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INFLUENCE DU CHANGEMENT CLIMATIQUE SUR LA PESSIÈRE DU QUÉBEC DE PART ET D'AUTRE DE LA LIMITE NORDIQUE D'ATTRIBUTION DES FORÊTS

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AVANT-PROPOS

Cette thèse, qui regroupe le travail effectué pendant mon doctorat à l'Université du Québec à Montréal, comprend une introduction, trois chapitres et une conclusion. Chaque chapitre constitue un article scientifique. Le premier chapitre, intitulé "Site index as a predictor of the climate warming on boreal tree growth", est publié dans Global Change Biology (https://doi.org/10.1111/gcb.16030). Le second, "Response of forest productivity to changes in growth and fire regime due to climate change", a été soumis pour publication auprès de Canadian Journal of Forest Research. Enfin, le troisième chapitre, intitulé "Current and future impacts of regeneration failures on boreal forest productivity", est actuellement en préparation pour une prochaine soumission.

Outre la rédaction de cette thèse et des trois chapitres qui la compose, j'ai analysé et procédé à la synthèse des données. J'ai aussi réalisé toutes les projections de croissance et de productivité. J'ai également réalisé toutes les figures et interpréter les résultats.

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RÉSUMÉ

La forêt boréale représente le biome terrestre le plus fortement affecté par le changement climatique, qui module à la fois les facteurs limitant la croissance des arbres et le régime des feux. Aucun consensus n'existe concernant les impacts de ces changements sur la croissance des espèces d'arbres qui s'y trouvent, alors que leurs effets sur l'activité du feu en forêt boréale nord-américaine vont dans le même sens en prévoyant une augmentation de l'occurrence des feux, de leurs intensités et des superficies brûlées. La croissance des arbres et les feux sont pourtant généralement projetés indépendamment. De plus, en territoire aménagé, deux risques sont liés aux feux de forêts : le premier étant que le peuplement brûle avant d'avoir été récolté, le second étant que le peuplement brûle avant d'avoir atteint l'âge minimal nécessaire à se régénérer. Pourtant, les impacts des accidents de régénération sur la forêt boréale restent une incertitude, et ce, dans un contexte de changement climatique.

L'objectif général de cette thèse est de contribuer à projeter quels seront les effets du changement climatique sur la capacité d'aménager de façon durable la forêt boréale du nord du Québec. Le but est donc d'évaluer les effets du changement climatique sur la productivité de la forêt boréale québécoise en tenant compte des impacts projetés sur la croissance des arbres (effets directs), sur leur densité et sur le régime des feux (effets indirects). De façon plus appliquée, l'objectif de ce doctorat est d'évaluer si la limite nordique d'attribution des forêts pourrait être déplacée (vers le nord ou le sud) avec le changement climatique afin de réduire l'impact du changement climatique sur cette limite.

La présente thèse est constituée de trois chapitres liés les uns aux autres dans une suite logique. Dans le premier chapitre, nous avons évalué les impacts du changement climatique sur la croissance de l'épinette noire (Picea mariana [Miller] BSP) et du pin gris (Pinus banksiana Lambert), deux espèces d'arbres dominantes dans les forêts boréales d'Amérique du Nord. Nous avons trouvé un effet positif du déficit de pression de vapeur sur la croissance des deux espèces, bien que l'effet sur l'épinette noire se soit stabilisé. Sur cette dernière, les températures ont eu un effet positif sur la croissance, effet qui a été atténué lorsque les conditions climatiques sont devenues plus sèches. Inversement, la sécheresse a eu un effet positif sur la croissance sous des conditions froides et un effet négatif sous des conditions chaudes.

Pour le deuxième chapitre, notre objectif est d'évaluer l'impact combiné des changements de croissance et de régime des feux dus au changement climatique sur la réserve de bois à la transition entre les forêts boréales de conifères fermées et ouvertes au Québec. La réserve de bois correspond au stock de tiges marchandes disponibles pour la récolte et dépend du taux de croissance des espèces d'arbres et du taux de perturbation. Afin d'identifier les zones susceptibles d'être les plus sensibles au changement climatique, nous avons projeté les impacts induits par le climat sur la croissance (avec le modèle du chapitre 1) et l'activité des feux sur différentes périodes. Notre étude montre l'importance d'intégrer le feu dans la planification stratégique de l'aménagement forestier, en particulier dans un contexte de changement climatique. Dans les scénarios les plus extrêmes, l'impact négatif de l'activité des feux sur la productivité annule en grande partie les effets positifs du changement climatique via l'amélioration de la croissance des arbres.

Dans le troisième chapitre, nous avons évaluer l'impact des accidents de régénération sur la productivité de la forêt boréale québécoise, pour l'épinette noire et le pin gris, en tenant compte des variations projetées de croissance, de densité de tiges et de taux de brûlage dues au changement climatique. Pour atteindre cet objectif, nous nous sommes servis des deux chapitres précédents en utilisant notamment la méthode du chapitre 2 pour déterminer le devenir de la productivité forestière face au changement climatique, en tenant compte des changements de croissance (grâce au modèle du chapitre 1) et de l'activité des feux. Pour estimer le risque d'accident de régénération, nous avons calculé un temps jusqu'à la maturité reproductive. Nos projections qui tiennent compte du risque d'accident de régénération dû au feu sont beaucoup plus inquiétantes et indiquent une possible surestimation de la superficie forestière productive de la forêt boréale québécoise. Il y a donc un besoin pressant de mieux suivre la régénération après une perturbation naturelle.

Les résultats de cette thèse montrent que la superficie forestière de la forêt boréale québécoise, qui peut être aménagée de façon durable, tendra à diminuer sous l'effet du changement climatique. Il semble donc impossible qu'à l'avenir un aménagement durable des forêts puisse être étendue au nord de la limite nordique d'attribution des forêts actuelle. Cette limite devrait au contraire être relocalisée vers le sud, notamment au niveau de la zone centrale qui semble particulièrement frappée par le changement climatique. En revanche, les parties sud-est et sud-ouest de notre zone d'étude ont le potentiel d'être gérées de manière durable et pourraient être privilégiées pour l'aménagement forestier. Ces zones semblent peu affectées par l'augmentation des feux et leur volume marchand pourrait être aussi favorablement influencé par une meilleure croissance. Nous recommandons toutefois avant d'y faire plus d'aménagement intensif d'y évaluer de manière plus dynamique les effets de l'aménagement intensif et du changement climatique sur la productivité des peuplements.

Mots clés : forêt boréale, croissance, activité des feux, accidents de régénération, changement climatique

ABSTRACT

The boreal forest is the terrestrial biome most strongly impacted by climate change, which modulates both the factors limiting tree growth and the fire regime. There is no clear consensus on the impacts of climate change on tree growth, while the effects of climate change on fire activity in the North American boreal forest point in the same direction, forecasting an increase in fire occurrence, fire intensity and area burned. However, tree growth and fires are generally projected independently. Furthermore, in managed areas, two risks are associated with forest fires: the first is that the stand burns before it is harvested, and the second is that the stand burns before it is old enough to regenerate. Yet, the impacts of regeneration failures on the boreal forest remain an uncertainty, even in the context of climate change.

The general objective of this thesis is to contribute to predicting the effects of climate change on the capacity to sustainably manage the boreal forest of northern Quebec. The goal is therefore to assess the effects of climate change on the productivity of Quebec's boreal forest, taking into account the projected impacts on growth (direct effects), density and fire regime (indirect effects). In a more practical way, the objective of this thesis is to assess whether the northern limit of commercial forest could be shifted (northward or southward) with climate change to reduce the impact of climate change on this limit.

This thesis consists of three chapters linked together in a logical sequence. In the first chapter, we evaluated the impacts of climate change on the growth of black spruce (Picea mariana [Miller] BSP) and jack pine (Pinus banksiana Lambert), two dominant tree species in North American boreal forests. We found a positive effect of vapor pressure deficit on the growth of both species, although the effect on black spruce stabilized. On black spruce, temperature had a positive effect on growth, which was attenuated when climatic conditions became drier. Conversely, drought had a positive effect on growth under cold conditions and a negative effect under warm conditions.

For the second chapter, our objective is to assess the combined impact of changes in growth and fire regime due to climate change on the wood supply at the transition between closed and open boreal coniferous forests in Quebec. Timber supply, that we define as the stock of merchantable stems available for harvesting, depends on tree species growth rate and disturbance rate. In order to identify areas likely to be most sensitive to climate change, we projected climate-induced impacts on growth (with the Chapter 1 model) and fire activity over different periods. Our study shows the importance of integrating fire into strategic forest management planning, particularly in the context of climate change. In the most extreme scenarios, the negative impact of fire activity on productivity largely offsets the positive effects of climate change through improved tree growth.

In the third chapter, we studied the impact of regeneration failures on boreal forest of Quebec productivity, for black spruce and jack pine, taking into account projected changes in growth, stem density and burn rate due to climate change. We used the two previous chapters, including the Chapter 2 method, to determine the changes in forest productivity due to climate change, taking into account changes in growth (using Chapter 1 model) and fire activity. To estimate the risk of regeneration failure, we calculated a time to reproductive maturity. Our projections that take into account the risk of regeneration failure due to fire are much more worrying and indicate a possible overestimation of the productive forest area of the Quebec boreal forest. There is therefore a pressing need to better monitor regeneration after natural disturbance.

The results of this thesis show that the forest area of Quebec's boreal forest, which can be managed in a sustainable way, tends to decrease under climate change. It therefore seems impossible that sustainable forest management can be extended north of the current northern limit of commercial forest in the future. Instead, this boundary should be relocated southward, especially in the central zone, which seems to be particularly affected by climate change. In contrast, the southeastern and southwestern parts of our study area have the potential to be managed sustainably and could be favored for forest management. These areas appear to be little affected by increased fire and their merchantable volume could also be favorably influenced by improved growth. However, we recommend that the effects of intensive management and climate change on stand productivity be evaluated in a more dynamic way prior to further intensive management.

Keywords: boreal forest, growth, fire activity, regeneration failures, climate change

INTRODUCTION

0.1 La forêt boréale québécoise et ses enjeux

Les forêts recouvrent 3 999 millions d'hectares au niveau mondial, soit environ 31% des terres émergées. À elle seule, la forêt boréale s'étend sur environ 1 224 millions d'hectares, soit 30% de la surface forestière totale (FAO, 2015; Keenan *et al.*, 2015), répartis sur seulement quelques pays. Au Canada, la forêt boréale, située entre ~ 45°N et 70°N (Larsen, 2013), occupe 270 millions d'hectares, ce qui équivaut à 22% de la superficie boréale (Brandt *et al.*, 2013). Elle est caractérisée par une faible productivité due à des températures faibles, une saison de croissance réduite et à des sols faibles en nutriments (Jarvis et Linder, 2000). Malgré cela, la forêt boréale fournit de nombreux services écosystémiques (MEA 2005) et est d'une importance capitale pour l'économie mondiale. En effet, 33% du bois et 20% du papier à l'exportation proviennent des forêts boréales (Gauthier *et al.*, 2015b), notamment au Canada, dont l'économie repose beaucoup sur l'industrie du bois (Burton *et al.*, 2010). Cette forêt permet aussi la régulation du climat (Steffen *et al.*, 2015), de la qualité de l'eau et des sols (Brandt *et al.*, 2013) et l'accueil de la biodiversité. En outre, elle fournit de nombreux services culturels, comme les loisirs et les valeurs éducatives, esthétiques, patrimoniales et spirituelles, utilisés par de nombreuses populations dont les peuples autochtones (Burton *et al.*, 2010). Un autre service écosystémique particulièrement important dans le contexte du changement climatique est la fixation et le stockage du CO2 par la forêt boréale (Kurz *et al.*, 2013). Cette dernière séquestre 32 % du carbone stocké dans les forêts mondiales, dont 20 % dans sa biomasse et 60 % dans le sol (Pan *et al.*, 2011). La forêt boréale constitue donc un écosystème essentiel à de nombreux niveaux (écologique, économique, culturel, …) qui risque pourtant d'être fortement impacté par le changement climatique (Steffen *et al.*, 2015).

En effet, le changement climatique est une préoccupation majeure pour les forestiers et d'importantes hausses de températures ont déjà pu être observées au cours des dernières décennies. Alors que, depuis 1950, la température moyenne a subi une hausse comprise entre 0,5 et 1,3°C au niveau mondial, les différents scénarios du GIEC prévoient tous une aggravation de cette tendance. En effet, d'ici 2100, la température moyenne globale devrait augmenter de 4 à 5°C. Cette hausse des températures devrait s'accompagner d'une augmentation de la fréquence et de l'intensité des épisodes de sécheresse (Christidis *et al.*, 2015; IPCC, 2013; Price *et al.*, 2013). Ces changements sont plus importants et rapides dans les régions nordiques et notamment au niveau de la zone boréale, la forêt boréale étant le biome forestier le plus sensible au changement climatique. Au Canada, une augmentation de la température annuelle moyenne de 2°C et jusqu'à 6°C est prévue d'ici la fin du siècle, s'ajoutant à une augmentation déjà observée de 1,7°C au cours du siècle dernier (Bush & Lemmen, 2019). Et là encore, les prévisions ne prévoient pas d'amélioration, bien au contraire, avec une augmentation des températures pouvant atteindre 11°C dans cette région du monde (Gauthier *et al.*, 2015b; Price *et al.*, 2013). On peut donc s'attendre à ce que le réchauffement continu ait des répercussions importantes sur la forêt boréale, en particulier au Canada (Gauthier *et al.*, 2015a; Price *et al.*, 2013).

0.2 La productivité de la forêt boréale québécoise face au changement climatique

La productivité forestière est généralement la base de l'évaluation de l'inventaire forestier actuel, de la planification de l'aménagement durable des forêts, et de l'évaluation de l'approvisionnement en bois actuel et futur (Li *et al.*, 2020). Ce terme est largement utilisé dans la littérature (Crow *et al.*, 2006; Keeling et Phillips, 2007; Zhang *et al.*, 2012; Van Bogaert *et al.*, 2015; Li *et al.*, 2020) mais il peut avoir différentes significations selon les auteurs. La productivité forestière, ou le rendement dans certaines études, est souvent définie comme le volume de la forêt sur pied à un moment donné, c'est-à-dire l'accumulation de bois de tige au-dessus du sol dans les arbres sur pied (Li *et al.*, 2020). Le rapport sur la limite nordique des forêts attribuables va plus loin en donnant comme définition de la productivité : "l'obtention d'un volume minimum de bois et des dimensions minimales d'arbres dans un temps donné (productivité) […] et que le risque associé à la récurrence des feux pas trop élevé pour affecter la durabilité de son aménagement" (Raulier *et al.*, 2013). Le changement climatique va donc influencer la productivité de la forêt boréale de différentes façons (non exhaustif) : (1) les effets directs via l'impact sur la croissance des arbres; (2) les effets indirects via l'impact sur les perturbations naturelles, tel que les feux ou les épidémies d'insectes. Les épidémies et notamment la tordeuse des bourgeons de l'épinette, ne seront pas étudié dans cette thèse. Par conséquent, pour déterminer si un peuplement est suffisamment productif pour être durablement exploité, il convient d'abord de mesurer son rendement (sa croissance et sa densité), puis d'évaluer sa vulnérabilité aux feux.

Les études sur les impacts du changement climatique sur la croissance des arbres de la forêt boréale sont nombreuses, mais leurs résultats divergent. Certains auteurs prévoient une augmentation de la croissance des forêts boréales (Price *et al.*, 2013; D'Orangeville *et al.*, 2016; Hember *et al.*, 2017). En effet, la hausse des températures permet l'allongement de la saison de croissance (Peñuelas & Filella, 2001) et l'amélioration du taux d'assimilation (Kauppi *et al.*, 2014; Ols *et al.*, 2020; Melillo *et al.*, 2011; Strömgren et Linder, 2002) ce qui serait donc bénéfique pour la croissance des arbres. À l'inverse, certains auteurs montrent que, dû à la hausse des températures estivales et à l'augmentation de la fréquence et de l'intensité des périodes de sécheresse, le principal facteur limitant la croissance et la survie des arbres en forêt boréale serait la disponibilité en eau (Silva *et al.*, 2010; Housset *et al.*, 2015; Dietrich *et al.*, 2016; Girardin *et al.*, 2008, 2011, 2014, 2016a, 2016b), induisant par conséquent une baisse de la productivité des forêts boréales (Zhang *et al.*, 2008; Beck *et al.*, 2011; Chen *et al.*, 2016). En effet, un fort stress hydrique peut induire la fermeture des stomates (Granier *et al.*, 2007), la mort des racines fines (Jany *et al.*, 2003), une baisse de la photosynthèse (Saxe *et al.*, 2001), une augmentation de la respiration (Girardin *et al.*, 2014) et même dans les cas extrêmes une défoliation (Bréda *et al.*, 2006) et la mort de l'arbre (Allen *et al.*, 2010; Ganey & Vojta, 2011; Michaelian *et al.*, 2011).

