UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

INFLUENCE DE LA VARIABILITÉ CLIMATIQUE À LONG TERME SUR LA CROISSANCE DES ARBRES DANS LES FORÊTS BORÉALES MIXTES DU QUÉBEC DE L'EST DU CANADA

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AVANT-PROPOS

The Thesis consists of five Chapters, three of which are written in manuscript form (Chapters two through four). Chapter one presents the general introduction and justification of the study, and Chapter five summarizes the results and discusses possible applications for boreal forest management and avenues for further research. Chapters two through four are accordingly based on the following three manuscripts for which I am the lead author:

1. Boakye, E.A., Bergeron, Y., Girardin, M.P., & Drobyshev, I. (2021). Contrasting growth response of jack pine and trembling aspen to climate warming in Quebec mixedwoods forests of eastern Canada since the early 20th century. JGR Biogeosciences, 126, e2020JG005873, https://doi.org/10.1029/2020JG005873.
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RÉSUMÉ

Les forêts de l’hémisphère nord stockent près de la moitié du carbone forestier mondial, et leur rôle dans le cycle mondial du carbone est essentiel pour l'atténuation des changements climatiques. La croissance des arbres dans ces forêts est limitée par une courte saison de croissance et de très faibles températures. La tendance du réchauffement climatique depuis le 19e siècle modifie les conditions de croissance des arbres qui en retour peuvent avoir un impact sur la croissance de ces derniers. À ce jour, les études montrent des tendances contrastées (tendances à la fois à la hausse et à la baisse) des taux de croissance des arbres. La période limitée couverte par ces études traitant principalement de la dynamique de croissance annuelle et décennale ne permettent pas de discuter des effets à long terme de la variabilité climatique sur la croissance des arbres.

L'objectif de la thèse est d'améliorer la compréhension de la réponse de croissance des principales espèces d'arbres de la forêt boréale mixte de l'est du Canada aux changements climatiques. En raison de l'augmentation des températures et des précipitations, nous nous attendions à une augmentation du taux de croissance des espèces dominantes du 19e siècle jusqu'à la fin du 20e siècle. De plus, comme la forêt boréale mixte est spatialement hétérogène en termes de peuplement et de caractéristiques environnementales, nous nous attendions à ce que la réponse de croissance des espèces à la variabilité des températures et des précipitations soit modulée par les conditions du site propres à chaque espèce. Enfin, nous nous attendions à ce que les changements dans les taux de croissance des arbres en réponse à la variabilité des températures et des précipitations affectent la composition future de la forêt boréale mixte. Les résultats de l'étude ont servi de

référence pour suggérer des stratégies et des pratiques sylvicoles pour améliorer la gestion des forêts mixtes dans la région boréale l'est canadien.

La thèse s'articule autour de trois articles de recherche individuels et interconnectés. Le premier article était basé sur un vaste ensemble de données sur les cernes de deux espèces intolérantes à l'ombre, le peuplier faux-tremble (*Populus tremuloides* Michx.) et le pin gris (*Pinus banksiana* Lambert) dans les forêts boréales mixtes du Québec. Ces données proviennent de l'inventaire provincial du ministère des Forêts, de la Faune et des Parcs au Québec. Dans le deuxième article, j'ai utilisé un ensemble de données de mesures de largeur des cernes de croissance de trois espèces d'arbres conifères, le sapin baumier (*Abies balsamea* (L.) Mill.), L'épinette blanche (*Picea glauca* (Moench) Voss) et le cèdre blanc (*Thuja occidentalis* L.), et de deux espèces d'arbres feuillus, peuplier faux-tremble et bouleau blanc *(Betula papyrifera* Marsh.) qui croissent et coexistent dans les forêts mixtes de la forêt d'enseignement et de recherche du lac Duparquet dans la région de l'Abitibi-Témiscamingue dans l'ouest du Québec. Les données cernes dans les premier et deuxième articles ont été standardisées en intégrant les attributs des arbres (c.-à-d. Taille et âge), les caractéristiques des peuplements (c.-à-d. Pente du terrain, indice de compétition) et les variables climatiques (c.-à-d. Température et indice climatique d'humidité (indicateur de l'eau disponible)) grâce à des modèles mixtes additifs généralisés non linéaires. Ont également été pris en considération dans le processus de modélisation, les perturbations périodiques liées à des épidémies de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.), un insecte défoliateur majeur du sapin baumier et de l'épinette blanche qui affecte les trajectoires de croissance des arbres et influence la dynamique des forêts dans l'est du Canada. Dans le troisième article, j'ai utilisé les résultats du deuxième articles pour simuler comment la réponse de la

croissance spécifique aux espèces au climat influencera la composition future de la forêt boréale mixte à l'aide d'un modèle dynamique de peuplement spatialement explicite, SORTIE-ND.

Dans le premier article, j'ai observé une réponse de croissance contrastée du pin gris et du peuplier faux-tremble au réchauffement climatique dans toute la forêt boréale mixte du Québec. Une augmentation significative de la croissance du peuplier faux-tremble a été observée alors que le pin gris montrait une tendance à la diminution qui n'était pas significative. Dans toute la région étudiée, les arbres poussant dans des sites où la concurrence est plus faible et ceux localisé en bas de pente ont montré des effets plus importants d'une hausse de la température sur la croissance. Ces résultats suggèrent que la réponse de la croissance des arbres au réchauffement climatique peut être spécifique à l'espèce et variera dans les forêts boréales mixtes.

Dans le deuxième article, j'ai observé une diminution du taux de croissance des espèces hôtes de la tordeuse des bourgeons de l'épinette, *A. balsamea* et *P. glauca* et une augmentation du taux de croissance des non-hôtes, *T. occidentalis, P. tremuloides* et *B. papyrifera* du lac Duparquet forêts de la région de l'Abitibi-Témiscamingue dans l'ouest du Québec. Le réchauffement climatique semble contribuer à l'augmentation de la croissance des arbres non hôtes dans les forêts mixtes étudiées. Dans l'épinette blanche et le sapin baumier, les infestations d'insectes peuvent contrebalancer les augmentations de croissance résultant d'un climat plus chaud. L'observation justifie l'inclusion de la défoliation par la tordeuse des bourgeons de l'épinette dans les modèles prédisant la productivité future des forêts.

Dans le troisième article, j'ai observé que les différentes réponses de croissance des feuillus et des conifères au réchauffement climatique pourraient ne pas modifier la trajectoire de succession des espèces dans la forêt boréale mixte du lac Duparquet. Nous n'avons trouvé aucune différence dans

la dynamique des surfaces terrières des arbres entre les scénarios impliquant des taux de croissance, avec et sans changements induits par le climat. Pour les deux scénarios, nous avons constaté un déclin plus précoce des espèces de feuillus et une augmentation plus précoce des espèces de conifères au cours de la période de simulation. Notre recherche montre que sous le changement climatique futur, la dynamique de succession forestière peut être cohérente avec la trajectoire de succession sous le climat historique. Pour améliorer la gestion forestière, nous recommandons que les gestionnaires tiennent compte du décalage plus précoce de la transition des combustibles des types feuillus vers les conifères, ce qui est probablement associé à des risques d'incendie accrus.

Dans l'ensemble, les différentes réponses de croissance des espèces d'arbres au réchauffement climatique suggèrent que les gestionnaires devraient être prudents quant à la généralisation des prescriptions de gestion. Au lieu de cela, ils devraient prendre en considération la réponse de croissance spécifique aux espèces au climat dans la planification forestière à long terme. Les interactions avec l'environnement local et les facteurs de perturbation ont également le potentiel de modifier les réponses de croissance spécifiques aux espèces au réchauffement climatique. Par conséquent, il est important qu'au fur et à mesure que les gestionnaires élaborent les outils de gestion forestière, ils tiennent également compte des facteurs locaux de modulation du site. Par exemple, la disponibilité de l'eau dans les pentes modérées à douces et les peuplements moins peuplés peut servir de refuge aux espèces menacées pour amortir l'effet négatif des températures élevées. De plus, une augmentation de la proportion de non-hôtes de la tordeuse des bourgeons de l'épinette (feuillus) dans les peuplements mixtes peut diluer les peuplements et réduire l'influence négative de la défoliation de la tordeuse des bourgeons de l'épinette sur la croissance de leur hôte, le sapin baumier et l'épinette blanche.

Mots clés: Forêt boréale mixte, dendrochronologie, changement climatique, croissance diamétrale, réponse de croissance des arbres, espèces intolérantes à l'ombre, conifères, feuillus, changements de composition, GAMM, SORTIE-ND.

ABSTRACT

Forests in northern latitudes store nearly half of the global forest carbon. Hence, their continuous role in the global carbon cycle is critical for climate change mitigation. The growth of trees in these forests is limited by a short growing season and low temperatures. The climate warming trend since the 19th century is modifying the growing conditions of trees, which can impact growth. It is important to know how trees have responded to the climatic changes that have taken place in their environment. Information is also lacking on the factors that may be modifying the growth response of the tree species to climate change.

The objective of the thesis is to enhance the understanding of the growth response of dominant tree species in the boreal mixedwoods of eastern Canada to the changes in climate and to explore the factors that may be modifying these growth responses. Owing to temperature and precipitation changes, we expected a growth rate increase among the dominant species from the 19th century until the late 20th century. Furthermore, because the boreal mixedwood is spatially heterogenous in terms of stand and environmental characteristics, we expected that the growth response of the species to the temperature and precipitation variability will be modulated by species-specific site conditions. Finally, we expected that the changes in tree growth rates in response to temperature and precipitation variability will affect the future forest succession trajectory of the boreal mixedwood forest. Collectively, the results from the study served as a reference to suggest strategies and silvicultural practices to improve mixedwood management in the Canadian boreal region.

The thesis is structured around three individual and interconnected research papers. The first paper was based on a large tree-ring dataset of two shade-intolerant species, trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lambert) across the boreal mixedwood forests of Quebec. The data was derived from the provincial inventory of the Ministère des Forêts, de la Faune et des Parcs in Quebec. In the second paper, I used a tree ring dataset of three conifers, balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss) and white cedar (*Thuja occidentalis* L.), and two hardwood trees, trembling aspen and white birch (*Betula papyrifera* Marsh) which co-occur in the mixedwoods of the lake Duparquet Teaching and Research Forest in the Abitibi-Temiscamingue region of Western Quebec. The tree ring data in the first and second papers were analysed (if data was available) by integrating their tree attributes (i.e. size and age), stand factors (i.e. terrain slope, competition index), and climatic variables (i.e. temperature and climate moisture index (i.e. indicator of available soil moisture)) through non-linear Generalized Additive Mixed Models. During the modeling process, I took into consideration, the periodic disturbance of spruce budworm (*Choristoneura fumiferana* Clem.), a major defoliating insect of balsam fir and white spruce that distort tree growth trajectories and influence forest dynamics in eastern Canada. In the Third paper, I used data from the Second paper to simulate how species-specific growth response to climate will influence the future succession trajectory of the boreal mixedwood forests using a spatially-explicit stand dynamic model, SORTIE-ND.

In the first paper, I observed the contrasting growth response of jack pine and trembling aspen to climate warming across the entire boreal mixedwood forest of Quebec between 1950 and 2012. A significant increase in the growth of trembling aspen was observed whereas that of jack pine decline was not significant. Over the whole study region, the trees growing in sites with lower competition, and those at the lower sections of the terrain slope experienced more of the positive effects of temperature on growth. The results suggested that the tree growth response to climate warming may be species-specific and will vary across the boreal mixedwoods.

In the second paper, I observed a decreasing growth rate of the spruce budworm host species, *A. balsamea* and *P. glauca* and an increasing growth rate of the non-hosts, *T. occidentalis, P. tremuloides* and *B. papyrifera* of lake Duparquet forests in the Abitibi-Temiscamingue region of western Quebec between 1967 and 1991. Climate warming appeared to contribute to the growth increases of the non-host trees in the studied mixedwood forests. In white spruce and balsam fir, insect outbreaks may offset growth increases resulting from a warmer climate. The observation warrants the inclusion of the spruce budworm defoliation into models predicting future forest productivity.

In the third paper, I observed that the different growth responses of deciduous hardwoods and coniferous trees to climate warming might not alter the succession trajectory of species in the boreal mixedwood forest of Lake Duparquet. We found no difference in the dynamics of the tree basal areas between scenarios involving growth rates, with and without climate-induced changes. For both scenarios, we found an earlier decline of deciduous species and an earlier increase of coniferous species during the simulation period. Our research shows that under future climate change, the dynamics of forest succession may be consistent with the succession trajectory under historical climate. To enhance forest management, we recommend that managers should account for the earlier offset of fuel transition from deciduous to coniferous types, which is likely associated with increased fire risks.

Overall, the different growth responses of the tree species to climate warming suggest that managers should be cautious of generalizing management prescriptions. Instead, they should take into consideration species-specific growth response to climate in the long-term forest planning. Local environment interactions and disturbance factors also have the potential to modify the species-specific growth responses to the warming climate. Therefore, it is important that as managers develop the tools for forest management, they also consider the local site modulating factors. For example, water availability in moderate to gentle slopes and less crowded stands can serve as refugium for threatened species to buffer the negative effect of high temperatures. In addition, an increase in the proportion of spruce budworm non-hosts (deciduous trees) in mixed stands can reduce the negative influence of spruce budworm defoliation on the growth of their host, balsam fir and white spruce.

Keywords: Boreal mixedwood, dendrochronology, climate change, above-ground growth, tree growth response, shade-intolerant species, conifer, hardwood, compositional changes, GAMM, SORTIE-ND.

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Problem statement

1.1.1 Boreal mixedwood forests of Canada

Canadian boreal forests account for about 9% of global forests. Canada's forest area is estimated to be 417.6 million hectares, of which the boreal mixedwood forests account for about 18% (Brassard & Chen, 2006; Natural Resources Canada, 2020). The boreal mixedwood forest is one of the most diverse ecosystems in the boreal region, comprising tree stands having a mixture of conifers and deciduous species (Bergeron, 2000). Compared with single-species stands, the mixedwood stands have the highest productivity. Mixedwoods provide greater resource availability, higher biodiversity, and are more resistant to wildfires, insects outbreaks, and windstorms (Bergeron, 2000; Brassard & Chen, 2006; Payne et al., 2019).

The composition of the boreal mixedwood varies over time due to differences in dominant species, environmental conditions, and disturbance regimes (Cavard et al., 2011; Bergeron et al., 2014). Following a stand-replacing disturbance, the stands at the early successional stage are composed of a mixture of fast-growing shade-intolerant species such as white birch *(Betula papyrifera* March), trembling aspen (*Populus tremuloides* Michx.), and jack pine *(Pinus banksiana* Lamb.)

(Bergeron et al., 2014). At the late-successional stage, the stands are composed of a mixture of slowing growing shade-tolerant species such as white spruce *(Picea glauca* [Moench] Voss), black spruce *(Picea mariana* [Mill.] B.S.P.), and eastern white cedar *(Thuja occidentalis* L.) (Bergeron et al., 2014).

Wildfire is a major disturbance factor in the boreal mixedwood. Wildfire severity and return interval dictate the dynamics of forest compositions (Bergeron et al., 2014). Short fire cycles favor the establishment and dominance of fire-adapted hardwoods, whereas longer fire cycles promote the establishment of conifers. Secondary disturbance factors such as insect outbreaks, windthrow, and aging-driven tree mortality create gaps to also facilitate the recruitment of individuals into the canopy to impact the forest dynamics (Bergeron et al., 2014). Tree mortality through insect outbreaks is mainly caused by forest tent caterpillar *(Malacosoma disstria*) and the spruce budworm (*Choristoneura fumiferana*). Forest tent caterpillars attack trembling aspen and white birch, whereas spruce budworms attack balsam fir, white spruce, and black spruce (Morin, 1994; Bergeron et al., 2002; Latutrie et al., 2015).

1.1.2 Climate change and tree growth in the boreal forests

Boreal forests play an important role in capturing and storing carbon to mitigate climate change. Owing to its slow decomposition rate, it accounts for about 32% of the global forest carbon (Buermann et al., 2014; Luo & Chen, 2015; Payne et al., 2019). Since the forests store and process large amounts of carbon, the net loss or absorption of carbon has a significant impact on the global biogeochemical cycle (Luo & Chen, 2015; Payne et al., 2019). Understanding the boreal forests' response to climate change is, therefore, critical as the forests can speed up climate change by acting as a source of CO_2 or mitigate it by sequestering carbon.

The boreal forests are warming up rapidly since the 1970s at rates of ~0.3–1.0°C/decade (Buermann et al., 2013; Price et al., 2013). This rate of change is higher than anywhere else on the earth and could have consequences on the growth of the trees across the boreal environment (Buermann et al., 2013). Increases in the growth rate have been attributed to the increasing photosynthetic rates due to elevated atmospheric CO_2 (Fang et al., 2014; Pretzsch et al., 2014; Stinziano et al., 2014; Hember et al., 2017; Marty et al., 2017; Babst et al., 2019), increased temperatures and precipitation (Hember et al., 2017; Boulanger et al., 2017; Luo et al., 2019). However, a decline in growth rates, reported for the Canadian boreal shield, Western Canada, and Alaska, has questioned the positive effects of the recent climate trends and increase in atmospheric CO_2 on growth (Silva et al., 2010; Chen et al., 2016; Girardin et al., 2014, 2016; Cahoon et al., 2018). Declining growth rate has been related to higher incidence of periods with extreme temperatures and low precipitation (Hogg et al., 2008; Cahoon et al., 2018). These studies, however, covered a short period and focused mainly on annual and decadal growth dynamics, which provide limited information on the long-term effects of climatic variability on trees growth.

1.1.3 Biotic and abiotic modifiers of tree growth response to climate change

Responses of the boreal forests to climate change depend on the species. Hardwoods are believed to be more adapted to changing environmental conditions due to their larger leaf area, diffuse-porous wood, larger diameter vessels, and deeper rooting depth (Carnicer et al., 2013; Cahoon et al., 2018). Faster growth of hardwoods under new climate has been speculated in several studies (Way & Oren, 2010; Di Filippo et al., 2015; Cahoon et al., 2018). The hardwoods, however, maintain higher stomatal conductance and are vulnerable to drought-induced xylem cavitation and embolism than the narrower tracheids of conifers (McDowell et al., 2008; Brodribb et al., 2014; Cahoon et al., 2018). It is necessary to understand if the hardwoods are responding more to climate variation compared to the conifers as speculated by many studies (Way & Oren, 2010; Di Filippo et al., 2015; Cahoon et al., 2018).

Insect outbreaks can impact how trees species respond to climate change. Spruce budworm for instance defoliates their host, balsam fir and white spruce in eastern Canada. On one hand, the defoliated species experience reduction of photosynthesis, which may reduce tree growth (Morin et al., 1993, 1994; Cooke & Lorenzetti, 2006). On the other hand, the non-host of spruce budworm such as trembling aspen, white birch and white cedar can enhance their growth due to the reduced competition for resources such as sunlight, nutrients and water (Bergeron et al., 2002).

Depending on the site, the sensitivity of the species to climate may vary. In sites where soil moisture does not limit growth, temperature rise increases the growth rate of trees, while trees on the sites with low moisture content decrease growth (Silva et al., 2010; Luo et al., 2019). Competition between trees can also change the response of trees to climate by changing the availability of light, nutrients, and water (Marchand et al., 2019). The large spatial and temporal variability in growing conditions in boreal forests coupled with the confounding effect of competition complicate partitioning between climatic and non-climatic growth responses (Marchand et al., 2019). Untangling climatic and non-climatic effects in tree growth helps quantify the impact of environmental changes on forest growth.

1.1.4 Detecting and modelling tree growth trends using dendrochronological approaches

Biases in growth trend detection

Tree-ring analysis is a powerful tool for retrospective assessment of growth rate response of trees to climate across a range of temporal frequencies (Béland et al., 1992; Johnson & Abrams, 2009; Gillis et al., 2005; Ricker et al., 2014). Tree ring analyses can nonetheless, be biased if key dendrochronological setbacks are not considered (Bowman e al., 2013; Peters et al., 2015). Traditional tree ring sampling requires a balance of age and soil fertility factors in regional samples. Since rotation age usually increases with decreasing site fertility, oldest stands are mostly located on poorer sites whereas a wider range of sites is covered by younger ones (Bontemps et al., 2009). If the most productive stands are subjected to frequent disturbances, younger age classes will be underrepresented in tree ring samples as most would not have reached the sampling diameter threshold whereas fast-growers at the same age are likely to be sampled (Duchesne et al., 2019; Hember et el., 2019). Another bias arises when the sampling of the population of individuals leads to the dominance of slow growers with high longevity compared to fast growers which are short-lived and may not be living at the time sampling (Bowman e al., 2013; Duchesne et al., 2019).

Estimating climate-related growth trends also become biased if a tree's biological age and size effects are not accurately removed. Of the numerous methods for removing trees biological growth trend (e.g. Regional Curve and linear regression standardizations) (Peters et al., 2015; Duchesne et al., 2019; Hember et el., 2019), tree standardization models that integrate tree size and age are effective in estimating growth trends in their resultant tree ring chronologies (Dietrich & Anand, 2019). This method is particularly useful to produce accurate estimates of external forcing when trees from different ages, sizes, or cohorts are not sampled (Dietrich & Anand, 2019).

Modeling forest growth and stand dynamics

The use of modelling approaches is quite critical in comprehending and projecting stand and tree growth. Of immediate benefits are the reduction in time requirements and operational costs associated with long-term monitoring of forests as applicable to climate change. Various modelling methods have been used to assess tree growth rate, but few have attempted to use statistical approaches to detect and quantify the magnitude of the long-term growth trends (Girardin et al., 2016; Marchand et al., 2019; Dietrich & Anand, 2019). Generalized Additive Mixed Model (GAMM) of basal area growth rate has the potential to assess growth trends and simultaneously identify the effects of environmental drivers on growth. Given the heterogeneity of factors influencing tree growing conditions in the mixedwoods, adoption of GAMM provides the advantage of exploring non-linear relationships between tree growth, stand factors such as inter-tree resource competition, and environmental factors (climate, soil, topography, etc.) (D’Orangeville et al., 2018).

In order to further understand the response of forests to climate change, gap models such as SORTIE-ND provides the opportunity to simulate the dynamics of forest succession (Canham et al., 2006). SORTIE-ND was developed in the early 1990s and has been tested across different boreal and temperate forests to simulate the forest succession dynamics in Europe, USA, and Canada (Coates et al., 2003; Canham et al., 2005; Ameztegui et al., 2015; 2017; Bose et al., 2015;

Cristal et al., 2019; Maleki et al., 2020). SORTIE-ND is best suited to understand the long-term dynamics of species composition in mixed forest stands (Ameztegui et al., 2015; 2017).

1.1.5 Thesis objectives and structure

Thesis objectives

The thesis was undertaken to enhance the understanding of the response of tree species in the boreal mixedwood of eastern Canada to the long-term changes in climate. The specific objectives were (1) to examine the century-long trends in the dynamics of the growth rate of two shade-intolerant species, trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lambert), that had been recruited during the 19th and 20th centuries; (2) to investigate how dominant tree species in the boreal mixedwood of eastern Canada respond to climatic variability and insect outbreaks; and (3) to project how species-specific growth response to climate variability will influence the future succession trajectory of the boreal mixedwood of eastern Canada.

Structure

The thesis is organized into five chapters, three of which are written in manuscript form (Chapters two to four). Chapter one presents the general introduction and justification of the study, and chapter five summarizes the results and discusses possible applications for boreal forest management and avenues for further research. Chapter two manuscript explores growth rate changes along the entire lifespan of shade-intolerant trembling aspen (*Populus tremuloides*

Michx.) and jack pine (*Pinus banksiana* Lambert) from the nineteenth century to modern times. In chapter three, I extended the analyses towards several co-occurring tree species of the boreal mixedwood and analyzed their responses to climate variability and insect outbreak using a tree ring dataset from the Lake Duparquet in the Abitibi region of Western Quebec. For the chapter Four, I used SORTIE-ND gap model to understand how the differences in the growth response of tree species to climatic variability may influence the future succession trajectory of the boreal mixedwoods of the lake Duparquet forest.

1.2 Study area

The study was conducted in mixedwood region of Québec, Eastern Canada (Fig. 1.1), extending from 47°N to 49°N and from 62°W to 79°W. The western portion of the study area has a continental climate while the eastern portion experiences a maritime influence (Reyes et al., 2013). The region features a precipitation gradient with drier conditions prevailing in the west (the average total annual precipitation 867 mm) and moister conditions in the east (average total annual precipitation 1050 mm), the latter being more affected by the advection of wet air masses from the Atlantic Ocean (Bergeron et al., 2014; Aussenac et al., 2016). The annual mean temperature is approximately 2ºC in the west and 3ºC in the east of the region (Reyes et al., 2013). The topography in the west is relatively flat to rolling and becomes increasingly hilly and montane towards the east. The main soil superficial deposit is till (Bergeron et al., 2014) except in the western clay belt where clay deposit is dominant. The soil drainage regimes vary from xeric to hydric (Duchesne et al., 2016; 2017).

The main tree species in the boreal mixedwoods are white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), eastern white cedar (*Thuja occidentalis* L.) and black spruce (*Picea mariana* [Moench] Voss) (Bergeron et al., 2014). In contrast, the temperate mixedwoods are dominated by balsam fir and yellow birch (*Betula alleghaniensis* Britt.) (Girard et al., 2004). Aspen and jack pine (*Pinus banksiana* Lambert) often mark areas subjected to fires in the mixedwood zone (Bergeron, 2000; Bergeron et al., 2014). Wildfire is the dominant disturbance factor that controls species distribution and successional pathways in this biome (Brandt et al., 2013). Spruce budworm (*Choristoneura fumiferana* Clemens, SBW) is the common factor of canopy tree mortality for balsam fir and black spruce (De Grandpré et al., 2019) whereas, outbreaks of forest tent caterpillar (*Malacosoma disstria* Hübner; FTC) can cause mortality of aspen (Brandt et al., 2013).

