconstructions for western Northern America, Graybill and Idso (1993) also detected CO_2 fertilization effect in tree rings of high-elevation bristlecone pine (*P. aristata* and *P. longaeva*) characterized by a strip bark morphology (partial cambial dieback). Nicolussi *et al*. (1995) associated the 25% increase in ring width of subalpine *P. cembra* L. from the central Alps, which occurred since the middle of the 19th century, with an increase in atmospheric CO_2. Based on the analyses of growth-climate associations of *Juniperus occidentalis* Hook. in arid Oregon using multiple regression models, Knapp *et al*. (2001) provided evidence for atmospheric CO_2 fertilization effect on the radial growth rates, especially during drought stress. A study of *P. ponderosa* carried out in the same region also showed evidence of CO_2 fertilization effect, i.e. significant increases in radial growth rates occurred post-1950, particularly during drought years, with the greatest increases generally found at the most-water-limited sites (Soulé and Knapp, 2006). Wang *et al*. (2006) compared the growth of young *Picea glauca* (Moench) Voss trees that are currently exposed to high atmospheric CO_2 to the early growth period of older trees that were exposed to low atmospheric CO_2 in a dry environment of southwestern Manitoba, Canada, and the results provided circumstantial evidence that atmospheric CO_2 fertilization increased radial growth in this dry environment. However, the authors could not exclude that atmospheric deposition of N contributed to the observed increase in growth. Another study from the Ozark Mountains in Missouri revealed that both hardwood (*Q. velutina* Lam. and *Q. coccinea* Muenchh.) and coniferous (*P. echinata* Mill.) species increased in stem growth coincidently with increases in atmospheric CO_2 over the past 150 years (Voelker *et al*., 2006). Other studies (see Spiecker, 1996) also found some indications of enhanced tree growth and attributed it, in some cases, to atmospheric CO_2 increase.

Table A. 1 Empirical dendrochronological studies detecting CO_2 fertilization effect in tree rings (I: finding evidence of CO_2 fertilization effect in tree rings; II: growth enhancement caused by favourable climate change; III: combined effects of several factors such as favourable climate change, CO_2 fertilization effect, anthropogenic atmospheric deposition (e.g. N); NA-northern America). Dentrending methods include some conservative methods such as negative exponential, regression line or straight line.

Results	**Study region**	**Species**	**Detrending (Yes/No)**	**Analysis Methods**	**Authors**
I	semiarid, western USA	*P. aristata* *P. longaeva*	Yes	comparisons of growth	LaMarche *et al*., 1984
	semiarid, western USA	*P. flexilis*	Yes	comparisons of growth	Graybill, 1987
	semiarid, high elevations western NA	*P. aristata* *P. longaeva*	Yes	comparisons of growth	Graybill and Idso, 1993
	subalpine, central Alps	*P. cembra*	No	age classes	Nicolussi *et al*., 1995
	semi-arid, CO_2 springs Mediterranean, Italy	*Q. ilex*	Yes	growth comparisons with CO_2 data	Hättenschwiler *et al*., 1997
	arid Oregon	*J. occidentalis*	Yes	detecting trends in residuals	Knapp *et al*., 2001
	arid Oregon	*P. ponderosa*	Yes	comparisons with drought years	Soulé and Knapp, 2006
	southeast Missouri	*Q. velutina* *Q. coccinea* *P. echinata*	Yes	comparisons of growth trends	Voelker *et al*., 2006
	dry environment, southwestern Manitoba	*P. glauca*	Yes	comparisons between young trees and old trees	Wang *et al*., 2006
II	tree line, NA		Yes	detecting trends in residuals	Jacoby and D'Arrigo, 1989
	Northeastern France	*A. alba*	Yes	analysis of residuals	Becker, 1989
	southwestern USA	subalpine conifers	Yes	response surface	Graumlich, 1991
	tree line, northern NA	*P. glauca*	Yes	detecting trends in residuals	D'Arrigo and Jacoby, 1993
	semiarid mountain, western NA	*P. balfouriana* *P. longaeva* *P. albicaulis* *P. occidentalis* *P. flexilis*	Yes	comparisons	Bunn *et al*., 2005
III	Finland	*P. sylvestris*	Yes	a four component model	Hari *et al*., 1984
	Finland	*P. sylvestris*	Yes	comparisons of time series models	Arovaara *et al*., 1984
	Finland	*P. sylvestris*	Yes	a four component model	Hari and Arovaara,
	Northern hemisphere	*Pinus, Picea, Abies, Cedrus,*	Yes	ß factor	Kienast and Luxmoore, 1988
	northeastern France	*Q. petraea* *Q. robur*	No	basal area increment	Becker *et al*., 1994
	European	European species	No	basal area increment	Briffa *et al*., 1998b
	tree-line French Alps	*P. abies* *L. decidua* *P. cembra* *P. uncinata*	Yes	average growth trend curve as a function of tree age; plotting ring-width as a function of the year of ring ormation for cambial ages	Rolland *et al*., 1998

CO_2 springs, i.e., places where CO_2 is emitted naturally from the soil, are places that permit us to study the effects of CO_2 enrichment on tree growth without the problems associated with climatic trends that are superimposed on CO_2 concentration trends. Hättenschwiler *et al*. (1997) and Tognetti *et al*. (2000) used these natural CO_2 springs (including the Bossoleto CO_2 spring and the Laiatico CO_2 spring, Italy) for dendrochronological studies. Hättenschwiler *et al*. (1997) found that radial stem width of *Q. ilex* was, indeed, initially enhanced but differences in growth rates flattened out when trees got older. Enhancement of radial growth was especially pronounced in years with a dry spring, indicating that CO_2 interacts with water stress. Tognetti *et al*. (2000) were unable to extend Hättenschwilers' results to four other species (*A. unedo*, *F. ornus*, *Q. pubescens*, and *Q. cerris*). They attributed the differences to the discrepancies in control sites, stand history, sampling methods, and sample replications (Tognetti *et al*., 2000). Saurer *et al*. 2003 used isotopic methods to understand the changes that occurred in these trees. Based on ^{14}C measurements, they found that CO_2 concentration (or the contribution of CO_2 spring to ambient CO_2 concentration) seemed to decrease with tree age. Changes in the ^{13}C discrimination and the oxygen isotopes indicated a progressive downscaling of photosynthesis with plant age, confirming Hättenschwilers' initial conclusions. All these studies (except Tognetti *et al*., 2000) support the hypothesis that elevated atmospheric CO_2 concentration could enhance tree growth.

Growth enhancement caused by favourable climate change

Jacoby and D'Arrigo (1997) pointed out that the analyses of LaMarche *et al*. (1984) and Graybill (1987) did not exclude possible contribution of favourable climatic change to growth increase. If non-climatic factors such as CO_2 significantly influence tree growth, the residuals of growth-climate models should show some trends (Graumlich, 1991; Jacoby and D'Arrigo, 1997). Jacoby and D'Arrigo (1989) did not detect significant trends of the residuals since 1973 for temperature-sensitive chronologies averaged for tree-line sites across North America. Through dendroecological investigation of *Abies alba* Miller. in the Vosges mountains of northeastern France, Becker (1989) suggested that indirect effects of CO_2 (increases in temperature and precipitation) may play a major role in changing radial growth. By using response surface models to account for the effects of interactions between climate variables on tree growth in southwestern United States, Graumlich (1991) did not find any evidence for CO_2 fertilization effect as a cause for enhanced growth among subalpine conifers in Sierra Nevada. D'Arrigo and Jacoby (1993) tested residual trends of growth-climate models of *P. glauca* at the northern boreal tree-line of North America, and reported that an equal or faster growth rate occurred since the mid-1800s than the prior period of tree-ring record, but CO_2 fertilization was not detectable as a major factor influencing growth on these sites. Bunn *et al*. (2005) investigated some 1000-year chronologies of five high-elevation conifers (*P. balfouriana* Balf.*, P. longaeva, J. occidentalis, P. flexilis,* and *P. albicaulis* Engelm.) in western North America, and found that their growth rates during the last half of the twentieth century differed from that any time during the past 1000 years, indicating a distinct biological signature of global climate change (mainly unprecedented warming). These studies attributed growth enhancements to favourable climate condition rather than to the CO_2 fertilization effect.