La dynamique de la forêt boréale nord-américaine est influencée par les perturbations naturelles dont la principale est le feu (Gauthier *et al.*, 2015c) dont la première cause de départ provoquant les plus grandes superficies brulées au Canada est la foudre (Stocks *et al.*, 2002). Le feu est un processus écologique essentiel permettant de modifier les attributs physiques et biologiques de la forêt (Girardin *et al.*, 2008; Weber et Flannigan, 1997). Il façonne la composition et la structure forestières (Boucher *et al.*, 2017; Gauthier *et al.*, 2000) et peut influencer la productivité de la forêt de façon positive, par exemple, en modifiant le sol (Anyomi *et al.*, 2014) ou de manière négative, notamment en réduisant la densité des arbres (Girard *et al.*, 2008; Michelot *et al.*, 2012; Payette *et al.*, 2000; Rapanoela *et al.*, 2016). Le feu de forêt étant étroitement lié aux conditions climatiques et météorologiques, son activité sera donc très sensible au changement climatique (Bowman *et al.*, 2009; Girardin *et al.*, 2008). Les effets de ces changements sur l'activité du feu en forêt boréale nord-américaine ont été grandement étudiés par la communauté scientifique. Ces études vont, pour la grande majorité, dans le même sens en prédisant une augmentation de l'occurrence des feux, de leurs intensités et des superficies brûlées (Boulanger *et al.*, 2014, 2013, 2017; de Groot *et al.*, 2013; Portier *et al.*, 2017) dues aux conditions de sécheresse (Portier *et al.*, 2016), ainsi qu'une augmentation des années de grands feux, durant lesquelles des superficies exceptionnellement grandes du territoire sont brûlées (Hanes *et al.*, 2018). Cette modification du régime de feu par le changement climatique pourrait avoir un impact dévastateur sur de la forêt boréale canadienne. En effet, ces effets indirects du changement climatique sur le paysage forestier boréal, en passant par le feu, devraient largement surpasser les effets directs du réchauffement climatique sur la végétation tels que les effets sur sa croissance, aussi bien en rapidité qu'en magnitude (Girardin *et al.*, 2008; Weber et Flannigan, 1997). En territoire aménagé, deux risques sont liés aux feux de forêts : le premier étant que le peuplement brûle avant d'avoir été récolté, ce qui affecte le taux de récolte réalisé ;

le second étant que le peuplement brûle avant d'avoir atteint l'âge nécessaire pour pouvoir se régénérer, ce qui entraine un accident de régénération et une ouverture du peuplement.

La forêt boréale est particulièrement bien adaptée aux feux de forêt avec lesquels elle a évolué. Les principales espèces de la forêt boréale ont d'ailleurs développé des cônes semi-sérotineux et sérotineux couverts d'un revêtement cireux et qui, en s'ouvrant sous la chaleur, libèrent leurs graines (Burns et Honkala, 1990). Les feux peuvent aussi produire des lits de germination favorables puisqu'ils vont brûler la matière organique du sol, exposer le sol minéral, et ainsi libérer les nutriments (Jayen *et al.*, 2006). De nombreuses espèces dépendent donc du feu pour se régénérer, mais leur résilience reste cependant limitée par la fréquence des feux (Brown et Johnstone, 2012 ; Baltzer *et al.*, 2021). Si ces derniers ne sont pas assez fréquents, le risque est d'avoir de plus en plus de vieilles forêts, avec des arbres sénescents aux graines stériles qui ne pourront pas se régénérer (Van Bogaert *et al.*, 2015). À l'inverse, si les feux sont trop fréquents, les arbres n'auront pas le temps d'atteindre l'âge nécessaire pour produire un stock de graines considéré comme adéquat pour régénérer un peuplement (Girard *et al.*, 2009; Johnstone *et al.*, 2010; Brown et Johnstone, 2012 ; Whitman *et al.*, 2018).

La sévérité des feux peut aussi influencer la régénération après feu. En effet, une sévérité trop faible limite les lits de germination favorables et peut ne pas dégager assez de chaleur pour libérer les graines des cônes, alors qu'une sévérité trop forte peut brûler les cônes et volatiliser l'azote du sol (Johnson, 1992; Greene *et al.*, 2006). Les accidents de régénération découlent donc à la fois du potentiel de régénération des arbres, c'est-à-dire de leurs âges au moment du feu, mais aussi des caractéristiques du feu lui-même. L'intervalle entre deux feux définira l'âge des peuplements alors que la sévérité déterminera la qualité et la quantité des lits de germination (Le Goff *et al.*, 2008). Plus une forêt est jeune, plus le risque d'avoir une régénération déficiente et donc un accident de régénération est grand (Le Goff et Sirois, 2004; Leduc *et al.*, 2004). Le feu peut donc avoir un impact significatif sur la densité du couvert forestier et modifier la structure et la composition des forêts. De nombreuses études ont d'ailleurs montré que les perturbations naturelles, dont le feu, sont la principale cause d'ouverture des peuplements dans la forêt boréale fermée (Payette *et al.*, 2000; Simard *et al.*, 2007; Girard *et al.*, 2008; Rapanoela *et al.*, 2016; Splawinski *et al.*, 2019; Baltzer *et al.*, 2021; Cyr *et al.*, 2022). L'augmentation de la fréquence, de l'intensité des feux et de la superficie brûlée avec le changement climatique pourraient donc entraîner une augmentation de l'occurrence des accidents de régénération entrainant une hausse de la proportion de peuplements ouverts. Cependant, les impacts des accidents de régénération sur la forêt boréale sont encore peu étudiés et restent une incertitude, d'autant plus dans un contexte de changement climatique.

0.3 Objectifs et structure de la thèse

Dans ce contexte, il semble donc important d'aménager la forêt boréale de façon durable (Gauthier *et al.*, 2008), ce que le Québec a fait, en mettant en place un aménagement forestier écosystémique pour garantir la durabilité des services offerts par la forêt boréale québécoise. L'utilisation de pratiques sylvicoles s'inspirant des effets des perturbations naturelles permet d'atténuer les différences entre les forêts aménagées et les forêts naturelles et ainsi de préserver et d'accroître la variété de structure et de composition du paysage forestier boréal. Cette diversité permettrait d'augmenter la capacité d'adaptation de la forêt boréale au changement climatique (Gauthier et *al.*, 2008). Dans le but de déterminer jusqu'où l'aménagement de la forêt boréale du nord du Québec est durable, une limite nordique des activités d'aménagement forestier a été proposée (Jobidon *et al.*, 2015). L'objectif étant de déterminer la capacité de districts écologiques à produire du bois dans un contexte d'aménagement durable des forêts, quatre critères ont été retenus : l'environnement physique, la capacité à assurer une production de bois adéquate, la vulnérabilité de la forêt au feu et la conservation de la biodiversité, notamment le caribou forestier (Gouvernement du Québec, 2013). Les districts ont ensuite été classés en trois catégories : légèrement sensibles, modérément sensibles et fortement sensibles à l'aménagement (Jobidon *et al.*, 2015). Cependant, les analyses effectuées ne prenaient pas en compte la sensibilité du territoire et des arbres face au récent changement climatique. Ainsi, une des recommandations émises par le comité scientifique chargé d'établir cette limite nordique des forêts attribuables était « de réévaluer la sensibilité des territoires à l'aménagement forestier lorsque des résultats de recherche, notamment sur l'effet dues changements climatiques, démontreront des modifications significatives de la capacité de production des forêts, du cycle de feu ou de la biodiversité » (Gouvernement du Québec, 2013). Il est donc primordial de mieux comprendre quelles sont les conséquences que pourraient avoir ces différents effets du changement climatique sur la forêt boréale.

Tout comme le territoire étudié pour établir la limite nordique, notre zone d'étude, qui s'étend du 48,60° au 53,00° Nord et du 79,52° au 57,12° Ouest, correspond au nord de la forêt boréale du Québec, Canada. Cette zone couvre la totalité du domaine bioclimatique de la pessière noire à mousses (forêt fermée) ainsi que la partie sud de la pessière noire à lichens (forêt ouverte). Dans cette zone, où se trouve la limite nordique d'attribution des forêts (Jobidon *et al.*, 2015), la température diminue du sud au nord et les précipitations augmentent d'ouest en est et du nord au sud (Gouvernement du Québec, 2019). Les principaux dépôts de surfaces sont organiques dans les régions de l'ouest, les tills profonds dans les régions du centre et du nord-est, et rocheux dans le sud (Gauthier *et al.*, 2015c). L'épinette noire (*Picea mariana* [Miler] BSP) domine largement cette zone, bien que le pin gris (*Pinus banksiana* Lambert) puisse aussi être présent à l'ouest où les feux sont plus fréquents. En effet, l'épinette noire est une espèce compétitive qui a tendance à dominer sur les sites mésiques, grâce à ses racines adventives localisées dans les couches superficielles du sol. Elle se régénère grâce à ses cônes semi-sérotineux après un feu ou par marcottage dans les zones où les feux sont peu fréquents. Grâce à son système racinaire plus profond, et notamment à sa racine pivot qui lui donne accès aux ressources du sol minéral, le pin gris peut quant à lui s'établir plus facilement sur les sites pauvres et sableux. Il se régénère essentiellement grâce à ses cônes sérotineux et dépend donc des feux (Burns et Honkala, 1990).

L'objectif général de cette thèse était donc de contribuer à évaluer quels seront les effets du changement climatique sur la capacité d'aménager de façon durable la forêt boréale du nord du Québec. Plus spécifiquement, le but est donc d'évaluer les effets du changement climatique sur la productivité de la forêt boréale québécoise en tenant compte des impacts projetés sur la croissance des arbres (effets directs), sur la densité des arbres dans les peuplements et sur le régime des feux (effets indirects). Pour ce faire, nous avons utilisé une méthodologie semblable à celle utilisée lors de la détermination de la limite nordique d'attribution des forêts en y ajoutant de nouveaux effets dus au changement climatique.

La productivité des peuplements est caractérisée par une limite d'exploitabilité définie à l'échelle du peuplement (supérieure à 50 m^3/ha) et à l'échelle de la tige (supérieure à 70 dm^3). Nous avons mesuré la capacité de régénération des peuplements à l'aide de deux seuils de densité de semis, un critique à 0,25 semis/m^2 nécessaire pour limiter l'ouverture d'un peuplement, et un maximal à 1 semis/m^2 nécessaire pour qu'un peuplement se régénère complètement (Greene *et al.*, 2002). La vulnérabilité aux feux est quant à elle estimée en fonction d'un temps requis à l'atteinte de la maturité commerciale et d'un temps requis à l'atteinte de la maturité reproductive. Enfin, pour évaluer l'impact du changement climatique, nous avons fait varier la croissance des arbres, la densité de tiges et le régime des feux en fonction du climat projeté pour différentes périodes futures (Figure 0.1). De façon plus appliquée, l'objectif de ce doctorat consiste à évaluer si la limite nordique d'attribution des forêts pourrait être déplacée (vers le nord ou le sud) avec le changement climatique afin de tenir compte de l'impact du changement climatique sur cette limite.

La présente thèse est constituée de trois chapitres liés les uns aux autres dans une suite logique (Figure 0.1). Dans le premier chapitre, intitulé “Site index as a predictor of the effect of climate warming on boreal tree growth”, nous avons étudié les relations entre le climat et la croissance en hauteur des arbres pour l’épinette noire et le pin gris dans la forêt boréale de l’est du Canada. Notre objectif était d’évaluer l’influence de la température, des précipitations et de la sécheresse sur la croissance en hauteur des arbres de ces deux espèces. Nous avons également regardé si les dépôts de surface jouaient un rôle dans ces relations climat-croissance. Trois variables ont été considérées pour ce chapitre : (1) l’indice de qualité de station (IQS), un indicateur temporel de croissance centré sur la hauteur des arbres, rarement utilisé en dendrochronologie mais moins affecté par la compétition environnante que d’autres substituts (proxy) de la croissance, reflétant donc mieux le potentiel d’un site (Spurr & Barnes, 1973; Monserud, 1984), (2) les normales climatiques correspondant à la période de croissance de chaque tige, et (3) le type de site (en fonction de la texture, de la pierrosité et du drainage) qui peut modifier les effets du climat sur la croissance des arbres. Finalement, à partir de ces analyses rétrospectives, nous avons prévu les tendances de la croissance en hauteur sur 30 ans des arbres de la forêt boréale du Québec aux transitions entre la forêt de conifères fermée et la forêt ouverte, jusqu'en 2100.

Le deuxième chapitre, intitulé “ Response of forest productivity to changes in growth and fire regime due to climate change”, se concentre sur la réponse de la réserve de bois de la forêt boréale du Québec, en termes de volume marchand et de superficie productive, aux changements de croissance des arbres et de taux de brûlage dus au changement climatique. La réserve de bois correspond au stock de tiges marchandes disponibles pour la récolte et dépend du taux de croissance des espèces d'arbres et du taux de perturbation. L’objectif général est d’identifier les zones de la forêt boréale québécoise qui sont susceptibles d’être les plus sensibles au changement climatique et d’évaluer la pertinence d’inclure le feu et le changement climatique dans la planification stratégique de l’aménagement forestier. Pour cela, nous avons utilisé le modèle d’IQS du chapitre 1 pour projeter les effets directs du changement climatique sur la croissance des arbres, et le modèle de feu de Boulanger *et al.* (2014) pour projeter les effets indirects via les changements du taux de brûlage. Pour estimer le volume marchand et combiner les impacts de ces effets directs et indirects, nous avons utilisé le temps maturité commerciale, la méthode d’appariement non paramétrique k-NN de Gauthier *et al.* (2015c) ainsi que les tables de production de Pothier et Savard (1998) (Figure 0.1). Pour ce chapitre, nous nous sommes concentrés sur l’épinette noire puisque cette espèce est largement dominante dans notre zone d’étude. Cependant, comme le pin gris semble être mieux adapté aux conditions sèches et aux feux, nous avons également voulu déterminer si la présence du pin gris, à la place de l'épinette noire, pouvait présenter des avantages dans ce contexte d'exposition à long terme à des risques accrus de déficit hydrique et de feux de végétation dus au réchauffement climatique.

Pour le troisième chapitre, intitulé "Current and future impacts of regeneration failures on boreal forest productivity", l'objectif est d'évaluer l'impact des accidents de régénération sur la productivité de la forêt boréale québécoise, pour l'épinette noire et le pin gris, en tenant compte des variations projetées de croissance, de densité de tiges et de taux de brûlage dues au changement climatique. . Cela permet d'identifier les zones de la forêt boréale québécoise qui risquent d'être particulièrement sensibles aux accidents de régénération dus au changement climatique. Pour atteindre cet objectif, une méthode semblable à celle du chapitre 2 a été utilisée pour projeter la productivité présente et future en tenant compte des effets directs (via la croissance) et indirects (via les feux) du changement climatique. Une méthode innovante, inspirée de Gauthier *et al.* (2015c), nous a permis de calculer un temps jusqu'à maturité reproductive et ainsi d'estimer le risque d'accident de la régénération. L'effet du changement climatique sur la densité des peuplements a aussi été pris en compte grâce à la fonction de transfert de densité de Cyr *et al.* (2022).

Enfin, les résultats majeurs de cette thèse ont été synthétisés dans la conclusion afin de déterminer de façon plus concrète le devenir de la limite nordique d'attribution des forêts. Pour faciliter la comparaison avec cette dernière, nous avons synthétisé nos résultats en utilisant des critères proches de ceux utilisés pour la création de la limite nordique. Nous avons classé les districts en 3 catégories : (1) peu vulnérable au feu (et donc aménageable) si ses peuplements ont en moyenne plus de 66% de probabilité de dépasser les seuils (productivité ou maturité reproductive), (2) vulnérable au feu (à risque mais toujours aménageable) si ses peuplements ont en moyenne plus de 33% mais moins de 66% de probabilité de dépasser les seuils, et enfin (3) très vulnérable (et donc non aménageable) si ses peuplements ont en moyenne moins de 33% de probabilité de dépasser les seuils (Gauthier et al., 2013).