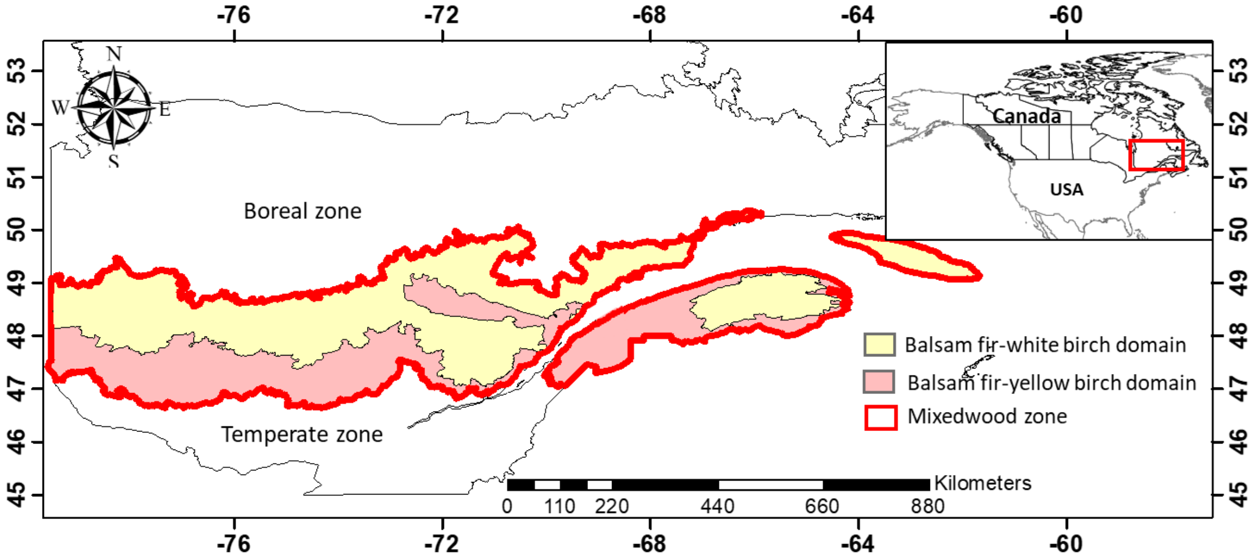

Figure 1.1 The study area in the mixedwood zone of Quebec, bioclimatic domains. The names of bioclimatic domains reflect dominant vegetation during the late serial stages

CHAPITRE II

CONTRASTING GROWTH RESPONSE OF JACK PINE AND TREMBLING ASPEN TO CLIMATE WARMING IN QUEBEC MIXEDWOODS FORESTS OF EASTERN CANADA SINCE THE EARLY TWENTIETH CENTURY

(RÉACTION CONTRASTÉE DE LA CROISSANCE DU PIN GRIS ET DU TREMBLE TREMBLANT AU RÉCHAUFFEMENT CLIMATIQUE DANS LES FORÊTS MIXTES DE L'EST DU CANADA DEPUIS LE DÉBUT DU XXE SIÈCLE)

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2.1 Résumé

Les études de suivi des forêts montrent des tendances contrastées dans les taux de croissance des arbres depuis le milieu du 20e siècle. Cependant, en raison de leur focalisation sur la dynamique annuelle et décennale, ils fournissent un aperçu limité des effets de la variabilité climatique à long terme sur la croissance des arbres. Ici, nous nous sommes appuyés sur un vaste ensemble de données sur les cernes (~ 2700 arbres) de deux espèces d'arbres communes nord-américaines intolérantes à l'ombre, le peuplier faux-tremble (*Populus tremuloides* Michx.) et le pin gris (*Pinus banksiana* Lambert), pour évaluer leur croissance à long terme dans les forêts mixtes du Québec. Nous avons également déterminé comment les conditions environnementales des peuplements influençaient la croissance des arbres. Nous avons observé une augmentation significative du taux de croissance radiale du peuplier faux-tremble au cours de la période d'étude, alors que le déclin du pin gris n'était pas significatif. Dans toute la région étudiée, les arbres poussant dans des sites où la concurrence est plus faible et ceux localisés en bas de pente ont montrés des reprises de croissance plus importante suite à l'augmentation de la température. Notre étude suggère que la réponse de la croissance des arbres au réchauffement climatique peut être spécifique à l'espèce et variera dans les forêts boréales mixtes.

Mots clés: dendrochronologie, croissance aérienne, changement climatique, réponse de croissance, espèces intolérantes à l'ombre, GAMM

2.2 Abstract

Forest monitoring studies show contrasting trends in tree growth rates since the mid-20th century. However, due to their focus on annual and decadal dynamics, they provide limited insight into the effects of long-term climatic variability on tree growth. Here, we relied on a large tree-ring dataset (~2700 trees) of two common North American shade-intolerant tree species, trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lambert), to assess their lifespan-long growth dynamics in the mixedwood forests of Québec. We also determined how the environmental conditions of the stands influenced tree growth. We observed a significant increase in the radial growth rate of trembling aspen during the study period, while the jack pine decline was not significant. Over the whole study region, the trees growing in sites with lower competition, and those at the lower sections of the terrain slope experienced more of the positive effects of temperature on growth rates. Our study suggests that the tree growth response to climate warming may be species-specific and will vary across the boreal mixedwoods.

Keywords: dendrochronology, above-ground growth, climate change, growth rate response, shade-intolerant species, GAMM

2.3 Introduction

In Canada, the annual temperature has increased at the rate of 0.3–1.0°C/decade since the 1970s (Buermann et al., 2013; 2014; Zhang et al., 2019). The changes in the length of the growing season, the atmospheric demand for water, and the precipitation that accompany warming have had undeniable effects on the growth rate of trees and forest productivity (Buermann et al., 2013; 2014; Girardin et al., 2016). Changes in tree growth affect the net uptake of carbon, biochemical cycles, and ecosystem services (Silva et al., 2010; Payne et al., 2019). Knowledge of tree growth responses to climate warming supports forestry planning, specifically – the management of the forest as a potential carbon sink (Silva et al., 2010; Boucher et al., 2018; Payne et al., 2019).

Repeated measurements on permanent forest plots and analyses of dendrochronological and satellite records have shown contrasting trends in tree growth and forest productivity in the boreal and temperate biomes (Marchand et al., 2018). Increases in growth have been attributed to the increasing photosynthetic rates due to elevated atmospheric CO_2 (Fang et al., 2014; Pretzsch et al., 2014; Stinziano et al., 2014; Hember et al., 2017; Marty et al., 2017) and increased temperature and precipitation (Hember et al., 2017; Boulanger et al., 2017; Luo et al., 2019). However, a decline in growth rates, reported for the Canadian boreal shield, Western Canada, and Alaska, has questioned the positive effects of the recent climate trends and increase in atmospheric CO_2 on growth (Silva et al., 2010; Chen et al., 2016; Girardin et al., 2014, 2016; Cahoon et al., 2018). Declining growth rates have been related to a higher incidence of periods with extreme temperatures and low precipitation (Hogg et al., 2008; Cahoon et al., 2018). These studies, however, covered a limited period, and focused mainly on annual and decadal growth dynamics, which provide limited information on the long-term effects of climatic variability on tree growth.

Tree-ring analysis is a powerful tool that is used to assess the response of growth rates to climate variability across a range of temporal frequencies (Béland et al., 1992; Johnson & Abrams, 2009; Gillis et al., 2005). Tree-ring sampling procedures, however, can introduce various biases in such estimations, since the sampled trees are not always representative of the general tree population in terms of their age or size. Sampled individuals from older age classes typically represent slow-growing trees, whereas younger classes commonly represent fast-growing trees (Duchesne et al., 2019; Hember et al., 2019). A particularly strong bias may arise from the variation in recruitment histories: trees representing a particular age class may predominantly recruit into the canopy following a stay in the understory (so-called *advanced regeneration*) while other age classes may reflect a wave of post-disturbance establishment followed by initial growth under the conditions of reduced competition. Such variability in regeneration histories could potentially mask the growth response to changes in climate (Ung et al., 2001; Duchesne et al., 2019; Hember et al., 2019). Competition among trees can further alter tree response to climate variability, by modifying the availability of light and soil resources (Marchand et al., 2019). Untangling climatic vs. non-climatic effects in tree growth is, therefore, a non-trivial but an important element in the analyses that help to correctly quantify the effect of climate on growth.

Site conditions modify the response of tree growth to regional climate. For example, differences in soil drainage can affect the sensitivity of tree growth to variation in precipitation. In the boreal forests of Ontario, where soil moisture is generally abundant, temperature rise during the 1950-2007 period has enhanced tree growth rates (Silva et al., 2010; Luo et al., 2019). However, trees on sites with limited available soil moisture have experienced reduced growth. The large spatial and temporal variability in growing conditions, together with the confounding effects of competition, complicates partitioning between regional climatic and stand-level growth responses (Marchand et al., 2018, 2019).

In this study, we examined the century-long trends in the dynamics of growth rates of trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lambert) that had regenerated between the years,1900 and 2000. Both species are shade-intolerant, typically regenerate following canopy disturbances, and experience limited variability in light conditions during their lifespans (Béland & Bergeron, 1996; Ung et al., 2001; Strimbu et al., 2017). The species shade-intolerance made them good models to study the effects of long-term climate variability on growth, since the variation in the growing conditions at the beginning of their lifespans was low. In particular, the trees, which reached forest canopy and were eventually sampled during the inventories, likely experienced the limited variability in light environments. This facilitated the comparison of tree growth rates among cohorts. To further enhance the climate signal in tree growth, we focused on the Eastern North American temperate and boreal mixedwoods, an ecosystem known to be sensitive to changes in regional climate regimes (Bergeron et al., 2014; Payne et al., 2019). We tested two hypotheses: (H1) the growth rates of jack pine and trembling aspen increased from the nineteenth century until the late twentieth century; and (H2) stand conditions (temperature, climate moisture index, terrain slope, and inter-tree competition) modified the long-term trends in the growth of jack pine and trembling aspen.

2.4 Material and Methods

2.4.1 Study area

The study was conducted in the mixedwood region of Québec, Eastern Canada (Fig. 2.1), extending from 47°N to 49°N and from 62°W to 79°W. The western portion of the study area has a continental climate, while the eastern portion experiences a maritime climate (Reyes et al., 2013). The continental climate is drier (the average total annual precipitation 866.6 mm; the annual mean temperature ~ 2° C), whereas the maritime climate is wetter (average total annual precipitation 1050.4 mm; annual mean temperature ~ 3° C) (Reyes et al., 2013; Bergeron et al., 2014; Aussenac et al., 2016). The topography in the west is relatively flat to rolling and becomes increasingly hilly and montane towards the east. The main soil superficial deposit is till (Bergeron et al., 2014). The soil drainage regimes vary from xeric to hydric (Duchesne et al., 2016; 2017).

The main tree species in the boreal mixedwoods are white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss) and eastern white cedar (Thuja occidentalis L.). In contrast, the temperate mixedwoods are dominated by balsam fir and yellow birch (*Betula alleghaniensis* Britt.) (Girard et al., 2004). Aspen and jack pine (*Pinus banksiana* Lambert) often mark areas subjected to fires in the mixedwood zone (Bergeron, 2000; Bergeron et al., 2014). Fire and insect outbreaks are the dominant disturbance factors that control species distribution and successional pathways in this biome (Brandt et al., 2013; Bergeron, 2000). Spruce budworm (*Choristoneura fumiferana* Clemens, SBW) is the common factor of canopy tree mortality for black spruce (De

Grandpré et al., 2019) whereas, outbreaks of forest tent caterpillar (*Malacosoma disstria* Hübner; FTC) can cause the mortality of aspen (Brandt et al., 2013).

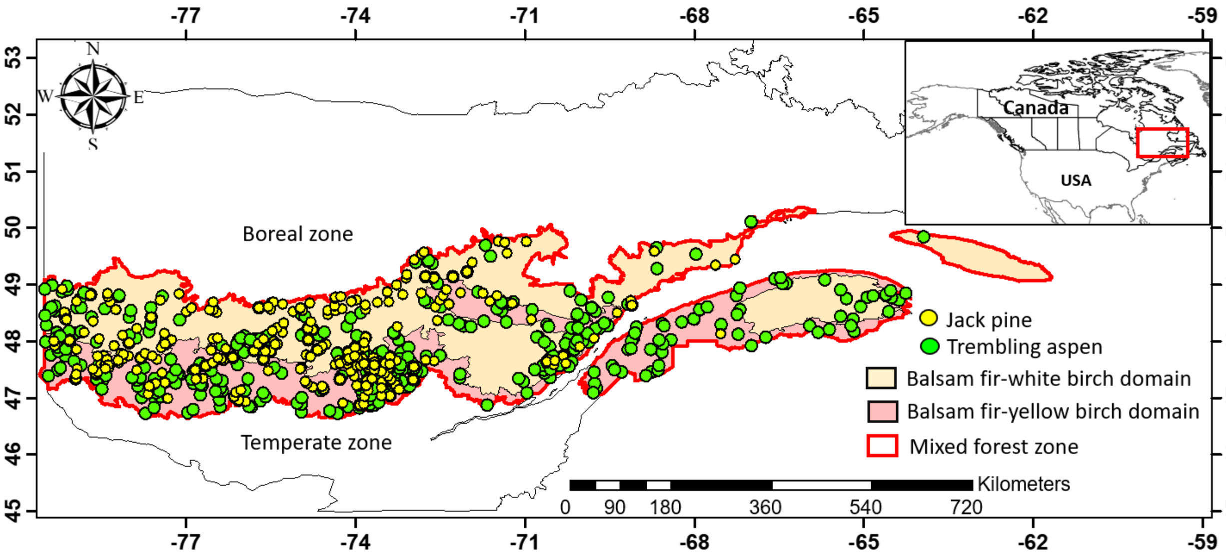

Figure 2.1 The study area in the mixed forest zone of Quebec, bioclimatic domains, and the locations of sampled plots. The names of bioclimatic domains reflect the dominant vegetation during the late seral stages.

2.4.2 Data collection

The data originated from permanent and temporary circular plots managed by Quebec's Ministère des Forêts, de la Faune et des Parcs (MFFP). The plots had the radii of 11.28 m, and the sampling is based on a stratified randomized design with proportional allocation of samples, according to surface area of each stratum (MFFP 2016 a, b). The different strata were determined from aerial photographs based on stand characteristics (composition, density, height, age), edaphic properties (slope, drainage, deposit), and the disturbance history (MFFP 2016 a, b).

For each plot, the following information was available: diameter at breast height (DBH) of every tree, composition of the understory, slope, soil and the type of superficial deposits (Table 2.1) (MRN 2001; MFFP 2009). We used data collected between 1970 and 2012.

In each permanent plot, up to nine trees were cored, five of which were selected randomly. Two trees were selected randomly among the four biggest trees (in terms of diameter at breast height, DBH) of the dominant species. One additional tree was selected to have a diameter closest to the mean diameter of the dominant tree species, and one more tree was selected to have a basal area at breast height closest to the 30th percentile of the distribution of stem basal area for the dominant species. In each temporary plot, three trees (DBH > 90 mm) were selected: one tree was selected randomly among all trees within the plot, another was selected randomly among the four biggest trees (in terms of DBH) of the dominant species, and the third had a diameter closest to the mean diameter of the dominant tree species (Duchesne et al., 2017). These trees were cored at the height of one meter. In 2012, the database included tree-ring measurements of close to 365,000 trees from 42 tree species covering the entire boreal and temperate regions of Quebec (Duchesne et al., 2019). In this study, we analyzed a total of 1454 jack pine trees and 1246 of trembling aspen trees, representing the mixedwood forest zone (Fig. 2.1).

Tree cores were dried, glued to wooden holders, and sanded successively with 120, 220 and 320 grit sandpaper to obtain a smooth surface. Annual rings were measured with the WinDendro Image Analysis System for tree-ring measurement (Regent Instruments Inc, Canada) at a resolution of 1000 dots per inch (Duchesne et al., 2017). A calendar year was attributed to each ring. Since these data have been developed for gaining information on forest productivity, they have not gone through a rigorous standard cross-dating process that is usually carried out in dendrochronological studies (MRN, 2001; MRNF, 2009). In order to test if the non-cross-dated tree ring data has an impact on the estimation of long-term growth trends, we compared the results of a sample of the tree ring data to that of the geographically nearest dated reference chronologies in Western Quebec (Hofgaard et al., 1999; Bergeron, 2000). We observed that in the same period both the cross-dated and non-cross-dated tree ring data produced a similar growth trend (Annexe Fig. A2.1). We would like to note that the use of non-cross-dated tree ring series for the assessment of decadal to century-long growth trends has similarly been used in tropical (Fichtler et al., 2003; Groenendijk et al., 2014) and boreal regions (Duchesne et al., 2019).

2.4.3 Acquisition of site-level variables

We obtained historical monthly weather data for all plots, using an interpolation of data from Environment Canada's weather stations network within the *BioSIM 10* software (Régnière et al., 2014) over the period between 1950 to 2012. This period was common across trees' lifespans and was believed to feature the data of the highest quality. To obtain the climatology of each plot, we averaged the following climate variables for each plot and growing season (May-September) over 1950-2012: mean maximum temperature (ºC), mean total precipitation (mm), and climate moisture index (CMI). CMI characterizes the available moisture and is the balance of monthly potential evapotranspiration (PET) and monthly precipitation (Preci) over a time period *i* in mm of water, $CMI = Preci_i - PET_i$ (Hogg, 1997; Berner et al., 2017). The CMI is a hydrologic index and is typically well-correlated with tree growth in boreal and temperate forest ecosystems (Hogg et al., 2013; Berner et al., 2017). PET was estimated with the R package *SPEI* using the Penman–Monteith algorithm with inputs of monthly average daily minimum and maximum temperature, latitude, incoming solar radiation, temperature at dew point, and altitude (Vicente-Serrano et al., 2010).

Terrain slope for each plot was originally recorded in classes. We converted them to quantitative values using the lower range value (e.g., 9–16% was replaced with 9%).

To account for the effect of competition for resources from neighboring trees on the growth of sampled trees, we calculated a plot-level competition index (CI) as the sum of all individual basal areas for trees with DBH > 1 cm in the plot and scaled it to a hectare (m^2 ha^{-1}). The choice of competition index was based on the results of an earlier study (Huang et al., 2013), which has indicated that the sum of basal areas could act as a simple yet robust representation of competition effects in the studied forests. We calculated the competition index (CI, m^2ha^{-1}) using the average of the estimates of the basal areas from 1970-2012 (permanent plots), and 1980-1993, 1992-2003, and 2004-2012 (temporary plots) inventory data. The distribution of environmental and stand variables for both species are shown in Annexe Fig. A2.2.

2.4.4 Statistical analyses

We converted ring-width data into chronologies of basal area increments (BAI) for each tree using the formula for the area of a circle: $BAI = \pi R^2_t - \pi R^2_{t-1}$ where R is the tree radius and *t* is the year when the ring was formed. Yearly growth rates were expressed as cm^2 $year^{-1}$. We used *bai.out* function in R package *dplR* to compute BAI (Bunn, 2008, R Core Team, 2018). Rings that formed during the first 10 years were removed, since at that age the climatic signal in growth tends to be weak due to the strong effect on growth exercised by the local conditions, such as snow loads, browsing, light/drought conditions, and proximity to taller trees. Removing rings representing the first decade in a tree's lifespan was also expected to remove sections of chronologies with the highest probability of dating mistakes (Marchand et al., 2019). As the initial exploratory step, we analyzed basal area growth rates as a function of calendar year and cambial age using the *interp* function in the R package *akima* (Akima & Gebhardt 2016). This bivariate function constructed a smooth interpolated surface of the median values of logarithmically-scaled BAI (logBAI). This step allowed us to get a graphical representation of variation in BAI along the lifespan of the trees.

At the second step, we quantified the drivers of tree growth, using the Generalized Additive Mixed Model (GAMM) (Wood 2017). We used GAMM to model the basal growth rate of tree j in a site k at specific year t as a function of tree basal area (variable *BA*) and cambial age (*Age*). We computed *BA* as the inner-bark basal area of tree i at specific year t. *Age* was the cambial age (1-m height ring count) of tree i at year t. Inclusion of *BA* and *Age* in the model helped us to retain low-frequency variation in chronologies (Dietrich & Anand, 2019).

To understand the influence of stand environmental conditions on growth, we included in the GAMM model the following variables as growth predictors: competition with neighboring trees (CI), terrain slope, maximum growing season temperatures (TMax), and the climate moisture index (CMI). The full fitted GAMM was:

$\log(\mathrm{BAI}_{jkt}) = \beta\,(\log(\mathrm{BA}_{jkt})) + f(\mathrm{Age}_{jkt}) + f(\mathrm{CI}_{k,}\ \mathrm{TMax}_{k}) + f(\mathrm{CI}_{k,,}\ \mathrm{CMI}_{k}), + f(\mathrm{Slope}_{k,}\ \mathrm{TMax}_{k}) + f(\mathrm{Slope}_{k,}\ \mathrm{CMI}_{k}) + Z_{jk} + \varepsilon_{jk} + \mathrm{AR1}_{jk}$ (Equation 2.1)

In this expression, β ($\log(BA_{jkt})$) is the parametric portion of the model, where β is the vector of the parameter associated with logarithmically-transformed tree inner-bark basal area (BA). The non-parametric part of the expression is formed by f, which is a smoothing function for *Age* effect resolved at tree level, stand and environmental effects. As smoothing functions, we used cubic regression splines. The interaction between each of the two variables (TMax and CMI) and terrain slope and CI was modeled with a tensor (te) product function to address the different units in which temperature, precipitation and terrain slope had been measured (Wood, 2017). To avoid over-fitting, we set the number of knots for the splines at the low value of 3. The subject tree identity (Z_{jk}) was used as a random effect in the GAMM. We included an auto-regressive (AR(1)) term to account for the temporal correlation of the data. The results from the GAMM growth model are associated with estimated degrees of freedom (EDF) that indicated whether the relationship was linear (EDF = 1) or non-linear (EDF > 1). GAMM was realized in R package *mgcv* (Wood 2017).

For each species, the full model was fit on a randomly selected subset of the database, comprising 80% of the trees of a studied species. We computed a correlation matrix among the stand and climatic variables to ascertain if multicollinearity will influence the growth model (Annexe Fig. A2.3). We also evaluated concurvity of the smoothing variables in the growth model terms. Concurvity refers to the degree to which a smooth model term can be approximated by one or more smooth model terms (Johnston et al., 2018). Like multicollinearity in a linear modeling framework, concurvity can lead to instability of the estimated coefficients of the smoothing terms in GAMMs. The concurvity index is calculated on a scale of 0 to 1, with 0 indicating no concurvity and 1 indicating high concurvity (Annexe Fig. A2.4) (Morlini, 2006). We further tested to know how each climate variable performs separately in competing GAMM for each species (Annexe Table

A2.1). We observed that the full model with both CMI and TMax had the lowest Akaike's information criteria with small sample bias adjustment (AICc).

The predictive capacity of the final model was validated using the remaining 20% of the trees to compute the root mean square error (RMSE) of predicted versus observed growth rates. The diagnostic plots of the GAMM model used to assess if the data gives a reasonable description of the relationships for estimating growth for each species are in Annexe Fig. A2.5. The GAMM model predicted BAI on a natural logarithmic scale. We back-transformed the prediction to the original scale (cm^2 year^{-1}), by following the procedure described by Girardin et al. (2016). We weighted the difference between observed (O) BAI (OBAI, cm^2) and predicted (P) BAI (PBAI, cm^2) by the PBAI and expressed it as percentage:

$$\mathrm{BAI} = \frac{OBAI_{jkt} - PBAI_{jkt}}{PBAI_{jkt}} \times 100$$

(Equation 2.2)

We estimated the long-term growth trend as a slope of the linear regression of BAI over the time period (1950-2012). This period is marked by significant increases in mean annual temperatures in eastern Canada (Price et al., 2013).

Methodological considerations

Estimating growth trends indirectly from growth patterns using Akima plots facilitates the understanding of growth dynamics over time and the identification of its driving factors. Although it is not based on a statistical model, an Akima plot is an illustration of the time-evolving plot commonly used in dendrochronology, making it possible to derive the growth rate at any given cambial age and a calendar year (Lenz et al., 2014).

The growth dynamics of a species may be attributed to the periodic oscillations in the climate system (Girardin et al., 2011), tree ontogeny (tree age and size), and inter-tree interactions that all can distort the climatic signal in growth chronologies (Marchand et al., 2019). Non-linear models, such as the general additive mixed effect model (GAMM) have the potential to minimize the fixed effect of tree age and size and adequately quantify effects of climate on growth (Dietrich & Anand, 2019; Marchand et al., 2019). While GAMM has more predictive power or is more flexible than typical statistical techniques employed in tree-ring science, we do caution that the amount of dating error will be reflected in the overall noise and goodness-of-fits. However, the predictors CI, Slope, CMI and TMax are here all time-irrelevant, which means that the impact of dating errors is not that important. For the other two time-related predictors, Age and BA, the shift of the year-recognition of the whole series also has no impact of the average growth rate.

2.5 Results

2.5.1 Growth temporal patterns

The *akima* plots (Fig. 2.2) revealed visible differences in the pattern of variation of the basal area growth rate (logBAI) between jack pine and trembling aspen over time. For jack pine, the plot showed a highly fluctuating growth rate over time: for the cambial ages 11 to 111 years, the growth revealed an approximately 20-year periodicity between 1840 and 1950 (Fig. 2.2 A). Higher growth rates were observed for cambial ages between 11 and ~31 years and between ~111 and ~171 years in the post-1950s period. For aspen, the growth rate at the cambial ages of ~11 and ~31 years was lower prior to1970 than post-1970 (Fig. 2.2 B). For aspen trees with cambial ages greater than 31 years, we observed a relatively constant growth rate over the period between 1960 and 2012.