Combined effects of several factors such as favourable climate change, CO_2 fertilization, and anthropogenic atmospheric deposition

It is not easy to clearly separate the direct CO_2 fertilization effect on vegetation from its effect as a greenhouse gas, which is its more or less important role in modifying the climate (Wigley and Jones, 1981). Several studies on *P. sylvestris* at the northern tree-line in Finland showed that several environmental factors were changing simultaneously and results were inconclusive despite suggesting a possible CO_2 or nutrient deposition (Hari *et al*., 1984; Arovaara *et al*., 1984; Hari and Arovaara, 1988). Kienast and Luxmoore (1988) found that 8 out of 34 chronologies showed increases in ring width in the post-1950, and attributed the increases to favourable climatic conditions and to factors other than CO_2 such as the better availability of nutrients due to atmospheric deposition. Briffa (1991) speculated that N fertilization could stimulate tree growth in some areas of Europe exposed to industrial pollution. In a dendroecological study of northeastern France, Becker *et al*. (1994) observed a 64% increase in radial growth of *Q. petraea* during the period 1888-1987 and 40% in *Q. robur*. The authors interpreted these growth increases as the effects of climate, CO_2 enrichment, and other factors such as anthropogenic atmospheric depositions, especially of N. Briffa *et al*. (1998b) reported that the BAI of a group of European tree species has steadily increased over recent centuries, and inferred that greater twentieth-century tree growth might be driven by a combination of factors such as warmer temperatures, rising CO_2 levels, and distant transport of nitrates. Rolland *et al*. (1998) observed increased radial growth of four conifer species (*P. abies* L., *Larix decidua* Mill., *P. cembra,* and *P. uncinata* Mill.) during the last two centuries in the French Alps near the upper treeline and ascribed these growth increases to climatic warming (especially minimum temperature) and some other factors such as atmospheric CO_2 enrichment, N deposition and human impact. Thus, these studies indicate that tree growth enhancements might be caused by the combined effects of several factors such as favourable climate change, CO_2 fertilization effect, and anthropogenic atmospheric deposition of nutrients, particularly of N.

A.7. EVIDENCE FOR CO_2 FERTILIZATION EFFECT DISPLAYING IN TREE RINGS IN NATURAL FORESTS

In natural forests, anthropogenic-caused increases in atmospheric CO_2 concentration might enhance forest growth in the following two ways: 1) through favorable climatic change associated with increasing greenhouse gas concentration, and/or 2) via direct

CO_2 or other nutrient fertilization such as nitrate (D'Arrigo and Jacoby 1993). As for the observed radial growth enhancements in natural forests attributing to three viewpoints that were summarized in the above section, correspondingly we have three different interpretations as follows:

Indeed occurrence of CO_2 fertilization effect in drought-stressed environments

Of three viewpoints, it is very likely that direct CO_2 fertilization effect does occur in trees growing in drought-stressed environments, as shown by most studies in the first viewpoint (LaMarche *et al*., 1984; Graybill, 1987; Knapp *et al*., 2001; Hättenschwiler *et al*. 1997; Wang *et al*., 2006; Soulé and Knapp, 2006). Drought-stressed trees might benefit from increased water use efficiency under elevated atmospheric CO_2 concentration and thus alleviate drought stress, which in turn delays the onset of reduced photosynthesis caused by stomata closure (Owensby *et al*., 1999), allowing trees to have an extended growing season (Knapp *et al*., 2001). Many field experiments have strongly suggested an increase in water use efficiency of trees under CO_2 enrichment (e.g. Ceulemans and Mousseau, 1994; Lloyd and Farquhar, 1996; Curtis and Wang, 1998; Norby *et al*., 1999; Schlesinger and Lichter, 2001). Since stable carbon ($^{13}C/^{12}C$) and oxygen ($^{18}O/^{16}O$) isotopes analyses has been an important tool to study water use efficiency and climate influences (Bert *et al*., 1997; Berninger *et al*. 2000; Helle and Schleser, 2004; Tardif *et al*., *in press*), several carbon isotope studies in natural forests have already discovered increased water use efficiency for the study period of past 100-200 years (Duquesnay *et al*., 1998; Feng, 1998, 1999; Liu *et al*., 2007). Increased water use efficiency was also revealed in *P. aristata*, showing full-bark and strip-bark morphology in arid White Mountains of California, but no significant differences between two growth forms were observed (Tang *et al*., 1999) (Figure 4). Graybill and Idso (1993) showed an enhanced growth trend of both strip-bark and full-bark trees over the past 150 years, but the growth rate increased more for strip-bark trees than for full-bark trees (Figure 5). It was supposed that the strip-bark trees are more sensitive to climate changes than trees with more complete cambial tissue (D'Arrigo and Jacoby, 1993), and more likely than full-bark trees to allocate any additional carbon to cambial production of stem tissue (Graybill and Idso, 1993). The discrepancy between the same rate of increased water use efficiency and different rates of cambial growth of two different tree forms was explained in the following ways: 1) carbon allocation to different parts of a tree differs in spite of increases in biomass in both tree forms, and 2) biomass may increase without any corresponding change in water use efficiency of plants (Tang *et al.*, 1999). In contrast, trees with entire bark collected from similar sites as strip-bark trees did not exhibit anomalous growth trends to support CO_2-fertilization hypothesis (Graumlich, 1991; Jacoby and D'Arrigo, 1997; Bunn *et al.*, 2003). All in all, there is increasing evidence to support the hypothesis of direct CO_2 fertilization effect in arid or sub-arid regions as based on studies of precipitation-limited *J. occidentalis* (Knapp *et al.*, 2001) and *P. ponderosa* (Soulé and Knapp, 2006) in arid central Oregon, as well as *P. glauca* growing on dry sites in southwestern Manitoba, Canada (Wang *et al.*, 2006).

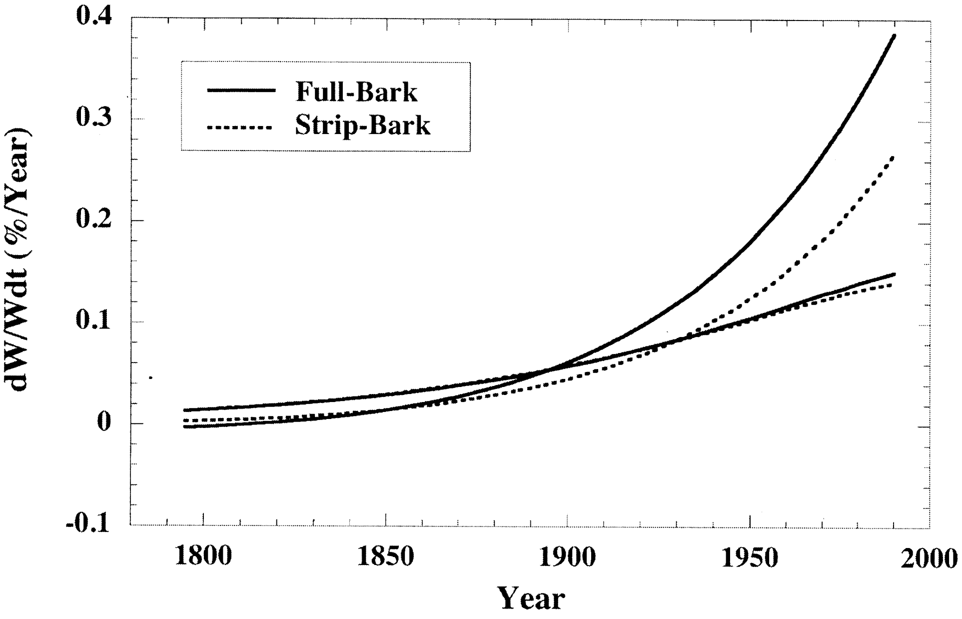

Figure A. 4 The relative rate of change in water-use efficiency (% per year) for the full-bark (solid lines) and strip-bark (dashed lines) bristlecone pine trees on Sheep Mountain of the White Mountains, California (after Tang *et al.*, 1999).