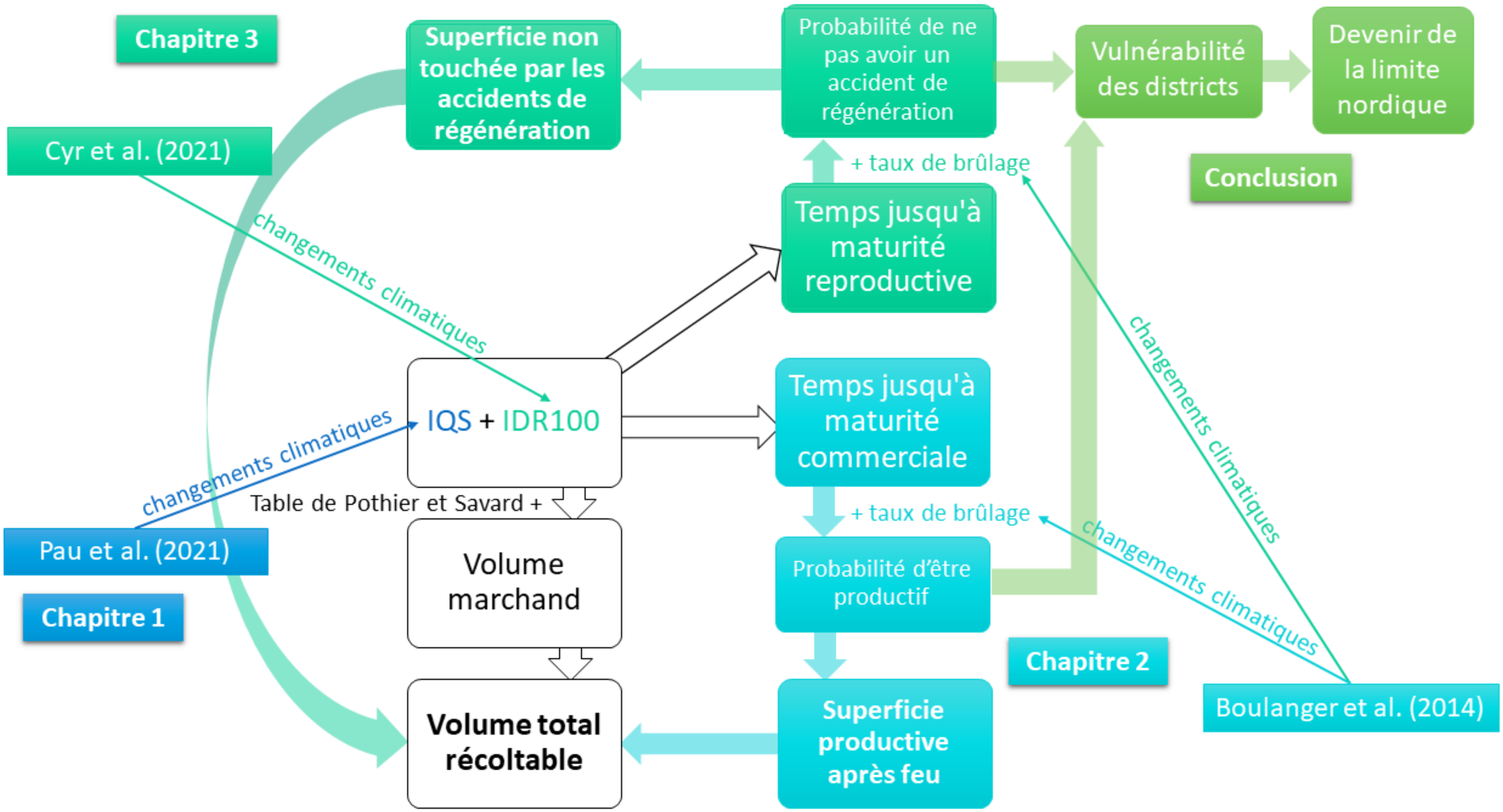

Figure 0.1 Schéma représentant la structure de cette thèse et des trois chapitres qui la composent.

CHAPITRE 1

SITE INDEX AS A PREDICTOR OF THE EFFECT OF CLIMATE WARMING ON BOREAL TREE GROWTH

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Résumé

La forêt boréale représente le biome terrestre le plus fortement affecté par le changement climatique. Cependant, aucun consensus n'existe concernant les impacts de ces changements sur la croissance des espèces d'arbres qui s'y trouvent. De plus, les évaluations de la réponse des jeunes arbres dans des paramètres transposables à l'aménagement forestier restent rares. Ici, nous avons évalué les impacts du changement climatique sur la croissance de l'épinette noire (*Picea mariana* [Miller] BSP) et du pin gris (*Pinus banksiana* Lambert), deux espèces d'arbres dominantes dans les forêts boréales d'Amérique du Nord. À partir d'une analyse rétrospective comprenant les données de 2591 épinettes noires et 890 pins gris, nous avons projeté les tendances de la croissance en hauteur sur 30 ans aux transitions entre les forêts boréales de conifères fermées et ouvertes au Québec, Canada. Nous avons considéré trois variables : (1) la croissance en hauteur, rarement utilisée mais reflétant mieux le potentiel du site que d'autres proxies de la croissance, (2) les normales climatiques correspondant à la période de croissance de chaque tige, et (3) le type de site (en fonction de la texture, de la pierrosité et du drainage), qui peut modifier les effets du climat sur la croissance des arbres. Nous avons trouvé un effet positif du déficit de pression de vapeur sur la croissance des deux espèces, bien que l'effet sur l'épinette noire se soit stabilisé. Pour l'épinette noire, les températures ont eu un effet positif sur la hauteur à 30 ans, effet qui a été atténué lorsque les conditions climatiques sont devenues plus sèches. Inversement, la sécheresse a eu un effet positif sur la hauteur sous des conditions froides et un effet négatif sous des conditions chaudes. La croissance de l'épinette noire était également meilleure sur les sites mésiques que sur les sites rocheux et sub-hydriques. Pour les parties des zones étudiées dont le climat futur projeté se situe dans notre plage de calibration, la variation médiane de la hauteur est de 10 à 31 % pour l'épinette noire et de 5 à 31 % pour le pin gris, selon la période et le scénario climatique. Les augmentations projetées étant relativement faibles, elles pourraient ne pas être suffisantes pour compenser les augmentations potentielles des perturbations futures comme les feux de forêt.

Mots-clés : forêts boréales, normales climatiques, croissance en hauteur, productivité, dépots de surface, épinette noire, pin gris

Abstract

The boreal forest represents the terrestrial biome most heavily affected by climate change. However, no consensus exists regarding impacts of these changes on the growth of tree species therein. Moreover, assessments of young tree responses in metrics transposable to forest management remain scarce. Here, we assessed the impacts of climate change on black spruce (*Picea mariana* [Miller] BSP) and jack pine (*Pinus banksiana* Lambert) growth, two dominant tree species in boreal forests of North America. Starting with a retrospective analysis including data from 2591 black spruces and 890 jack pines, we forecasted trends in 30-year height growth at the transitions from closed to open boreal coniferous forests in Québec, Canada. We considered three variables: (1) height growth, rarely used, but better reflecting site potential than other growth proxies, (2) climate normals corresponding to the growth period of each stem, and (3) site type (as a function of texture, stoniness and drainage), which can modify the effects of climate on tree growth. We found a positive effect of vapor pressure deficit on the growth of both species, although the effect on black spruce leveled off. For black spruce, temperatures had a positive effect on height at 30 years, which was attenuated when and where climatic conditions became drier. Conversely, drought had a positive effect on height under cold conditions and a negative effect under warm conditions. Spruce growth was also better on mesic than on rocky and sub-hydric sites. For portions of the study areas with projected future climate within the calibration range, median height-change varied from 10 to 31% for black spruce and from 5 to 31% for jack pine, depending on the period and climate scenario. As projected increases are relatively small, they may not be sufficient to compensate for potential increases in future disturbances like forest fires.

Keywords: boreal forests, climate normal, height growth, productivity, surficial deposits, black spruce, jack pine

1.1 Introduction

With a predicted rise in global temperatures and a predicted increase in the frequency and intensity of droughts by many climate scenarios (Stocker *et al.*, 2013), the boreal forest would be the biome most strongly affected by global warming (Price *et al.*, 2013). An increase of mean annual temperature between 4° and 11°C was projected across the boreal forest by the end of this century, adding to an already observed increase of 1.5°C during the past century (IPCC, 2013; Gauthier *et al.*, 2015b; Price *et al.*, 2013). It can be expected that continuing warming will have significant impacts therein on a variety of ecological services such as timber supply, wildlife conservation, and carbon storage provided by the forest, particularly in Canada (Gauthier *et al.*, 2015a, Kurz *et al.*, 2013).

In the boreal forest, individuals of a given tree species usually grow better at warmer temperatures than at colder ones (Way et Oren, 2010). Low temperatures are associated with a short growing season and nutrient-poor soil conditions, which are factors limiting growth (Jarvis et Linder, 2000). Increases in temperature have a positive effect on growth by extending the growing season and stimulating photosynthesis rates (Menzel et Fabian, 1999; Chmielewski et Rötzer, 2001; Menzel *et al.*, 2006; Ibáñez *et al.*, 2010; Price *et al.*, 2013). However, at southernmost margins of species ranges and within low-moisture environments, tree growth is often limited by soil moisture availability (Girardin *et al.*, 2021a). There, dry and hot conditions are typically associated with a decrease in growth (Girardin *et al.*, 2008; Zhang *et al.*, 2008; Silva *et al.*, 2010; Beck *et al.*, 2011; Housset *et al.*, 2015; Chen *et al.*, 2016; Marchand *et al.*, 2019). In particular, extreme drought conditions can cause trees to modify their carbon allocation strategy belowground or prioritizing the accumulation of reserves at the expense of growth (Way et Sage, 2008; Muller *et al.*, 2011). Recent tree-ring work suggests that large areas of the boreal forests have recently seen tree growth becoming increasingly limited by soil water availability due to rising atmospheric water demand, especially from summer months (Girardin *et al.*, 2016a; Babst *et al.*, 2018). These changes occurred under mild warming, and it is anticipated that continued climate change will trigger a major redistribution in growth responses to climate and in growth rates (Charney *et al.*, 2016; Girardin *et al.*, 2016b; D'Orangeville *et al.*, 2018).

In forestry, the Site Index (SI) is a commonly used temporal indicator of growth focusing on tree height. SI integrates the effects of climate on growth over a long period in the life of the tree, thus facilitating predictions for stand productivity at maturity (Messaoud et Chen, 2011). Growth in height reflects site fertility and consequently the potential productivity of a forest stand (Monserud, 1984). Given that height growth is negligibly affected by stand density, SI mostly depends on site quality and climate being less affected by surrounding competition compared to diameter at breast height (DBH 1.3 m above ground) (Spurr et Barnes, 1973). As height reflects site production potential as conditioned by both the physical arrangement and architecture of the stand, and the climatic conditions under which a tree grows, it can be a good indicator for studying slow- and long-term processes such as the effect of climate warming on tree growth in boreal environments.

The productive potential of a site may be described generally as a function of moisture availability based on climate (Landsberg et Sands, 2011; Anyomi *et al.*, 2012). For example, interaction between snow and temperature influences the timing of snowmelt, which is a robust indicator of the start of the growing season for many boreal tree species (Frolking *et al.*, 1996; Frolking, 1997). Apart from climate, surficial deposits, which can provide information on the soil drying potential, can also affect moisture availability (Mansuy *et al.*, 2010). Surficial deposits with excessive stoniness and a sandy texture facilitate water flow in the soil and, therefore, can decrease the amount of water that is available for trees (Mansuy *et al.*, 2010).

Site characteristics and climate can have different impacts on species depending on their morphological characteristics (Nothdurft *et al.*, 2012). In the case of two important eastern Canadian boreal forest species, black spruce (*Picea mariana* [Miller] BSP) and jack pine (*Pinus banksiana* Lambert) exhibit different rooting patterns and, as a result, acquire nutrients and water at different depths. Black spruce takes up nutrients from the organic soil, while jack pine acquires them from deeper in the mineral soil via taproots (Burns et Honkala, 1990; Houle *et al.*, 2014). Moreover, black spruce is a generalist species that usually grows on wet organic soils, but can also be found on a variety of soils. Jack pine, on the other hand, is a pioneer species and usually grows on well drained sandy soils (Burns et Honkala, 1990).

In this study, we investigated climate and tree height growth relations (hereafter, "climate–growth relations") for black spruce and jack pine in the eastern Canadian boreal forest. Our objective was to assess the influence of temperature, precipitation, and drought on tree height growth for these two species. We also assessed whether surficial deposits had the potential to modulate climate–growth relations. We hypothesized that 1) higher temperature affects tree growth positively, 2) increased drought limits tree growth, and 3) tree growth on dry deposits is more negatively affected by climate change than those growing on more mesic deposits. Ultimately, from these retrospective analyses, we aimed to forecast the trends in tree-height growth in our study area, the coniferous boreal forest of Québec, i.e., in the area transition from closed to open forest, until 2100 AD.

1.2 Material and methods

1.2.1 Study area

Our study area extends from 48.60°–53.00° N and 79.52°–57.12° W in the province of Québec, Canada (Figure 1.1). This area is located at the transition between the spruce-feather moss and the southern portion of the spruce-lichen bioclimatic domains. This area is also located at the northern limit of commercial forestry (Jobidon *et al.* 2015). Beyond the northern limit harvesting operations are absent, thus natural dynamics dominate (Girardin *et al.*, 2012). Black spruce is the main tree species in the area, and dominant surficial deposits are organic in western regions, deep till in central and northeastern regions, and rock in the south (Gauthier *et al.*, 2015c).

1.2.2 Tree stem dataset and sampling area

We used a large dataset of tree stem samples with 2591 black spruces (distributed across 570 plots) and 890 jack pines (distributed across 177 plots; Table 1.1; Supporting Information S1.1 in Annexe A) obtained from the Direction des inventaires forestiers of the Ministry of Forests, Wildlife and Parks of Québec (Laflèche *et al.* 2013) to calculate the Site Index (SI). The plots come from a wide range of climatic and site conditions, in a sampling area mostly south of our study area, located from 46.69°–51.38° N and 79.42°–60.44° W across Québec (Figure 1.1). The area encompasses the northern part of the temperate vegetation zone and the boreal zone extending over three bioclimatic domains including the spruce-feather moss, balsam fir-yellow birch, and balsam fir-white birch domains (Saucier *et al.*, 2011). In the sampling area, dominant surficial deposits are undifferentiated tills, outwash plains, and juxta-glacial deposits (Supporting Information S1.2 in Annexe A). In this area, temperature decreases from south to north and precipitation increases from west to east and north to south (Gouvernement du Québec, 2019) (Supporting Information S1.3 in Annexe A).

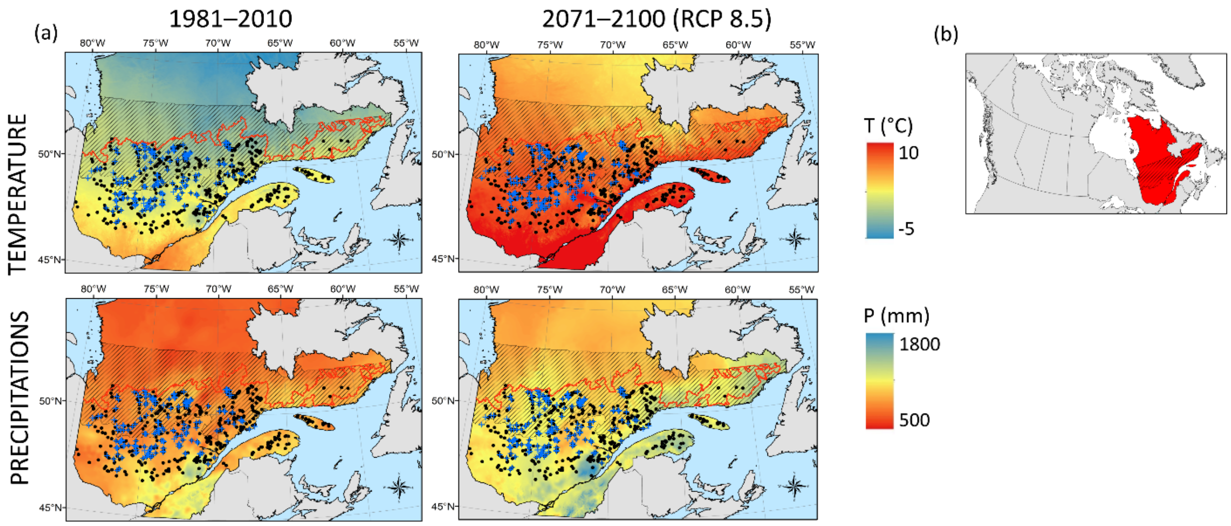

Figure 1.1. (a) Black spruce and Jack pine plot locations (as black dots and blue crosses, respectively; Supporting Information S1.1) according to the database developed by the Direction des inventaires forestiers of the Ministry of Forests, Wildlife and Parks of Québec (Laflèche *et al.*, 2013), with annual mean temperature and annual precipitation for 1981–2010 (baseline) and 2071–2100 (ESM2–RCP 8.5 scenario) (b) in Québec, Canada. The red line indicates the 2018 limit for commercial forests (Jobidon *et al.*, 2015), and hatching indicates our study area.

Table 1.1. Number of plots, number of trees, and number of trees with juvenile suppression for each species and each site type (SAND = sandy, MT = mesic, ROC = rock, SHT = sub-hydric) according to the database developed by the Direction des inventaires forestiers of the Ministry of Forests, Wildlife and Parks of Québec (Laflèche et al., 2013). Bold numbers are totals.

Species	Black spruce				Jack pine			
Site type	SAND	MT	ROC	SHT	SAND	MT	ROC	SHT
No. of plots	38	363	47	122	31	128	12	6
	570				**177**			
No. of trees	186	1655	217	533	158	651	51	30
	2591				**890**			
No. of trees with juvenile suppression	50	519	88	148	14	33	3	0
	805				**50**			

1.2.3 Sampling design

Samples used in our study were originally collected by the Direction des inventaires forestiers of the Ministry of Forests, Wildlife and Parks of Québec to determine SI for dominant commercial species based on ecological types in southern Québec (Laflèche *et al.*, 2013). We summarized the sampling design and collection methods used hereafter. Up to twenty-five stems per species from at least five plots were sampled in each ecoregion's ecological types, i.e., a local area presenting a permanent combination of potential vegetation and physical characteristics of the environment. Sampled jack pine trees were almost always in mixed stands, with black spruce in the majority of cases, but sometimes with other species. Sampled black spruce trees were mostly in pure stands or mixed with one or two other species. To be sampled, stands needed a minimum of 40–60% cover density. For each sample plot, a description of the ecological and physical environment, and dendrometric characteristics of the stand were recorded. Stems ≥50-years old in the dominant or codominant classes were sampled and characterized for stem analysis. Sampling was designed to reduce the potential influence of competition and past disturbance history; thus, sampled trees were dominant trees sampled in stands older than 50 and if possible 70 years, most likely in non previously harvested stands. Disk samples were collected at heights of 0.15 m, 0.60 m, 1 m, 1.30 m and 3 m, then every 2 m up to the stem apex. Disks were then sanded and dated to obtain an age-height curve.