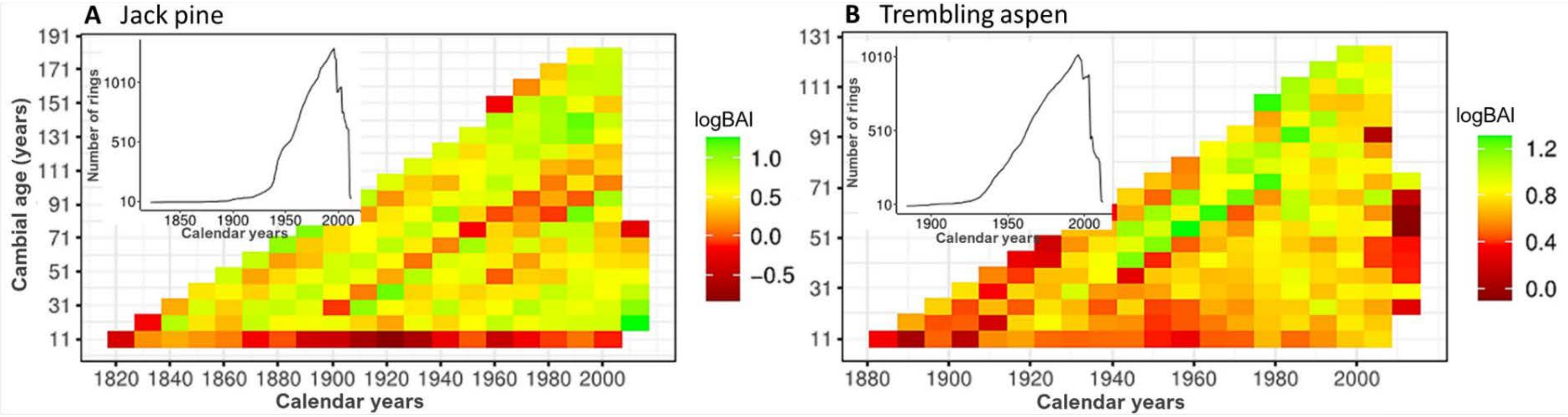

Figure 2.2 The dynamics of log-transformed basal area growth rates (logBAI) in relation to the cambial age and the calendar year chronology for trembling aspen and jack pine.

The color scale denotes the median values of logBAI with low values being in purple and high values - in green. The number of tree rings analyzed as a function of time, is shown in the inserts.

2.5.2 Stand and environmental drivers of growth

The GAMM models (Table 2.1) for jack pine (Fig. 2.3) and trembling aspen (Fig. 2.4) had an identical list of predictors, which included the inner-bark basal area (a proxy of tree size), cambial age, terrain slope, competition index, mean growing season CMI and maximum temperature. There were relatively low absolute correlation (< 0.6) and estimated concurvity (<0.3) among the model individual variables, suggesting weak functional relationships (i.e. low collinearity) among them. Each species-specific GAMM had a root mean square error (RMSE) lower than 0.5, indicating a good predictive skill of the models (Table 2.1).

Tree cambial age (Table 2.1) had a significant non-linear effect on the growth of jack pine (Fig. 2.3 A) and trembling aspen (Fig. 2.4 A). It had a positive effect during the first ~60 years of growth (juvenile stage), after which the age-growth relationship flattened for another ~40-year period (peak growth). Following the peak growth, age had a negative effect on growth (i.e. a growth decrease with age after ~100 years). For both species, the inner-bark basal area had a significant and positive effect on growth rate (Table 2.1; Figs. 2.3 G and 2.4 G).

Stand environmental variables were strong predictors of the growth rate of jack pine and trembling aspen. The interaction between maximum temperature (TMax) and competition (CI) has a significant effect on the growth of trembling aspen (Fig. 2.4 B), but not jack pine (Fig. 2.3 B). The interaction between climate moisture index (CMI) and CI on the other hand has a significant effect on the growth of jack pine (Fig. 2.3 C) but not trembling aspen (Fig. 2.4 C). Tree growth was higher in sites with higher CMI and lower competition.

The interaction between TMax and terrain slope has a significant effect on the growth of jack pine

(Fig. 2.3 D) but not trembling aspen (Fig. 2.4 D). Tree growth was lower on steep slopes and higher on flatter parts of landscapes with higher temperature. The interaction between CMI and terrain slope also has a significant effect on the growth of both jack pine (Fig. 2.3 E) and trembling aspen (Fig. 2.4 E). For jack pine trees, the growth was relatively higher at the lower sections of the slope and at lower CMI. Trembling aspen growth was however, higher at the lower sections of the slope, and at higher CMI.

Table 2.1 Summary of generalized additive mixed model of the effect of tree size, age and stand environmental variables on the growth rates of jack pine and trembling aspen.

Characteristic	Jack pine	Trembling aspen
Leaf type	Needleaf	Broadleaf
Number of trees	1454	1246
Max tree age (years)	188	130
Min tree age (years)	11	12
Mean values (±SE)		
BAI (cm^2 year^{-1})	4.60±0.01	5.84±0.02
Basal area (cm^2)	331.09±0.88	479.23±1.44
CI (m^{2}ha^{-1})	7.52±0.02	9.54±0.03
Slope (%)	10.37±0.12	10.25±0.04
T_{Mean} (°C)	13.08±0.00	13.24±0.00
T_{Max} (°C)	18.31±0.00	18.55±0.00

Table 2.1 (follow)

CMI (mm)	8.61±0.03	5.05±0.03
Model fit		
Deviation explained (%)	51.30	58.20
RMSE	0.27	0.25
Parametric coefficients (±SE, P-value)		
log(BA)	0.60±0.03, <0.001*	0.31±0.03, <0.001*
Significance of smoothing terms (edf, F, P-value)		
Cambial age	2.00, 643.32, <0.001*	2.00, 1598.72, <0.001*
T_{Max*} CI	4.24, 3.14, 0.063^{ns}	6.59, 2.18, 0.018*
CMI_{*} CI	3.69, 2.70, 0.018*	3.24, 0.56, 0.404^{ns}
T_{Max*} Slope	2.87, 6.58, 0.000*	1.00, 1.83, 0.176^{ns}
CMI_{*}Slope	3.02, 5.13, 0.002*	3.00, 3.76, 0.010*
Subject tree	1344.80, 13.23, <0.001*	1126.66, 22.95, <0.001*

CI - competition index, TMean - growing season (May-September) mean temperature of site, TMax – growing season maximum temperature of site, CMI - growing season climate moisture index, BA – tree basal area, edf - estimated degrees of freedom, SE - standard error. P values indicate significance of the effect, with the star indicating values of P lower than 0.05, “ns” indicates non-significant effects.

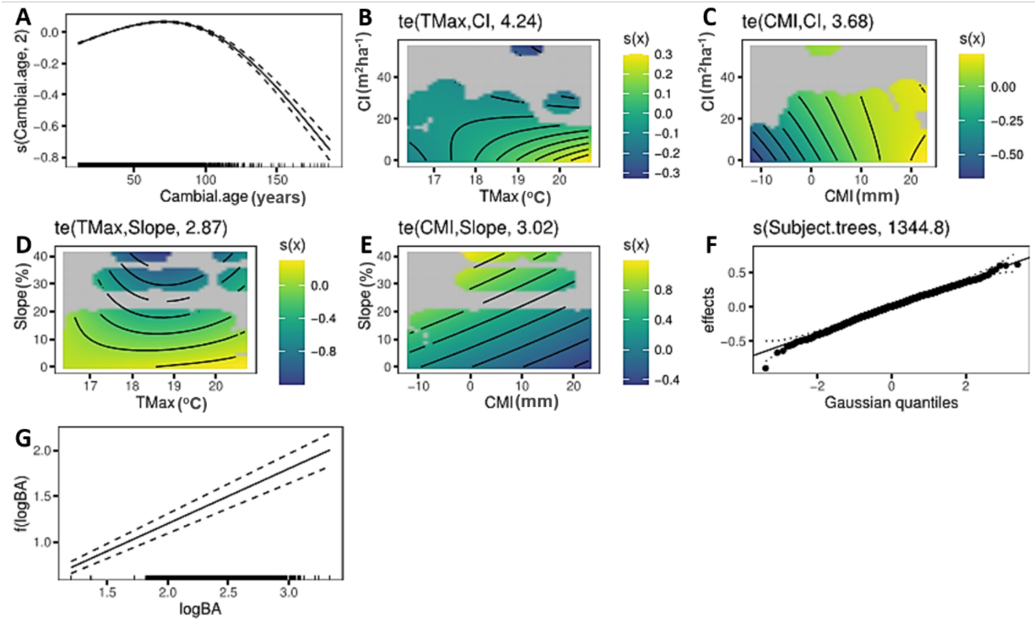

Figure 2.3. The isolated effects of tree size (expressed as basal area, BA), age, and stand environmental variables on the growth rate of jack pine. Stand variables are the competition index, expressed as the sum of basal areas for all trees in the plot, scaled to a hectare (m^2ha^{-1}), terrain slope (%), maximum temperature (TMax, ºC) and climate moisture index (CMI, mm) of the growing season (May-September). In the plots A and G, the OX axis represents a covariate, while the OY axis represents effect values, labeled *s or f (cov, edf)*, where *cov* is the covariate name, and *edf* is the estimated degrees of freedom of the smooth. Plot F shows a diagnostic quantile–quantile plot of the estimated random effects vs. Gaussian quantiles. Dash lines on effect plots denote the 95% confidence intervals. In the plots B, C, D and E, the axes represent the covariates. Colored areas in plots B though E refer to the regions in two-dimensional covariate space with significant effects ($p < 0.05$) interactions.

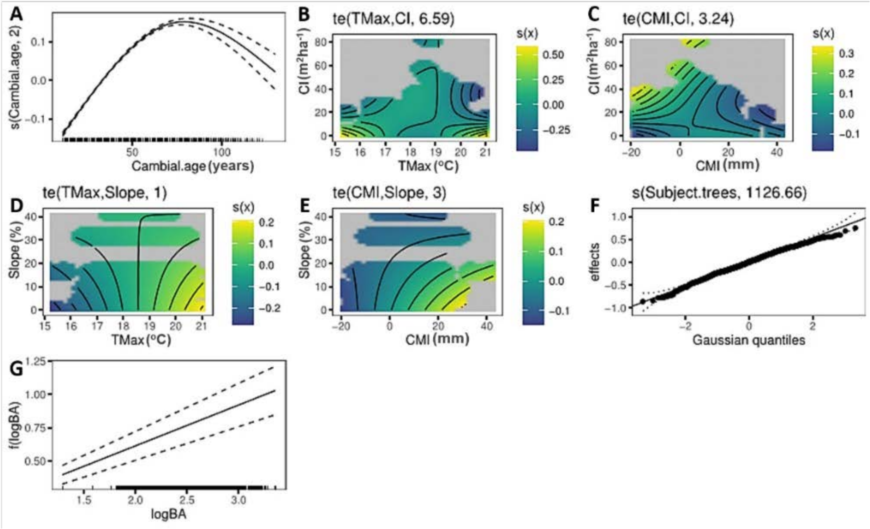

Figure 2.4. The isolated effects of tree size (expressed as basal area, BA), age, and stand environmental variables on the growth rate of trembling aspen. Stand variables are the competition index, expressed as the sum of basal areas for all trees in the plot, scaled to a hectare (m^2ha^{-1}), terrain slope (%), maximum temperature (TMax, °C) and climate moisture index (CMI, mm) of the growing season (May-September). In the plots A and G, the OX axis represents a covariate, while the OY axis represents effect values, labeled *s or f (cov, edf)*, where *cov* is the covariate name, and *edf* is the estimated degrees of freedom of the smooth. Plot F shows a diagnostic quantile–quantile plot of the estimated random effects vs. Gaussian quantiles. Dash lines on effect plots denote the 95% confidence intervals. In the plots B, C, D and E the axes represent the covariates. Colored areas in plots B though E refer to the regions in two-dimensional covariate space with significant effects ($p < 0.05$) interactions.

2.5.3 Quantification of growth trends

We observed contrasting temporal growth trends between jack pine and trembling. Jack pine showed an increasing growth trend until the 1960s, when growth declined up to 1990. The growth increase occurred between 1990 and 2012 (Fig. 2.5 A). Linear regression showed a non-significant growth rate (-0.068 % year^{-1} ± (std) 0.010% year^{-1}, $p = 0.056$, $R^2 = 0.105$) from 1950 to 2012. Trembling aspen showed a constant increase in growth until the 1990s and a slightly decreasing growth rate afterwards (Fig 2.5 B). Between 1950 and 2012, linear regression suggested a significant growth increase (0.111 % year^{-1} ± 0.022% year^{-1}, $p =< 0.000$, $R^2 = 0.291$).

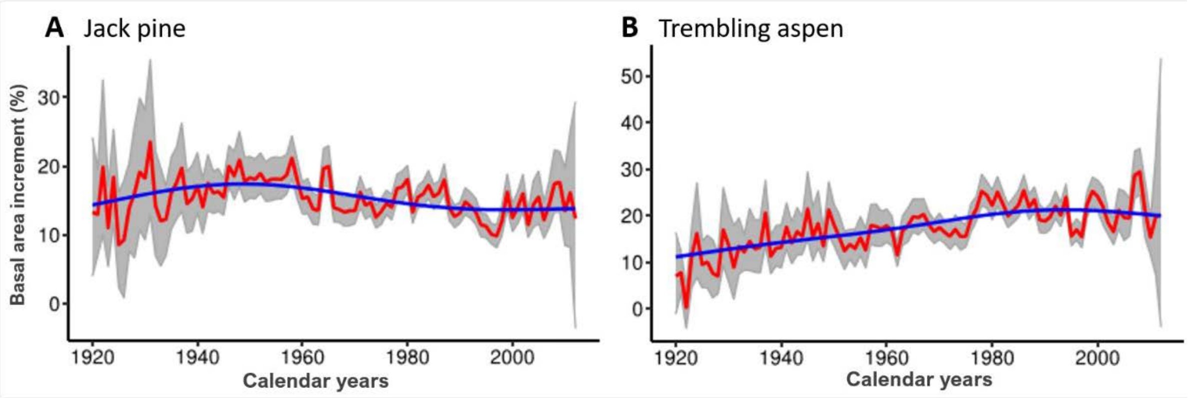

Figure 2.5. Temporal variability of basal area growth (BAI) of jack pine and trembling aspen. The Y-axis is the ratio of observed BAI (cm^2) to GAMM predicted BAI back-transformed to cm^2, and the X-axis is the calendar time. Ratios (red curves) of jack pine (left panels) and trembling aspen (right panels). Gray shading delimits the bootstrapped 95% confidence intervals. The GAM smoothing curve is shown by blue color. The length of temporal variability has been adjusted to cover the period between 1920 and 2012.

2.6 Discussion

Our study documented generally increased growth of trembling aspen and stable growth of jack pine in the mixedwood forests of Quebec between 1950 and 2012, although we observed a strong variability in growth rates. The accelerated growth of trembling aspen and the lack of a long-term trend in jack pine are consistent with trend assessments from the forest inventory in the boreal region of Quebec, since the second half of the 20th century (Anyomi et al., 2012; Girardin et al., 2011; 2012). The trend estimates, however, varied across the boreal mixedwood and depended on stand conditions and local climate features.

2.6.1 Ontogeny effects on tree growth

The observed effect of cambial age on growth rate was consistent with the classical non-linear sigmoidal model (Table 2.1, Figs. 2.3 A and 2.4 A), suggesting a higher growth rate at the early stages of tree lifespan, constant growth in mature trees and a growth decline in trees approaching the end of their lifespan (Johnson & Abrams, 2009; Groover, 2017). The increase in growth rate is primarily related to the increase in canopy size and the photosynthetic capacity of the tree. Stabilization of the growth rate at approximately 60 to 100 years (Fig 2.3 A and 2.4 A) reflects an increasing allocation of photo-assimilates towards maintenance functions and marks the onset of the period with relatively constant canopy volume (Weiner & Thomas, 2001; Johnson & Abrams, 2009; Groover, 2017). Further increasing maintenance and defense costs, higher hydraulic resistance with increase in tree height contribute to decline in growth rates in older (>100 years) trees (Figs. 2.3 A and 2.4 A) (Weiner & Thomas 2001).

Tree growth increased continuously with tree size in both jack pine (Fig. 2.3 G) and trembling aspen (Fig. 2.4 G). The result reflects the fact that these species establish canopy dominance early in stand development, that results from stand replacing disturbance events benefiting from high sunlight availability (Luyssaert et al., 2008; Stephenson et al., 2014; Matsushita et al., 2015). Being well-exposed to sunlight, tree canopies can, therefore, provide high levels of photosynthesis throughout the tree lifespans (Strimbu et al., 2017; Zhang et al., 2017). Basal area increment models have typically reported a positive effect of size on growth and a negative effect of age, when both covariates have been included in the same model (Foster et al., 2016; D'Orangeville et al., 2018), as in the current study.

2.6.2 Stand conditions and climate-growth relationship

The stand environmental conditions altered the tree growth response to climate and often in a non-linear manner. Trees growing on sites with lower competition, in particular trembling aspen (Fig. 2.4 B) experienced the positive effect of temperature on growth because trees tend to increase growth in uncrowded stands where light energy is sufficiently available (Cavard et al., 2011; Huang et al., 2013). Jack pine (Fig. 2.3 C) trees growing on sites with lower competition on the other hand experienced the positive effect of climate moisture index (CMI) on growth because of the increased moisture availability in the less competitive site. Increased temperatures under no deficit in moisture availability generally favors photosynthetic activity and, subsequently, the tree growth (Anderegg et al., 2012; Dietrich et al., 2016).

Jack pine trees (Fig. 2.3 D) at the flatter sections of the slope experienced the positive effect of temperature on growth because of the good availability of soil water at the lower portions of the slopes, combined with the increased in temperatures, that favored the tree growth there. Nevertheless, because Jack pine typically grows on dry sites, excess moisture can constrain growth and impact negatively on the trees (Fig. 2.3 E). Trembling aspen grows in high moisture areas which could have resulted in the more positive effect of CMI at the lower portions of the slope (Fig. 2.4 E) (Anyomi et al., 2012; Marchand et al., 2019).

The growth of trembling aspen (Fig. 2.5 B) increased between 1920 and 2012. Climate warming since the end of the Little Ice Age around 1850, coupled with increasing precipitation, likely favored that increase (Bergeron & Archambault, 1993; Bergeron et al., 2002; Girardin & Wotton, 2009; Girardin et al., 2013; Drobyshev et al., 2017). Although trembling aspen is found in predominantly mesic sites where soil moisture is generally considered as not limiting, a combination of a warmer and wetter climate appears beneficial for this species. In line with this observation, enhanced growth rates of trembling aspen have been documented in tundra regions in western Canada (Zhang et al., 2008) and in boreal and temperate forests of eastern Canada (Anyomi et al., 2012; Girardin et al., 2013). However, a decreasing trend in growth has been reported for trembling aspen along the entire stretch of southern boreal forests in western Canada from 1983 to 2005 (Zhang et al., 2008). These results suggest that the growth of aspen is controlled by both regional trends and variability in site-level conditions within single landscapes/watersheds. Patterns of growth variability at larger geographical scales appear to reflect interactions among regional climatology, biotic agents, and tree growth.

Jack pine did not show a region-wide growth trend over the studied period (Fig. 2.5 A), supporting the result of an earlier study done for the 1983-2005 period (Girardin et al. 2012). Jack pine dominates on mesic to xeric soils, where an increase in temperature and a subsequent increase in evapotranspiration demand are more likely to constrain photosynthesis and lead to reduced growth (Anderegg et al., 2012; Dietrich et al., 2016). However, increased growth in this species has been observed in the northern boreal Quebec (Girardin et al., 2011). This suggests that the growth of trees at the northern fringes of jack pine population range in Eastern North America is temperature limited.

For both species, the lack of consistency in the study's result may arise from the differences in species demography, variability among stand conditions, analyzed time periods and the complexity of analytical setups. Competition and site conditions appear to be the most important modifiers of the climate-growth relationships. Selection of shade-intolerant species for this study and the statistical correction of estimates for BAI trends (Girardin et al., 2016; Dietrich & Anand, 2019) both insured that the trends in growth rate, observed in this study, are climatically-driven. We realize that our methodology might not account for the influence of insect outbreaks, one of the main disturbing agents in the North American mixedwoods. This may be particularly true for aspen, which is affected by the forest tent caterpillar. Disregard for this factor could make the direct (e.g. not modified by biotic agents) climate signal appear less strong in tree ring chronologies (Brandt et al., 2013; Girardin et al., 2013; Boucher et al., 2018).

2.6.3 Management implications

Our study pointed to species-specific sensitivity of growth to changes in climate, modulated by stand-level environmental variables. This implies that growth trends will likely diverge between the two species in the future, with potentially important implications for regional biogeochemical cycles and forestry. The faster growth rate of trembling aspen stands may increase the carbon sequestration capacity of forests with a tangible aspen component. However, it is not clear what the overall effect of the observed trends may be, since higher growth rates will likely be associated with the shorter lifespans of the trees that, in turn, will lower carbon residence time in the living biomass (Büntgen et al., 2019), possibly even limiting the capacity for carbon sequestration in early successional and mixed forests. Shorter rotation periods of aspen stands and an increased production rate of aspen timber should favor the profitability of aspen-oriented forest management programs. The earlier maturation and shorter lifespan would likely cause a decrease in overall wood density, negatively affecting the quality of aspen wood for oriented strandboards, laminated veneer lumber and production of pulp and paper (Balatinecz & Kretschmann, 2001; Bigler, 2016).

For the jack pine, the slowing growth could increase stand rotation age and increase the contribution of this species to the pool of carbon stored in the living biomass (Bigler, 2016). However, the management programs focusing on this species will likely suffer from lower profitability, although increased wood density, which often accompanies decrease in growth, may partially offset the drop in the long-term economic value of jack pine stands used for pulpwood and lumber production (Zhang & Koubaa, 2008).

The apparent lack of similarity in growth trends between trembling aspen and jack pine should make managers cautious in generalizing on the effects of climate change for long-term planning. For both species, a projected change in the frequency of natural disturbances could increase the incidence of background mortality, which may promote a higher rate of deadwood production and carbon release into the atmosphere through wood decomposition (Brandt et al., 2013; Boucher et al., 2018).

2.7 Acknowledgements

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CHAPITRE III

INSECT DEFOLIATION MODULATES INFLUENCE OF CLIMATE ON THE GROWTH OF TREE SPECIES IN THE BOREAL MIXED FORESTS OF EASTERN CANADA

(LA DÉFOLIATION DES INSECTES MODULE L'INFLUENCE DU CLIMAT SUR LA CROISSANCE DES ESPÈCES D'ARBRES DANS LES FORÊTS MIXTES BORÉALES DE L'EST DU CANADA)

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3.1 Résumé

L'augmentation de la température de l'air et la modification des modèles de précipitations en raison du changement climatique peuvent affecter la croissance des arbres dans les forêts boréales. Les épidémies périodiques d'insectes affectent la trajectoire de croissance des arbres, ce qui rend difficile la quantification du signal climatique dans la dynamique de croissance à des échelles supérieures à un an. Nous avons étudié les tendances de croissance induites par le climat et l'influence des épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) sur ces tendances en analysant l'accroissement de la surface terrière (BAI) de 2058 arbres *d'Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss, *Thuja occidentalis* L., *Populus tremuloides* Michx. et le marais à *Betula papyrifera*, qui coexiste dans les forêts boréales mixtes de l'ouest du Québec. Nous avons utilisé un modèle mixte additif généralisé (GAMM) pour analyser les tendances spécifiques aux espèces dans la dynamique des BAI de 1967 à 1991. Le modèle reposait sur la taille des arbres, l'âge cambial, le degré de défoliation de la tordeuse des bourgeons de l'épinette et les variables climatiques saisonnières. Dans l'ensemble, nous avons observé une diminution du taux de croissance des espèces hôtes de la tordeuse des bourgeons de l'épinette, *A. balsamea* et *P. glauca* entre 1967 et 1991, et une augmentation du taux de croissance des non-hôtes, *P. tremuloides, B. papyrifera* et *T. occidentalis*. Nos résultats suggèrent que les épidémies d'insectes peuvent compenser les augmentations de croissance résultant d'un climat plus chaud. L'observation justifie l'inclusion de la défoliation de la tordeuse des bourgeons de l'épinette dans les modèles prédisant la productivité future des forêts.

Mot-clé: dendrochronologie; changement climatique; Épidémie d’insectes forêt mixte boréale; conifère; feuillu

3.2 Abstract

Increasing air temperatures and changing precipitation patterns due to climate change can affect tree growth in boreal forests. Periodic insect outbreaks affect the growth trajectory of trees, making it difficult to quantify the climate signal in growth dynamics at scales longer than a year. We studied climate-driven growth trends and the influence of spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks on these trends by analyzing the basal area increment (BAI) of 2058 trees of *Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss, *Thuja occidentalis* L., *Populus tremuloides* Michx. and *Betula papyrifera* Marsh, which co-occurs in the boreal mixedwood forests of western Quebec. We used a Generalised Additive Mixed Model (GAMM) to analyze species-specific trends in BAI dynamics from 1967 to 1991. The model relied on tree size, cambial age, degree of spruce budworm defoliation, and seasonal climatic variables. Overall, we observed a decreasing growth rate of the spruce budworm host species, *A. balsamea* and *P. glauca* between 1967 and 1991, and an increasing growth rate for the non-host, *P. tremuloides, B. papyrifera* and *T. occidentalis.* Our results suggest that insect outbreaks may offset growth increases resulting from a warmer climate. The observation warrants the inclusion of the spruce budworm defoliation into models predicting future forest productivity.