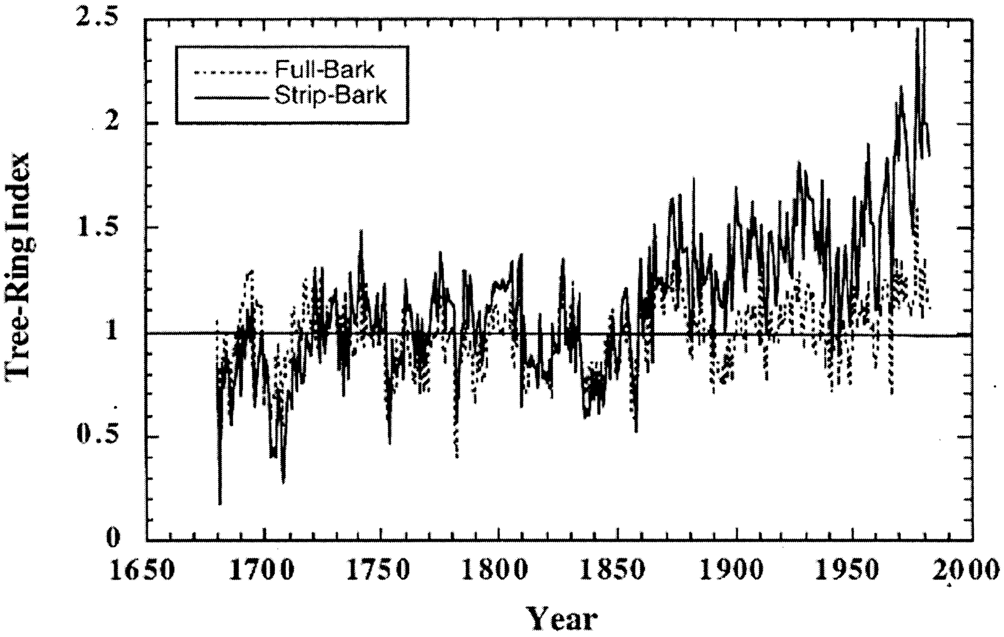

Figure A. 5 Bristlecone pine tree-ring index chronologies of full-bark (dashed line) and strip-bark (solid line) growth forms from Sheep Mountain, California (after Graybill and Idso, 1993).

Underestimation for CO_2 fertilization effect

The second viewpoint attributes growth enhancements to climate warming rather than CO_2 fertilization. Long-term increases in tree growth during the last century were detected in many tree-ring studies (e.g. Payette *et al.*, 1985; Jacoby and D'Arrigo, 1989; Luckman, 1989; Graumlich, 1991; Archambault and Bergeron, 1992; D'Arrigo and Jacoby, 1992; Cook *et al.*, 1991, 1992; Rolland, 1996; Zhang *et al.*, 2003; Huang and Zhang, 2007). This trend was supposed to be associated mostly with greenhouse-induced temperature or precipitation increases during that period. IPCC (2001) reported that within the 20th century a 0.6°C±0.2°C rise of mean global surface temperature and an increase of precipitation by 0.5 to 1% per decade over most mid- and high latitudes of the Northern Hemisphere were observed with the increase of atmospheric CO_2 from 295 ppm to 350 ppm between 1900 and 1990 (Keeling and Wort, 1994). Lloyd and Farquhar (1996) commented that both ring-width and temperature data are auto-correlated and need to be prewhitened (a procedure that removes the potentially differing level of serial correlation between climate data and climate-sensitive tree ring series, such as temporal autocorrelation, Cook *et al*., 1999) to remove underlying trends, otherwise one could find correlations between unrelated parameters. However, most previous studies (D'Arrigo and Jacoby, 1993; Jacoby and D'Arrigo, 1989; Graumlich, 1991) did not prewhiten climate data and the results may thus be questionable (Lloyd and Farquhar, 1996). D'Arrigo and Jacoby (1993) ascribed their failure to detect CO_2 fertilization effect to the following possible reasons: 1) There exists a threshold of CO_2 level that trees may need to be reached, but current CO_2 level may not yet be reached for trees at the temperature-limiting sites such as northern tree-line and high elevations, and 2) Close to the boreal tree-line, cold temperatures, short growing seasons, and N shortage could preclude a direct CO_2 growth response (Jacoby and D'Arrigo, 1997). Their first hypothetical explanation lacks a theoretical basis and is not supported by any experimental evidence. Berninger *et al*. (2004) and Tardif *et al*. (in press) have partially supported their second explanation for the tree-line. In contrast, several high-elevation or tree-line studies provided clear evidence for greater efficiency of CO_2 uptake at any given CO_2 partial pressure in plants from high altitudes (Körner and Diemer, 1987; Körner *et al*., 1991; Handa *et al*., 2005), suggesting potentially greater sensitivity to CO_2 enrichment compared to plants from lower altitudes (Hättenschwiler *et al*., 2002). Without a critical and convincing comparisons with Mann *et al*. (1999), in which they found that the 20th century warming was abrupt and truly exceptional, Bunn *et al*. (2005) conclusion that recent growth enhancement might be caused by global climate change (mainly unprecedented warming) was doubted (McIntyre, 2005). Since dendroclimatological studies focus on old trees past half of their maximum life expectancy, the small increase in biomass increment due to CO_2 fertilization effect might be diminished. Therefore, Voelker *et al*. (2006) proposed to consider the purported CO_2 effect relative to age by species. Recently, researchers such as Cherubini *et al*. (1998) and D'Arrigo *et al*. (2007) recognized the potential problem in age-related detrending methods, which could also remove some CO_2-related long-term trends in tree-ring growth. In addition, translation of a photosynthetic CO_2 response into a growth response is not 1:1 ratio (Körner, 2006). Furthermore, carbon partitioning and growth within a plant is species specific (Körner *et al*., 2005). In any case, with increasing CO_2-fertilization evidence from many CO_2-enriched experiments and increasing tree ring studies, it is possible that the studies ascribing growth increase solely to climate change underestimate direct atmospheric CO_2 fertilization effect.

Possible occurrence for synergistic effects of several factors

The third viewpoint insists that the long-term increase of tree growth could be attributed to the combined effects of several factors such as favourable climate change, CO_2 fertilization effect, and anthropogenic atmospheric deposition of nutrients (e.g. N). Tree growth is a complex process and influenced by multiple factors (Fritts, 1976; Schweingruber, 1996). Recent studies showed that associations between tree growth and climate are changing. Tree growth at high latitudes maybe less sensitive to variations in temperature today than in the past (Briffa *et al*., 1998a, 1998b; Barber *et al*., 2000; Jacoby *et al*., 2000; Wilson and Luckman, 2003; Wilmking *et al*., 2004, 2005; Büntgen *et al*., 2006; D'Arrigo *et al*., 2007). Climate variability alone seems to be insufficient to explain trends observed in trees like *Q. petraea* (Becker *et al*., 1994). With N deposition from urban-industrial pollution during the last several decades (Kauppi *et al*., 1992), tree growth might also benefit from N fertilization, especially in nutrient-limited soil. Previous studies did not find any N fertilization effect in natural forests (Miller *et al*., 1991), but a CO_2 and N interactive experiment on *Q. robur* seedlings showed a significantly higher growth (139%) in the elevated CO_2/high-N environment compared to the elevated CO_2/low-N treatment (Maillard *et al*., 2001). On the other hand, studies (Tognetti *et al*., 2000; Saurer *et al*. 2003) in semi-arid, N-limited Mediterranean ecosystem (Cherubini *et al*., 2003) failed to discover long-term significant growth enhancements in several species close to natural CO_2 springs, providing an inverse evidence for N fertilization effect in natural forests. In other words, if soil N is sufficient in this ecosystem, these species might have shown significant growth enhancements as a result of CO_2 and N fertilization effects. Therefore, while the residuals of growth-climate models show obvious trends (Wang *et al*., 2006), it is very likely that tree growth is influenced by complex and synergistic effects due to several factors, including CO_2 fertilization and anthropogenic atmospheric deposition (e.g. N). To clearly separate CO_2 fertilization and N fertilization effects on tree growth in tree-ring studies, it will be necessary to establish CO_2 /N-fertilization experiments in natural forests, while precluding N fertilization.