1.2.4 Tree height at 30 years of age (H30)

To represent SI, we used the height of dominant trees at 30 years of age (H30). We selected 30 years such that the growth period would correspond to 30-year climate normals. We obtained H30 using annual height increments, which are calculated from the difference in height between two successive disks divided by the number of years separating the two disks (Grondin *et al.*, 2000). The Direction des inventaires forestiers of the Ministry of Forests, Wildlife and Parks of Québec screened each tree for juvenile suppression by identifying slow-growth periods following tree establishment and growth delays at the seedling stage (Laflèche *et al.*, 2013). Juvenile suppression is frequent for many tree species (Seymour et Fajvan, 2001); for example, growth of a young tree is likely inhibited or slowed under a stand canopy that intercepts light. To limit this effect, the year in which the tree reached a height of 1 m was selected as the starting year for SI calculation. Of the two species in our study, black spruce should be much more subject to juvenile suppression than jack pine due to its shade tolerance (Burns et Honkala, 1990). The year at 1 m varied from 1900 to 1967 for black spruce and from 1900 to 1972 for jack pine, and that age at ground level varied from 45 to 141 for black spruce and from 33 to 115 for jack pine.

1.2.5 Climate data

We extracted daily weather records from 1901–2017 for each plot using the BioSIM 11 software (Régnière *et al.*, 2017). BioSIM interpolates weather records from nearby Environment and Climate Change Canada meteorological stations using inverse distance weighting output, while adjusting for elevation, latitude, and longitude. From the interpolated weather records, we calculated 30-year climate normals for the following variables: mean annual temperature (°C), mean April–October Drought Code (DC; dimensionless, and representing soil water availability), mean April–October Vapor Pressure Deficit (VPD; kPa, and representing atmospheric water demand), and annual total snowfall (mm; as water equivalent) given that normals of annual precipitation were strongly correlated with DC. DC indicates the moisture content in deep compact organics in forest soils (Van Wagner, 1987). It requires maximum daily temperature to estimate a day's potential evapotranspiration and daily rainfall to track moisture content (Van Wagner, 1987). With DC, higher values are associated with more severe drought conditions (Girardin et Wotton, 2009). VPD corresponds to the difference between the amount of water in the atmosphere and the amount of water the atmosphere could hold at saturation; and was calculated following Landsberg et Sands (2011) (Supporting Information S1.4 in Annexe A). For each climate variable, we calculated their normals as the mean value over 30-years, from the year when the tree reached 1 m until the year at 1 m + 30 years (Figure 1.2).

1.2.6 Physical environment data

To characterize soil drying potential, we grouped sites based on their surficial deposit texture, stoniness, drainage and morphology (adapted from Mansuy *et al.*, 2010). We identified four groups of sites with different characteristics: coarse-sand deposits (SAND), rock outcrops (ROC), mesic undifferentiated till and outwash plains (MT), and sub-hydric undifferentiated till and organic deposits with black spruce (SHT). These four groups represented the variable 'site type' (Supporting Information S1.5 in Annexe A). Due to the smaller sample size for jack pine (Tables 1.1 and 1.2), we grouped SAND and ROC (hereafter SAND/ROCK site type), and MT with SHT (hereafter MT/SHT site type).

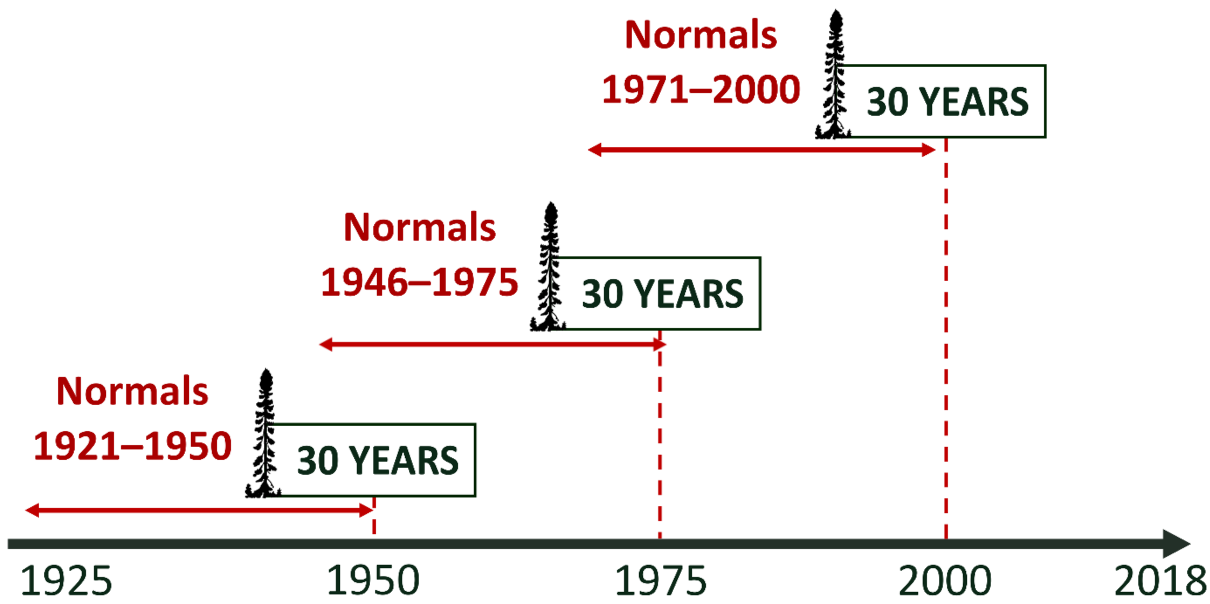

Figure 1.2. Graphical representation of the climate normals used as a function of the year in which the tree reaches 30 years (1 m + 30 years since the starting year, where the starting year is the year in which a given tree reaches a height of 1 m). For example, we applied 1971–2000 climate normals to trees that were 30-years old in 2000.

Table 1.2. Mean, standard deviation and range of each modelled variable for each species and each site type in the sampling area (SAND = sandy, MT = mesic, ROC = rock, SHT= sub-hydric). Bold numbers are totals.

Species	Black spruce				Jack pine	
Site type	SAND	MT	ROC	ST	SAND/ROC	MT/SHT
Height at 30-years (m)	7.8 ± 1.9 3.2 - 12.9	8.1 ± 2.3 1.9 - 14.8	7.5 ± 2.2 2.0 - 13.8	7.3 ± 2.1 2.2 - 13.5	9.1 ± 2.0 4.6 - 14.8	10.4 ± 2.4 4.6 - 16
	7.8 ± 2.3 **1.9 - 14.8**				**10 ± 2.4** **4.6 - 16**	
Age at ground level (yrs)	83 ± 12 50 - 106	83 ± 16 45 - 141	85 ± 18 55 - 106	90 ± 17 46 - 140	87 ± 14 58 - 111	80 ± 14 33 - 115
	85 ± 16 **45 -141**				**82 ± 14** **33 - 115**	
Year at 1 m	1935 ± 12 1904 - 1961	1933 ± 14 1900 - 1967	1934 ± 14 1901 - 1959	1927 ± 15 1900 - 1963	1925 ± 13 1900 - 1951	1930 ± 13 1900 - 1972
	1932 ± 14 **1900 - 1967**				**1929 ± 13** **1900 - 1972**	
Temperature normals (°C)	-0.6 ± 1.1 -2.3 - 2.4	0.1 ± 1.3 -2.7 - 2.7	0.4 ± 0.9 -2.0 - 2.4	-0.1 ± 1.3 -2.5 - 3.2	-0.6 ± 1.1 -2.3 - 1.8	0.0 ± 1.1 -2.2 - 2.5
	0.1 ± 1.3 **-2.7 - 3.2**				**-0.1 ± 1.1** **-2.3 - 2.5**	
Precipitation normals (mm)	940 ± 49 812 - 1046	940 ± 82 693 - 1516	928 ± 77 768 - 1070	924 ± 87 730 - 1335	890 ± 66 746 - 1034	925 ± 66 762 - 1138
	936 ± 81 **693 - 1516**				**917 ± 68** **746 - 1138**	
Snowfall normals (mm)	343 ± 29 277 - 439	348 ± 46 224 - 570	362 ± 48 263 - 458	343 ± 49 241 - 531	324 ± 24 264 - 380	327 ± 26 254 - 409
	348 ± 46 **224 - 570**				**326 ± 26** **254 - 409**	
Drought Code normals	109 ± 16 79 - 161	118 ± 23 41 - 179	125 ± 22 82 - 169	120 ± 23 45 - 182	123 ± 19 86 - 177	118 ± 19 78 - 180
	118 ± 23 **41 - 182**				**119 ± 19** **78 - 180**	

Vapor pressure deficit normals (kPa)	0.47 ± 0.05 0.36 - 0.59	0.49 ± 0.07 0.25 - 0.65	0.47 ± 0.07 0.36 - 0.61	0.49 ± 0.08 0.29 - 0.66	0.48 ± 0.04 0.40 - 0.57	0.50 ± 0.05 0.37 - 0.59
		0.49 ± 0.07 **0.25 - 0.66**			**0.50 ± 0.05** **0.37 - 0.59**	

1.2.7 Statistical analyses

To test non-linear relationships between H30, climate, and site type for black spruce and jack pine, we applied Generalized Additive Models (GAM) with the 'mgcv 'package in R (Wood, 2016). We conducted separate analyses for black spruce and jack pine, and modelled sampling plots as a random effect. To avoid collinearity among variables, we calculated Pearson's correlations between variables with the 'stats' package in R (R Core Team, 2019) (Supporting Information S1.6 in Annexe A) and did not include highly correlated (thresholds of -0.7 or 0.7) variables in the same model. We assessed multicollinearity among variables using variance inflation factors (VIF) with the 'fuzzySim' package in R (Barbosa, 2015) (Supporting Information S1.7 in Annexe A).

To test our hypothesis, we created a base model that included our climate and site variables. Age at ground level was also included in the model to control for sampling bias associated with the absence of large, fast-growing trees, and presence of slow-growing trees with relatively small diameters in the older age class compared to the younger age classes (Duchesne *et al.*, 2019). As no distinction for the regeneration mode was made when sampling, it was not possible to know if trees originated from layers or fire-originating established seedlings, which can also be a source of bias due to the effect of juvenile suppression (Paquin *et al.*, 1999). We therefore also included juvenile suppression in the base model. We finally accounted for spatial autocorrelation in the base model with the interaction of latitude and longitude. To explore for significant interactions, we also developed a model composed of our base model and all possible two-way interactions between climate variables and site type, and among climate variables. When more than one interaction was significant, we used the 'MuMIn' package in R (Bartoń, 2020) to select models according to the Bayesian Information Criterion (BIC) over the Akaike Information Criterion (AIC) due to the stronger penalty afforded (Brewer *et al.*, 2016) (Supporting Information S1.8 in Annexe A). To verify model assumptions, we used observed vs. predicted, and residual vs. predicted plots (Supporting Information S1.9 in Annexe A). To estimate a given model's predictive power, we used 10 repeated 10-fold cross-validations. Due to the random effect in our sampling structure, we created folds according to trees belonging to the same plot. Based on the 10 repeated 10-fold cross-validations, we calculated for each model its Root-Mean-Square Error (RMSE) and adjusted R^2, to estimate the model's prediction error, and the proportion of variance explained by predictors (Supporting Information S1.10 in Annexe A).

1.2.8 Climate effects on boreal conifer productivity

To assess the effect of climate on productivity, we applied the selected model to project gains or declines in height growth assuming that the study area was covered by either species. To represent the study area, we created a grid with a cell size of 6 km x 6 km using ARCGIS v.10.4 (ESRI, 2016). Using BioSim 11 (Régnière *et al.*, 2017), we calculated past and current climate normals for 1901–1930 and 1981–2010 (baseline), respectively, and we calculated future climate normals for 2011–2040, 2041–2070, and 2071-2100 based on 4.5 and 8.5 Representative Concentration Pathway (RCP) scenarios (Supporting Information S1.3 in Annexe A). For the Global Climate Model (GCM), we used 2003–2017 adjusted weather station observations from the fourth generation Canadian Regional Climate Model (CanRCM4) and driven by the second generation Canadian Earth System Model (CanESM2)/fourth generation coupled GCM (CGCM4) to mimic 1981–2010 normals (Dunne *et al.*, 2012). For the RCPs, we used medium-low (RCP 4.5) and high (RCP 8.5) emission scenarios (Meinshausen *et al.*, 2011). Age was set at 30 years with no juvenile suppression and minimum height was set at 1 m as in the observed data. We estimated percent increases in height growth between baseline and past, and between future and baseline as follows:

$$Percent\ increase\ between\ baseline\ and\ past\ (H30_{1995-1915}) = \left(\frac{H30_{baseline} - H30_{past}}{H30_{past}}\right) \times 100$$

$$Percent\ increase\ between\ future\ and\ baseline\ (H30_{Future-1995}) = \left(\frac{H30_{future} - H30_{baseline}}{H30_{baseline}}\right) \times 100$$

For each species, period, and RCP scenario, we calculated standard errors (Supporting Information S1.11 in Annexe A). We interpolated percent increases across the study area using the empirical bayesian kriging algorithm with an empirical transformation of the data, an exponential type semivariogram model, a search radius of 1^{o}, and a smoothing factor of 0.2. Because our model was calibrated over a limited climate range (Supporting Information S1.3 in Annexe A) and we could not know how trees would react to more extreme climate than what we modelled, we determined the area outside our calibration climate range for each scenario and for each period. We chose to present our results for the entire study area as well as for parts of our study area included in our climate range.

1.3 Results

1.3.1 Effects of climate and environmental factors on height growth

1.3.1.1 Black spruce

The black spruce model had good predictive capacity (Table 1.3; Supporting Information S1.9 in Annexe A) and showed, as expected, that tree age and juvenile suppression influenced spruce height growth. These results confirmed that age and juvenile suppression were required in the models to avoid bias. Latitude/longitude and plot also had important effects on H30, which confirmed the need to account for spatial autocorrelation and sampling plots as a random effect.

The best model revealed a significant interaction between temperature and DC. Spruce H30 increased with temperature. However, this positive effect was influenced by DC (Figure 1.3a). Increase in growth with temperature was more pronounced when DC was low. In contrast, higher DC values were associated with a lower positive effect of temperature on growth. Thus, the effect of temperature on height growth was stronger under wet conditions than dry conditions. Similarly, temperature influenced the effect of DC on H30. DC had a positive effect on H30 under cold conditions and a negative effect under warm conditions. Height growth was greater under dry conditions than wet conditions when the temperature was cold, whereas height growth was lower under dry conditions than wet conditions when the temperature was warm (Figure 1.3b). Increasing VPD was associated with increasing H30 until VPD reached 0.53 kPa (Figures 1.3c). Above this threshold, spruce H30 remained stable. Snowfall was not a significant predictor (Table 1.3).

Spruce height growth was greater on mesic and sandy sites than on rocky or sub-hydric sites (Figure 1.3d). Specifically, H30 on MT was significantly greater than on ROC and SHT. No other significant difference was detected across site types for black spruce.

Table 1.3. Results of the Generalized Additive Models (GAM). Estimated degrees of freedom (EDF), F-value and p-value for each smooth term of the GAM and regression slopes (β), standard deviations (Std.error), and t-values and p-values for qualitative variables. Adjusted R^2 values and number of observations for each model are also presented. For the site type (SAND = sandy, MT = mesic, ROC = rock, SHT = sub-hydric), intercept is set to MT for black spruce and MT/SHT for jack pine. For juvenile suppression (SUPP), intercept is set to no juvenile suppression.