Keyword: dendrochronology; climate change; insect outbreak; boreal mixedwood; conifer; hardwood

3.3 Introduction

Forests in the northern latitudes store nearly half of the global forest carbon and play a central role in the global carbon cycle (Pan et al. 2011). Changes in tree growth rates can affect the net carbon uptake and feedback to the planetary biogeochemical cycles, by altering the concentration of the atmospheric carbon dioxide (Silva et al., 2010; Bastin et al., 2019). Increases in average mean temperatures, changes in rainfall patterns and extreme weather events since the early twentieth century have already been documented to impact the growth rates of many tree species across the boreal zone (Lloyd & Bunn, 2007; Girardin et al. 2016; Babst et al., 2019). These impacts result from the direct forcing of climate changes upon the tree physiology (e.g., the timing of budset, photosynthesis, and respiration rates) and the indirect interactions with natural disturbances, such as insect and pathogen outbreaks, fires, and windstorms (Pureswaran et al., 2015). It is anticipated that continuing climate warming will affect the natural disturbance regimes in the boreal biome, indirectly impacting tree growth (Boucher et al., 2018).

In the eastern Canadian boreal mixedwoods, coniferous and hardwood species may differ in their capacity to respond to climate change. Hardwood trees may be more adaptable to a future warmer climate, as compared to coniferous trees, due to their larger vessel diameter and deeper rooting depth allowing for more efficient water uptake (Carnicer et al., 2013; Cahoon et al., 2018). Faster growth of hardwoods under warmer climates has been suggested (Way & Oren, 2010; Di Filippo et al., 2015; Cahoon et al., 2018). The hardwoods, however, maintain a higher rate of stomatal conductance and, therefore, are more vulnerable to drought-induced xylem cavitation and embolism than the conifers with their narrower tracheids (McDowell et al., 2008; Brodribb et al., 2014; Cahoon et al., 2018). Anatomical differences among these species may, therefore, lead to a variation in trees' response to climate.

Spruce budworm (*Choristoneura fumiferana* Clem.) is one of the major defoliating insects of balsam fir (*Abies balsamea* [L.] Mill.) and white spruce (*Picea glauca* [Moench] Voss) in eastern Canada. The insect usually kills the host trees and those that survive the outbreak experience significant depletion of carbohydrate reserves, leading to growth reduction (Morin et al., 1993, 1994; Cooke & Lorenzetti, 2006). In the mixedwood stands, however, the diversity of the forest canopy reduces the damage by species-specific insects due to spatial resource (Jactel et al., 2021; Poeydebat et al., 2021). In the less diverse forests, the death or the growth decline of the host trees may enhance the availability of resources, such as sunlight, nutrients, and water to non-hosts, such as trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.). It follows that biotic agents can attenuate or exacerbate climate change effects on growth in both host and non-host trees (Bergeron et al., 2002).

There are indications that the current rate of climate warming exceeds the natural adaptability of forests to environmental changes, which may impact tree growth and lead to changes in insect activity, shifts in species ranges, and modify the composition of forest communities (Gauthier et al., 2015; Astrup et al., 2018). Current management strategies may not be able to effectively deal with the forest changes related to the climate warming, warrantying adjustment of timber harvesting and production strategies. These adjustments could include minimizing disturbance during harvesting activities and reducing the susceptibility of the forest stands to water stress and wildfire (Gauthier et al., 2015; Government of Québec, 2015; Keenan, 2015).

To quantify the effects of climate and insect outbreaks on growth, we studied the growth response of dominant species in boreal mixedwood forests in western Quebec. Since 1950, this region has been experiencing both rising temperatures and increasing precipitation (Girardin & Wotton, 2009; Price et al., 2013; Girardin et al., 2014). During the second half of the twentieth century, extensive outbreaks of spruce budworm have been documented in the conifer-dominated forests of the region, especially during 1972-1987 period (Morin et al., 1993). The spruce budworm outbreaks have been reported to change the structure and composition of the boreal forests (Navarro et al., 2018; Labadie et al., 2021). The region is, therefore, a good location to study the effect of climate-outbreak interaction upon tree growth.

To study tree growth patterns affected by climate and insect outbreaks, we used 2058 tree-ring chronologies of *Abies balsamea* (L.) Mill*.*, *Picea glauca* (Moench) Voss*, Thuja occidentalis* L*.*, *Populus tremuloides* Michx and *Betula papyrifera* Marsh growing on the interface between temperate and boreal mixedwoods in Western Quebec. Specifically, we hypothesized that (H1) the increase of temperatures and changing precipitation patterns generally favored tree growth, and (H2) the combined impacts of temperature and precipitation changes, as well as the emergence of insect epidemics, were overall more positive for the growth of non-host trees and more negative for hosts.

3.4 Material and methods

3.4.1 Study area

We conducted the study in mixedwood stands growing in the balsam fir-white birch domain in the Abitibi region of Quebec, Eastern Canada (Fig. 3.1). The study was located in the Research and Teaching Forest of Lake Duparquet (48.46 N, 79.24 W) at 270–275 m above sea level. The long-term average annual temperature between 1961 and 1990 was 0.8°C. Also the annual precipitation was, on average, 856.8 mm (Bergeron, 2000). The main soil type is clay (Bergeron, 2000; Aussenac et al., 2017a). The dominant canopy species include white birch (*Betula papyrifera Marsh.*), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), and eastern white cedar (*Thuja occidentalis* L.) (Bergeron et al., 2014). The stands originated from seven different fires that occurred in 1760, 1797, 1823, 1847, 1870, 1916, and 1944 (Leduc et al., 2020). The studied stands have not been affected by logging and can be viewed as a result of natural succession (Bergeron et al., 2002).

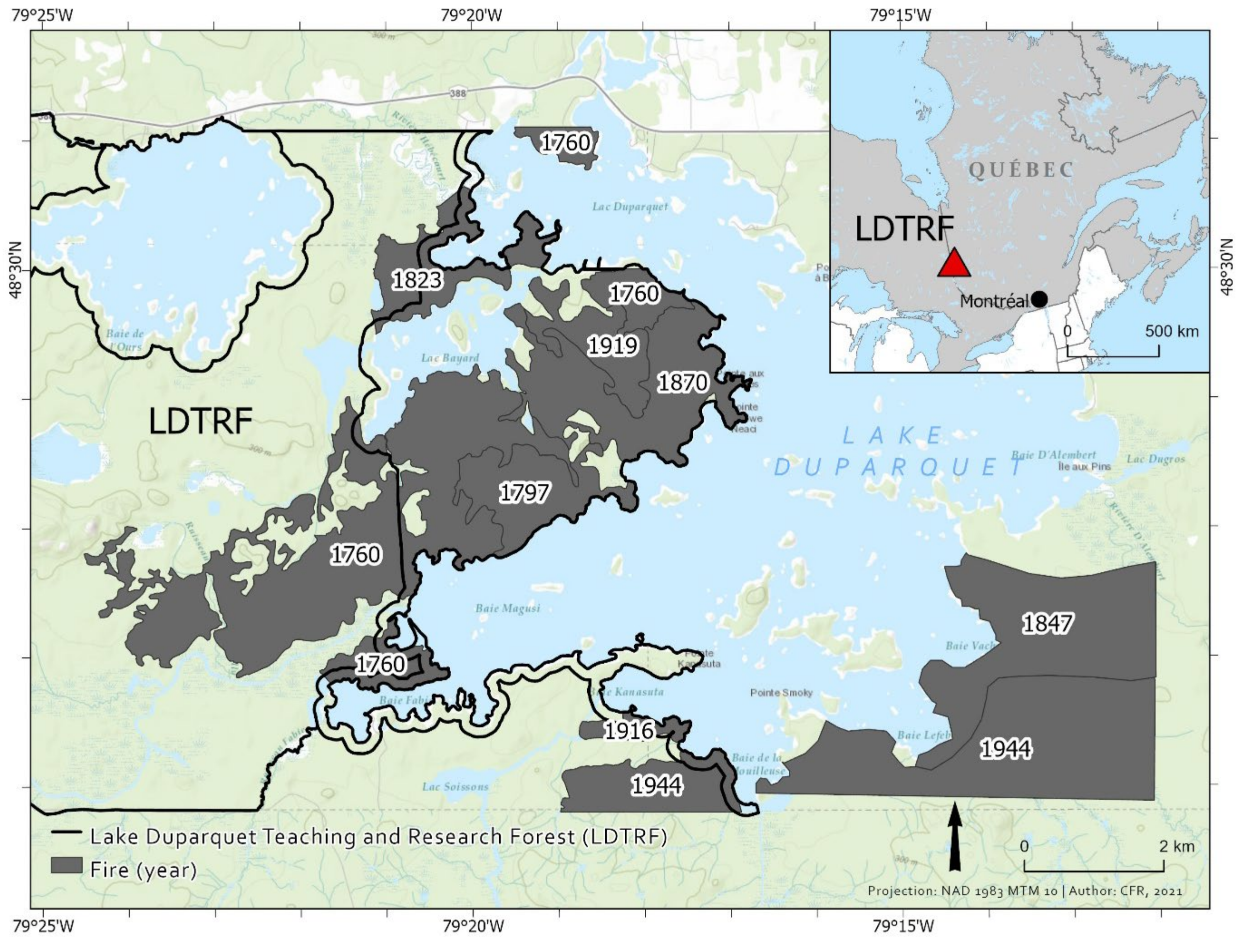

Figure 3.1. Map of the study area, Lake Duparquet Teaching and Research Forest (LDTRF) in Western Quebec, Canada.

3.4.2 Data collection and preparation

We studied balsam fir, white spruce, eastern white cedar, trembling aspen, and white birch. These species were selected because they are the dominant species in the forest successional dynamics of Lake Duparquet. Younger forest stands (74 and 120 years) were dominated by trembling aspen and white birch, mid-aged stands (143 and 167 years) were dominated by balsam fir and white spruce, whereas older stands (193 and 230 years) were dominated by white cedar. Trembling aspen (10 m^2 ha^{-1}) had the highest basal area in the forest stand, followed by balsam fir (9 m^2 ha^{-1}), white birch (5 m^2 ha^{-1}), white spruce (4 m^2 ha^{-1}), and the least being white cedar (3 m^2 ha^{-1}) (Bergeron, 2000).

We retrieved dated chronologies of the species from the tree-ring databank of the dendrochronological laboratory of the Université du Québec en Abitibi-Témiscamingue. The tree ring data were derived from sampling the cross-section of trees at the height of 1m with a diameter $\geq$ 2cm in 1990 (Bergeron, 2000) and increment cores taken at the height of 1.3 m in 2012 and 2013 (Aussenac et al., 2017b). The samples were dried, glued to a wooden holder, and sanded with sandpaper to obtain a smooth surface. Ring boundaries were first detected and identified under x40 magnification, cross-dated through the use of pointer years, and then measured to the nearest 0.01 mm precision with the WinDendro Image Analysis System (Regent Instruments Inc.) and Henson incremental measuring device (Mission Viejo, California, USA). The total number of tree-ring series for all species was 2058 (Table 3.1, Annexe Fig. A3.1).

Table 3.1 Characteristics of sampled trees of the studied species in Lake Duparquet Teaching and Research Forest of Western Quebec.

Species characteristics	White cedar	White spruce	Balsam fir	White birch	Trembling aspen
Leaf type	Conifer	Conifer	Conifer	Deciduous	Deciduous
Total sample of trees	481	136	856	173	412
Inter-series correlation	0.81	0.75	0.73	0.87	0.71
Expressed Population Signal	0.91	0.96	0.95	0.92	0.88
Max tree age	183	162	151	224	87
Basal area increment ± standard deviation, cm^2/year	3.64±4.7	6.61±5.60	2.26±3.60	7.61±9.6	5.24± 7.65
Variance measure	0.39	0.14	0.38	0.44	0.36

Ring width does not give a correct approximation of growth trends, due to its inability to account for the changes in trunk diameter throughout the tree lifespan (Biondi & Qeadan, 2008; Sullivan et al., 2016). Accordingly, we converted ring width into basal area increment (BAI) to improve the representation of the growth rate and biomass accumulation with the formula for the area of a circle: $BAI = \pi (R^2_t - R^2_{t-1})$, where R is tree radius, *t* is the year when the ring was formed and π is 3.142. The function *bai.out* in the R package *dplR* was used to compute BAI (Bunn, 2008, R Core Team, 2018). We expressed annual growth rates as cm^2 $year^{-1}$. Inter-series correlation and expressed population signal (EPS) were used to assess the strength of the population-wide growth signal in the chronologies (Table 3.1). EPS values for all species were above 0.85, indicating that the population signal in chronologies was sufficiently strong (Wigley et al., 1984). Rings that formed during the first 10 years of growth were removed from analyses, since at that age the climatic signal in growth tends to be weak, due to the strong and varying effects on growth, exercised by the local conditions, such as snow load on the crown, browsing, light/drought conditions, and proximity to taller trees (Marchand et al., 2019). Annexe Fig. A3.2 shows the temporal pattern of the BAI for each species between 1800 and 2013.

We compiled historical records of defoliation severity that were incurred by spruce budworm for the study area between 1967 and 1991 from Quebec's annual provincial surveys of the Ministère des Forêts, de la Faune et des Parcs (MFFP). These annual surveys provide aerial estimates of the intensities of damage caused by spruce budworms across Québec. The intensity of the damage is expressed in percentage with 0 indicating no defoliation and 100 indicating severe defoliation (MFFP, 2018). Since the trembling aspen and white birch chronologies extended only to 1991, we limited the analyses for all studied species to 1967 - 1991.

We obtained a historical temperature and climate moisture index (CMI) for the study site. CMI characterizes the available moisture and reflects the balance of monthly potential evapotranspiration (PET) and monthly precipitation (Preci) in mm of water, $CMI = Preci_i - PET_i$, over a time period *i* (Hogg, 1997; Berner et al., 2017). The CMI is typically well-correlated with tree growth in boreal and temperate forest ecosystems (Berner et al., 2017). Potential evapotranspiration was estimated with the R package *SPEI*. The package used the Penman–Monteith algorithm with inputs of daily minimum and maximum temperatures averaged per month, latitude, monthly incoming solar radiation, monthly temperature at dew point, and altitude (Vicente-Serrano et al., 2010). The temperature and CMI were calculated using the *BioSIM 10* software (Régnière et al., 2014), operating on the Environment Canada's weather station network. We obtained temperature and climate moisture index (CMI) chronologies for three seasons of the focal year: winter (December to February), spring (March to May) and summer (June-August). We also obtained previous summer and fall CMI and temperature data to assess the influence of the previous year's weather on tree growth. In Fig. 3.2 we show a correlation matrix of the climatic variables to evaluate the potential impact of multicollinearity on model results. In order to understand the temporal trends in climate variables, we regressed seasonal temperatures and CMI against time, using linear regression.

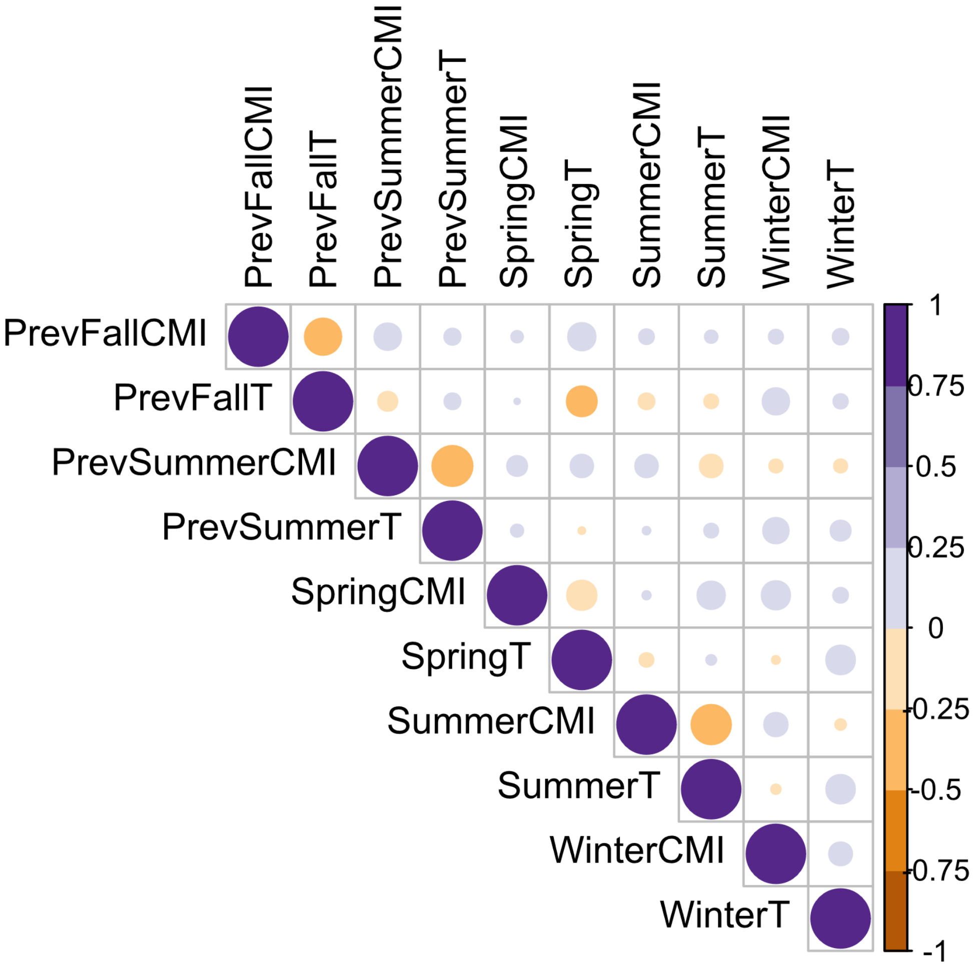

Figure 3.2. Pearson correlation matrix between seasonal climate variables. Suffixes CMI and T denote Climate Moisture Index and Temperature respectively. The prefix Prev denotes previous.

GAMM model

We used GAMM to model the basal growth rate (BAI) of tree *j* at specific year *t* as a function of the tree basal area (variable *BA*) and its cambial age (variable *Age*). To understand the influence of climate variability and insect outbreak, we included seasonal climatic variables (Temperature, *T* and Climate Moisture Index, *CMI*) and the spruce budworm defoliation levels (*DFI*) into the model. A single GAMM was fitted for all species and, therefore, species (*S*) was introduced as a factor. The global model took the following form:

$\log(\mathrm{BAI}_{jt}) = \beta\,(\log(\mathrm{BA}_{jt}, \mathrm{S})) + f(\mathrm{Age}_{jt}, \mathrm{S}) + f(\mathrm{T}_{t}, \mathrm{S}) + f(\mathrm{CMI}_{t}, \mathrm{S}) + f(\mathrm{DFI}_{\mathrm{t}}, \mathrm{S}) + \mathrm{Z}_{j} + \varepsilon_{j} + \mathrm{AR1}_{j}$ (Equation 3.1)

where BA_{jt} is the inner-bark basal area of tree *j* at specific year *t* (computed as the sum of BAI of previous years), *Age* is the cambial age of tree *j* at year *t,* T_t is the temperature at year *t* and CMI_t is the climate moisture index at year *t*. The tree code (Z_j) was used as a random effect in the GAMM. We included an auto-regressive term (AR(1)*j*) to account for the temporal correlation between successive values of BAI data. GAMM was realized in R package *mgcv* (Wood, 2017). The inclusion of *BA* and *Age* in the model helped us increase the model realism and address low-frequency variation in the initial data, thereby improving the model prediction skill (Dietrich & Anand, 2019).

As an initial step in the analysis of the model output, we evaluated the concurvity of the smoothing variables in the GAMM model (Annexe Fig. A3.3). Concurvity refers to the degree to which a smooth model term that detects trends can be approximated by one or more smooth model terms (Johnston et al., 2018). It describes the instability of the estimated coefficients of the smoothing terms in GAMM models. The concurvity index is calculated on a scale of 0 to 1, with 0 indicating no concurvity and 1 indicating high concurvity (Morlini, 2006). We further tested how each climatic variable, T_t and CMI_t, performed separately in competing GAMMs for each species. We also tested the full GAMM model with or without random effects. The model with the lowest value of Akaike's information criterion was selected, using the R package *AICcmodavg* (Mazerolle, 2020).

The model was fit on a randomly sampled subset of 1646 trees, corresponding to 80% of all trees. The predictive capacity of the model was then validated using the remaining 20% of the data (412 trees). For validation, we computed the adjusted R^2 and the root means square error (RMSE) of predicted versus observed growth rates. The normality and homoscedasticity of GAMM residuals were assessed visually (Annexe Fig. A3.4).

To estimate the effect of the insect defoliation on the growth trajectory, we predicted spruce budworm defoliation in the full GAMM model (Equation 1) by allowing DFI_t, and Z_j to vary and keeping the seasonal climatological means (T_t and CMI_t), BA_{jt}, and Age_{jt} , constant at zero. We estimated the effect of climate, by allowing variation of seasonal climate (T_t and CMI_t), and Z_j variables and keeping DFI_t , BA_{jt} and Age_{jt} variables constant at zero. Finally, we predicted the growth, allowing all variables in the full version of the GAMM model to vary, by keeping their effects in the model.

To test for temporal trends in BAI chronologies of each species, we relied on a linear mixed effect models (LME), which used the BAIs predicted by the GAMM as dependent variables. In the LME, we included the calendar year (*Year*) of tree *j* as the fixed effect, tree identity (Z_j) as the random effect, and the auto-regressive term (AR(1)). The model took the following structure:

$$\log(\mathrm{GAMMPredictedBAI}_j) = \beta\,(\mathrm{Year}_j) + Z_j + \varepsilon_j + \mathrm{AR1}_j \quad \text{(Equation 3.2)}$$

3.5 Results

3.5.1 Climate dynamics

Regression analysis on climate variables in the study area showed that average winter and spring temperatures increased between 1967 and 1991 (Fig. 3.3). Summer, previous fall, and previous summer temperatures visibly had little to no overall change during the period between 1967 and 1991. The seasonal climate moisture index (CMI) showed that the study area is becoming wetter, due to the increases in CMI. The correlation between the seasonal temperature and moisture index did not exceed 0.30 (Fig. 3.2), allowing us to retain all the variables in the GAMM model.

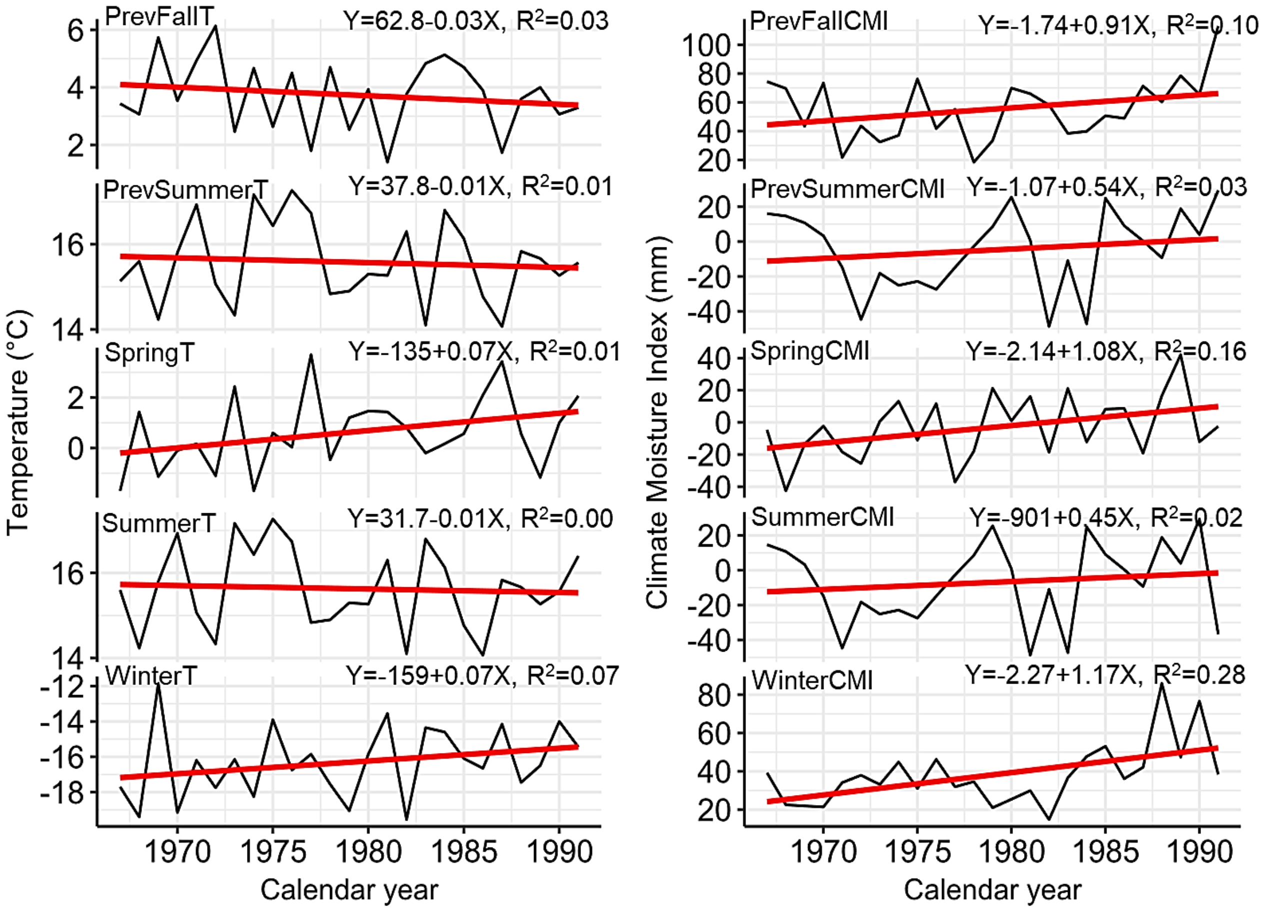

Figure 3.3. Changes in seasonal climate variables during the period between 1967 and 1991. The prefix, *Prev*, denotes previous, whereas the suffixes, CMI and T denote Climate Moisture Index and temperature, respectively.