A.8. CONCLUSIONS

CO_2 fertilization effect hypothesis, i.e. rising atmospheric CO_2 has a positive effect on tree growth due to increasing availability of carbon, was extensively tested by CO_2 enrichment experiments and empirical dendrochronological studies. In this paper, we compared and synthesized the literature from both CO_2 enrichment experiments on seedlings or young trees and empirical tree-ring studies detecting CO_2 fertilization effect to assess whether CO_2 fertilization effect occurs in tree rings in natural forests. Considerable of CO_2 enriched experiments demonstrated significantly positive physiological and growth responses of trees to CO_2, providing strong evidence to support the direct CO_2 fertilization effect (increased photosynthesis, water use efficiency, above- and below- ground growth) and thus allowing predication of which ecosystems might be most responsive to CO_2. We propose that warm, moderately drought-stressed ecosystems with an ample nitrogen supply might be the most CO_2 responsive ecosystems. Empirical tree-ring studies took the following three viewpoints on detecting CO_2 fertilization effect in tree rings: 1) finding evidence of CO_2 fertilization effect in tree rings, 2) attributing growth enhancement to favorable climate change rather than CO_2 fertilization, and 3) considering that tree growth enhancement might be caused by synergistic effects of several factors such as favorable climate change, CO_2 fertilization, and anthropogenic atmospheric deposition, especially of nitrogen. Correspondingly, we interpreted these three viewpoints as 1) indeed occurrence of CO_2 fertilization effect in drought stress environments, 2) underestimation for CO_2 fertilization effect, and 3) possible occurrence for synergistic effects of several factors, respectively. Our review supports the atmospheric CO_2 fertilization effect hypothesis, at least in trees growing in semi-arid or arid conditions because the drought-stressed trees could benefit from increased water use efficiency to enhance growth. However, a CO_2 spring study in semi-arid (mean total precipitation during dry summer (May-August) from 1918-1982 below 200 mm in the study region), N-limited Mediterranean ecosystem did not observe significant growth enhancements in several species, even in extremely dry years (Tognetti *et al*. 2000). In addition, Nowak *et al*. (2004) did not find strong evidence to support greater response of productivity to elevated CO_2 concentration in drier ecosystems or in dry years within an ecosystem. Rather, they suggested that it would occur at some intermediate precipitation (annual precipitation between 300 mm and 500 mm from the empirical results). This indicates that there might exist extreme drought thresholds that could limit CO_2 fertilization effect in semi-arid and arid environments. Hence, questions on how to define it in dry environments will need to be considered.

In contrast, studies in cold, arid Chaidamu basin with relatively fertile loess (annual mean total precipitation from 1958-2000 around 200 mm, with 80% dropped between May and August in the study area) of the Qinghai-Xizang Plateau (also referred to the Tibetan Plateau (Huang *et al*., 2007)) showed significant growth enhancements (Zhang *et al*., 2003; Shao *et al*., 2005; Liang *et al*., 2006; Huang and Zhang, 2007; Zhang and Qiu, 2007) as well as increased water use efficiency (24.7% and 33.6% for each species, respectively) (Liu *et al*., 2007) in Qilian juniper (*Sabina przewalskii* Kom.) and Qinghai spruce (*P. crassifolia* Kom.) since the 1850s. These contrasting results suggest that the thresholds of extreme drought that could limit CO_2 fertilization effect might be related to the interactions among temperature, N, and drought, as well as to site- and species-specific. To clarify this, however, will need more CO_2 fertilization effect studies focusing on sites conditions (fertility, drought, and temperature) and growth increases of different species in semi-arid and arid environments in the future. Further extensive research on CO_2 fertilization effect in semi-arid and arid environments will certainly contribute to better understanding of global carbon sinks and modification of the current global carbon cycle models, as well as adjustment of long-term reforestation policy in semi-arid and arid regions, which could potentially mitigate the continuing increases in atmospheric CO_2 concentration.

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APPENDIX II

SUPPORTING MATERIALS FOR THE CHAPTERS II & IV

Appendix II. 2.1 Characteristics of sampling sites and sampled stands (trembling aspen TA, paper birch PB, black spruce BS, and jack pine JP) along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest. I: Sugar maple-yellow birch bioclimatic zone; II: Yellow birch-balsam fir, and paper birch-balsam fir climax zone; III: Black spruce-lichen, and black spruce-moss climax zone. The mean distance between sites pertaining to the same species is 1.11° latitude for TA, 1.11° latitude for PB, 0.85° latitude for BS, and 0.96° latitude for JP, respectively.

Site ID	Latitude (N)	Longitude (W)	Elevations (m, a.s.l.)	Species	Stand types	Site types	Slopes(°)/ Aspect	Sample types	Note (°N)
Petawawa	45°58.916'	77°27.602'	183	BS	Even-aged/ Mixed	Mesic	0	Cores	46
	45°59.687'	77°31.707'	184	PB	Uneven-aged/ Mixed	Mesic	7/N	Cores	I
	45°59.687'	77°31.707'	184	TA	Uneven-aged/ Mixed	Mesic	7/N	Cores	
	46°00.419'	77°25.092'	160	JP	Even-aged/ Pure	Submesic	0	Cores	
Laniel	47°02.517'	79°20.746'	258	JP	Uneven-aged/ Mixed	Mesic	0	Cores	47
	47°03.417'	79°20.432'	273	BS	Uneven-aged/ Mixed	Mesic	0	Cores	II
	47°09.539'	79°25.341'	210	PB	Uneven-aged/ Mixed	Mesic	9/NE	Cores	
	47°09.539'	79°25.341'	210	TA	Uneven-aged/ Mixed	Mesic	9/NE	Cores	
Opasatica	48°06.000'	79°18.000'	260	BS	Uneven-aged/ Mixed	Mesic	0	Cores	48
Kanasuta	48°09.203'	79°30.065'	330	JP	Even-aged/ Mixed	Mesic	0	Cores	II
Lac Dasserat	48°14.189'	79°21.822'	285	PB	Uneven-aged/ Mixed	Mesic	0	Cores	
	48°14.189'	79°21.822'	285	TA	Uneven-aged/ Mixed	Mesic	0	Cores	

Plamonton	49°08.905'	78°32.038'	440	BS	Uneven-aged/ Mixed	Submesic	2/N	Cores	49
	49°08.905'	78°32.038'	440	JP	Uneven-aged/ Mixed	Submesic	7/N	Cores	II
	49°08.905'	78°32.038'	440	PB	Uneven-aged/ Mixed	Mesic	2/NE	Discs	
	49°09.592'	78°32.885'	341	TA	Uneven-aged/ Mixed	Mesic	0	Cores	
Collines	49°56.754'	78°42.881'	290	TA	Uneven-aged/ Mixed	Mesic	0	Cores	50
Muskuchii	50°03.098'	78°45.512'	260	BS	Uneven-aged/ Pure	Mesic	4/S	Discs	III
	50°08.674'	78°48.804'	245	JP	Even-aged/ Pure	Submesic	10/SE	Discs	
	50°09.375'	78°41.651'	292	PB	Uneven-aged/ Mixed	Mesic	3/SE	Discs	
Broadback	51°02.312'	77°34.481'	240	BS	Uneven-aged/ Mixed	Mesic	0	Discs	51
River	51°11.775'	77°27.184'	215	JP	Uneven-aged/ Mixed	Submesic	4/S	Discs	III
Rupert River	51°20.957'	77°25.343'	172	TA	Uneven-aged/ Mixed	Mesic	5/SE	Discs	
Nemiscau	51°37.000'	76°41.908'	250	PB	Uneven-aged/ Mixed	Mesic	8/N	Cores	
Eastmain	51°52.209'	77°26.152'	177	BS	Uneven-aged/ Mixed	Mesic	0	Discs	52
	51°56.060'	77°22.123'	200	JP	Uneven-aged/ Mixed	Submesic	0	Discs	III
Wemindji	52°39.180'	77°24.019'	237	PB	Uneven-aged/ Mixed	Mesic	0	Discs	53
	52°39.180'	77°24.019'	237	TA	Uneven-aged/ Mixed	Mesic	0	Discs	III
	52°53.953'	77°15.704'	226	JP	Uneven-aged/ Mixed	Mesic	0	Discs	
	52°53.953'	77°15.704'	226	BS	Uneven-aged/ Mixed	Mesic	0	Discs	
Chisasibi	53°39.493'	78°21.713'	82	BS	Uneven-aged/ Mixed	Mesic	5/E	Discs	54
	53°42.028'	78°04.350'	125	JP	Uneven-aged/ Mixed	Mesic	3/N	Discs	III
Radisson	53°48.402'	77°35.785'	36	TA	Uneven-aged/ Mixed	Mesic	25/S	Discs	
	53°48.461'	77°37.054'	32	PB	Uneven-aged/ Mixed	Mesic	27/N	Discs	

Appendix II. 2.2 Bootstrapped correlation between the PCs (PCI to PCIV) and the climate data (monthly mean temperature, total precipitation, and drought code) from 46°N to 54°N. Only significant climate variables in the previous year (e.g., Jun) and current year (e.g., *jan*) at different latitudes were listed in the table. Significant positive and negative correlation (P ≤ 0.05) was indicated by ‘p’ and ‘n’, respectively. The abbreviations 51PB, 53BF, 53CON, 54BF, and 54CON represent the climate data for the paper birch site at 51°N, both deciduous sites at 53°N, both coniferous sites at 53°N, both deciduous sites at 54°N, and both coniferous sites at 54°N, respectively.