	Black spruce			Jack pine		
	EDF	F-value	p-value	EDF	F-value	p-value
Age	1	447.048	**<0.001**	2.443	13.558	**<0.001**
Longitude,Latitude	16	3.346	**<0.001**	6.414	3.209	**<0.010**
Vapor Pressure Deficit	4.167	2.335	**<0.050**	3.869	4.466	**<0.001**
Drought Code				1.176	3.125	0.091
Snowfall	2.202	0.849	0.366	1.115	0.291	0.717
Temperature				1	3.711	0.054
Temperature x Drought Code	11.288	6.257	**<0.001**			
Plot	426.149	3.780	**<0.001**	147.007	8.273	**<0.001**

	Black spruce				Jack pine			
	β	Std. error	t value	p-value	β	Std. error	t value	p-value
Intercept	7.831	0.108	72.708	**<0.001**	10.184	0.110	92.323	**<0.001**
SUPP	-1.071	0.058	-18.476	**<0.001**	-0.901	0.170	-5.289	**<0.001**
Site type SAND (SAND/ROC)	-0.160	0.197	-0.814	0.416	-0.269	0.235	-1.114	0.253
SHT	-0.447	0.124	-3.857	**<0.001**				
ROC	-0.408	0.184	-2.214	**<0.050**				

	Black spruce	Jack pine
Adjusted R^2	0.802	0.872
Number of observations	2591	890

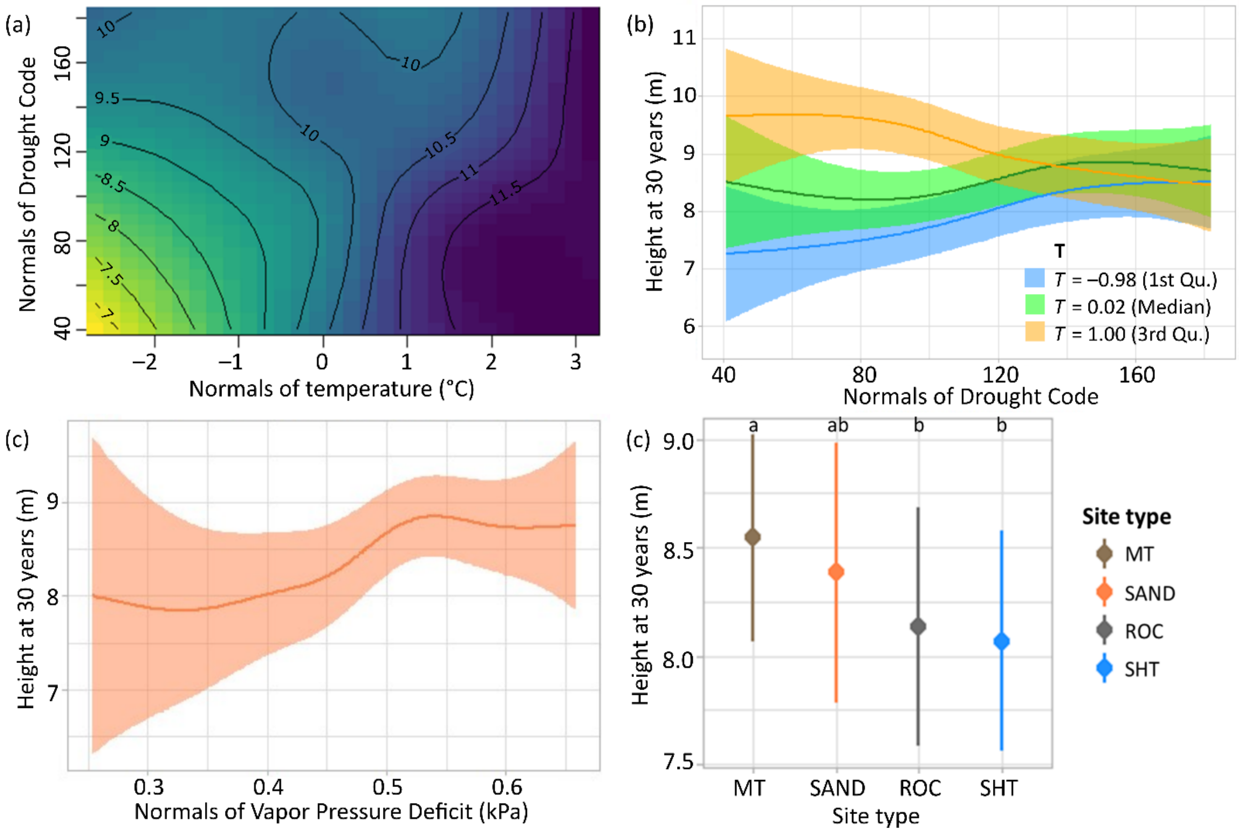

Figure 1.3. Environmental drivers for the height at 30 years of age (m; predicted values) for black spruce without juvenile suppression. (a) Contour plot depicting interaction effects between temperature (range of observed values from -2.70 to 3.18°C) and the Drought Code (DC; range of observed values from 78 to 180, unitless) on height growth. Darker colors indicate higher predicted height at 30 years of age. (b) Illustrative example detailing the relationship between height growth and DC at three different levels of temperature normals: first quantile (-0.98°C, cold); median quantile (0.02°C, intermediate); third quantile (1.00°C, warm). (c) Effects from Vapor Pressure Deficit (range of observed values from 0.25 to 0.66 kPa). (d) Effects from site type (MT (mesic), SAND (sandy), ROC (rock), and SHT (sub-hydric)). All other variables were set to their mean observed value and to MT for site type. Colored areas in panels (b) and (c) represent 95% confidence bands and error bars in panel (d). Letters at the top of panel (d) highlight significantly different H30 mean values (α = 0.05).

1.3.1.2 Jack pine

Like the black spruce model, the jack pine model had good predictive capacity (Table 1.3; Supporting Information S1.9 in Annexe A), and showed that age and juvenile suppression had significant effects on H30. This confirmed the importance of including both age and juvenile suppression in the models for jack pine to avoid biases related to these two factors. Latitude/longitude and plot also had effects on H30, confirming the need to account for spatial autocorrelation and sampling plots as a random effect (Table 1.3).

We found no significant interaction for jack pine. Temperatures, DC, snowfall and site type were not significant predictors (Table 1.3). Jack pine H30 increased with increasing VPD (Figure 1.4).

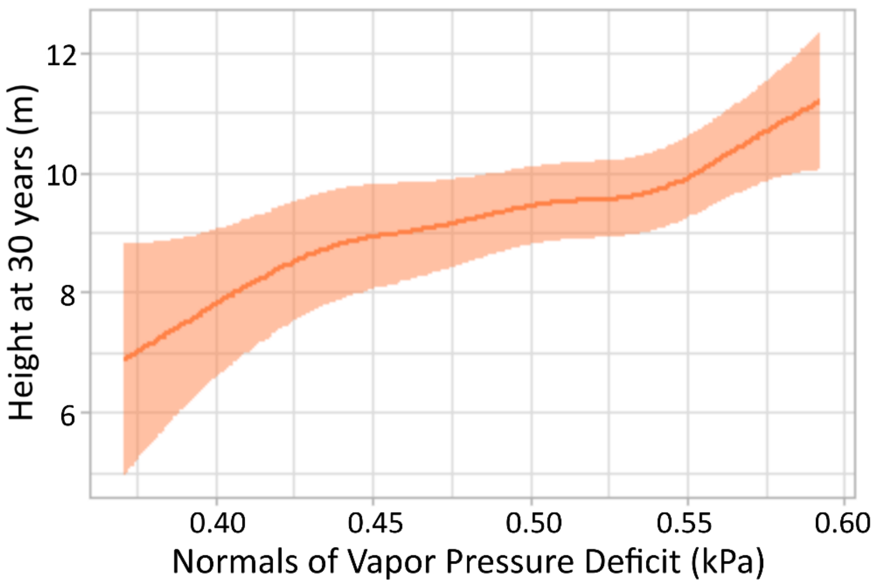

Figure 1.4. Effect of Vapor Pressure Deficit (range of observed values from 0.37 to 0.59 kPa) on height of dominant trees at 30 years (m; predicted values) for jack pine for mesic sites and without juvenile suppression. All other variables were set to their mean observed value. Colored shading represents the 95% confidence bands.

1.3.2 Potential climate change effects on height growth in boreal forests

1.3.2.1 Black spruce

Projected impacts of climate change on height growth varied. Over 1981–2010, black spruce H30 was estimated to range from 9.1 m to 14.5 m with slower growth in central and eastern regions (Figure 1.5a; Supporting Information S1.11; S1.12 in Annexe A). In comparison to 1901–1930, black spruce experienced a decrease in H30 in eastern, northwest and southern regions, whereas in the rest of the study area, H30 increased (Figure 1.6a). Most trees (90% intervals) had $H30_{1995–1915}$ ≥-6% and ≤16% with a median increase of 5%. Interestingly, most of the study area (77%) was located in areas inside the climate calibration range (Table 1.2). For this subregion, $H30_{1995–1915}$ (90% intervals) were between ≥-5% and ≤17% (Figure 1.6a) with a median increase of 6%.

For $H30_{2025–1995}$, black spruce height was projected to increase, except in a few areas, notably in the north and northwest regions of the study area (Figure 1.6b). $H30_{2025–1995}$ (90% intervals) were between 4% and 16% with RCP 4.5 and between 4% and 17% with RCP 8.5, with respective medians of 8% and 9%. Almost the entire study area (66% for RCP 4.5 and 71% for RCP 8.5) was inside the climate calibration range. For this subregion, most trees (90% intervals) revealed a change ≥4% and ≤17% with RCP 4.5 and between 5% and 18% with RCP 8.5, with a median of 10% for both RCPs.

For $H30_{2055–1995}$, projected increases in black spruce height were more substantial. Most trees (90%) had $H30_{2055–1995}$ of ≥10% and ≤27% with RCP 4.5 and ≥16% and ≤37% with RCP 8.5, with respective medians of 17% and 24%. Only portions of the study areas (59% for RCP 4.5 and 21% for RCP 8.5) were located inside the climate calibration range. For this subregion, most trees (90% intervals) had a $H30_{2055–1995}$ ≥10% and ≤28% with RCP 4.5 and between 24% and 40% with RCP 8.5, with respective medians of 20% and 31%.

For $H30_{2085–1995}$, height continued to increase. Most height increases (90%) were between 13% and 33% with RCP 4.5 and between 42% and 75% with RCP 8.5, with respective medians of 22% and 52%. Important sections of the study area (67% for RCP 4.5 and 100% for RCP 8.5) were outside of the climate calibration range. For the area within the calibration range, most trees (90% intervals) had a $H30_{2085–1995}$ ≥20% and ≤36% with RCP 4.5 with a median of 28% (Figure 1.6b).

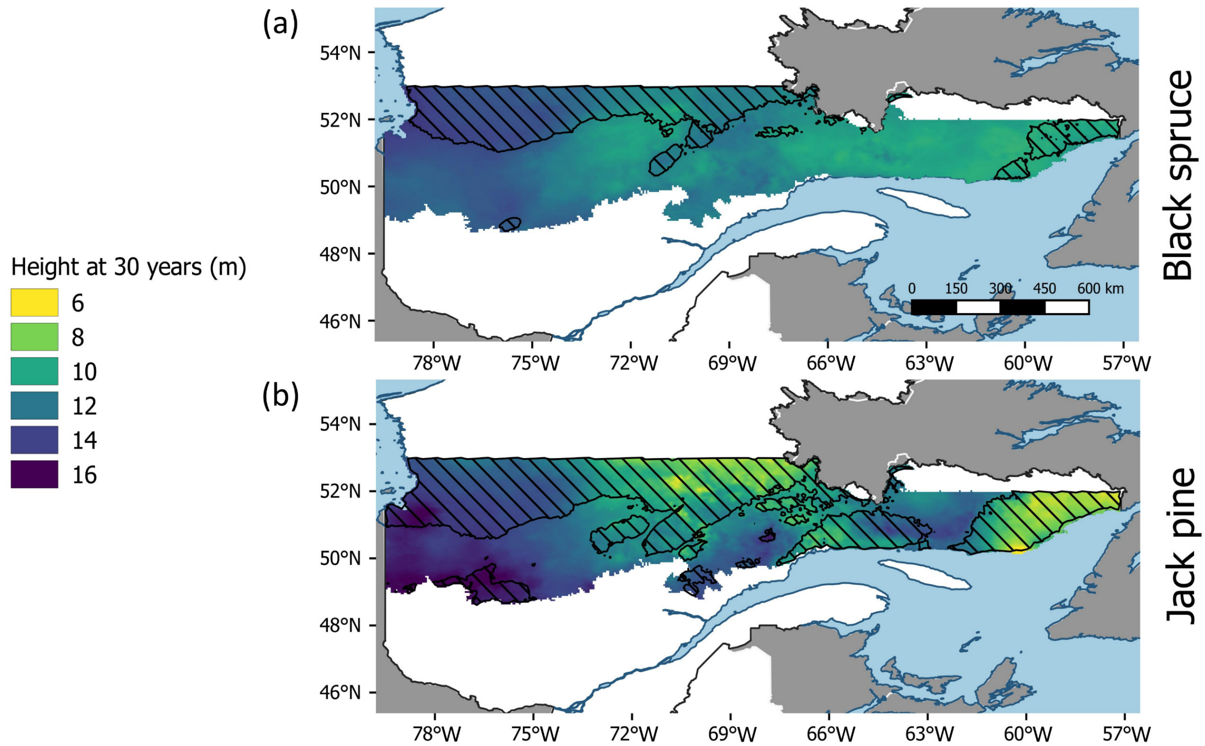

Figure 1.5. Projected height at 30 years (m) for the baseline period 1981–2010 for (a) black spruce and (b) jack pine. Hatched areas are outside the climate calibration range.

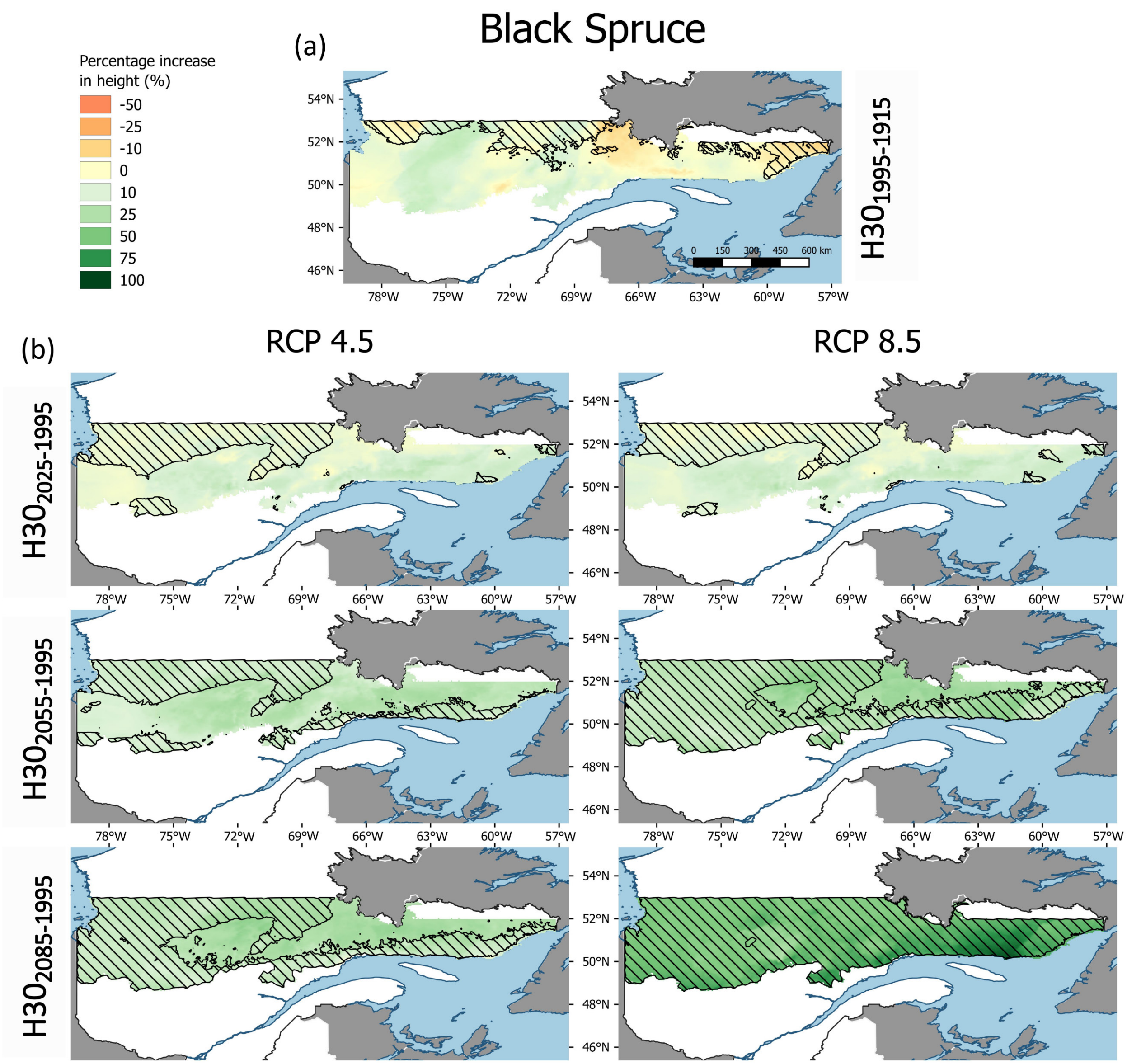

Figure 1.6. (a) Projected percentage change in height for black spruce between baseline (1995) and past (1915), and (b) between future periods (2025, 2055, 2085) and baseline (1995) for two different climatic scenarios (ESM2–RCP 4.5 and 8.5). Hatched areas are outside the climate calibration range.

1.3.2.2 Jack pine

For jack pine and over 1981–2010, H30 varied between 5.3 m and 17.3 m, with lower growth in central north and eastern regions (Figure 1.5b; Supporting Information S1.11; S1.12 in Annexe A). $H30_{1995–1915}$ decreased in central and eastern regions, whereas other regions showed increases. Most height growth changes (90%) were between -10% and 63% with a median of 11%. Part of the study area (40%) was inside the calibration range. For this subregion, $H30_{1995–1915}$ (90% intervals) were between ≥-1% and ≤22% with a median of 10% (Figure 1.7a).

For $H30_{2025–1995}$, jack pine height increased, except in some central regions, which showed a decrease. Most $H30_{2025–1995}$ changes (90%) were between 0% and 21% with RCP 4.5 and between -3% and 19% with RCP 8.5, with respective medians of 8% and 5%. Only portions of the study areas (27% for RCP 4.5 and for RCP 8.5) were inside the calibration range. For this subregion, most trees (90% intervals) had a $H30_{2025–1995}$ ≥0% and ≤23% with RCP 4.5 and between 0% and 20% with RCP 8.5, with respective medians of 7% and 5%.