3.5.2 GAMM growth model

The GAMM model with the lowest AIC had the following set of predictors: basal area (a proxy of tree size), cambial age, defoliation intensity, seasonal temperatures, and climate moisture index (Table 3.2; Annexe Fig. A3.4). We observed low estimated concurvity (concurvity < 0.50) between the model variables, which suggests that the functional relationship between them is weak (i.e., low collinearity) (Annexe Fig. A3.3). Overall, the proportion of variance explained by the GAMM model was 85% (Table 3.2). The GAMM model also showed that all variables included in the model were significant at $P < 0.05$.

3.5.3 Spruce budworm defoliation versus climate effects

Temporal dynamics (Fig. 3.4) of the tree growth showed that the non-host of spruce budworm, trembling aspen and white cedar grew at a slower rate between 1967 and 1980. Following 1980, the growth of the two species increased over time. White birch, on the other hand, had been increasing in growth over time between 1967 and 1991. The growth of the spruce budworm host, white spruce decreased over time between 1967 and 1991. The growth of balsam fir, however, decreased over time between 1967 and 1985, after which growth increased slightly.

Overall, the combined effects of the climate variability and spruce budworm defoliation negatively affected the growth of balsam fir and white spruce, and positively affected the growth of white cedar, trembling aspen, and white birch (Fig 3.5). Similarly, the climate variability and spruce budworm separately had a significant negative effect on the growth of white spruce and balsam fir

(Fig. 3.5). Raw basal area increment series revealed growth releases in non-host species, in particular, white cedar and trembling aspen, during the suppression of the host species (white spruce and balsam fir) from the spruce budworm outbreak of 1972-1987 (Annexe Fig. A3.2).

Table 3.2 Summary of generalized additive mixed model of the effect of tree size, age and seasonal climatic variables on growth rates.

The prefix, Prev denotes previous, whereas the suffixes, CMI and T denote Climate Moisture Index and Temperature respectively. BA= basal area, RMSE=Root Mean Square Error, P values indicate the significance of the effect of variables at lower than 0.05.

A. GAMM growth model comparison				
Characteristics	df	AICc	RMSE	R^2
Full model with random factor as in Equation 3.1	1519.54	6778.39	0.28	0.85
Model without random factor in Equation 3.1	128.03	11928.59	0.33	0.79
Characteristics	df	AICc	RMSE	R^2
Full Model with all variables as in Equation 3.1	1519.54	6778.39	0.26	0.85
Model with CMI excluded from Equation 3.1	1486.84	7990.28	0.42	0.84
Model with T excluded from Equation 3.1	1473.54	7955.45	0.42	0.84
B. Summary of the full GAMM growth model (Equation 3.1)				
R^2 adjusted (%)	0.85			

Table 3.2 (follow)

Parametric coefficients (± SE, p-value)			
Intercept	0.37±0.17	0.029	
Significance of smoothing predictors (edf, F, p-Value)			
log.BA	8.81	36169.72	<0.001
Cambial age (years)	9.76	1150.33	<0.001
PrevSummerT (ºC)	8.98	20.27	<0.001
PrevSummerCMI (mm)	9.87	39.39	<0.001
PrevFallT (ºC)	9.49	40.79	<0.001
PrevFallCMI (mm)	9.32	15.02	<0.001
WinterT (ºC)	9.01	41.07	<0.001
WinterCMI (mm)	12.08	41.70	<0.001
SpringT (ºC)	8.66	9.89	<0.001
SpringCMI (mm)	9.19	15.97	<0.001
SummerT (ºC)	9.65	38.08	<0.001
SummerCMI (mm)	8.91	12.35	<0.001
Defoliation index	9.53	36.27	<0.001
Subject trees	1390.11	4.46	<0.001

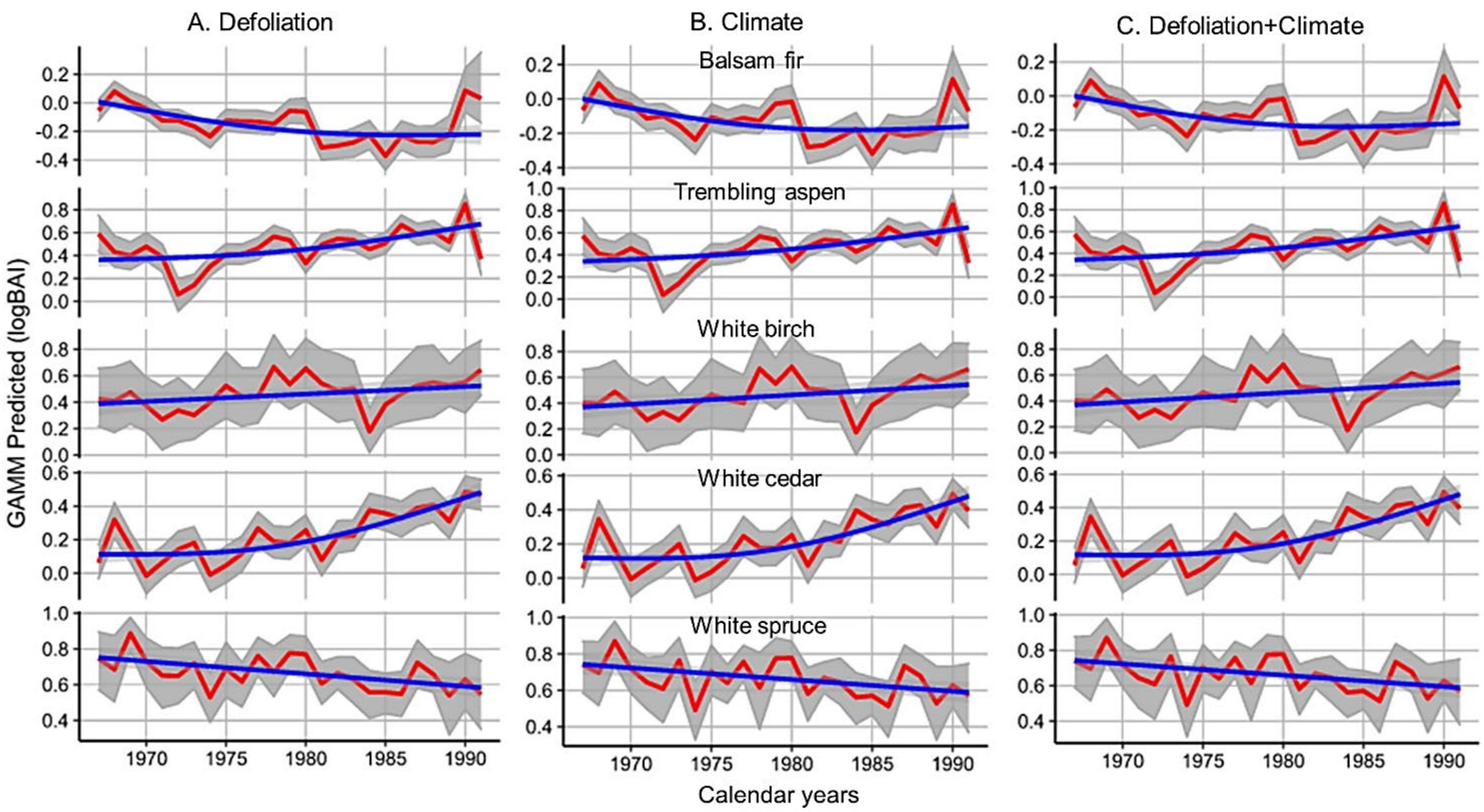

Figure 3.4. Temporal variability of predicted basal area increment (log BAI) of the species in relation to spruce budworm defoliation, climate and the two factors combined. The Y-axis is the log of BAI, as predicted by GAMM. Blue lines are curves representing fitted generalised additive models using a knot of 3. Red lines represent the predicted values from GAMM. Gray shading delimits the bootstrapped 95% confidence intervals. Each row of places represents a species.

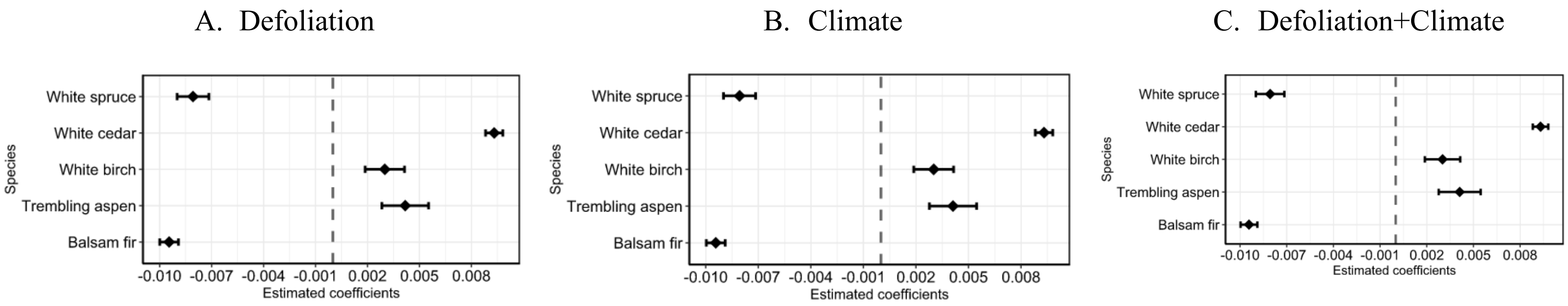

Figure 3.5 Species-specific linear mixed model estimates of the effects of defoliation, climate and all factors combined (full GAMM model, Equation 3.1) on the growth of tree species.

3.6 Discussion

Our results highlight the importance of climate variability and insects in controlling tree growth in the mixedwood forests of eastern Canada. We observed a decreasing growth rate of the spruce budworm host species, balsam fir and white spruce, and an increasing growth rate of the non-hosts, trembling aspen, white birch and white cedar (Figs 3.4, 3.5). Our results partially supported H1, which proposed that the increase of temperatures and changing rainfall patterns generally favored tree growth. Our results supported H2, since we observed that the combined effects of temperature and precipitation changes, as well as the emergence of insect epidemics, were overall more positive for the growth of non-host trees and more negative for hosts. Climate warming increases moisture availability and the length of the growing season, which correlates positively with tree growth (Price et al., 2013). However, the lengthening of the growing season makes it possible for insects to produce several generations within the same season, increasing the risk of insect outbreaks and associated growth declines. The enhancement of the deciduous species growth and the reduction of conifer growth have been widely reported across the northern hemisphere, including northern Japan (Tsutom et al., 2019), Eastern (Anyomi et al., 2012; Boakye et al., 2021) and Western Canada (Zhang et al., 2008; Searle & Chen, 2018).

The defoliation of the spruce budworm hosts, balsam fir and white spruce, might indirectly promote the growth of non-hosts trees, trembling aspen, white birch and white cedar (Figs. 3.4, 3.5). Tree defoliation by the insects creates large openings, where non-host trees likely experience reduced competition from the surviving host trees for sunlight, water, and nutrients. This promotes tree growth of the non-host species (Bergeron, 2000; Anderegg et al., 2015; Boulanger et al., 2017). Consistent with our observations, studies have reported the spruce budworm defoliation as a factor driving an increase in the growth of non-host species in eastern and western Canadian boreal forests (Duchesne & Ouimet, 2008; Itter et al., 2019).

The growth of the spruce budworm host species, balsam fir and white spruce (Figs 3.4, 3.5), declined between 1967 and 1991. The pattern might be due to the higher temperatures accelerating transpiration, stomata closure and limited access to atmospheric carbon. The growth decline of the conifers provides adequate canopy openings that promote the regeneration of the shade-intolerant species (Barber et al., 2000; Anderegg et al., 2012, 2015). This compositional change can impact the climate system, since the reduced evergreen conifer cover will expose the landscape in winter, increasing the surface reflectance and the cooling of the boreal mixedwoods (Mcdowell, et al., 2016).

The defoliation by spruce budworm might also contribute to the growth decline of the balsam fir and white spruce (Figs 3.4, 3.5). Between 1960 and 1980, the budworm caused massive defoliation in the study area, likely leading to carbon starvation and subsequent growth decline in surviving trees (Morin et al., 1993). Mined needles have shown a reduced water transport efficiency, lower carbon absorption potential, and the affected trees have revealed a limited investment of resources into defensive compounds (Morin, 1994; Anderegg et al., 2012; 2015).

Differences in xylem anatomy, plant allometry, stomatal behavior, rooting strategies, stand density and forest management can all modify the response of tree species to environmental variability. For example, deciduous trees such as white birch and trembling aspen have a deeper root system than conifers, enabling them to access water from deeper soil layers to better overcome seasonal water deficits, as compared to coniferous species (Oltchev et al., 2002; Mekontchou et al., 2020).

Different stand densities modulate tree response to spruce budworm outbreaks and climate variability by controlling competition between trees (De Grandpré et al., 2019; Steckel et al., 2020). Higher densities of host species and warmer climates can increase the intensity of tree defoliation, and promote growth reduction and mortality in the host trees. The resulting canopy openings will increase the availability of light and water to promote the growth of the hon-hosts (Steckel et al., 2020; Chavardès et al., 2021).

The studied stands experienced no silvicultural treatments such as thinnings or selective fellings as the stand management has been based on the natural disturbance dynamics (Harvey, 1999).

Implication for forest management

Climate warming and insect outbreaks influence the growth of the studied mixedwood forests of eastern Canada. These influences have a significant and likely long-lasting impact on the forest ecological and economic value and forest management. There is a need to develop and implement the necessary changes to mitigate the adverse effects and to take advantage of the changing environmental settings.

The decreased growth rate of the spruce budworm host species (balsam fir and white spruce) will increase the time needed for the trees to reach maturity and, subsequently, the rotation time of the stands (Bigler, 2016). An increased rotation time means that the trees could provide more long-term storage of sequestrated carbon in the living biomass. Furthermore, if the rotation periods are increased, the economically optimal number of thinnings may increase, which could incur additional costs for the forest owners. On the other hand, extended rotation may also diversify the stand composition and promote mature and old-forest features such as multilayered canopies, down deadwood and standing snags which will benefit local wildlife (Martin et al., 2018).

Climate warming may increase the survival of spruce budworms, potentially leading to more frequent and/or more severe outbreaks and offsetting effects of longer rotation period on carbon storage capacity (Logan et al., 2003; Dymond et al., 2010; Jactel et al., 2019). More severe budworm outbreaks will cause higher tree mortality and greater revenue loss from forestry operations. We, however, caution against the proposed use of pesticides to control the spruce budworm due to potentially extensive and long-term negative effects on forest ecosystems (James et al., 2017).

We expect that the growth increases among the non-hosts of the spruce budworm, especially in trembling aspen, may contribute to a short-term increase in the deciduousness of the mixedwood forests that may increase the production of hardwood, such as lumber and wood biomass used in the production of pulp and paper (Balatinecz & Kretschmann, 2001). However, the rapid growth of the deciduous hardwoods would mean that the trees will mature and die earlier, which may lower the residence time of carbon in their biomass (Büntgen et al., 2019). The earlier maturity of the trees may also ensure a faster transition to a forest dominated by the slow-growing conifers (Bigler, 2016; Leduc et al., 2020). Jointly, these effects will likely affect the rotation periods for the deciduous and coniferous components of mixed stands.

3.7 Acknowledgements

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CHAPITRE IV

SUCCESSION TRAJECTORY OF THE BOREAL MIXEDWOODS IS RESILIENT AGAINST VARYING GROWTH RESPONSES OF TREES TO CLIMATE

(LA TRAJECTOIRE DE SUCCESSION DES FORÊTS MIXTES BORÉALES EST RÉSILIENTE AUX VARIATIONS DE LA CROISSANCE DES ARBRES AU CLIMAT)

Emmanuel A. Boakye, Kobra Maleki, Daniel Houle, Danielle Charron, Yves Bergeron, Igor Drobyshev

(Article in preparation)

4.1 Résumé

Les changements climatiques modifient le taux de croissance des espèces d'arbres et peuvent entraîner un changement dans la composition des forêts boréales mixtes dans l'est de l'Amérique du Nord. Nous avons utilisé un simulateur de forêt spatialement explicite SORTIE-ND pour comprendre l'effet des changements de taux de croissance induits par le climat sur la succession forestière future et la composition du peuplement qui en résulte. Nous nous sommes concentrés sur deux espèces de feuillus (*Populus tremuloides* Michx. et *Betula papyrifera* Marsh.) et trois conifères (*Abies balsamea* [L.] Mill., *Thuja occidentalis* L. et *Picea glauca* [Moench] Voss) dans un paysage de l'ouest du Québec. Nous avons constaté que dans une simulation de 60 ans, il n'y a pas de différence dans la dynamique des surfaces terrières des arbres entre les scénarios impliquant des taux de croissance, avec et sans changements induits par le climat. Pour les deux scénarios, nous avons constaté un déclin plus précoce des espèces à feuilles caduques et une augmentation plus précoce des conifères au cours de la période de simulation. Notre recherche montre que sous le changement climatique futur, la dynamique de succession forestière peut être cohérente avec la trajectoire de succession sous le climat historique. Pour améliorer la gestion forestière, nous recommandons que les gestionnaires tiennent compte du décalage plus précoce de la transition des combustibles des types feuillus vers les conifères, ce qui est probablement associé à des risques d'incendie accrus.

Mot-clé : changement climatique, bois mélangé boréal, conifère, bois franc, changements de composition

4.2 Abstract

Climate change alters the growth rate of tree species and may cause a shift in the composition of the boreal mixedwood forests in eastern North America. We used a spatially explicit forest simulator SORTIE-ND to analyse the effect of climate-induced growth rate changes on future forest succession and resulting stand composition between 1991 and 2051. We focused on two deciduous species (*Populus tremuloides* Michx. and *Betula papyrifera* Marsh.) and three conifers (*Abies balsamea* [L.] Mill., *Thuja occidentalis* L. and *Picea glauca* [Moench] Voss) in a western Quebec landscape. We found that in a 60-year simulation, there is no difference in the dynamics of the tree basal areas between scenarios involving growth rates, with and without climate-induced changes. For both scenarios, we found an earlier decline of deciduous species and an earlier increase of conifers during the simulation period. Our data suggests that under future climate change, the forest succession trajectory will remain unchanged. To enhance forest management, we recommend that managers should account for the earlier offset of fuel transition from deciduous to coniferous types, which is likely associated with increased fire risks.

Keyword: climate change, boreal mixedwood, conifer, deciduous, compositional changes, forest model

4.3 Introduction

Boreal forests play a key role in the maintenance of biogeochemical cycles, species diversity, and carbon pools (Buermann et al., 2013, 2014). Changes in tree growth rates can affect forest functioning due to the effects on species distribution, forest composition and net carbon uptake (Silva et al., 2010; Cahoon et al., 2018). Such changes are predicted under the future climate as increases in temperature and declines in precipitation reduce tree growth rate and induce tree mortality across Western (Silva et al., 2010; Peng et al., 2011; Hogg & Michaelian, 2015) and eastern North America (Hember et al., 2017; De Grandpré et al., 2018) and Eurasia (Kharuk et al., 2017; Neumann et al., 2017). Increases in growth have been reported in areas where abundant soil moisture compensates for the temperature-driven increase in evapotranspiration demand (Silva et al., 2010; McCollum & Ibáñez, 2020). It is therefore of value to mechanistically link trends in the future growth rates with forest succession and ecosystem-level properties such as dynamics of C pools and stands composition.

Presently, boreal mixedwoods of eastern Canada are dominated by shade-tolerant and more slow-growing conifers and shade-intolerant fast-growing deciduous species. Balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), white spruce (*Picea glauca* (Moench) Voss), and eastern white cedar (*Thuja occidentalis* L.) form the former group, and trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.) dominate in the second (Bergeron, 2000; Bose et al., 2015). The stands in that region are commonly initiated by fire and clear-cuts. Non-stand replacing disturbances such as insect outbreaks and windthrows, together with tree- and stand-level processes, such as competition and senescence act as important modifiers of succession

(Morin et al., 1993; Cavard et al., 2011; Boulanger et al., 2017; Ford et al., 2017). The interplay of disturbance histories and the effects of local site conditions allow for a variety of successional pathways often involving a gradual transition from the dominance of early successional hardwoods to admixtures of hardwood–conifer species and, finally, to conifer-dominated stands (Bergeron, 2000). Temporal changes in canopy tree compositions ultimately reflect the variation in species shade tolerance, lifespan, and growth rates (Bergeron, 2000).

The effect of climate change on the relative dominance of coniferous versus deciduous species in the boreal mixedwoods remains a subject of debate. In the boreal mixedwoods, conifer-dominated stands follow deciduous-dominated stands in the successional development. This pathway may be disrupted under the future climates, as the deciduous may be more adapted to a warmer climate than the conifers. Deciduous trees have higher photosynthesis rates and hydraulic conductance that cause them to grow faster and produce more shade in the canopy to limit the growth of the conifers over a longer period (McDowell et al., 2008; Cahoon et al., 2018). The conifers are, however, more resistant to droughts and cold temperatures than the deciduous trees due to the diameter of their tracheids being narrower than the vessels of the deciduous trees. This distinctive adaptation feature enables the conifers to survive and dominate under extreme climatic conditions (McDowell et al., 2008; Kreyling et al., 2015; Cahoon et al., 2018).

Spatially explicit forest gap models such as SORTIE-ND help project the dynamics of forest stand composition (Canham et al., 2005; Ameztegui et al., 2015; 2017; Cristal et al., 2019) and may be instrumental in modelling responses of mixedwood to changes in growth rates. SORTIE-ND operates with tree neighborhood processes such as competitive interactions for resources between individuals to simulate forest dynamics (Cristal et al., 2019). Recent studies have employed

SORTIE-ND to explore the effects of harvesting regimes and post-fire disturbance on the dynamics of conifer-hardwood mixed stands in the boreal region of western Quebec in eastern Canada (Bose et al., 2015; Maleki et al., 2020). However, these studies did not discuss how changes in tree growth rates may influence forest succession and the future forest composition. In this study, we assessed whether the future changes in relative growth rates will affect the stand structure characteristics of mixedwoods.

Specifically, we hypothesized that under future climate, entailing faster growth rates of deciduous species, we should observe (H1) a higher basal area of deciduous species in the canopies than the conifers during the first 30 years, and (H2) a shorter period between the dominance of the deciduous species and the period with the dominance of coniferous species. H1 assumed that faster growth rates of deciduous trees (trembling aspen and white birch) would foster the faster accumulation of deciduous biomass following the stand-replacing disturbance as compared to balsam fir, white spruce, and white cedar. In turn, H2 assumed that faster growth would lead to earlier tree mortality that would accelerate the transition to conifer-dominated stands (Purves et al., 2008). To test the hypotheses, SORTIE-ND was used to predict the changes in the tree basal area of the forests over time at the Lake Duparquet Teaching and Research Forest (LDRTF) located in the boreal mixedwood forest of western Quebec. LDTRF has been sampled repeatedly in recent years and offered the opportunity to monitor the basal area dynamics of the forests. We used inventory data sampled from 431 permanent plots in 1991 (Bergeron, 2000) to parameterize the SORTIE-ND model to simulate the basal area composition of the forest over 60 years. Another empirical data collected in 2013 (Aussenac et al., 2017) were compared with the SORTIE-ND simulation over the first 22 years to understand how much the modelled future deviates from the present.

4.4 Materials and methods

4.4.1 Study area

We conducted the study in mixedwood stands growing in the balsam fir-white birch domain in the Abitibi region of Quebec, Eastern Canada (Fig. 4.1). The study was located in the Research and Teaching Forest of Lake Duparquet (LDTRF) (48.46 N, 79.24 W) at 270–275 m above sea level. The stands originated from seven different fires that occurred in 1760, 1797, 1823, 1847, 1870, 1916, and 1944 (Leduc et al., 2020). The main soil type is clay (Bergeron, 2000; Aussenac et al., 2017). The dominant canopy species include white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), and eastern white cedar (*Thuja occidentalis* L.) (Bergeron et al., 2014). The long-term monthly average temperature ranged between -16.6°C in January and 17.3°C in July. Annual total precipitation was, on average, 894.6 mm (Aussenac et al., 2017). The LDTRF forests experience periodic insect outbreaks, particularly spruce budworm (*Choristoneura fumiferana* Clem.) which cause large reductions in tree diameter growth of the hosts, balsam fir, and white spruce. The forests have not been affected by logging and can be viewed as a result of natural succession (Bergeron et al., 2000).