PCI

Latitude	Temperature										Precipitation								Drought code			
(°N)	Jun	Jul	Aug	Dec	*Jan*	*mar*	*apr*	*may*	*jul*	*aug*	Jun	Aug	Oct	Nov	Dec	*feb*	*mar*	*jul*	Jul	Aug	*jul*	*Aug*
46		n	n	p		p	p		p							n		n			p	p
47	n	n	n			p	p		p						p							
48	n	n	n	p	p	p	p		p		p		n						n			
49	n	n	n	p	p	p	p		p	p	p		n									
50		n	n		p	p	p		p	p	p											
51		n	n		p	p	p				p								n			
51PB		n	n		p	p	p				p								n			
52		n	n		p	p	p				p								n	n		
53BF					p	p	p	p			p	p							n		n	n
53CON					p	p	p	p			p	p					p		n	n	n	n
54BF					p	p	p	p			p	p					p		n	n		
54CON					p	p	p	p			p	p		n	p		p		n	n		

PCII

Latitude	Temperature					Precipitation						Drought code				
(°N)	Jul	Sep	Nov	Dec	*feb*	May	Oct	Nov	Dec	*mar*	*apr*	Jul	Oct	*may*	*jul*	*aug*
46			p							p				p		
47			p			p			n	p	n			p	p	p
48		n	p		p		n	n		p				p		p
49		n	p				n			p		n				
50		n	p				n			p						
51			p				n			p						
51PB			p	n			n			p						
52			p	n			n			p		p				

53BF		n	n	p	p	
53CON		n	n	p	p	
54BF	p	n				
54CON	p	n				p

PCIII

Latitude	Temperature					Precipitation						Drought code					
(°N)	May	*mar*	*jun*	*jul*	*aug*	Jun	Jul	Aug	*jan*	*may*	*jun*	Jul	Aug	*may*	*jun*	*jul*	*Aug*
46			n	n	n				n		p	n				n	n
47			n	n		p	p			n		n	n	p	p		
48	n		n	n		p	p	n		n				p			
49			n	n		p		n		n					p		
50	n		n	n		p				n					p		p
51			n	n						n							
51PB			n	n						n							
52			n	n						n						n	n
53BF			n	n						n						n	n
53CON			n	n						n						n	n
54BF			n	n						n						n	n
54CON		p	n	n												n	n

PCIV

Latitude	Temperature		Precipitation				Drought code					
(°N)	Sep	Nov	Aug	*may*	*jun*	*aug*	Sep	Oct	*may*	*jun*	*jul*	*aug*
46	n	n	p			n	n					
47	n		p		p		n				n	
48					p					n	n	n
49					p					n	n	
50					p					n	n	n
51				p	p					n	n	n
51PB				p	p					n	n	n
52				p	p	p			n	n		n
53BF					p	p		p				
53CON					p	p		p				
54BF						p	p	p				
54CON						p	p	p				

Appendix II. 3.1 The calibrated full-period climate-growth (Tree-Ring Index, TRI) models for the four species trembling aspen (TA), paper birch (PB), black spruce (BS), and jack pine (JP) along the latitudinal gradient from 46ºN to 54ºN.

Latitude (ºN) / Species	Calibrated full-period climate-growth models along the latitudinal gradient
46 / TA	TRI=1.48482+0.00092552*(p5p+p6p+p7p+p8p+p9p)-0.00040307* (p3+p4+p5+p6+p7+p8+p9)-0.03997* ((tmax3+tmax4+tmax5+tmax6)/4)-0.04082*((tmin8p+tmin9p+tmin10p+tmin11p)/4)+0.03366*((tmin2+tmin3+tmin4+tmin5+tmin6) /5)+0.00078905*((dc7p+dc8p+dc9p+dc10p)/4)
47 / TA	TRI =0.84163+0.00064779*(p9p+p10p+p11p)-0.00090518*(p4+p5+p6+p7+p8+p9)+0.03218*((tmax3+tmax4+tmax5)/3)+0.04228* ((tmax7+tmax8)/2)-0.04802*((tmin6+tmin7+tmin8+tmin9)/4)-0.00193*((dc6+dc7+dc8)/3)
48 / TA	TRI =1.20669-0.00050084*(p11p+p12p+p1+p2)+0.05291*((tmax12p+tmax1+tmax2+tmax3+tmax4+tmax5)/6)-0.02077* ((tmax9p+tmax10p+tmax11p)/3)-0.0147*tmin5p-0.01294*((tmin12p+tmin1)/2)-0.00059883*((dc5+dc6+dc7+dc8)/4)
49 / TA	TRI =1.19092-0.02183*((tmax1+tmax2)/2)+0.03537*((tmin6p+tmin7p+tmin8p+tmin9p+tmin10p+tmin11p+tmin12p)/7)+0.03398* ((tmin2+tmin3+tmin4+tmin5+tmin6)/5)-0.00109*((dc5+dc6+dc7+dc8)/4)
50 / TA	TRI =0.78183+0.00125*(p5p+p6p)-0.00111*p8+0.00072492*(p3+p4+p5+p6+p7)+0.02968*((tmin3+tmin4+tmin5+tmin6+tmin7)/5)
51 / TA	TRI =0.59569+0.00106*(p5p+p6p+p7p)+0.0006362*(p4+p5+p6+p7+p8)-0.03022*((tmax6p+tmax7p+tmax8p+tmax9p+tmax10p +tmax11p)/6)+ 0.0513*((tmin6+tmin7+tmin8+tmin9)/4)
53 / TA	TRI =0.53665+0.00153*(p3+p4+p5+p6+p7+p8)-0.06643*((tmax12p+tmax1+tmax2)/3)+0.05133*((tmin12p+tmin1+tmin2)/3) +0.05593* ((tmin6+tmin7+tmin8)/3)-0.00118*((dc5p+dc6p+dc7p+dc8p+dc9p+dc10p)/6)+0.0011*((dc5+dc6+dc7+dc8+dc9)/5)
54 / TA	TRI =0.76525+0.00276*p5p-0.00134*p9+0.01517*tmax3+0.06864*((tmin7+ tmin8)/2)-0.00075441*((dc8p+dc9p+dc10p)/3)