For $H30_{2055–1995}$, projected increases in jack pine height were more substantial. Most trees (90%) had a $H30_{2055–1995}$ ≥8% and ≤38% with RCP 4.5 and ≥22% and ≤60% with RCP 8.5, with respective medians of 17% and 35%. The area inside the calibration range represented 13% of the study area for RCP 4.5 and 8% for RCP 8.5. For this subregion, most trees (90% intervals) had a $H30_{2055–1995}$ ≥8% and ≤34% with RCP 4.5 and between 22% and 46% with RCP 8.5, with respective medians of 16% and 31%.

For $H30_{2085–1995}$, jack pine height continued to increase. Most $H30_{2085–1995}$ (90%) were between 14% and 49% with RCP 4.5 and between 57% and 110% with RCP 8.5, with respective medians of 27% and 74%. Rare portions of the study area (2% for RCP 4.5 and 0% for RCP 8.5) were inside the calibration range. For this subregion, most trees (90% intervals) had a height growth change ≥12% and ≤47% with RCP 4.5 with a median of 23% (Figure 1.7b).

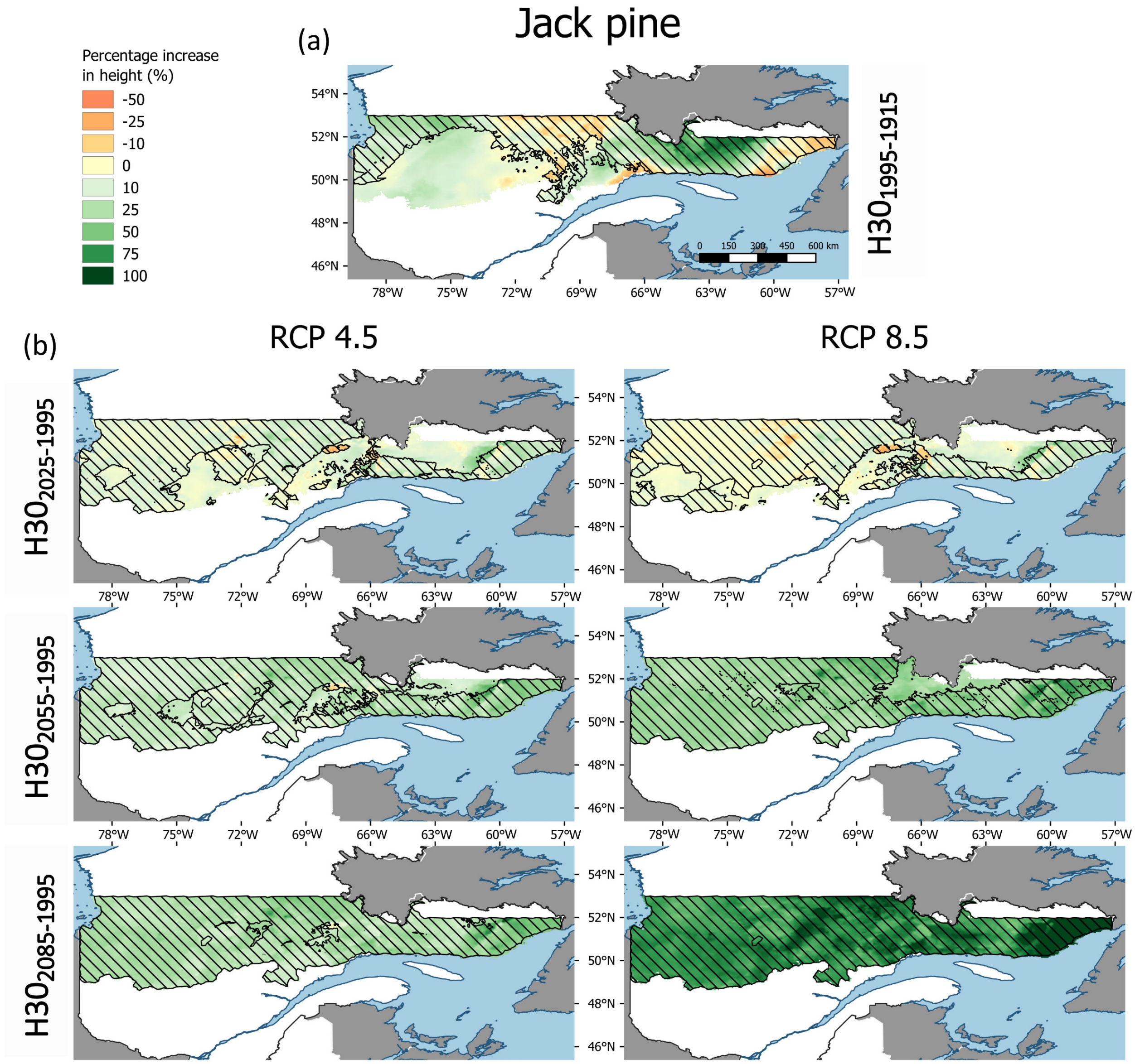

Figure 1.7. (a) Projected percentage change in height for jack pine between baseline (1995) and past (1915), and (b) between future periods (2025, 2055, 2085) and baseline (1995) for two different climatic scenarios (ESM2–RCP 4.5 and 8.5). Hatched areas are outside the climate calibration range.

1.4 Discussion

Within our sampling area, increasing temperature normals had a positive effect on black spruce height growth even if this effect was mitigated when and where climate conditions became drier. Warmer conditions can lead to a longer vegetative season and thus promote height growth of trees (Moreau *et al.*, 2020; Menzel et Fabian, 1999; Chmielewski et Rötzer, 2001; Messaoud et Chen, 2011; Price *et al.*, 2013; D'Orangeville *et al.*, 2016; Hember *et al.*, 2017; D'Orangeville *et al.*, 2018). Pedlar et McKenney (2017) found a similar increase in height for black spruce at 33 years of age with a mean annual temperature increase up to 4°C. Above this threshold; however, the effect reverses and further warming has a negative effect on height growth (Pedlar et McKenney, 2017). Given that our observed temperature varied from -2.7°C to 3.2°C for black spruce, it is possible these ranges were not wide enough to reach the threshold at which warming becomes detrimental for growth.

Our results shed light on a non-linear relationship for black spruce, whereby soil water availability was found to be a limiting factor for height growth at high temperatures (mean annuals >0.5°C; Figure 1.3a). Although height growth for both species was positively influenced by increasing VPD normals, the positive effect on black spruce growth ended once a threshold (0.53 kPa) was reached. In our study area, pronounced and prolonged multiyear droughts likely pushed atmospheric water demand beyond the threshold and limited black spruce growth, more so than less drought sensitive jack pine. Black spruce has a lower capacity to fully recover after a drought compared to jack pine, likely due to more stringent stomatal control under dry conditions, which can reduce carbon inputs (Marchand *et al.*, 2021). Often, drought is associated with lower tree growth (Chaste *et al.*, 2019; Girardin *et al.*, 2016a, b; Housset *et al.*, 2015; Marchand *et al.*, 2019; Way et Sage, 2008) and many studies have shown that high VPD conditions have a negative effect on trees by increasing transpiration, and reducing stomatal conductance and photosynthesis (Grossiord *et al.*, 2020). The non-linear response to VPD was not observed within our jack pine samples, perhaps because of the more limited climatic range of jack pine relative to black spruce.

Differences in tree height growth were associated with climate and also the type of surficial deposit, particularly for black spruce. Spruce height growth was greater on mesic and sandy sites than on rocky or sub-hydric sites. Rock outcrops consist of sedimentary rock formations that are only sometimes covered by a thin layer of mineral or organic material; thus, compared to the other surficial deposits, rock outcrops are poorer in nutrients. Sub-hydric sites are characterized by poor drainage (Supporting Information S1.5 in Annexe A) and are more prone to soil water saturation.

Unlike with black spruce, the jack pine model showed a greater sensitivity to VPD than to temperature or DC, independent of soil type. Black spruce and jack pine exhibit different rooting patterns and thus acquire water and nutrients at different depths, which could be responsible for differences in climate sensitivity and responses to climate change (Girardin *et al.*, 2008). Black spruce acquires water and nutrients from the organic layers, while jack pine acquires them from deeper horizons within the mineral soil (Houle *et al.*, 2014). These species-specific differences in climate sensitivity could represent the manifestation of the limited distribution of jack pine across the ecological and climatic extent that characterizes the territory under study, relative to black spruce. This interpretation is supported by previous work showing that under similar environmental settings and stand ages, the two species have covariant behavior across years and similar climate sensitivities (Girardin *et al.*, 2012).

The relationship between height growth and radial growth is well documented (Huang *et al.*, 1992; 2000; Sharma et Zhang, 2004; Newton et Amponsah, 2007; Sharma et Parton, 2007), including within our sampling area (Fortin *et al.*, 2009; 2013; Schneider *et al.*, 2013; 2018). Diameter at breast height is closely related to height (Fortin *et al.*, 2009). Resources are usually allocated to the area of the tree collecting the resource that is most limiting to its growth, although trees can modify their allocation patterns based on environmental or local factors (Mccarthy et Enquist, 2007; Schneider *et al.*, 2018). Within our sampling area as elsewhere, the height-diameter ratio increases with density and thus competition (Zeide et VanderSchaaf, 2002; Huang *et al.*, 2009), but this effect should be limited given the sampling of dominant trees. Additional factors, such as stand species mixture, can also affect height and radial growth. Species mixture can enhance litter decomposition and nutrient cycling (Prescott *et al.*, 2000; Cavard *et al.*, 2010), increase soil nutrient availability (Houle *et al.*, 2014; Oboite et Comeau, 2019), but also increase competition if there is a strong niche overlap between species (Oboite et Comeau, 2019; 2020). Species mixture can also influence the impact of climate on growth (Oboite et Comeau, 2019; Chavardès *et al.*, 2021). The effects of stand species mixture could become more important in the future with the northward migration of deciduous species associated with climate change, and the anticipated increase in proportion of deciduous-coniferous mixed stands (McKenney *et al.*, 2011; Terrier *et al.*, 2013). Clearly, more research is warranted on how different environmental and local factors influence the growth of boreal tree species.

Our approach facilitated assessments of tree responses to climate at the same life stage, namely young trees, whereas most studies focus on mature- and overmature trees. As our model revealed good predictive capacity within the calibration range (Table 1.3; Supporting Information S1.9 in Annexe A), we projected height growth according to future climate in the study area. These projections can be easily transposable to forest management where SI is used widely. Depending on the period and climate scenario, only part of the study area was located in areas inside the climate calibration range (non-hatched areas in Figure 1.6 and 1.7). We avoided interpretations outside our climate range because we did not know how trees would react to extreme future climate. Within the observed calibration range, future warming suggested mostly positive effects on black spruce and jack pine growth in the area where the forest transitions from closed- to open-forest. Depending on the period and climate scenario, this positive effect remained limited and was consistent with other studies (D'Orangeville *et al.*, 2018; Chaste *et al.*, 2019). These results also showed that there was little difference between the jack pine and black spruce projections. Although medians were similar, the height-change range was wider for jack pine than for black spruce. In some regions, our results showed greater increases in height growth for jack pine compared to black spruce, for both past and future climates. In those regions, jack pine may be better adapted than black spruce to future climate including warmer and drier conditions and more frequent fires, which is in agreement with previous studies (Subedi et Sharma, 2013; Marchand *et al.*, 2019; Sharma, 2021). On the contrary, other regions showed greater decreases for jack pine compared to black spruce. Black spruce is a competitive species and tends to dominate on mesic sites, whereas jack pine can establish more easily on poor sites, especially following fire (Burns et Honkala, 1990).

Our approach that smoothed the climate signal over 30 years did not allow the capture and, consequently, the prediction of the effect of single year or short-term climate extremes on tree growth, such as spring frosts or intra-annual droughts. Our predictions could be optimistic, especially considering forecasts of more frequent hotter and drier extremes than over past decades (Stocker *et al.*, 2013). Northern boreal forests may differ in sensitivity to climate change relative to southern boreal forests because of specific adaptations linked with distinct physical environments (Moreau *et al.*, 2020; Klesse *et al.*, 2020; Girardin *et al.*, 2021b). Drought sensitivity is not the same over the entire Canadian boreal forest (Girardin *et al.*, 2021b), and climate is also drier in central and western Canada than in Québec, over the baseline and also over the future (Girardin *et al.,* 2016b). It would therefore be interesting to use our approach in other regions of Canada to assess the impact of a warmer-drier climate. By using the Site Index, we were able to test the effect of climate variables on tree growth over several decades. This allowed us to focus on detecting the cumulative/average effects of climate on trees at the same maturity phase.

An increase of fire activity due to climate change is anticipated across boreal forests of Canada (Balshi *et al.*, 2009; Wotton *et al.*, 2010; de Groot *et al.*, 2013; Boulanger *et al.*, 2014; 2017; Wang *et al.*, 2017) and may cancel out potential growth increases. According to Gauthier *et al.* (2015a), it would take an increase of at least 50% in average growth compared to current growth to compensate for the loss of biomass due to the expected increase in annual area burned, an increase rarely projected by our models. Moreover, short fire intervals that will also become more prevalent in the future can have a significant impact on post disturbance forest density. Numerous studies have shown that natural disturbances including fire were the main cause of stand opening (Payette *et al.*, 2000; Simard *et al.*, 2007; Girard *et al.*, 2008; Rapanoela *et al.*, 2016, Blatzer *et al.*, 2021). Thus, increases in fire frequency, intensity, and area burned as a result of climate change could induce an increase in the proportion of open stands and a decrease in productivity (Rapanoela *et al.*, 2016; Splawinski *et al.*, 2019). It is therefore unlikely that climate change will have a positive impact on forest management in our study area, despite the positive results on height growth suggested in our findings.

1.5 Acknowledgements

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CHAPITRE 2

RESPONSE OF FOREST PRODUCTIVITY TO CHANGES IN GROWTH AND FIRE REGIME DUE TO CLIMATE CHANGE

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Résumé

Le changement climatique a des impacts complexes sur la forêt boréale, modulant à la fois les facteurs limitant la croissance des arbres et le régime des feux. Cependant, ces derniers sont généralement projetés indépendamment lors de l'étude de l'effet du changement climatique sur la forêt boréale. En utilisant une combinaison de 3 méthodes différentes, notre objectif est d'évaluer l'impact combiné des changements de croissance et de régime des feux dus au changement climatique sur le stock de bois à la transition entre les forêts boréales de conifères fermées et ouvertes au Québec, Canada. Afin d'identifier les zones susceptibles d'être les plus sensibles au changement climatique, nous avons projeté les impacts induits par le climat sur la croissance et l'activité des feux à trois périodes différentes : 2011-2040 RCP 8.5, 2071-2100 RCP 4.5, et 2071-2100 RCP 8.5. Notre étude montre l'importance d'intégrer le feu dans la planification stratégique de l’aménagement forestier, en particulier dans un contexte de changement climatique. Dans les scénarios les plus extrêmes, l'impact négatif de l'activité des feux sur la superficie productive et le volume total annule en grande partie les effets positifs du changement climatique via l’amélioration de la croissance des arbres.

Mots-clés : forêts boréales, changement climatique, productivité, croissance, régime des feux

Abstract

Climate change is having complex impacts on the boreal forest, modulating both tree growth limiting factors and fire regime. However, these aspects are usually projected independently when estimating climate change effect on the boreal forest. Using a combination of 3 different methods, our goal is to assess the combined impact of changes in growth and fire regime due to climate change on the timber supply at the transitions from closed to open boreal coniferous forests in Québec, Canada. In order to identify the areas that are likely to be the most sensitive to climate change, we projected climate-induced impacts on growth and fire activity at three different time periods: 2011-2040 RCP 8.5 for low growth change and minimum fire activity, 2071-2100 RCP 4.5 for moderate growth change and medium fire activity, and 2071-2100 RCP 8.5 for high growth change and maximum fire activity. Our study shows the importance of incorporating fire in strategic forest management planning especially in a context of climate change. Under the most extreme scenarios the negative impact of fire activity on productive area and total volume mostly offsets the positive effects of climate change via improved tree growth.

Keywords: boreal forests, climate change, productivity, growth, fire regime

2.1 Introduction

The boreal forest is a key ecosystem on many levels (ecological, economic, cultural, etc.), particularly in Canada where the timber industry is one of the most important in the world (Burton *et al.,* 2010). It is therefore important to manage the boreal forest in a sustainable way through ecosystem management (Gauthier *et al.,* 2008; Gauthier *et al.,* 2015a). With a predicted rise in global temperatures and a predicted increase in the frequency and intensity of droughts with increasing atmospheric CO_2 (Stocker *et al.,* 2013), the boreal forest would be the forest biome most strongly affected by global warming (Price *et al.,* 2013). In fact, an increase of mean annual temperature of 2°C and up to 6°C is projected across Canada by the end of this century, adding to an already observed increase of 1.7°C during the past century (Bush and Lemmen 2019). It can therefore be expected that continuing warming will have significant impacts on boreal forest, particularly in Canada (Gauthier *et al.,* 2015a; Price *et al.,* 2013).