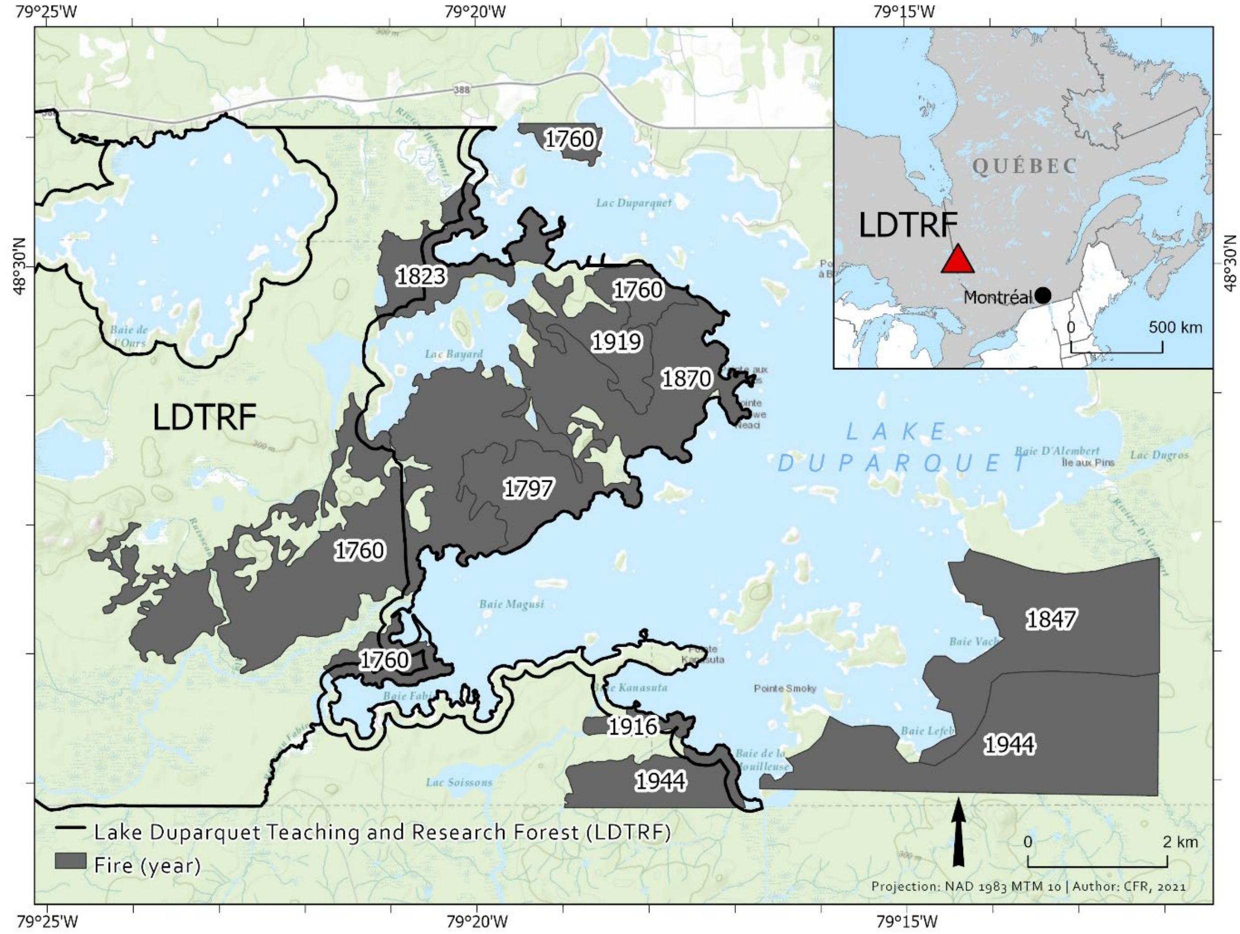

Figure 4.1 Lake Duparquet Teaching and Research Forest (LDTRF) in western Quebec (Canada) with the dates of stand initiating fires dated with the help of dendrochronological methods.

4.4.2 SORTIE-ND Model

SORTIE-ND is a spatially explicit, individual-based forest dynamics model that simulates changes in tree populations over time (Canham et al., 1999; 2005; 2006). In the SORTIE-ND, each tree is a discrete object, described by various attributes such as size, growth rate, age and crown morphology. SORTIE-ND tracks the specific location of each tree and takes into account neighborhood effects to simulate the recruitment, growth, and mortality of every individual within the plot (Canham et al., 1999; 2005; 2006). It also allows modelling of natural disturbance and harvesting. The trees in the model belong to one of the following life-history stages: seedling, sapling, adult, snag, and woody debris. The sub-models control transition along life stages at defined time intervals.

SORTIE-ND works through a parameter file that describes the initial conditions of a stand and the processes (e.g. climate) that act to change these conditions during the stand development for modelling seedlings, saplings, and adult trees (Murphy, 2011). Seedlings’ and saplings’ growth are modelled as a function of understory light requirements of a species. The growth model for the mature trees is based on the maximum growth per year (MaxG, cm/year) of each species. MaxG is the maximum diameter growth the tree can attain, in cm/year. The MaxG is modified by light availability, tree size, climate and neighborhood competition (Maleki et al., 2020).

SORTIE-ND parameter file has been developed to simulate the stand dynamics of the LDTRF in Western Quebec concerning the tree species, which are common in the region: balsam fir, white birch, white spruce, trembling aspen, eastern white cedar, jack pine (*Pinus banksiana* Lamb.), and mountain maple (*Acer spicatum* Lamb.) (Bose et al., 2015). The SORTIE-ND parameter file for the LDTRF has been calibrated and validated successfully by Maleki et al. (2020).

4.4.3 Estimation of growth parameters for SORTIE-ND simulation

We estimated the tree growth response of each species to the climate through dendrochronology techniques. The value of the growth response to climate (GRC) is intended to either increase (MaxG+GRC) or decrease the maximum growth rate (MaxG) (Table 4.1) for the SORTIE-ND simulations.

To estimate the tree growth response to climate (GRC), first, we used Generalized Additive Mixed Models (GAMM) (Wood, 2017) to evaluate the effect of tree age, size, spruce budworm defoliation level, and climate on tree ring basal area increment (BAI) over the period 1967 and 1991. GAMM modelled the basal growth rate of tree *j* at specific year *t* as a function of the tree basal area (variable *BA*) and its cambial age (*Age*) to minimize age and size effects (Dietrich & Anand, 2019). We also included seasonal climatic variables (Temperature, *T* and Climate Moisture Index, *CMI*) and spruce budworm defoliation level (DFI) into the model. The global model took the following form:

$$\log(\mathrm{BAI}_{jt}) = \beta\,(\log(\mathrm{BA}_{jt})) + f(\mathrm{Age}_{jt}) + f(\mathrm{T}_{t}) + f(\mathrm{CMI}_{t}) + f(\mathrm{DFI}_{\mathrm{t}}) + \mathrm{Z}_{j} + \varepsilon_{j} + \mathrm{AR1}_{j} \quad \text{(Equation 4.1)}$$

where BA_{jt} is the inner-bark basal area of tree *j* at specific year *t* (computed as the sum of BAI of previous years), *Age* is the cambial age of tree *j* at year *t,* T_t is the temperature at year *t* and CMI_t

is climate moisture index at year *t*. The tree identity (Z_j) was used as a random effect in the GAMM. We included an auto-regressive term ($AR(1)j$) to account for the temporal correlation between successive values of BAI data. GAMM was realized in R package *mgcv* (Wood, 2017).

For each species, the model was fit on a random subset of 70% of the trees. The predictive capacity of the model was then validated using the remaining 30% of the trees, computing the adjusted R^2 (i.e. measure of goodness of fit for GAMM) and the root means square error (RMSE) of predicted versus observed growth rates.

We modelled the effect of climate by allowing variation of climate (T_t and CMI_t) and Z_j variables and keeping BA_{jt}, Age_{jt}, DFI_t variable constant at zero. We back-transformed the prediction to the original scale (cm^2/year) of each species by following the procedure described by Girardin et al. (2016).

To assess the growth rate changes (GRC) in the BAI chronologies (Table 1), we relied on linear mixed effect models (LME), which used the species-specific BAI as dependent variables. In the LME, we included the calendar year (*Year*) of tree *j* as the fixed effect, tree identity (Z_j) as the random effect, and the auto-regressive term (AR(1)). The model took the following structure:

$$BAI_j = \beta\,(Year_j) + Z_j + \varepsilon_j + AR1_j \qquad \text{(Equation 4.2)}$$

SORTIE-ND has been structured to operate at a rate of increase in diameter per year (GRC, cm/year). Therefore, we converted the basal area growth rate in cm^2/year to diameter growth rate change in cm/year as used in SORTIE-ND.

Table 4.1 Growth rates of species for SORTIE-ND simulation

NoClim represents the simulation scenario with the maximum growth rate of the tree species determined through several experiments for Lake Duparquet, and *ClimChange* represents the simulation with a modified maximum growth rate due to climate variability. For the *ClimChange* we assumed that the rate of climate changes will be the same throughout the simulation period 60 years

	Tree maximum growth rate, MaxG (cm/year)	Growth rate change (GRC) due to climate (cm/year)	Future growth rate (cm/year), (MaxG+/-GRC)
	NoClim		ClimChange
Trembling aspen	0.739	0.050	0.789 (increase)
White birch	0.616	0.062	0.678 (increase)
White cedar	0.377	0.101	0.478 (increase)
Balsam fir	0.722	-0.113	0.609 (decrease)
White spruce	0.821	-0.080	0.741 (decrease)

4.4.4 Simulation runs

We created 431 initial starting conditions representing the empirical data that were collected from the 431 plots in 1991. The size of each plot for simulation runs was set to 4 ha (200 m × 200 m). It is the realistic minimum size that is recommended for SORTIE-ND simulation (Murphy, 2011). We set the timestep to one year as some of the behaviors (e.g., competition, mortality) in the LDTRF parameter file cannot handle timesteps longer than one year (Bose et al., 2015; Maleki et al., 2020). These were one-year intervals in our study.

To evaluate the effects of climate on post-fire stand dynamics, we ran the simulations (60 years, from 1991 to 2051) in two scenarios; MaxG without climate modification and MaxG with climate modification. For the first simulation (i.e. MaxG without climate modification), we used the original LDTRF parameter file that had been parameterized and validated through several studies (Poulin & Messier, 2008; Beaudet et al., 2011; Leduc & Coates, 2013; Bose et al., 2015; Maleki et al., 2020). In this way we modelled the changes in stand composition, assuming no changes in climate on tree growth in the forest succession dynamics.

For the second simulation (i.e. MaxG with climate modification), we accounted for the effect of changing climate by altering MaxG as shown in Table 4.1. This simulation enabled us to reconstruct the stand dynamics, accounting for changes in climatic variables and their effects on individual tree growth, and consequently on stand composition. We admit that climate influence is non-linear and will continue to change in the future, so is the impact on growth. However, for this study, we assumed a constant climate influence on tree growth rate over time to understand how it will influence the forest successional dynamics.

An earlier study (Morin et al., 1993) suggested that spruce budworm outbreaks for the study region occur every 30 to 35 years. Therefore, as the most recent outbreak took place during 1972-1987, we expected the next outbreak to occur around 2021–2022. We implemented a spruce budworm outbreak simulation after a 30-year run (year > 2021). Thus from the 30-year run, we allowed SORTIE-ND to kill a predefined number of trees (episodic mortality in terms of SORTIE) based on three DBH classes for balsam (5-10 cm (mortality rate=63.7%), 10-15 cm (75.8%), and > 15 cm (82.5%)) and one DBH class (>10cm (mortality rate=29%)) for white spruce until the 60-year run was reached. The mortality rates were obtained from Bergeron et al. (1995) for balsam fir in the study area, and Blais (1981) for white spruce in the boreal forests of eastern Canada.

We examined the dynamics of tree composition overtime to answer H1 and H2. First, we compared the stem basal area of the tree species simulated from the two scenarios (i.e., MaxG without climate modification and MaxG with climate modification) to empirical data collected in 2013 to better understand how much the modelled futures deviates from the climate of the present. The comparison was made for stands that regenerated from fires in 1847 and 1823 for 22-year simulation time as the data collected in 2013 only covered these two stands.

Second, we regressed the basal area against the 60-year simulation time for the two scenarios using polynomial regression built within the R package *ggplot2* (Wickham, 2016). We similarly regressed the basal area against the time since the stand-replacing fire for the two scenarios (i.e. MaxG without climate modification and MaxG with climate modification) using the polynomial regression to understand the basal area changes with stand development.

We used one-way ANOVA to assess if there existed differences in the means of the basal area over the entire simulation period (60 years) for each post-fire stand and the total basal area of a species under the two scenarios (MaxG without climate modification and MaxG with climate modification). Tukey test for multiple pairwise comparisons was used to test for significant differences in the mean basal area between the two scenarios. We further visualized the structural output of the simulation as histograms of the species' basal area (m^2 ha^{-1}). All analyses were done using the R software (R Core Team, 2018).

4.5 Results

4.5.1 Differences in tree basal areas between climate scenarios

Comparison of the empirical (2013) and simulated data in the short-term (22 years) showed that the SORTIE-ND slightly underestimated the stem basal area for trembling aspen (~4%), followed by balsam fir (~20%) and then white birch (~23%) for the 1823 stand (Table 4.2). The model underestimation for the 1823 stand was higher for the white cedar (~40%) and white spruce (~48%). In the case of the 1847 stand, the model underestimation was lower for the white birch (~15%) and balsam fir (~16%). The magnitude of underestimation was, however, higher for trembling aspen (~30%), white cedar (~39%), and white spruce (~43%).

The two scenarios, i.e. MaxG without climate modification and MaxG with climate modification did not differ significantly ($p>0.05$) in the magnitude of the basal areas of the tree species at the end of the long-term simulation (60 years) (Table 4.2; Fig 4.2). The difference in the overall stem basal area between the scenarios was approximately 0.2m^2/ha (Table 4.2). We also observed that, for the two scenarios (Fig 4.3), the basal area of balsam fir, white spruce, and white cedar increased over time until the end of the 60-year simulation. The basal area of the white birch decreased during the simulation period, while the trembling aspen increased slightly during the first 30 years, followed by a decrease until the end of the 60-year simulation (Fig 4.3).

The magnitude and diameter distribution of basal areas of the species changed significantly between the scenarios and the baseline data of 1991 (Table 4.2; Fig 4.2). For the scenario, MaxG with climate modification, the basal area of trembling aspen and white birch decreased by 8.7% and 20.3% respectively in comparison to the baseline data, whereas balsam fir, white cedar, and white spruce increased by 120.9%, 73.6%, and 37.6% respectively (Table 4.2; Fig 4.2). In the case of the scenario, MaxG without climate modification, however, the basal area for trembling aspen and white birch decreased by 9.9% and 21.6% respectively in comparison to the baseline data, whereas balsam fir, white cedar, and white spruce increased by 121.9%, 70.8%, and 41.8% respectively (Table 4.2; Fig 4.2).

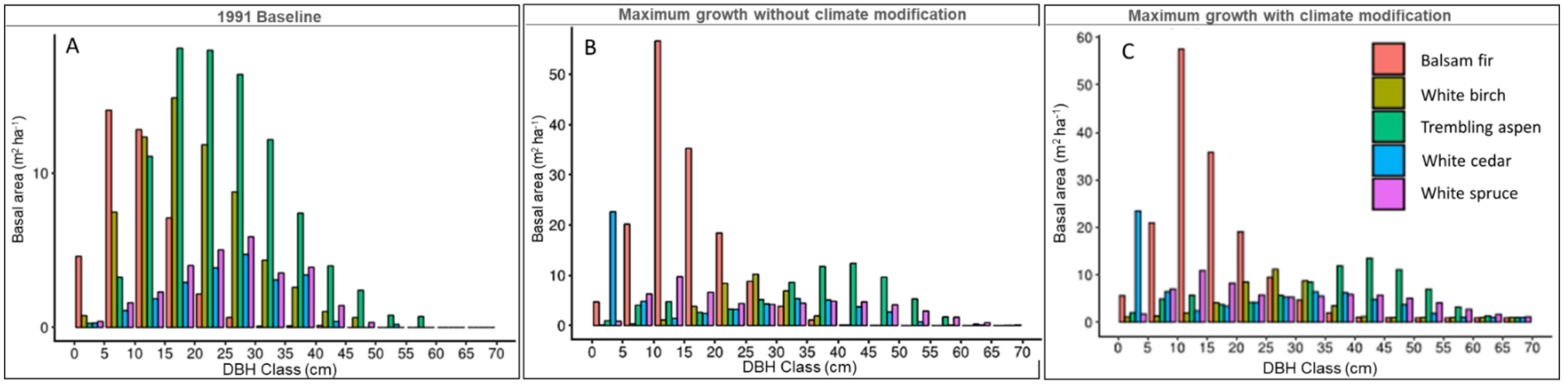

Figure 4.2 Observed (A) and simulated basal area distributions for maximum growth without climate modification (B) and maximum growth with climate modification (C) over 60 year period of the 431 simulations

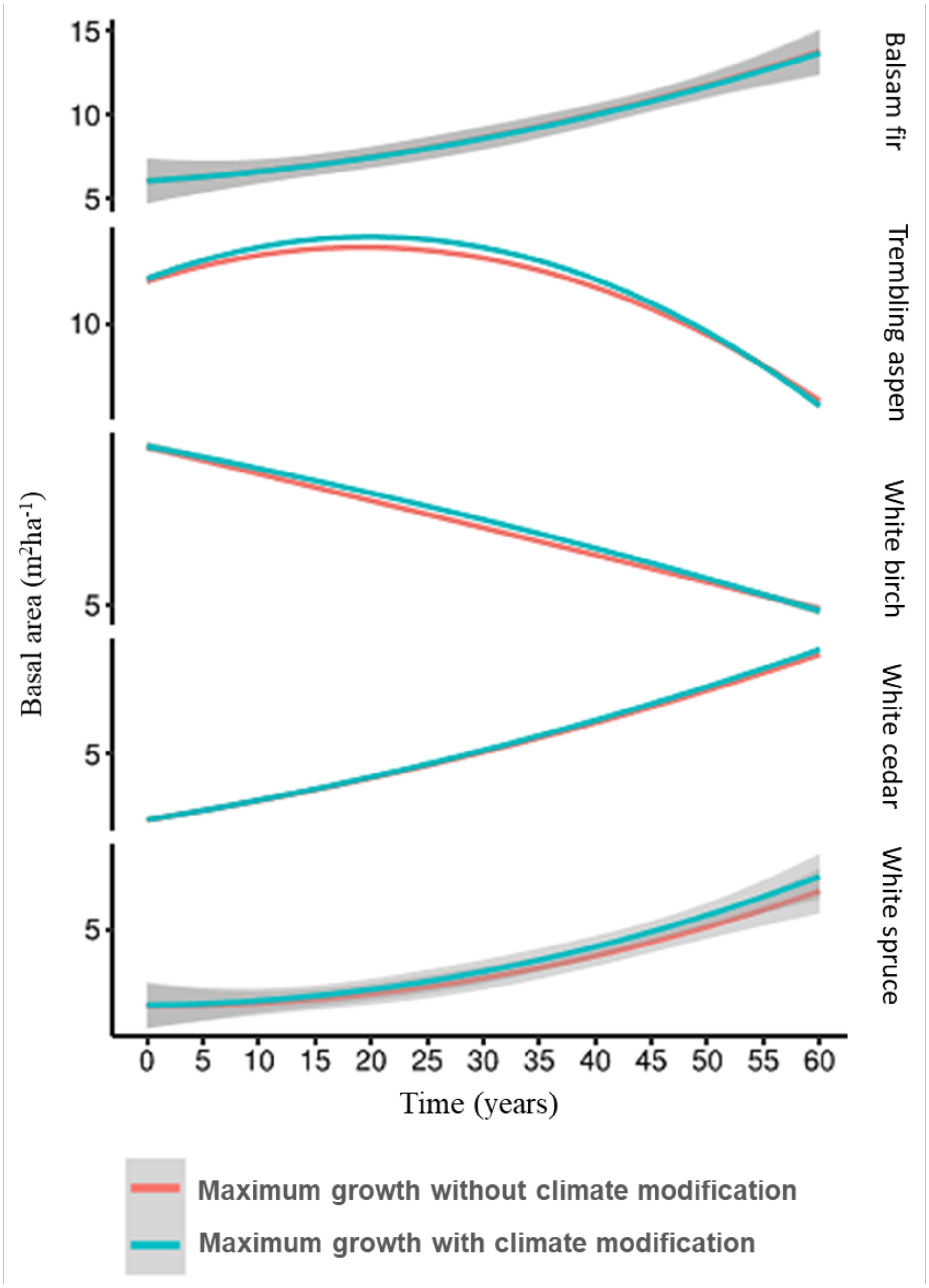

Figure 4.3 SORTIE-ND simulations for scenarios, Maximum growth without climate modification and Maximum growth with climate modification over 60 years. Gray shading delimits the 95% confidence interval.

Table 4.2 Baseline measurements and simulated basal area (m^2 ha^{-1}, ±SE) of studied species. *Baseline* represents the measurement values of the 1991 field survey, *Constant clim.* represents a simulation with a maximum growth without climate modification, and *Clim. change* represents a simulation with a maximum growth with climate modification over the 60-year or 22-year simulation period. Stand initiation refers to the dates of stand-replacing fires. The simulation produced basal areas which were significantly different from the observed baseline data at $p < 0.05$.

Stand initiation	Scenarios	Trembling Aspen	Paper Birch	Balsam Fir	White Spruce	White Cedar
1760	Baseline 1991	1.74±0.33	4.77±0.38	1.84±0.18	1.46± 0.19	7.79± 0.54
	Constant clim (60 years)	0.92±0.168	2.09±0.27	5.53± 0.55	2.99±0.32	18.73±1.22
	Clim. Change (60 years)	0.94±0.18	2.09±0.27	5.45±0.54	2.89±0.34	19.08±1.22
1797	Baseline 1991	0.35±0.09	5.66±0.41	1.98±0.17	1.49±0.16	2.74±0.27
	Constant clim (60 years)	0.58±0.16	2.49±0.29	11.94±1.02	3.63±0.28	8.38±0.81
	Clim. Change (60 years)	0.62±0.157	2.48±0.29	11.90±1.02	3.49±0.29	8.56±0.82
1823	Baseline 1991	5.73±0.40	2.77±0.19	3.08±0.19	1.75±0.16	0.38±0.07
	Constant clim (60 years)	6.25±0.41	1.35±0.15	13.83±0.97	4.48±0.28	1.07±0.23
	Clim. Change (60 years)	6.29±0.40	1.33±0.15	13.67±0.96	4.28±0.28	1.08±0.23
	Empirical data 2013	6.15±0.39	3.31±0.47	7.9± 0.03	5.73±0.57	2.07±0.06
	Simul Constant clim (22 years)	5.93±0.07(4%)	2.56±0.03(23%)	6.32±0.07(20%)	2. 94±0.04(49%)	1.11±0.02(46%)
	Simul Clim change (22 years)	6.03±0.07(2%)	2.59±0.03(22%)	6.29±0.07(20%)	2.98±0.04(48%)	1.24±0.02(40%)
1847	Baseline 1991	8.49±0.48	3.30±0.21	4.90±0.29	3.86±0.25	0.55±0.09
	Constant clim (60 years)	5.27±0.29	1.29±0.15	14.5±0.87	5.32±0.27	1.22±0.23
	Clim. Change (60 years)	5.31±0.29	1.28±0.15	14.35±0.87	5.07±0.27	1.24±0.23

Table 4.2 (follow)

	Empirical data 2013	9.10±0.47	3.11±0.32	7.91±0.03	6.36±0.41	3.98±0.04
	Simul Constant clim (22 years)	6.36±0.09(30%)	2.64±0.04(15%)	6.68±0.08(16%)	3.65±0.07(43%)	2.41±0.03(39%)
	Simul Clim change (22 years)	6.45±0.08(29%)	2.68±0.04(14%)	6.66±0.078(16%)	3.69±0.07(42%)	2.42±0.07(39%)
1870	Baseline 1991	9.13±0.59	4.19±0.29	2.47±0.16	3.19±0.25	0.02±0.01
	Constant clim (60 years)	8.84±0.53	1.22±0.12	8.97±0.62	6.68±0.36	0.04±0.02
	Clim. Change (60 years)	8.76±0.51	1.19±0.12	8.87±0.62	6.48±0.37	0.04±0.02
1916	Baseline 1991	11.95±0.82	5.45±0.39	3.25±0.22	1.42±0.209	0.69±0.11
	Constant clim (60 years)	5.38±0.45	3.63±0.37	10.58±0.78	3.50±0.29	2.17±0.41
	Clim. Change (60 years)	5.15±0.43	3.64±0.37	10.56±0.78	3.29±0.31	2.21±0.41
1944	Baseline 1991	8.26±0.57	6.67±0.37	2.72±0.21	0.58±0.07	0.16±0.04
	Constant clim (60 years)	6.19±0.48	4.56±0.36	8.23±0.59	1.85±0.22	0.46±0.16
	Clim. Change (60 years)	6.17±0.48	4.52±0.36	8.19±0.59	1.75±0.23	0.48±0.17
Overall	Baseline 1991	6.78±0.62	4.68±0.44	3.20±0.29	1.70±0.17	1.06±0.11
	Constant clim (60 years)	6.11±0.30	3.67±0.29	7.101± 0.49	2.41±0.11	1.81± 0.14
	Clim. Change (60 years)	6.19±0.30	3.73±0.29	7.07±0.49	2.34±0.11	1.84±0.14

4.5.2 Species successional dynamics following stand replacing disturbance

The trends in the accumulation of the basal area of the species in the post-fire stands were identical in the scenario with the maximum growth (MaxG) without climate modification and the scenario, MaxG with climate modification (Fig 4.3). In both scenarios, the basal area of deciduous trees (trembling aspen and white birch) was higher in the youngest post-fire stand (<50 years) and it decreased with time as the post-fire stand got older. For the conifers, the basal area of both balsam fir and white spruce increased until the post-fire stand reached the age of ~150 years. After ~150 years since the stand-replacing fire, the basal area of the balsam fir and white spruce declined. The basal area of white cedar was lower in the young post-fire stand (<100 years) and it increased exponentially after ~100 years (Fig 4.3).