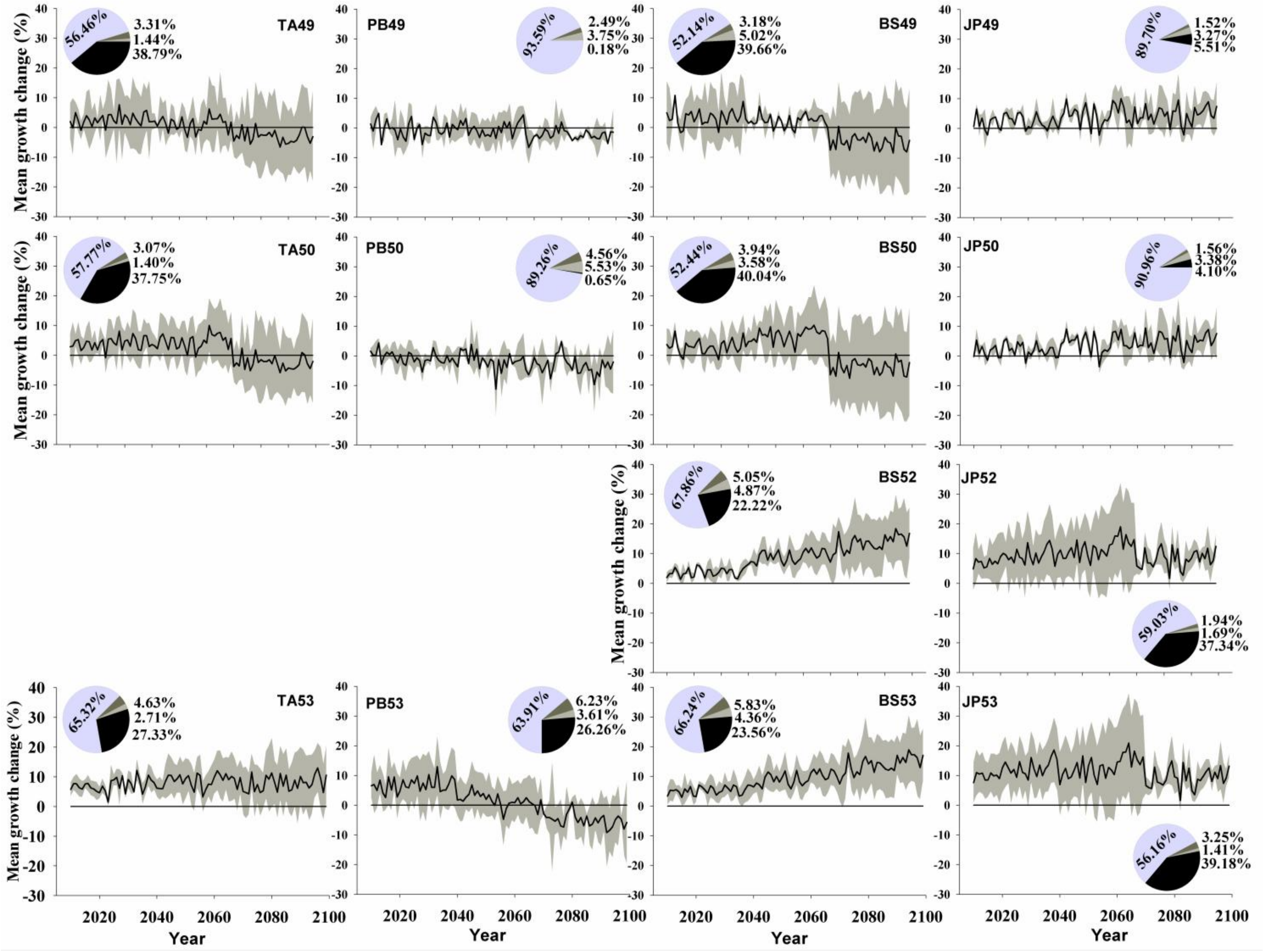
Latitude (ºN) / Species	Calibrated full-period climate-growth models along the latitudinal gradient
46 / PB	TRI =1.49196+0.00097013*(p7p+p8p+p9p)-0.06971*((tmax2+tmax3+tmax4+tmax5+tmax6)/5)+0.05194*((tmin2+tmin3+tmin4+tmin5+tmin6)/5) +0.00058924*dc10p
48 / PB	TRI =1.39767-0.00127*(p8+p9)-0.00149*((dc6+dc7+dc8+dc9)/4)+0.00213*dc5
49 / PB	TRI =1.5191-0.07925*((tmax1+tmax2+tmax3+tmax4+tmax5+tmax6)/6)+0.1167*((tmin3+tmin4+tmin5+tmin6+tmin7+tmin8)/6) -0.0467*tmin9-0.00122*((dc5+dc6+dc7+dc8)/4)
50 / PB	TRI =2.02279+0.02234*tmax5p+0.02508*((tmax12p+tmax1+tmax2)/3)-0.05002*((tmax6p+tmax7p+tmax8p)/3)
51 / PB	TRI =1.00859+0.00127*(p5+p6+p7+p8)-0.00165*p9+0.06151*((tmax7+tmax8+tmax9)/3)-0.05855*((tmax3+tmax4+tmax5+tmax6)/4)-0.03045*((tmax6p+tmax7p+tmax8p)/3)+0.07503*((tmin3+tmin4+tmin5+tmin6+tmin7)/5)-0.04072*tmin9
53 / PB	TRI =0.2017+0.00099563*(p4+p5+p6+p7+p8)+0.01445*tmax5p+0.04589*((tmax6+tmax7+tmax8+tmax9)/4) +0.0272*((tmin9p+tmin10p+tmin11p+tmin12p)/4)-0.00196*((dc5p+dc6p+dc7p)/3)
54 / PB	TRI =1.39771+0.07637*((tmax9p+tmax10p+tmax11p+tmax12p+tmax1+tmax2+tmax3)/7)-0.00074111*((dc8p+dc9p+dc10p)/3)

Latitude (ºN) / Species	Calibrated full-period climate-growth models along the latitudinal gradient
46 / BS	TRI =2.16894+0.05301*((tmax11p+tmax12p)/2)-0.05155*((tmax6+tmax7+tmax8+tmax9)/4)-0.05799*((tmin9p+tmin10p+tmin11p+tmin12p)/4)
47 / BS	TRI =1.57534-0.00092835*(p5+p6)+0.02562*((tmax8+tmax9)/2)+0.02739*((tmin2+tmin3+tmin4)/3)-0.04264*((tmin6+tmin7+tmin8)/3)- 0.00105*((dc6+dc7+dc8)/3)
48 / BS	TRI =1.86219+0.00095323*(p5p+p6p+p7p)-0.03547*((tmax7+tmax8+tmax9)/3)+0.02419*((tmin12p+tmin1+tmin2+tmin3+tmin4)/5)-0.0012*((dc6+dc7+dc8)/3)+ 0.00224*dc5+0.00057414*dc9
49 / BS	TRI =1.90837+0.00071661*(p5p+p6p+p7p)-0.00050706*(p4+p5+p6+p7+p8)-0.00108*(p8p+p9p+p10p)+0.02955*((tmax9p+tmax10p+tmax11p+tmax12p)/4)-0.04644*((tmax5+tmax6+tmax7+tmax8)/4)+0.07141*((tmin4+tmin5+tmin6+tmin7+tmin8)/5) +0.00089305*((dc7p+dc8p+dc9p)/3)-0.00126*dc10p
50 / BS	TRI =1.50701+0.00094755*(p5p+p6p)+0.03345*((tmax12p+tmax1+tmax2+tmax3+tmax4+tmax5)/6)-0.03636*((tmax6+tmax7+tmax8+tmax9)/4) +0.00045703*((dc7p+dc8p)/2)+0.00068851*((dc5+dc6+dc7+dc8)/4)
51 / BS	TRI=0.74844+0.00059553*(p5p+p6p+p7p+p8p+p9p+p10p)+0.05205*((tmax9p+tmax10p+tmax11p+tmax12p+tmax1+tmax2+tmax3+tmax4+tmax5)/9)-0.0354*((tmin5p+tmin6p+tmin7p+tmin8p+tmin9p+tmin10p+tmin11p+tmin12p)/8)-0.0007636*((dc5p+dc6p+dc7p+dc8p)/4)+0.00042744*((dc9p+dc10p)/2)
52 / BS	TRI =1.01148+0.00056153*(p5+p6+p7+p8)+0.02607*((tmax1+tmax2+tmax3+tmax4+tmax5)/5)-0.00105*((dc5p+dc6p+dc7p+dc8p+dc9p)/5)+0.00037843*dc10p
53 / BS	TRI =0.55886+0.00101*(p6+p7+p8)+0.01962*((tmax6+tmax7+tmax8+tmax9)/4)-0.00098141*((dc5p+dc6p+dc7p+dc8p+dc9p)/5)
54 / BS	TRI =1.09988-0.00063977*(p11p+p12p+p1)+0.00088221*(p6+p7+p8)-0.00095704*p9+0.00844*((tmin3+tmin4)/2)-0.0006434*((dc5p+dc6p+dc7p+dc8p+dc9p+dc10p)/6)+0.00067757*((dc6+dc7)/2)