Climate change is having complex impacts on the boreal forest, modulating both tree growth limiting factors and forest disturbances. At its northward margin in eastern Canada, many studies predict an increase in tree growth with global warming (Price *et al.,* 2013; Girardin *et al.,* 2016b; D'Orangeville *et al.,* 2016; Hember *et al.,* 2017; Chaste *et al.,* 2019; Pau *et al.,* 2022). There, low temperatures are associated with a short growing season and nutrient-poor soil conditions, which are factors limiting growth (Jarvis and Linder 2000). Increases in temperature could have a positive effect on growth by extending the growing season and stimulating photosynthesis rates (Menzel et Fabian, 1999; Chmielewski et Rötzer, 2001; Menzel *et al.,* 2006; Ibáñez *et al.,* 2010; Price *et al.,* 2013). On the other hand, warming and shifting water availability could cause forest losses along the warmer southern margins and within low-moisture environments, where tree growth is often limited by soil moisture availability (D'Orangeville *et al.,* 2016; Chaste *et al.,* 2019; Girardin *et al.,* 2021a).

Wildfire is a major disturbance in Canada’s boreal forest, contributing to an average 2M ha of stand renewal annually (Stocks *et al.,* 2002). Fire activity is anticipated to increase with climate change across boreal forests of Canada (Balshi *et al.,* 2009; Wotton *et al.,* 2010; de Groot *et al.,* 2013; Boulanger *et al.,* 2014; 2017; Wang *et al.,* 2017) and may cancel out potential increase in forest stock (Gauthier *et al.,* 2015b; Rapanoela *et al.,* 2015; Beaudoin *et al.,* 2017; Chaste *et al.,* 2019). In the context of sustainable boreal forest management, it seems particularly important to assess the combined impact of climate change via growth changes and changing fire activity.

Timber supply, that we herein define as the stock of merchantable stems available for harvesting, depends on tree species growth rate and disturbance rate. In order to take into account these two factors when calculating timber supply (Savage *et al.,* 2010; Leduc *et al.,* 2015; Gauthier *et al.,* 2015c), it seems important to project and combine growth changes and fire activity changes due to climate change, which few studies have yet investigated.

In this study, we investigate the response of Quebec's boreal forest timber supply, in terms of merchantable wood volume and productive area, to changes in growth and fire regime due to climate change. The goal will also be to assess which of the factors has the greatest impact on the current and future timber supply. This assessment will allow us to identify areas of the Quebec boreal forest that are likely to be the most sensitive to climate change and to assess the relevance of including fire and climate change in strategic forest management planning. This concern is particularly important in our study area, the area transition from closed to open forest in the coniferous boreal forest of Québec, given the socio-economic impacts associated with the Quebec boreal forest. Under current climatic conditions, the southern part of the study area, forest management is considered to be sustainable (Jobidon *et al.,* 2015), but the effects of climate change on timber supply are still uncertaint and need to be investigated (Leduc *et al.,* 2015; Daniel *et al.,* 2017).

To achieve this investigation, we made use of the site index (SI, height in m at 50 years) model of Pau *et al.,* (2022) to project the direct effects of climate change on tree growth, and the fire model of Boulanger *et al.,* (2014) to project the indirect effects via changing burn rates. The method of Gauthier et al. (2015c) and the production tables of Pothier and Savard (1998) were used to estimate mean merchantable volume and to combine the impacts of these direct and indirect effects. Since black spruce (Picea mariana (Mills.) B.S.P.) largely dominates throughout the study area, the species' timber supply was the main focus of our work. However, since jack pine (Pinus banksiana Lamb.) is a species better adapted to dry conditions than black spruce, due to its deeper root system and faster growth (Burns and Honkala 1990; Houle *et al.,* 2014), we also wanted to determine if any advantages could be conferred to jack pine in a context of long-term exposure to increased risks of moisture deficit and wildfires.

2.2 Methods

2.2.1 Study Area

Our study area extends from ~49°–53°N and ~79°–57° W in the province of Québec, Canada. This area is located at the northern limit of commercial forest (Jobidon *et al.,* 2015), at the transition between the spruce-feather moss forest (closed forest) and the southern portion of the spruce-lichen bioclimatic domains (open forest). Beyond (northward) the northern limit, harvesting operations are absent, thus natural dynamics dominate (Jobidon *et al.,* 2015). Black spruce is the main tree species in the area, and dominant surficial deposits are organic in western regions, deep till in central and northeastern regions, and rock in the south (Gauthier *et al.,* 2015c). Mean annual temperature decreases from south to north (from –4.9 to 1.6 °C) and total annual precipitation increases from west to east and north to south (from 651 to 1236 mm) (Gauthier *et al.,* 2015c). Our study area is divided into 1113 districts. A land district is defined as "an area of land characterized by a unique pattern of relief, geology, geomorphology, and regional vegetation" (Jurdant *et al.,* 1977). At the regional level, the land district emphasizes the geographic pattern that defines certain permanent ecological aspects of the environment (Gauthier *et al.,* 2015c; Saucier *et al.,* 2009).

2.2.2 Productivity estimation

To estimate the productivity, we used the method of Gauthier *et al.,* (2015c) based on site index (SI) and the relative density index at 100 years (RDI100). The SI, or the height at 50 years, is a commonly used temporal indicator of growth in forestry. Growth in height reflects site fertility and consequently the potential productivity of a forest stand (Monserud 1984). Given that height growth is negligibly affected by stand density (Skovsgaard and Vanclay 2008), SI mostly depends on site quality and climate being less affected by surrounding competition compared to diameter at breast height (DBH 1.3 m above ground) (Spurr and Barnes 1973). The RDI100 corresponds to "the density of a stand relative to that of a very dense stand in which all the trees are assumed to be of the same mean diameter size, normalized to 100 years" (Gauthier *et al.,* 2015c). Given that our study area is mostly covered by black spruce, we assumed that all stands were composed only of black spruce (see Gauthier *et al.,* 2015c). We did the same for jack pine to be able to compare the two species assuming that jack pine could be dominant in the context of long-term exposure to increased risks of water deficit and forest fires.

2.2.2.1 Forest data

Two data sets from the Gouvernement du Québec were used. To estimate productivity, we used SI and RDI100 derived from dendrometric characteristics from 9884 black spruce and 619 jack pine sample plots distributed over the entire study area. This dataset is composed in the south of sample plots from the regular Gouvernement du Québec forest survey conducted between 1990 and 2001 and in the north and east, of northern ecodendrometric northern plots surveys conducted by the Gouvernement du Québec annually from 2006 to 2009. To spatialize productivity, we used the Gouvernement du Québec detailed integrated map of forest polygons (an average of 2700 polygons larger than 4 ha for each 1114 districts over the study area). In the south, this map is composed of information acquired using aerial photographs from the third decennial forest inventory program, from 1990 to 2001, while in the north, a method based on the analysis of Landsat satellite corroborated by aerial photography (between 2005 and 2008) was adopted (Gauthier *et al.,* 2015c; Robitaille *et al.,* 2015).

Both datasets contain a wide variety of information on environmental and forest stands variables, such as aspect, elevation, surficial deposit, hydrologic regime, partial disturbance, ecological type, forest cover, height class, understory vegetation, and development stage. These biophysical variables were used to characterize the similarity among sites (see below in the 'Growth' section).

2.2.2.2 Climate Data

Climate data necessary to this study were obtained using the software BioSim 11 (Régnière *et al.,* 2017). As part of the procedure, daily weather data were interpolated from Environment and Climate Change Canada's historical climate database using the four nearest weather stations to each plot, adjusted for elevation and location differentials with regional gradients. Data were used for calculation of climate normals for the 1971–2000 period and for the following variables (see Gauthier *et al.,* (2015c) for more details): cumulative growing degree-days (°C), days in the growing season (days), consecutive days without frost (days), first frost day (Julian day), total growing season precipitation (mm), portion of total precipitation as snow (mm of water equivalent), aridity index (cm), and total radiation ($MJ \cdot m^{-2}$).These variables were chosen for their impact on vegetation dynamics and growth and were also used to characterize the similarity among sites (see below in the 'Growth' section).

2.2.2.3 Growth

SI and RDI100 values were available only for our 9884 black spruce and 619 jack pine plots. As such, we used the non-parametric k-NN matching method, which consists of estimating the indices of a given polygon with the weighted mean of the indices of the *k* most similar plots (*k* = 13 for black spruce and *k* = 14 for jack pine) to assign an SI and RDI100 to each of the forest polygons using those of the plots. Climatic, environmental, and forest stand variables described above, were used to characterize the similarity between sites. The weighting of a reference plot of a target polygon is based on the inverse of the distance computed from these variables (Raulier et *al.*, 2013). To include the uncertainty in the estimation of the SI and RDI100 of the polygons, a bootstrap resampling of *k* plots among the *k* plots used for each of the polygons was repeated 100 times to calculate productivity. Then the weighted mean of the SI and RDI100 by stand area was calculated for each of the 1113 districts.

2.2.2.4 Production classes and exposure times

Using SI and RDI100 and the production tables of Pothier et Savard (1998), Gauthier *et al.,* (2015c) calculated the minimum age at which stands of given SI and RDI100 exceed the two-parameter productivity threshold (50 m^3/ha and 70 dm^3/stem), which is equivalent to exposure time to fire (Table 2.1). This two-parameter productivity threshold of 50 m^3/ha and 70 dm^3/stem correspond to a minimum operable threshold for harvesting in Quebec. The determination of this minimum harvestable limits at stand level and at stem level was based on a harvest history. These limits represent the first decile of the cumulative frequency distributions of merchantable stand and stem volumes that were harvested between 1995 and 2005 (Raulier *et al.,* 2013) in the coniferous boreal forest of Quebec (Gauthier *et al.,* 2015c).

Table 2.1. Exposure time or minimum age at which a stand of given site index (SI, height in m at 50 years) and relative density index at 100 years (RDI100) exceeds the two-parameter productivity threshold (50 m^3/ha and 70 dm^3/stem).

		SI											
		Black spruce						Jack pine					
		12	14	16	18	20	22	12	14	16	18	20	22
RDI100	0.1	130	110	100	95	90	90	110	90	80	75	70	70
	0.3	100	85	75	70	65	65	85	70	65	60	55	55
	0.5	90	60	50	50	45	45	130	55	45	45	40	40
	0.7	160	55	40	30	25	25	140	65	40	30	25	25
	0.9	185	70	50	40	35	30	140	95	55	40	35	30

2.2.2.5 Volume

From the SI and RDI100 and using the equations of Pothier and Savard (1998), we calculated merchantable volume (m^3/ha) by district and by exposure time at 100 years.

2.2.2.6 Fire regime

Under the current climate, we defined the fire regime as in Gauthier *et al.,* (2015c). The fire map from MFFP, based on data from aerial surveys and satellite images, was used. Data since 1972 are complete and have been subject to quality control; therefore, only the period between 1972 and 2009 was used to define the territory's current regional fire activity. Our study area is divided into 10 homogeneous fire regime (HFR) zones from Gauthier *et al.,* (2015c) where burn rate varies between 2.272% HFR y^{-1} and 0. 012% HFR y^{-1}. Indeed, HFR reflects the spatial heterogeneity of the fire regime unlike other ecological classifications (Boulanger *et al.,* 2012). The fire regime defines the patterns of fire seasonality, frequency, size, spatial continuity, intensity, type and severity. Therefore, using a model based on HFR allows a more accurate spatial estimate of climate effects on fire regimes and thus a better projection of the future fire regime.

Based on the burn rate of each HFR, we then calculated the probability that a stand with a given SI and RDI100 would exceed the two-parameter productivity threshold while accounting for fire. The proportion of stands reaching the age where the two-parameter productivity threshold is reached is calculated using the equation of Johnson and Gutsell (1994) (Appendix 6 in Ministère des Ressources naturelles du Québec 2013):

$$(1)\quad Probability\ of\ exceeding\ the\ two\ parameter\ productivity\ threshold\ \ taking\ into\ account\ fires = exp(-exposure\ time\ x\ burn\ rate)$$

This gives a frequency distribution of the probability of reaching the two-parameter threshold against fire for each polygon. This procedure was repeated 10 times. Then, the weighted by stand area mean of the probabilities of exceeding the two-parameter productivity threshold taking into account fire were calculated for each district.

2.2.2.7 Productive area and total volume

We were then able to calculate the post-fire productive area as well as the total pre- and post-fire volume for each district and for each exposure time:

$$(2)\quad Post\ fire\ productive\ area$$
$$= Suitable\ areas\ for\ management\ before\ fire\ x$$
$$Probability\ of\ \ exceeding\ the\ two\ parameter\ productivity\ threshold$$

$$(3)\quad Total\ volume\ before\ fire\ = Volume\ x\ suitable\ areas\ for\ management\ before\ fire$$

$$(4)\quad Total\ volume\ after\ fire\ = \ Volume\ x\ \ post\ fire\ productive\ area$$

Suitable areas for management exclude areas with high physical limitations, without vegetation or considered unproductive (SI too low or negative RDI100).

2.2.3 Effects of climate change on growth and fire regime

To evaluate climate change impacts on forest productivity, we projected future fire regimes and tree growth according to specific future climate scenarios. We projected height growth of 9884 black spruce plots and 619 jack pine plots, and the fire regime within the 10 HFR (from Gauthier *et al.,* (2015c)) as explained below. The same process as described above (see section Productivity estimation) was then used to extrapolate plot-level growth to district-level productivity.

2.2.3.1 Future climate projection

Our goal was to assess the combined impact of changes in growth and fire regime on the timber supply for different levels of climate change. For reference, except for 2071-2100, there is little difference in our study area between two Representative Concentration Pathway (RCP) for the same time period. Indeed, for 2011-2040 with a 4.5 RCP, we have a projected mean temperature of 0.995 and with a 8.5 RCP, mean temperature is 1.11. Therefore, we projected climate-induced impacts on growth and fire activity at three selected periods/RCPs that seemed most relevant for our purpose: 2011-2040 RCP 8.5 for low growth change and minimum fire activity, 2071-2100 RCP 4.5 for moderate growth change and medium fire activity, and 2071-2100 RCP 8.5 for high growth change and maximum fire activity (Table 2.2). We used the period 1981–2010 as the reference climate (baseline). RCP scenario climate data were retrieved from the fourth generation Canadian Regional Climate Model (CanRCM4) which was driven by the second-generation Canadian Earth System Model (CanESM2)/fourth generation coupled GCM (CGCM4) to mimic 1981–2010 normals (Dunne *et al.,* 2012). From these datasets, we then calculated future normals (30 years values) for all climate variables used by Pau *et al.,* (2022) and Boulanger *et al.,* (2014) models to project future growth and fire, for each of our four periods/RCPs. All climate data have been calculated with BioSim 11 (Régnière *et al.,* 2017).

For black spruce, 20 scenarios were run to simulate independent growth or fire regime changes which allows us to see what the productivity would be if the growth or fire regime changes were over- or underestimated. For jack pine, only joint change scenarios were tested, in order to make a comparison with black spruce (Table 2.3).

Table 2.2. Level of growth and fire change, their corresponding Period/RCP and their corresponding increase in mean temperature as averaged over the whole study area.

Period/RCP	Present	2011-2040 ESM2–RCP 8.5	2071-2100 ESM2–RCP 4.5	2071-2100 ESM2–RCP 8.5
Increase in mean temperature	T= 0ºC	+1.3ºC	+3.7ºC	+6.6ºC
Black spruce growth change	**No change** SI = 12.82m	**Low** +10.5%	**Moderate** +23.2%	**High** +59.7%
Jack pine growth change	**No change** SI= 13.38m	**Low** +4%	**Moderate** +17%	**High** +82.1%
Fire activity	**Current** Burn rates = 0.0079% y^{-1}	**Minimum** +84%	**Medium** +326%	**Maximum** +620%

Table 2.2. Climate scenarios for black spruce (BS) and jack pine (JP).

		Growth Change			
		No change	Low	Moderate	Hight
Fire activity	Without fire	BS JP	BS	BS	BS
	Current	BS JP	BS	BS	BS
	Minimum	BS	BS JP	BS	BS
	Medium	BS	BS	BS JP	BS
	Maximum	BS	BS	BS	BS JP

2.2.3.2 Climate effects on growth

To project growth change in response to climate change, we used the black spruce and jack pine growth models developed by Pau *et al.,* (2022). Originally calibrated on data from 2591 black spruces and 890 jack pine plots using Generalized Additive Models (GAM), the formulation implements height growth based on climate normals corresponding to the growth period of each stem, and site type (as a function of texture, stoniness and drainage). With this model, we projected trends in height growth for our 9884 black spruce and 619 jack pine plots and for the future periods/RCP (Table 2.2). We then estimated percent increases in height growth between future and baseline as follows:

$$(5)\quad Percent\ increase\ between\ future\ and\ baseline\ (Height\ growth_{Future-baseline}) = \left(\frac{Height\ growth_{future} - Height\ growth_{baseline}}{Height\ growth_{baseline}}\right) \times 100$$

These percentage increases in height growth were then applied to our current SI, giving us a future SI for each plot and period/RCP (Table 2.2). In order to avoid incoherent projected SI and according to observed values and production tables of Pothier and Savard (1998), we have limited SI to a maximum value of 22 for both species.