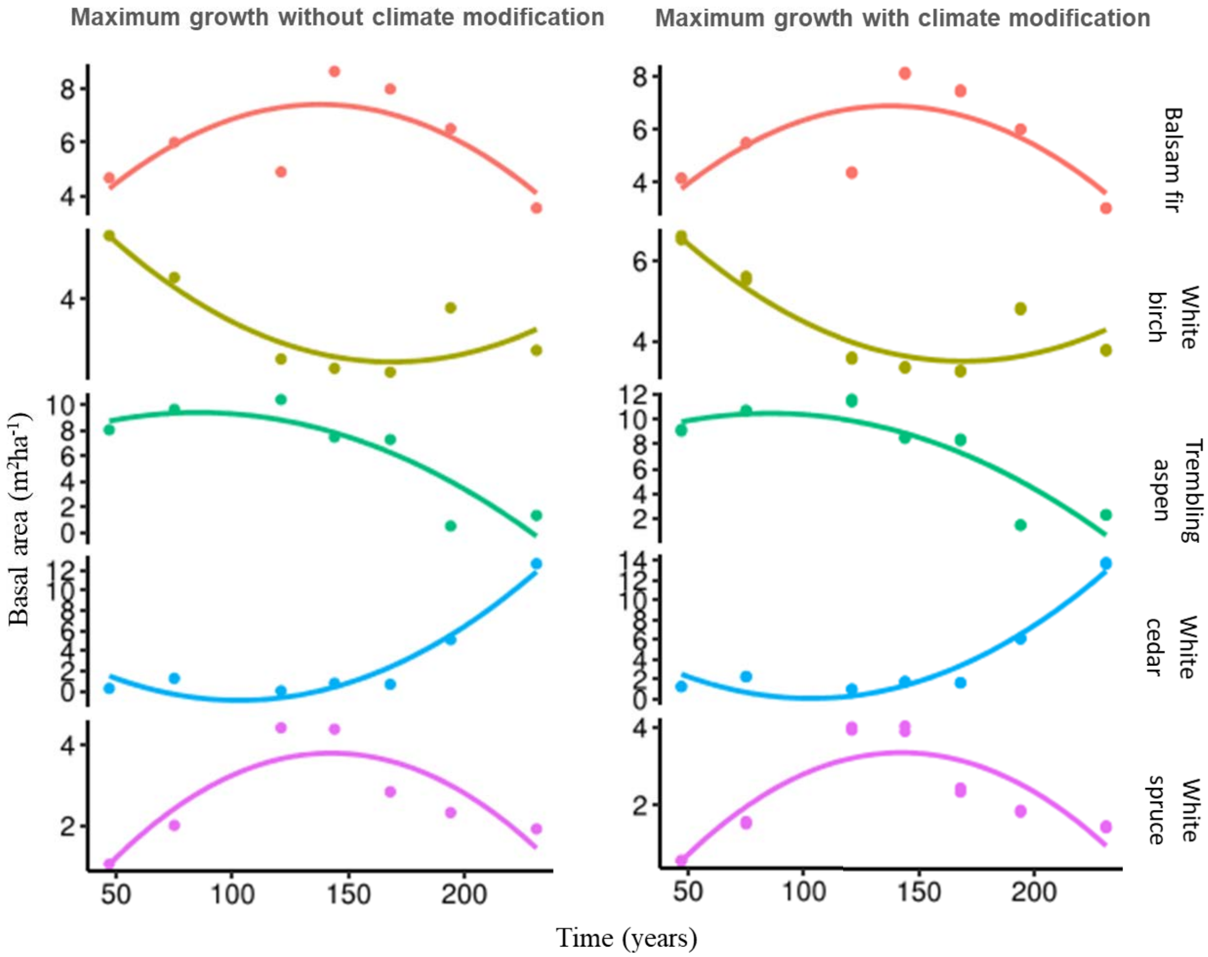

Figure 4.4 Simulated successional dynamics of the species basal area as a function of time since stand establishment under two scenarios: (A) MaxG without climate modification and (B), and a MaxG with climate modification. Actual data points for the regression curves, significant at $p < 0.05$.

4.6 Discussion

The empirical and simulated stem basal area (Table 4.2) over the short-term (22 years) were generally similar for trembling aspen, white birch, and balsam fir compared to the white spruce and white cedar. One of the most important causes of the disagreement between the empirical and simulated data for the white spruce and white cedar may be due to the inability of the SORTIE-ND model to capture the changes in growing season length in the simulation. The length of the growing season has increased for up to two months longer in the boreal zone (Price et al., 2013; Girardin et al., 2016), which presents opportunities for more forest growth as reflected in the empirical data.

The results of the long-term simulation (60 years) showed a significant increase in the basal area of conifers (balsam fir, white cedar, and white spruce) over the simulation period (Table 4.2, Fig 4.3). We expected that the basal area of the deciduous species would be greater than that of conifers at the end of the simulation because they experienced a stronger growth response to changes in climate, as compared to the conifers (Chapitre 3). We, however, observed the opposite situation. The results suggest that even faster growth of deciduous species in the future will shorten their period in the canopy through the earlier onset of age-related mortality (Bigler, 2016; Fridley & Wright, 2018).

Dynamic of forest species succession in post-fire stands were similar under MaxG without climate modification and MaxG with climate modification (Fig 4.4). The younger post-fire stands (< 100 years) were dominated by trembling aspen and white birch. The pattern exemplified the tendency of these species to establish immediately after the disturbance by either re-sprouting from surviving root systems or by growing rapidly from seeds that persisted in the soil. These deciduous trees dominate the stand canopy composition in the first few decades since the stand-replacing event and over-compete conifers (white spruce, balsam fir, white cedar) (Bergeron, 2000, 2004).

The post-fire forest stands older than 100 years experienced a decline in the basal area of trembling aspen and birch (Fig 4.3). Age-related mortality of the trembling aspen and white birch could have created space and allowed sunlight penetration into the forest floor, to facilitate the recruitment of the conifer saplings (balsam fir, white spruce, and white cedar) and the germination of seeds on litter, ground moss, and deadwood into the canopy (Simard et al., 1998). The oldest post-fire stands (> 150 years), however, exhibited a decline in the basal area of white spruce and balsam fir. Spruce budworm outbreak is a likely driver of this pattern. The outbreaks kill the hosts and facilitate the recruitment of white cedar (Bergeron, 2000; Rogers et al., 2018). The increased dominance of the white cedar in the oldest postfire stands is also attributed to the reduced availability of the deciduous species, whose litter inhibited the regeneration of the species (Bergeron, 2000).

The transition from deciduous to coniferous forests at the later succession stage can result in a large number of spruce budworm host species, which may intensify their defoliation activities and tree mortality. The mortality of the conifers would generate more fuels to increase the risk of wildfire, especially, if there is reduced moisture in the fuels under the canopy (Banerjee et al., 2020). The increased risk of wildfire will favour the repopulation of pioneer species, in particular trembling aspen (Boulanger & Puigdevall, 2021).

Our finding is consistent with D'Orangeville et al. (2016) who found that Quebec's boreal forests may not be affected by climate change due to the increasing wetness of the region. This lack of forests changes may be beneficial for biodiversity in the boreal region as the forests can continue to act as a climatic refugium for threatened species in a warmer climate.

Our SORTIE-ND model simulation was based on the historical variability of climate. This assumption may be biased because climate change is non-linear and therefore, the impact on tree growth and forest composition will change in the future, warrantying the inclusion of projected climate change scenarios in further SORTIE-ND simulations to better project future forest composition.

4.7 Acknowledgements

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CHAPITRE V

CONCLUSION GÉNÉRALE

The study assessed the influence of climatic variation on the long-term growth rate of dominant tree species in the entire boreal mixedwoods of the province of Quebec in eastern Canada. In chapter two, we used an inventory and tree ring dataset (~2700 trees) to assess the growth rate changes of shade-intolerant trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lambert) from the nineteenth century until the late twentieth century. In chapter three, I used a tree ring dataset (2058 trees) of three conifers, balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss) and white cedar (*Thuja occidentalis* L.), and two hardwood trees, trembling aspen and white birch (*Betula papyrifera* Marsh) which co-occur in the mixedwoods forest of Lake Duparquet Teaching and Research Forest in the Abitibi-Temiscamingue region of Western Quebec to assess their growth response to climate. I also examined the influence of spruce budworm outbreaks on tree growth trajectories. In Chapter Four, we demonstrated the use of a stand dynamics simulation tool, SORTIE-ND adapted for the mixedwoods of eastern Canadian boreal forest to assess the potential influence of the different responses of trees species to climate variability on the future succession trajectory of the boreal mixedwood forests. Finally, I used the results of the three Chapters (2, 3, 4) as guides to suggest strategies to improve mixedwood management in the eastern Canadian boreal forest.

5.1 Growth rate response to climate warming is species-specific

Trembling aspen, white birch, and white cedar (Chapters 2 and 3) showed a positive response to climate warming whereas balsam fir and white spruce showed a negative response (Chapter 3) with jack pine showing no significant growth trend (Chapter 2). Climate warming across the boreal mixedwood may have stimulated photosynthetic activity, thereby promoting the growth of trembling aspen, white birch, and white cedar (Fang et al., 2014; Loehle & Solarik, 2019).

The outbreak of spruce budworm from 1972 to 1987 likely induced a growth decline in the hosts, balsam fir, and white spruce during the short period of analysis (i.e., 1967 and 1991) (Chapter 2). In addition, the defoliation of the spruce budworm host may create large openings, and reduce competition for sunlight, water, and nutrients among surviving trees, further promoting the growth of the non-hosts trees, namely trembling aspen, white birch, and white cedar (Bergeron, 2000; Anderegg et al., 2015; Boulanger et al., 2017).

5.2 Trees growth rates are modulated by local factors

The influence of climate on growth rate is confounded by the effects of competition and the slope of the terrain. These factors altered the growth response of trees to climate (Chapter 2), suggesting that the effects of climate change on growth will vary according to the local environmental conditions. Earlier studies in the boreal region found that site variables (e.g., competition and terrain slope) modified the availability of resources such as soil moisture that impact the response of the tree species to the climate variability (Silva et al., 2010; Luo et al., 2019; Messaoud et al., 2019).

The trees grow better in the flat sections of the study area (Chapter 2), which may be due to the generally higher water availability in such habitats (Anyomi et al., 2012; Marchand et al., 2019). Furthermore, the availability of water combined with sustained warmer temperatures at such lower portions of the slope possibly favored the growth of trees. On the contrary, the trees on the steeper and uninterrupted portion of the terrain suffer from runoff and warm-season water deficits. Hence, tree growth is not favored under these conditions (Marchand et al., 2019).

Competition between trees plays an important role in influencing growth because it changes the resource availability for growth (Cavard et al., 2011; Huang et al., 2013). Trees growing on sites with lower competition experienced the positive effect of temperature on growth (Chapter 2) because trees tend to increase growth in uncrowded stands where light and moisture are fully utilized to increase photosynthesis (Cavard et al., 2011; Anderegg et al., 2012; Huang et al., 2013).

5.3 Differential growth rates and boreal species composition

The differences in the growth rate of tree species have demographic consequences because it is a temporal determinant of tree species domination in the boreal forest (Bigler, 2016; Seidl et al., 2017; Büntgen et al., 2019). Nonetheless, the climate-induced growth rate differences among species (Chapter 3) appear not to alter the long-term succession dynamics in the studied mixedwood forests (Chapter 4). SORTIE-ND simulation showed no difference in the dynamics of the tree basal areas between scenarios involving growth rates, with and without climate-induced changes (Chapter 4). For both scenarios, we found an earlier decline of deciduous species and an earlier increase of coniferous species during the simulation period. Our research shows that under future climate change, the dynamics of forest succession may be consistent with the succession trajectory under historical climate.

5.4 Management implication

In ecosystem-based forest management, forest practitioners use the natural dynamics of the forest as a reference to set management strategies and develop or adapt silvicultural practices (Dhital et al., 2015). The results of the study suggest that climate change is altering the growth dynamics of the boreal mixedwood forests which need to be taken into consideration in the management of the forests.

The enhanced growth response of trembling aspen, white birch, and white cedar to climate change (Chapter 2 and 3) would benefit forestry as it can increase the profitability of forest management programs (Bigler, 2016). Fast growth causes trees to mature early, which can reduce the rotation time for timber production. This means that the intensity and frequency of silvicultural practices such as thinning, pruning, and harvesting could be changed to reflect the current understanding of tree growth variability (Thiffault et al., 2021).

Local environmental and disturbance factors have the potential to alter species-specific growth responses to climate change (Chapter 2 and 3). Therefore, it is important that as managers develop the tools for forest management, they consider the local site modulating factors. For example, moderate to gentle slopes and less crowded forest stands are characterised by soil moisture availability that can buffer the negative effects of extreme temperatures and heatwaves (Marchand et al., 2019; Thiffault et al., 2021). These places can serve as sanctuaries for species that are under physiological stress due to high temperatures.

Spruce budworm defoliation reduces the growth and survival of the host tree, balsam fir and white spruce (Chapter 3). To reduce the impact of the insect activity on the host trees, active methods such as the use of natural insect predators can minimize the rapid reproduction of spruce budworms to reduce their defoliation activity on the host. In addition, it might be important to increase the proportion of spruce budworm non-host (deciduous trees) to reduce the susceptibility of the host to insect attack (Volney & Fleming, 2000; MacLean & Clark, 2021).

5.5 Limitation of the study

There were key limitations during the study. The tree ring data for the study consisted of tree samples that were live and dominant at the time of sampling. The absence of information on the trees that died before the sampling could have, therefore, introduced biases in the estimation of growth responses to climate change (Duchesne, et al., 2019).

A significant portion of the data (Chapter 2) was from managed forests that are severely disturbed by harvesting activities. This means that the harvesting activities in the stands could have impacted the tree canopy conditions and influenced the estimation of tree growth trends (Duchesne, et al., 2019). Another disturbance factor is the forest tent caterpillar, which can defoliate the hosts, trembling aspen and white birch and may affect the growth of the host and response to climate (Cooke & Lorenzetti, 2006).

5.6 Knowledge gaps and avenues for further research

The boreal mixedwood forests have multiple and diverse components. The forests vary in terms of tree species mixtures, vertical stratification and horizontal tree canopy structure, biomass within species and across species, and habitats (Payne et al., 2019). At the same time, the forests are managed for a variety of objectives including biodiversity, wildlife habitat, products, and recreation (Brandt et al., 2013). Besides these factors, there are external forces such as climate, fire, and insect outbreaks, whose magnitudes of effects on forests have become uncertain since the mid of 20th Century (Boulanger et al., 2017). It is important to explore how these interacting factors impact trees' long-term growth.

Climate change effects are non-linear and will continue to change in the future, as will the effects on tree growth. It is unclear the influence of the projected climate change from global climate models on the future forest succession trajectory of the mixedwood forests. Future climate change scenarios can be integrated into SORTIE-ND to make credible projections of forest dynamics (Ameztegui et al., 2015, 2017; Cristal et al., 2019). This is an interesting avenue for research as SORTIE-ND can help to improve our knowledge of forest stand dynamics, particularly dynamics related to changes in climate, biotic and abiotic factors.

ANNEXE A

INFORMATIONS COMPLÉMENTAIRES CHAPITRE II

Table A2.1 GAMM model comparison

Models	**Jack pine** **AICc**	**Trembling aspen** **AICc**
$\log(\mathrm{BAI}_{jkt}) = \beta\,(\log(\mathrm{BA}_{jkt})) + f(\mathrm{Age}_{jkt}) + f(\mathrm{CI}_{k,}\ \mathrm{TMax}_{k}) + f(\mathrm{CI}_{k,,}\ \mathrm{CMI}_{k}), + f(\mathrm{Slope}_{k,}\ \mathrm{TMax}_{k}) + f(\mathrm{Slope}_{k,}\ \mathrm{CMI}_{k}) + Z_{jk} + \varepsilon_{jk} + \mathrm{AR1}_{jk}$	14959.41	4645.048
$\log(\mathrm{BAI}_{jkt}) = \beta\,(\log(\mathrm{BA}_{jkt})) + f(\mathrm{Age}_{jkt}) + f(\mathrm{CI}_{k,}\ \mathrm{TMax}_{k}) + f(\mathrm{Slope}_{k,}\ \mathrm{TMax}_{k}) + Z_{jk} + \varepsilon_{jk} + \mathrm{AR1}_{jk}$	14961.81	4645.999
$\log(\mathrm{BAI}_{jkt}) = \beta\,(\log(\mathrm{BA}_{jkt})) + f(\mathrm{Age}_{jkt}) + f(\mathrm{CI}_{k,,}\ \mathrm{CMI}_{k}), + f(\mathrm{Slope}_{k,}\ \mathrm{CMI}_{k}) + Z_{jk} + \varepsilon_{jk} + \mathrm{AR1}_{jk}$	14970.27	4648.790

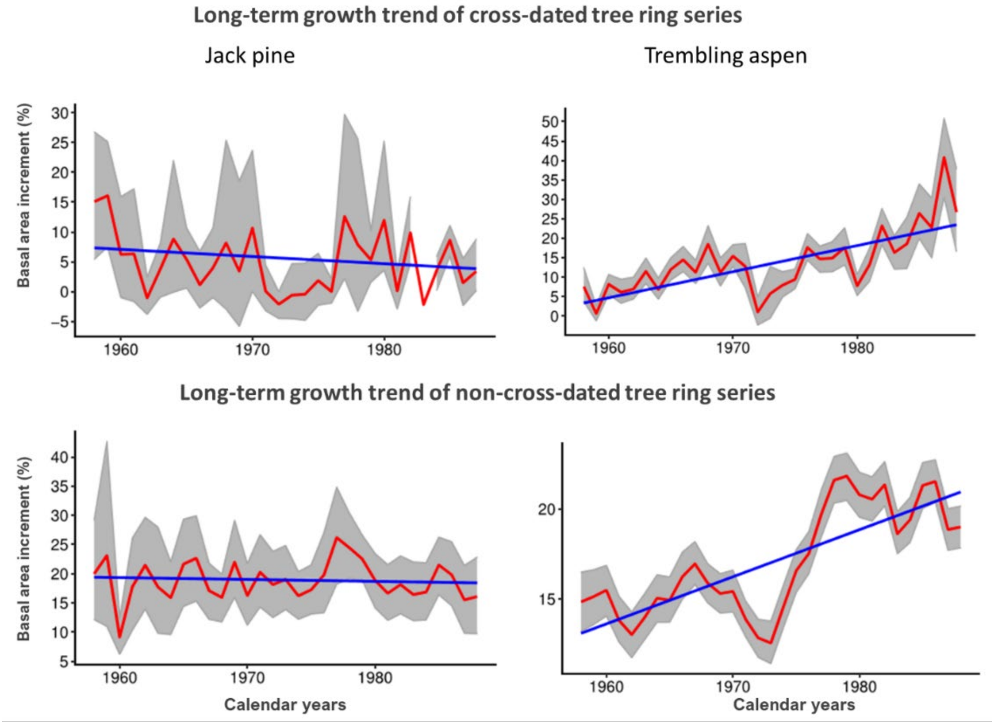


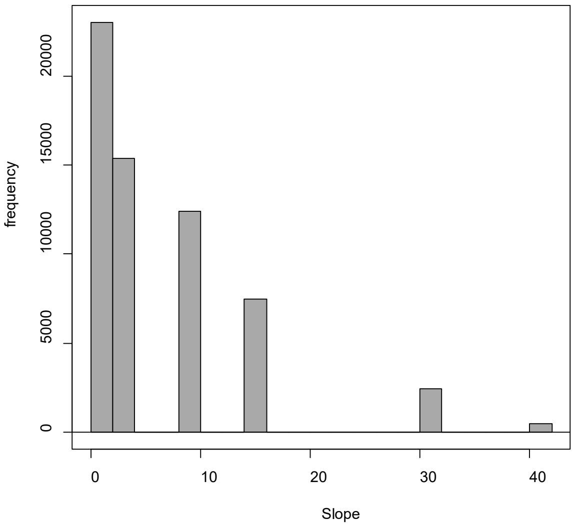
Figure A2.1 Long-term growth trend of cross-dated (top) and non-cross-dated (bottom) tree ring series of jack pine (left panel) and trembling aspen (right panel) for the western Quebec.

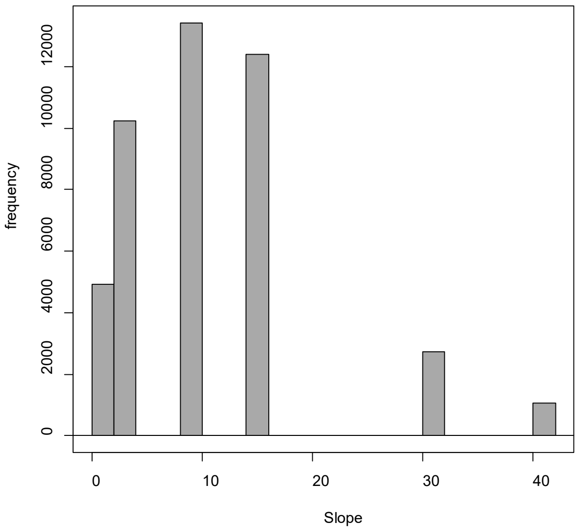
The period of analysis was adjusted to ensure the species chronologies were of the same length (1958 -1988). The blue line is the trend line, the red is the average growth trajectory, and the grey is the 95% confidence interval. The growth trend was estimated using GAMM as detailed in the Methods section of the main text. Since the analysis was based on a small subset of trees in Western Quebec, we excluded the environmental variable from the GAMM and retained only the age (Age) and the size (BA) effects with subject trees (Z) as random effects and accounted for the auto-regressive (AR1) effect as follows: $\log(BAI) = \beta(\log(BA)) + f(Age) + Z + \varepsilon + AR1$. The number of the cross-dated tree ring series for jack pine and trembling aspen were 147 and 412 respectively. Similarly, the number of the non-cross-dated tree ring series for jack pine and trembling aspen were 251 and 327 respectively.

Jack pine

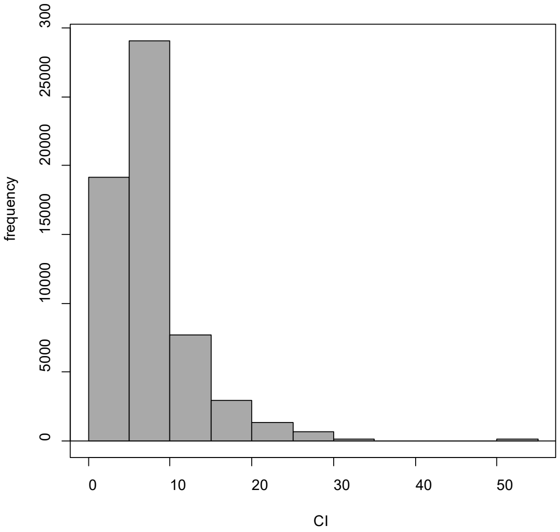
Trembling aspen

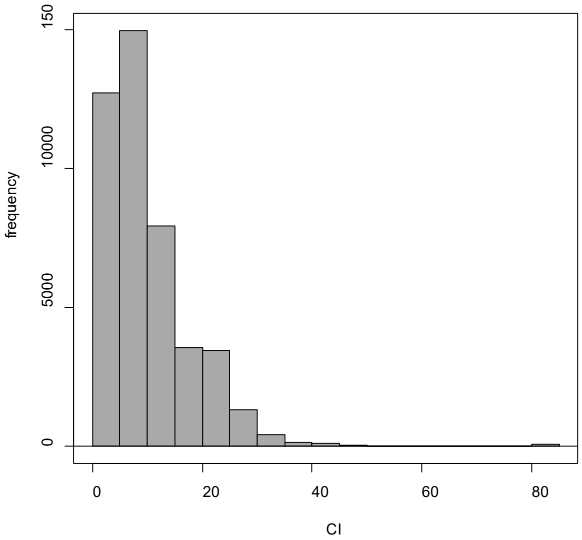
Terrain slope (%)



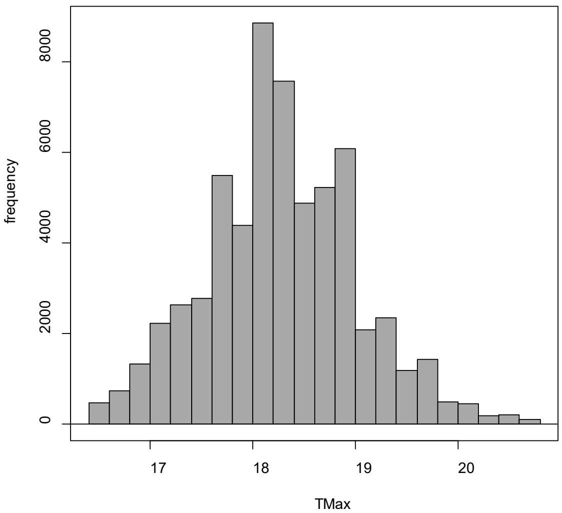


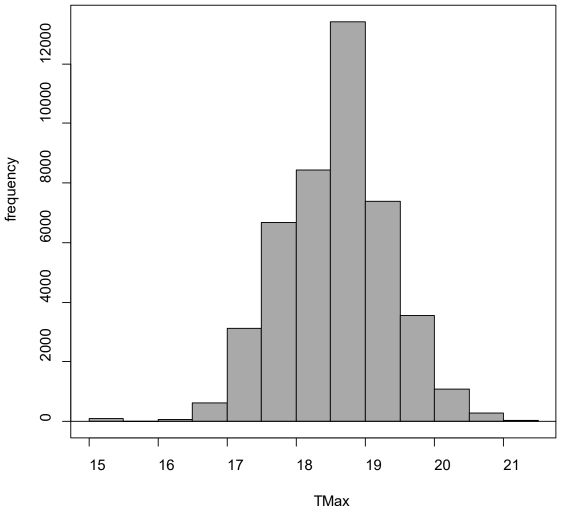
Basal area per hectare, CI (m^2ha^{-1})