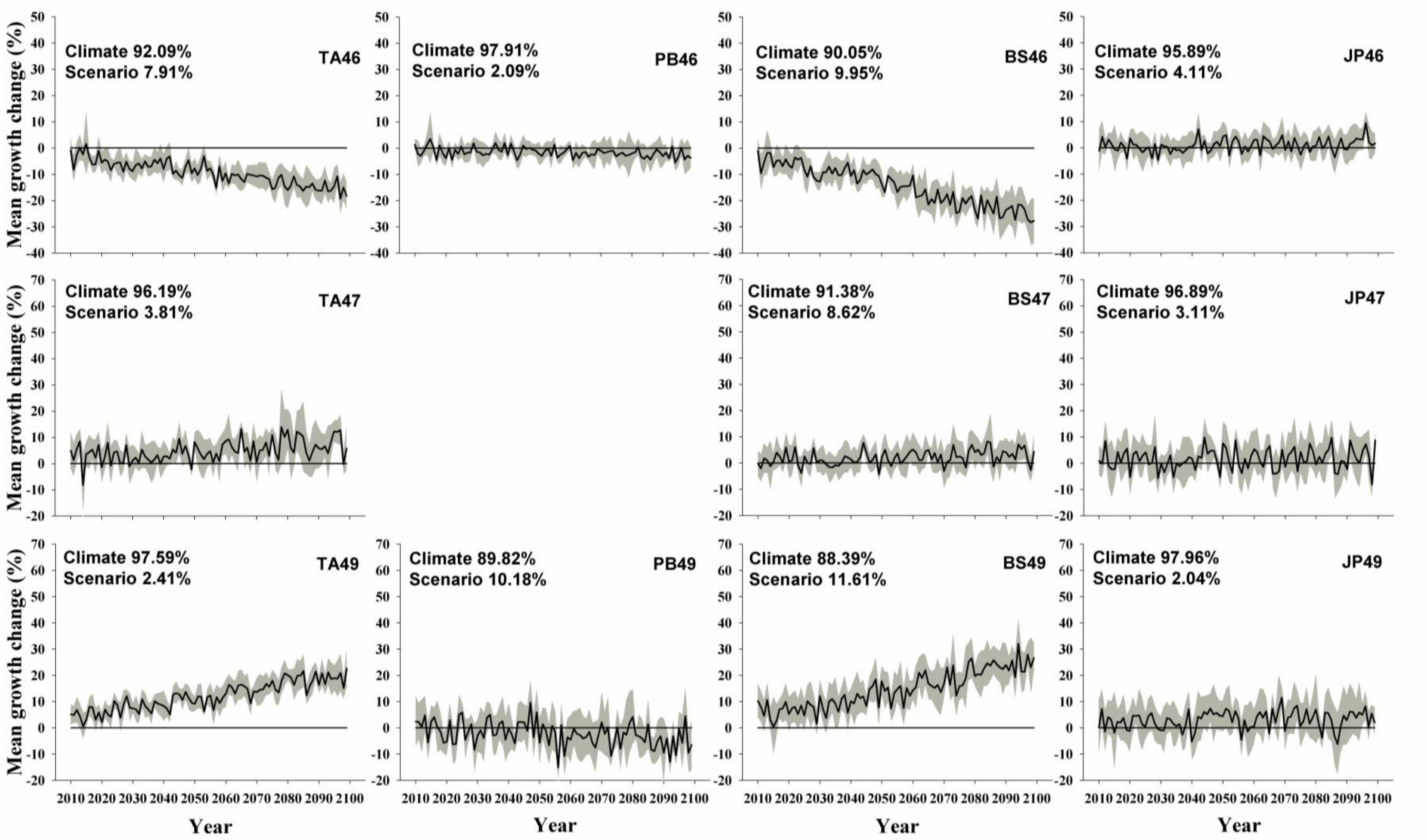
Latitude (ºN) / Species	Calibrated full-period climate-growth models along the latitudinal gradient
46 / JP	TRI =1.50634-0.06341*((tmax9p+tmax10p+tmax11p+tmax12p+tmax1)/5)+0.03637*((tmax2+tmax3+tmax4+tmax5+tmax6+tmax7)/6)-0.03229* ((tmin6p+tmin7p+tmin8p+tmin9p)/4)+0.04769*(tmin10p+tmin11p+tmin12p+tmin1)/4)-0.00072391*((dc5p+dc6p+dc7p)/3)+0.00072059* ((dc8p+dc9p+dc10p)/3)
47 / JP	TRI =1.35416+0.04425*((tmax2+tmax3+tmax4+tmax5+tmax6)/5)-0.05398*((tmin7p+tmin8p+tmin9p)/3)+0.02386* ((tmin10p+tmin11p)/2) +0.00075418*((dc7p+dc8p+dc9p)/3)-0.00044001*dc10p-0.00156*((dc5+dc6+dc7+dc8)/4)
48 / JP	TRI =1.2853-0.00070978*(p4+p5+p6+p7+p8)+0.06574*((tmax3+tmax4+tmax5+tmax6)/4)-0.05006*((tmin7p+tmin8p+tmin9p)/3)+0.02151* ((tmin10p+tmin11p)/2)-0.00154*((dc5+dc6+dc7+dc8)/4)
49 / JP	TRI =0.5291+0.0007898*(p5p+p6p+p7p+p8p+p9p)+0.02997*((tmax10p+tmax11p)/2)+0.04688*((tmax3+tmax4+tmax5+tmax6)/4)-0.0726* ((tmin7p+tmin8p+tmin9p)/3)+0.00082412*dc10p
50 / JP	TRI =1.5187-0.00109*(p10p+p11p+p12p)+0.02977* ((tmax11p+tmax12p+tmax1+tmax2+tmax3)/5)-0.04198*((tmin8p+tmin9p+tmin10p)/3)+ 0.0273*((tmin4+tmin5+tmin6+tmin7+tmin8)/5)
51 / JP	TRI =0.09386+0.03502*((tmax8p+tmax9p+tmax10p)/3)+0.02065*tmax9+0.05463*((tmin4+tmin5+tmin6+tmin7+tmin8)/5)+0.00092871* ((dc5+dc6+dc7+dc8)/4)-0.00060938*dc9
52 / JP	TRI =0.33041+0.00261*p3+0.05238*((tmax8p+tmax9p+tmax10p)/3)-0.05803*((tmin8p+tmin9p+tmin10p)/3)+0.05373* ((tmin4+tmin5+tmin6+tmin7+tmin8)/5)
53 / JP	TRI =0.85127+0.00158*(p1+p2+p3)+0.0486*((tmax4+tmax5+tmax6+tmax7)/4)-0.06068*((tmax8+tmax9)/2)+0.06534* ((tmin8+tmin9)/2)
54 / JP	TRI =1.13453+0.01976*((tmax5p+tmax6p)/2)+0.02507*((tmax4+tmax5+tmax6)/3)-0.0553*((tmax7+tmax8+tmax9)/3)+0.07702* ((tmin7+tmin8+tmin9)/3)-0.00108*((dc5p+dc6p+dc7p+dc8p)/4)

Note: The chronology full period and adj R^2 of each model were listed in Table 3. Monthly climate variables were abbreviations in the model, for example climate variables in May, p5p and p5 indicates precipitation in the previous and current May, respectively; tmax5p and tmax5 indicates maximum temperature in the previous and current May, respectively; tmin5p and tmin5 indicates minimum temperature in the previous and current May, respectively; dc5p and dc5 indicates drought code in the previous and current May.