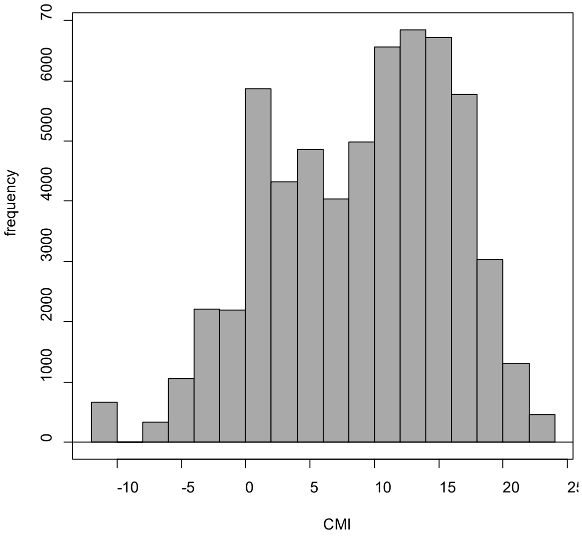


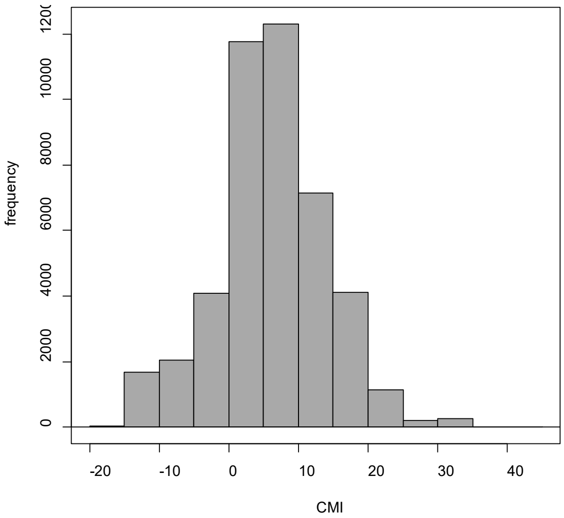
Maximum temperature (TMax, °C)



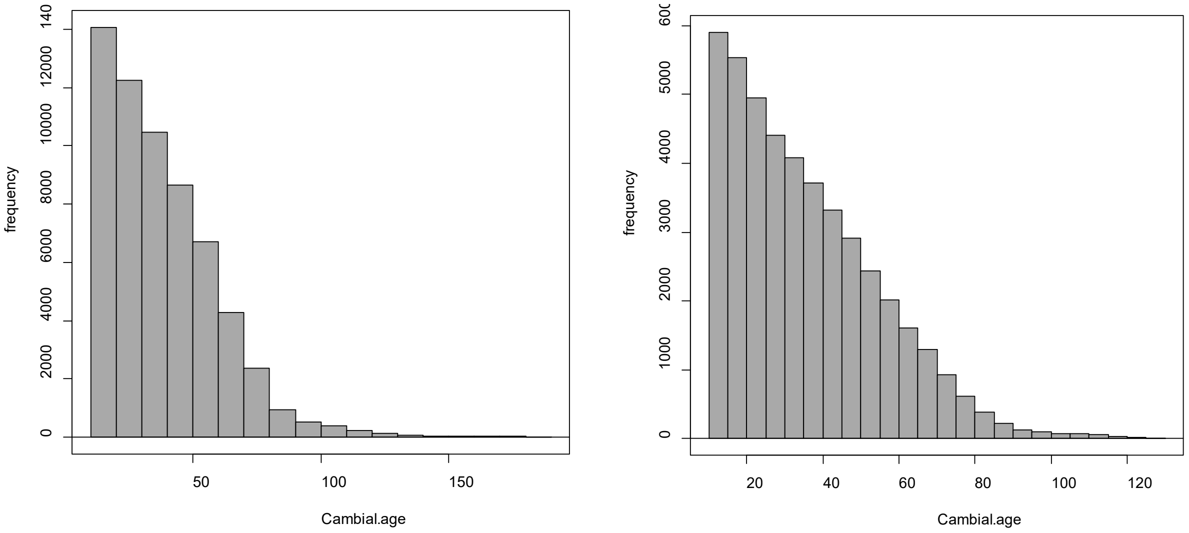


Climate moisture index (CMI, mm)

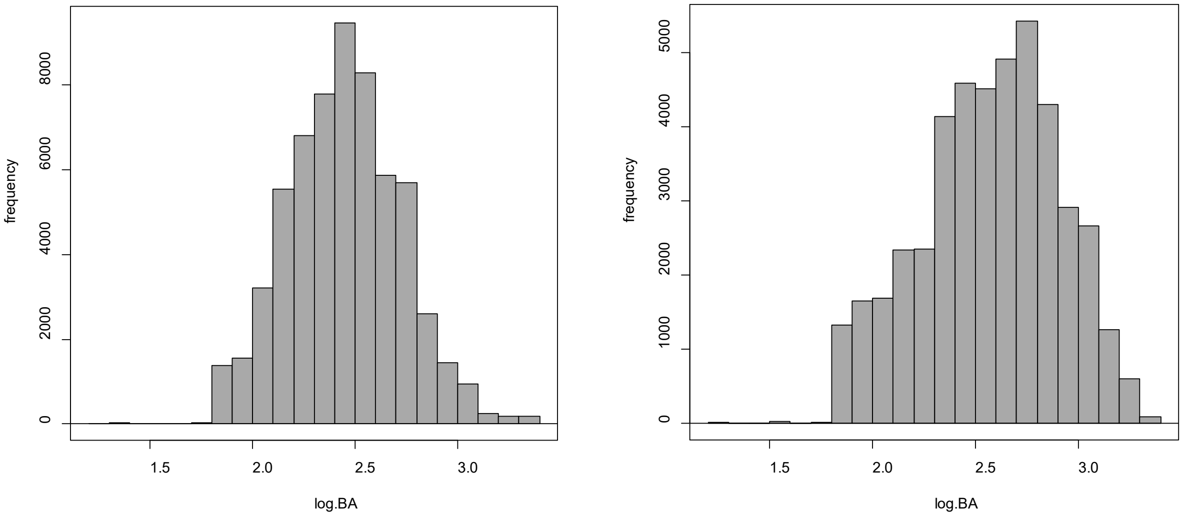




Cambial age (years)



Log(Basal area, BA)



Jack pine Trembling aspen

Figure A2.2 Distribution of the variables used in the GAMMs for trembling aspen and jack pine

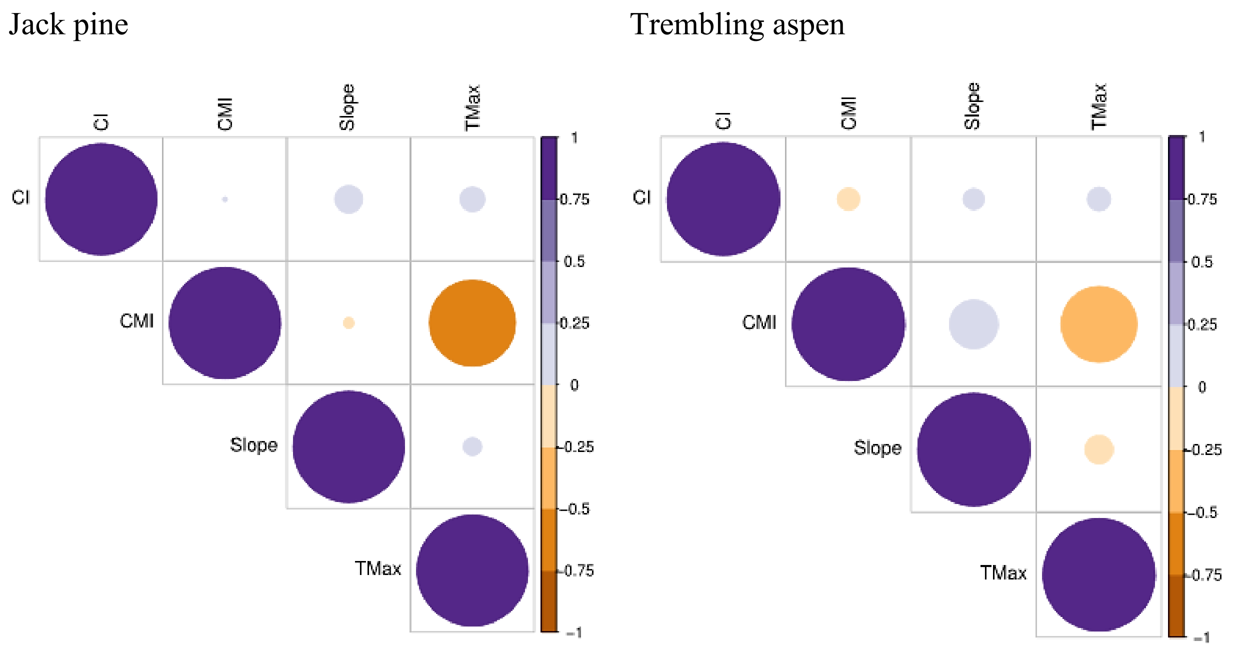
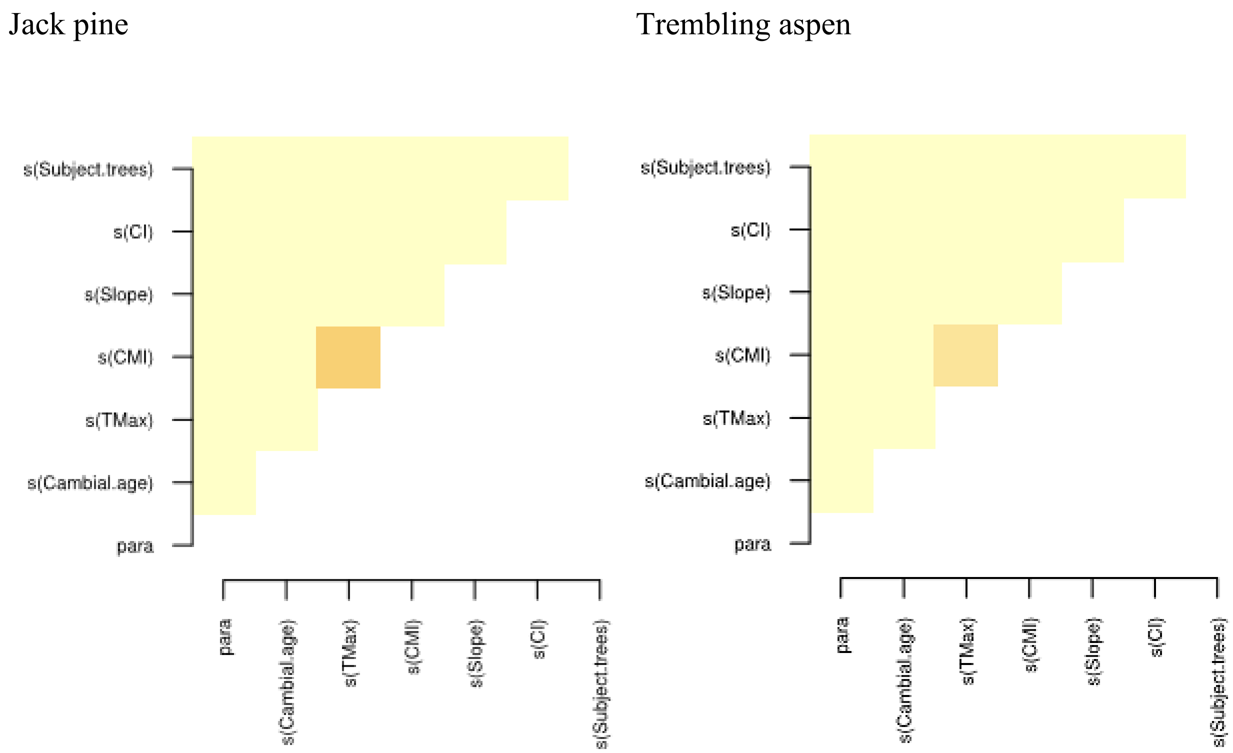


Figure A2.3 Pearson correlation matrix among stand and climatic variables



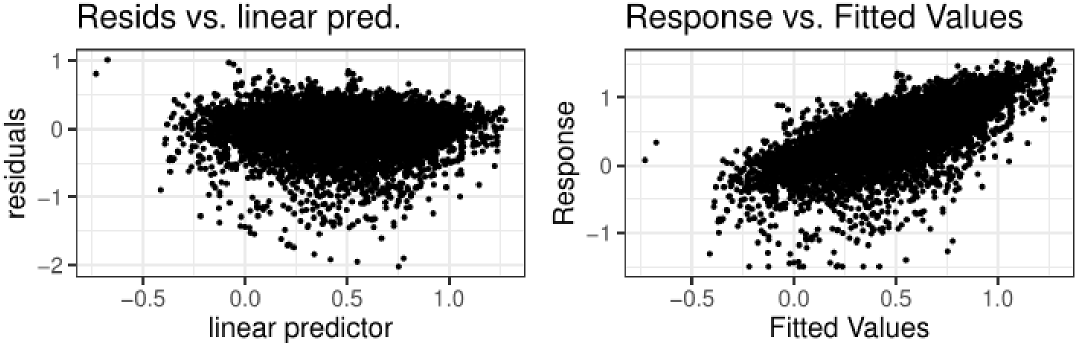
Jack pine

Trembling aspen

Figure A2.4 Estimated pairwise concurvity values between smoother terms in the model predicting trees growth rates.

Pairwise concurvity with 0 and 1 indicating low and high concurvities respectively.

Jack pine



Trembling aspen

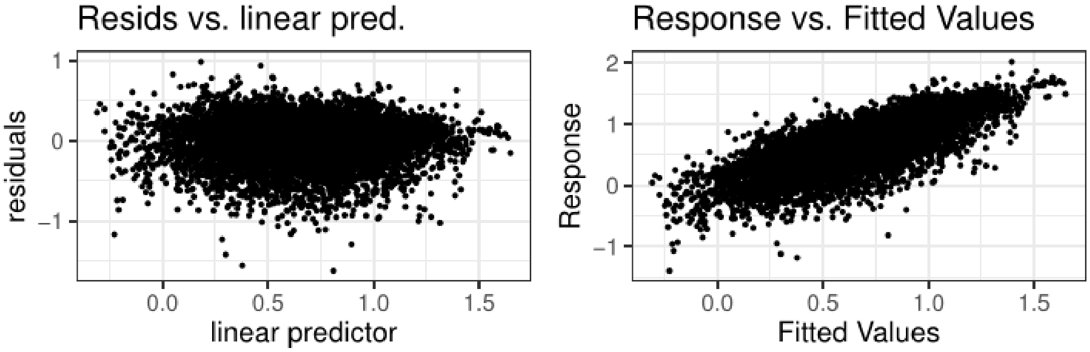
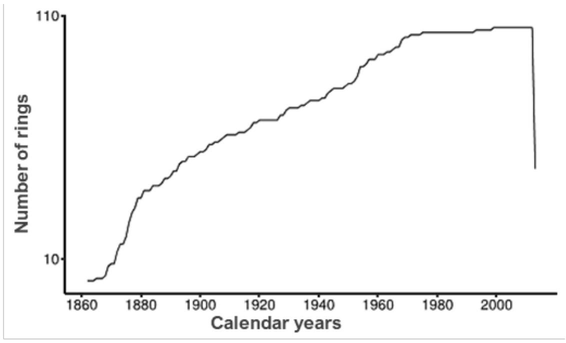


Figure A2.5 GAMM checking plot for the full model fit for the basal area growth rates of jack pine and trembling aspen

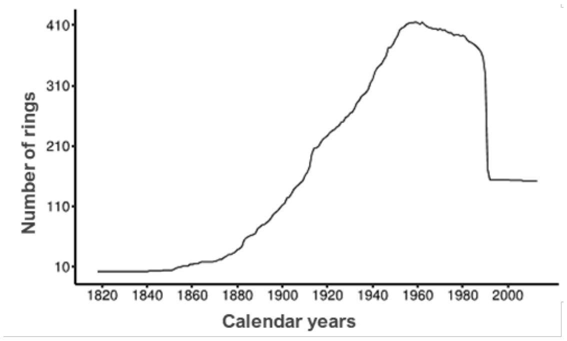
ANNEXE B

INFORMATIONS COMPLÉMENTAIRES CHAPITRE III

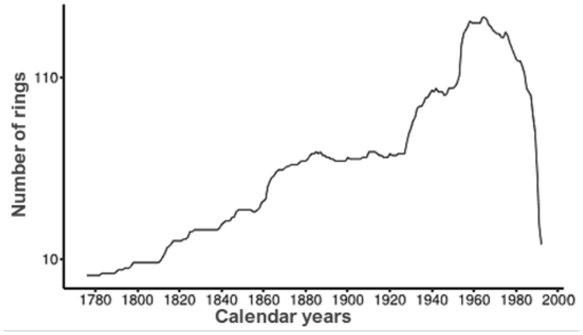
White spruce



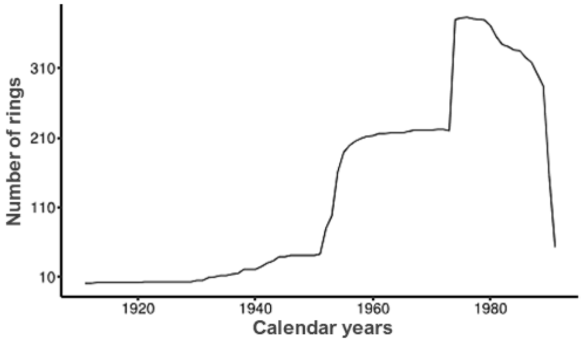
White cedar



White birch



Trembling aspen



Balsam fir

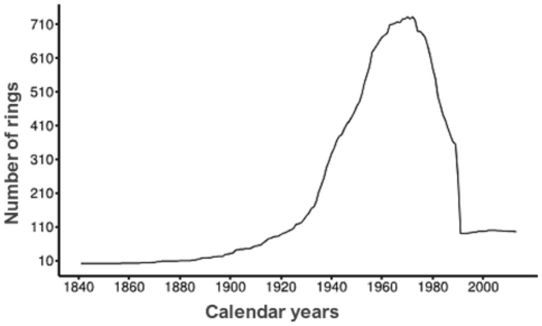


Figure A3.1 Sample depth, i.e. the number of tree rings analyzed as a function of time and species

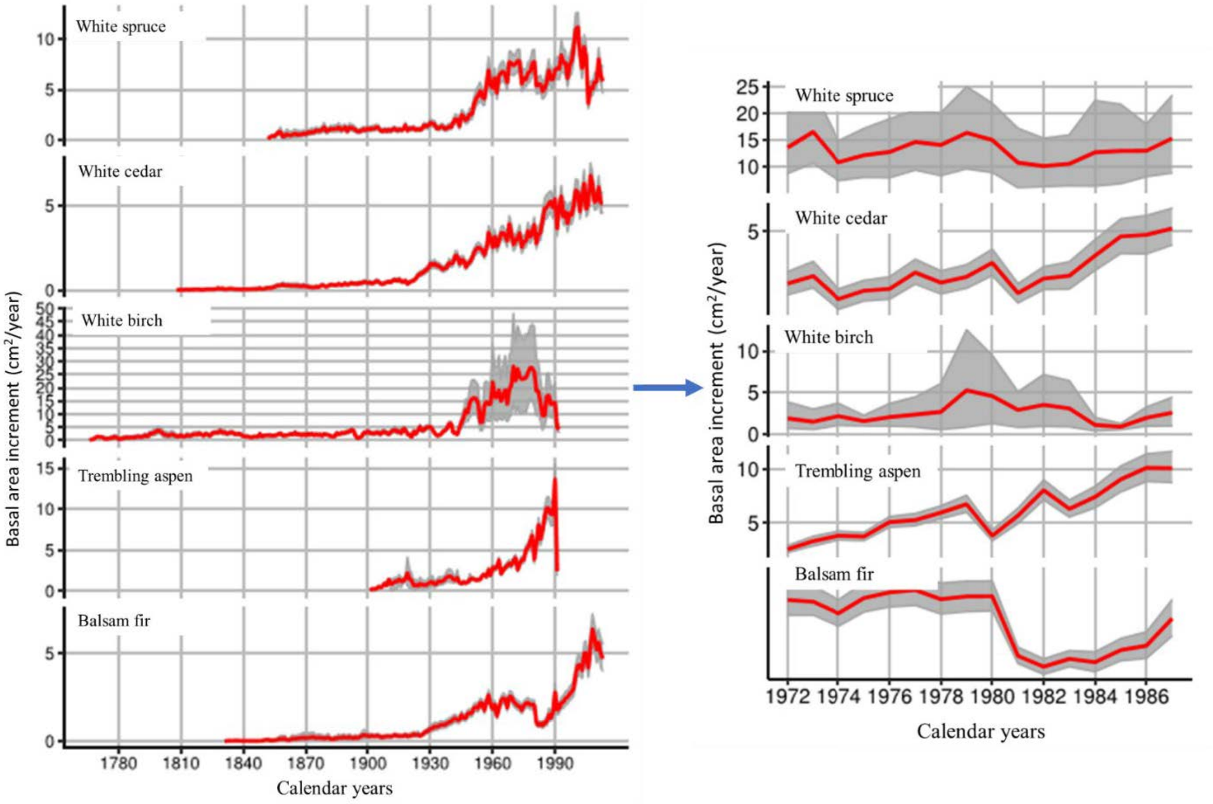


Figure A3.2 Temporal pattern of basal area increment of each tree species over their lifespan. The graph on the left shows the growth pattern of the entire chronology, and the graph on the right shows the period between 1972-1987, when spruce budworm defoliation was intensive.

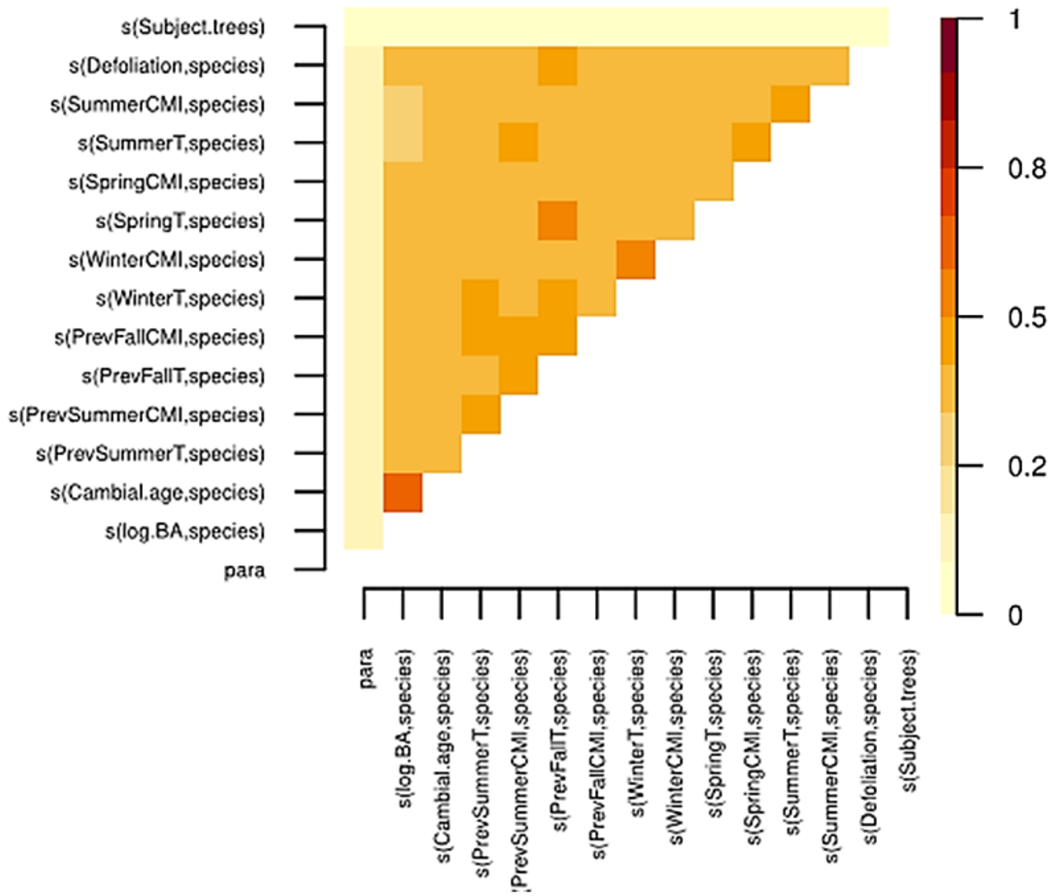


Figure A3.3 Estimated pairwise concurvity values between smoother terms in the model predicting trees growth rates.

Pairwise concurvity with 0 and 1 indicates low and high concurvities respectively. CMI and T denote Climate Moisture Index and Temperature respectively

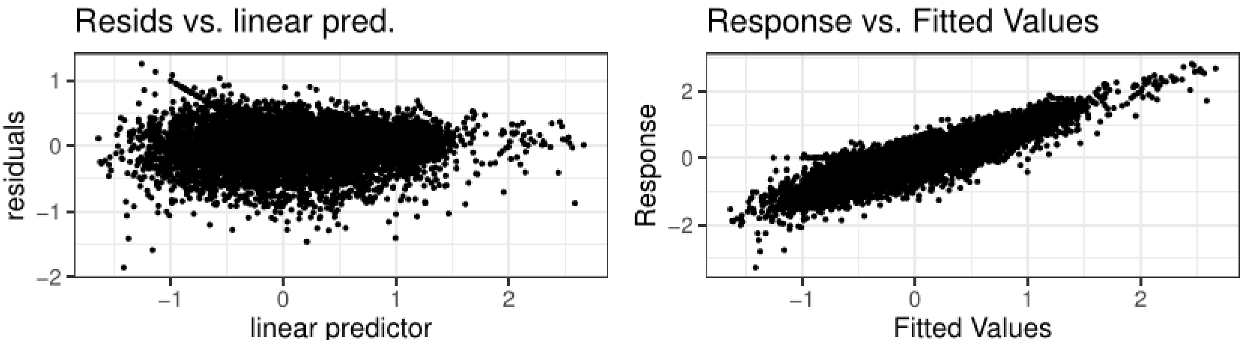


Figure A3.4 GAMM checking plot for the full model fit for the basal area growth rates

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