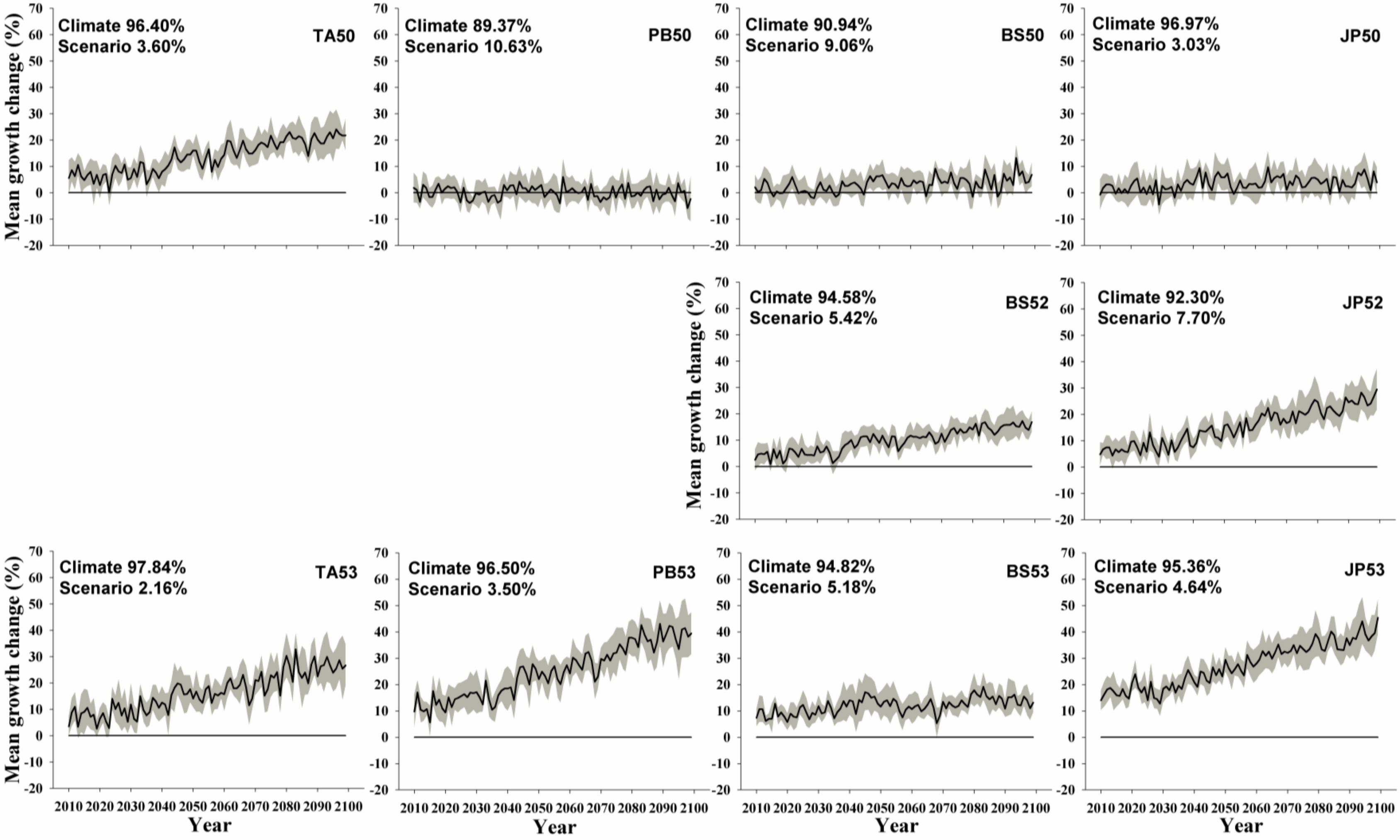
Appendix II. 3.2 The predicted mean growth change of the four species trembling aspen (TA), paper birch (PB), black spruce (BS), and jack pine (JP) at latitudes 49-50ºN and 52-53ºN under the AP1.


TA49
56.46%
3.31%
1.44%
38.79%
PB49
93.59%
2.49%
3.75%
0.18%
BS49
52.14%
3.18%
5.02%
39.66%
JP49
89.70%
1.52%
3.27%
5.51%
TA50
57.77%
3.07%
1.40%
37.75%
PB50
89.26%
4.56%
5.53%
0.65%
BS50
52.44%
3.94%
3.58%
40.04%
JP50
90.96%
1.56%
3.38%
4.10%
BS52
67.86%
5.05%
4.87%
22.22%
JP52
59.03%
1.94%
1.69%
37.34%
TA53
65.32%
4.63%
2.71%
27.33%
PB53
63.91%
6.23%
3.61%
26.26%
BS53
66.24%
5.83%
4.36%
23.56%
JP53
56.16%
3.25%
1.41%
39.18%
Mean growth change (%)
40
30
20
10
0
-10
-20
-30
2020
2040
2060
2080
2100
Year

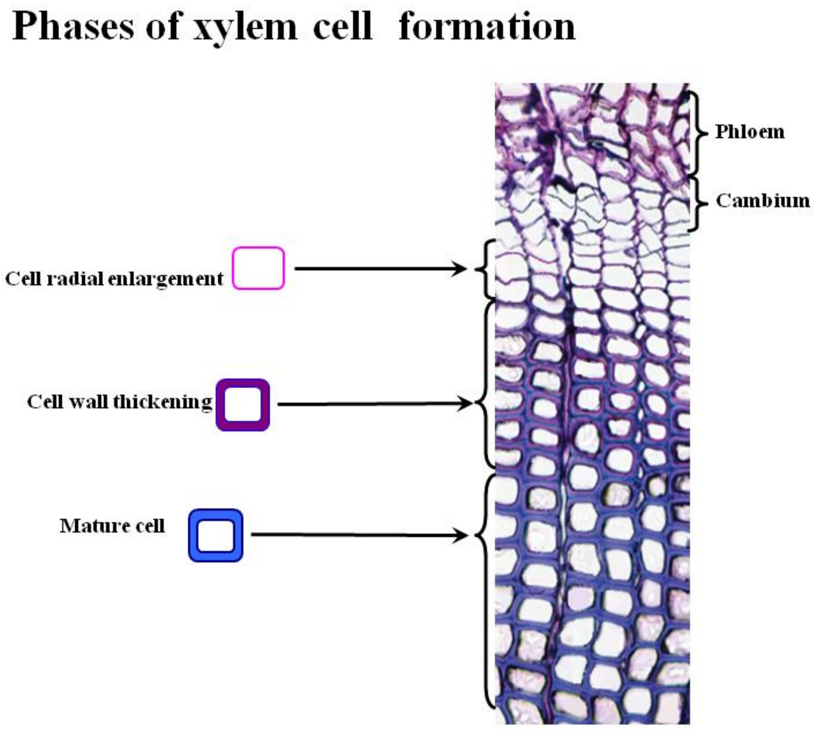
Appendix II. 3.3 The predicted mean growth change of the four species trembling aspen (TA), paper birch (PB), black spruce (BS), and jack pine (JP) at latitudes 46-47ºN, 49-50ºN, and 52-53ºN under the AP2. The calibrated model for paper birch at 47°N was not established and thus the predicted mean growth change was not shown.



To be continued.


Climate 96.40%
Scenario 3.60%
TA50
Climate 89.37%
Scenario 10.63%
PB50
Climate 90.94%
Scenario 9.06%
BS50
Climate 96.97%
Scenario 3.03%
JP50
Climate 94.58%
Scenario 5.42%
BS52
Climate 92.30%
Scenario 7.70%
JP52
Climate 97.84%
Scenario 2.16%
TA53
Climate 96.50%
Scenario 3.50%
PB53
Climate 94.82%
Scenario 5.18%
BS53
Climate 95.36%
Scenario 4.64%
JP53
Mean growth change (%)
70
60
50
40
30
20
10
0
-10
-20
2010 2020 2030 2040 2050 2060 2070 2080 2090 2100
Year

Appendix II. 4.1 Cell radial enlargement (pink), cell wall thickening (violet), and mature cell phases (blue) observed during the xylem cell production.



APPENDIX III

OTHER PUBLICATIONS

Other papers that I sacrificed many of my nights, weekends, and holidays to accomplish and publish in the peer-reviewed international journals as the author or coauthor during my Ph.D study are listed as below. Together with the five papers presented in this thesis and the thesis itself, all these papers may constitute the footprints of my Ph.D life in Canada.

1. Zhai L.H., Bergeron Y, **Huang J.G**., and Berninger F. Variation in intra-annual wood formation of the three major boreal tree species in western Quebec, Canada. (to be submitted)
2. Lapointe-Garant M.P., **Huang J.G.,** Guillermo G.I., Raulier F., Bernier P. and Berninger F. (2009) Use of tree rings to study the effect of climate change on trembling aspen in Quebec. *Global Change Biology,* doi: 10.1111/j.1365-2486.2009.02048.x (online early view) (IF 2008: **5.876**)
3. Li J.B., Cook E.R., D'Arrigo R., Chen F., Gou X.H., Peng J.F., and **Huang J.G.** (2008) Common tree growth anomalies over the northeastern Tibetan Plateau during the last six centuries: Implications for regional moisture change. *Global Change Biology*, **14**, 2096-2107. doi:10.1111/j.1365-2486.2008.01603.x (IF 2008: **5.876**)
4. **Huang J.G**., Lin J.D., and Miao S.L. (2007) Tibet: holy place, not ‘‘Western Storehouse’’! *Frontiers in Ecology and the Environment*, **5(3)**, 122-123. (IF 2008: **5.065**)
5. **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. *Climatic Change* **80**, 369-377, DOI 10.1007/s10584-006-9135-1. (IF 2008: **3.202**)