2.2.3.3 Climate effects on fire regime

Since no models have been developed to project future burn rate within each of the 10 HFR zones developed by Gauthier *et al.,* (2015c), we rather used models developed for Canadian-based HFR zones (Boulanger *et al.,* 2014). These Canadian-based HFR zones were delimited at a much coarser scale and do not represent a higher hierarchical level classification of the Gauthier *et al.,* (2015c) HFR zones. As such, we intersect both classifications and we identified which Canadian-based HFR zones pertained to each resulting portion of the Gauthier *et al.,* (2015c) HFR zones. Future burn rate for each of these portions was then assessed by first calculating the percent change in future burn rate at the Canadian-based HFR level as follows:

$$(6)\quad Percent\ change\ between\ future\ and\ baseline\ (Area\ burned_{Future-baseline}) = \left(\frac{Area\ burned_{future} - Area\ burned_{baseline}}{Area\ burned_{baseline}}\right) \times 100$$

We then weighted the percent changes for each Gauthier *et al.,* (2015c) HFR zone according to the intersected areas, giving us a future burn rate for each HFR and period/RCP (Table 2.2).

2.2.4 Statistical Analyses

In order to evaluate which factors would be most influential on the future productivity of the study area, we realized a two-way ANOVA to determine the influence of level of change in growth and fire regime on mean merchantable volume (m^3/ha) with the 'rstatix' package in R (Kassambara 2021).

2.3 Results

Both growth and fire activity significantly affected future total volume. Increasing growth with climate change is increasing total volume while concomitant increase in fire activity has the opposite effect (Figure 2.1). There is a significant interaction between the effects of level of growth change and the level of burn rate change on merchantable volume ($p < .0001$) (Table 2.4). The climate-induced effect of growth improvement fades out as fire activity conditions become more extreme. However, as growth change increases, the negative effect of burn rate change is stronger (Figure 2.1).

Table 2.4. Results from the two-way ANOVA on the influence of level of change in growth and burn rate on mean merchantable volume (m^3/ha).

Climate-induced effect	Sum of squares	Mean of squares	DF	F value	p value
Growth change	2351522	783841	3	6603.098	<.0001
Fire activity	2523996	841332	3	7087.407	<.0001
Growth change x Fire activity	33187	3687	9	31.063	<.0001

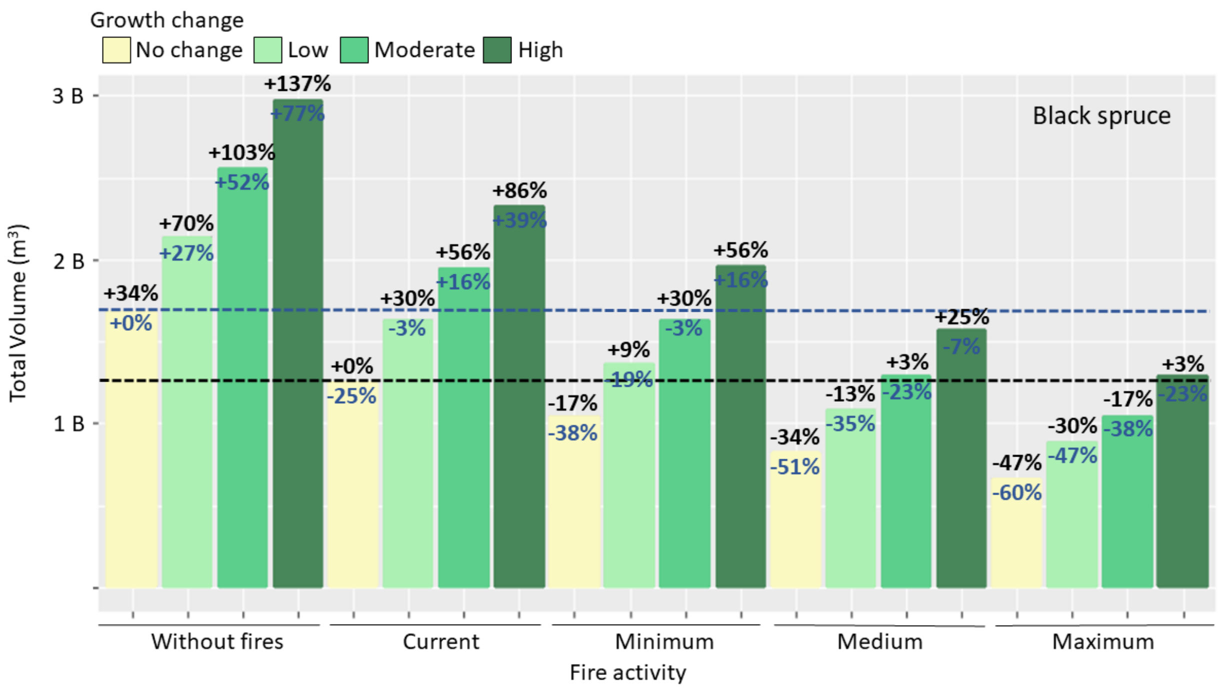

Figure 2.1. Projected total volume (m^3) for black spruce for four levels of change (growth/fire activity): no change/current (present), low/minimum (2011-2040 ESM2–RCP 8.5), moderate/medium (2071-2100 ESM2–RCP 4.5) and high/maximum (2071-2100 ESM2–RCP 8.5) and without fires. Percentages in blue report the changes in volume compared to no change in growth without considering fires (dotted blue line) and in black, percentage change in volume compared to no change in growth and no change in fire (dotted black line).

Omitting fire impacts would overestimate, total volume by 34% with no growth change, by +70% with low growth change, by +103% with moderate growth change and by +137% with high growth change (Figure 2.1). Taking into account only current fire activity would also overestimate the total volume but to a lower extent, i.e., by +30% with low growth change, by +56% with moderate growth change and by +86% with high growth change (Figure 2.1).

Conversely, omitting the impact of climate-induced growth change would underestimate future total volume by -17% with low growth change, by -34% with moderate growth change and by -47% with high growth change (yellow/no change bars in Figure 2.1).

When considering both climate-induced growth change and fire activity (i.e., same period and same RCP), there are minor differences between projected and current total volumes (Figure 2.1). Under joint change scenarios (same period/RCP), total volume remains similar or increases slightly and the positive effects of climate change on growth offset negative effects from changing fire regime.

Compared with black spruce, jack pine total volume would be higher by +43% without fire and no growth change, by +40% with current fire activity and no growth change, by +15% with minimum fire activity and low growth change, by +20% with medium fire activity and moderate growth change, and by +33% with maximum faire activity and high growth change (Figure 2.2).

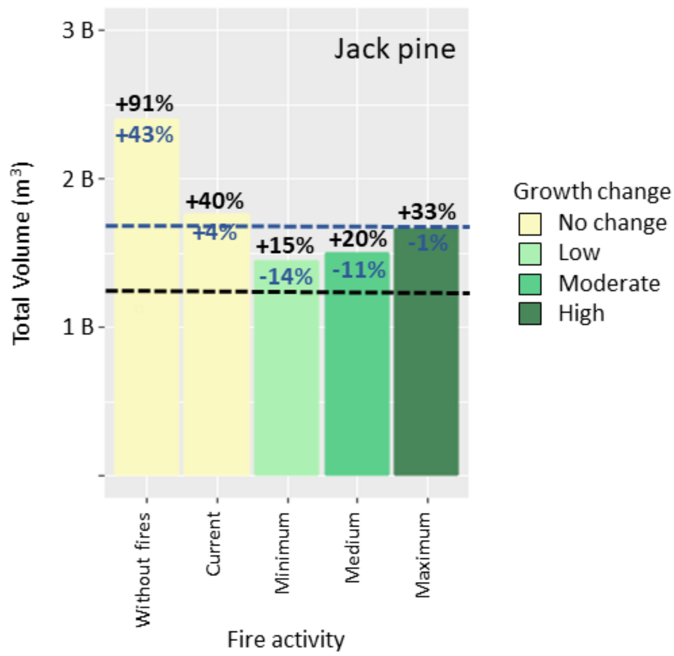

Figure 2.2. Projected total volume (m^3) for jack pine for four levels of change (growth/fire activity): no change/current (present), low/minimum (2011-2040 ESM2–RCP 8.5), moderate/medium (2071-2100 ESM2–RCP 4.5) and high/maximum (2071-2100 ESM2–RCP 8.5) and without fires. Percentages in blue report the changes in volume compared to no change in growth without considering fires for black spruce (dotted blue line) and in black, percentage change in volume compared to no change in growth and current fire for black spruce (dotted black line).

Again, for black spruce, omitting projected fire impacts would overestimate the productive areas by +42% with no growth change, by +74% with low growth change, by +128% with moderate growth change, and by +166% with high growth change (Figure 2.3). The level of change in fire regime negatively influences the productive areas while the level of change in growth positively influences both merchantable volume and available forest area (Figures 2.1 and 2.3).

Currently (no growth change and current fire activity), for black spruce, we observe a productive area of 14.3 M ha with a maximum merchantable volume of 139 m^3/ha, and half of the area exceeding 76 m^3/ha (Figure 2.3 top left panel). Although the productive area is greatly reduced with changes in the fire regime, the merchantable volume of the available forest area increases with changes in growth. With high growth changes and maximum fire activity, the productive area is 9.9 M ha, i.e., a decrease of -31% compared to the current situation. The maximum merchantable volume increases to 192 m^3/ha, whereas half of the productive area exceeds 121 m^3/ha.

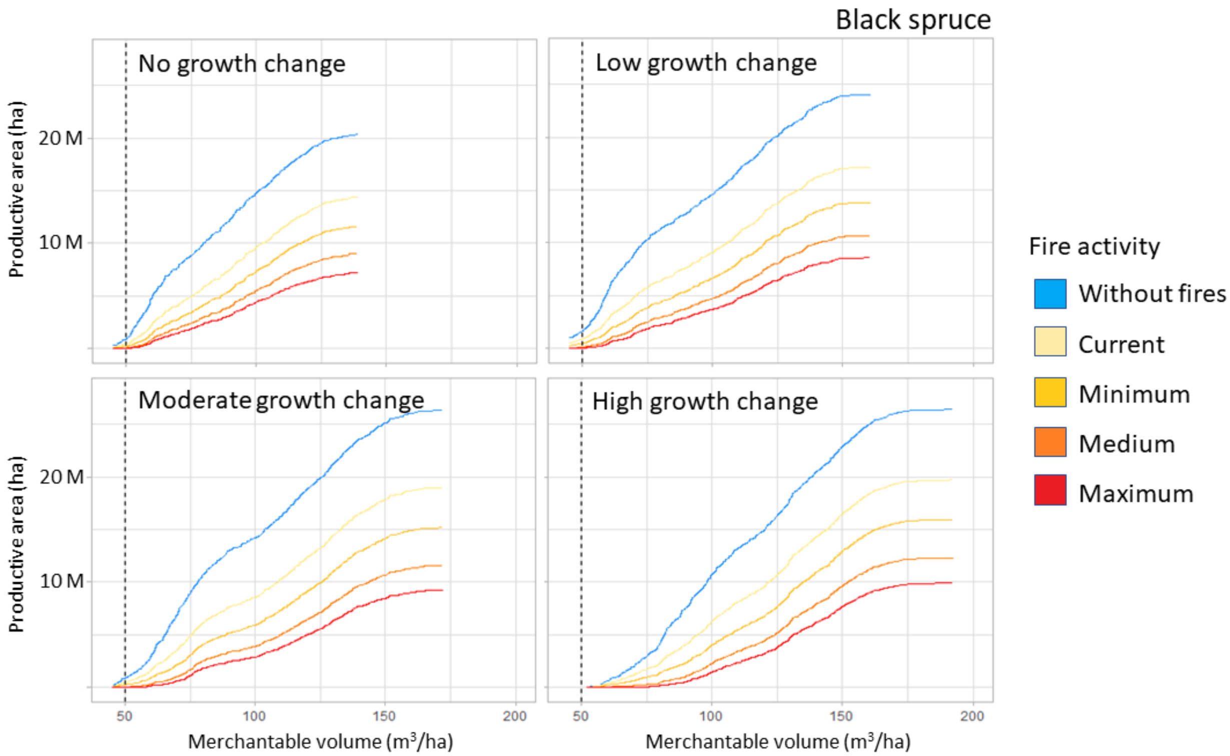

Figure 2.3. Projected cumulated productive area (ha) according to merchantable volume (m3/ha) for black spruce for four levels of change (growth/fire activity): no change/current (present), low/minimum (2011-2040 ESM2–RCP 8.5), moderate/medium (2071-2100 ESM2–RCP 4.5) and high/maximum (2071-2100 ESM2–RCP 8.5) and without fires.

Without considering climate-induced fire and growth changes, for black spruce, most of the districts (90%) would be productive (≥ $50m^3/ha$), except for a small area in the north (Figure 2.4 top left panel). As opposed, when the current fire regime is taken into account, the productive area is divided in two, with most of the productive area (60% of districts) being restricted to the southern part of the study area (Figure 2.4 top right panel).

As burn rates increase with anthropogenic climate forcing, unproductive areas increase and expand southward (Figure 2.4 third column panels). As the level of change in growth increases, the merchantable volume of productive areas increases (Figure 2.4 first and second column panels), although the area of such productive forest decreases to varying levels as a function of fire regime changes (Figure 2.4 fourth column panels).

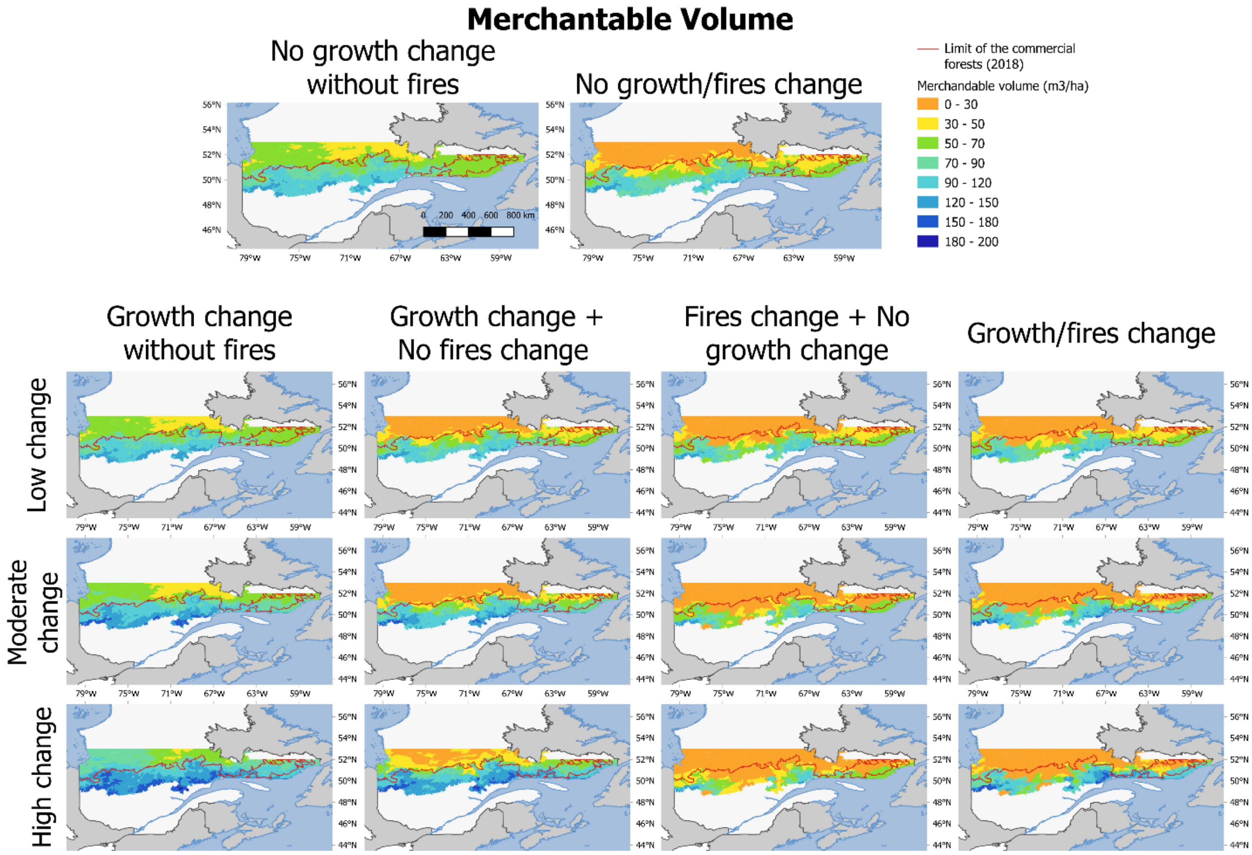

Figure 2.4. Projected merchantable volume (m^3/ha) (relative to the area without fire at each level of growth change) for black spruce for four levels of change: no change/current (present), low/minimum (2011-2040 ESM2–RCP 8.5), moderate/medium (2071-2100 ESM2–RCP 4.5) and high/maximum (2071-2100 ESM2–RCP 8.5) in growth/fire activity, and without fires.

Without considering fires, for black spruce, most of the districts (53%) would encompass more than 50% of productive area, except for a small area in the north and in the west (Figure 2.5 top left panel). When considering the current fire regime, most districts in the northernmost part of the study area (63%) are mostly unproductive while these proportions drop to 37% in the south (Figure 2.5 top right panel).

As the level of change in the fire regime increases with climate change, areas with a low percentage of productive area increase and expand southward (Figure 2.5 third column panels). On the contrary, as the level of change in growth increases, areas with a low percentage of productive area decrease and move northward (Figure 2.5 first and second column panels). Currently (no change in growth and in fire regime), 69% of the districts ≥ 20% of productive area, 37% ≥ 50%, 2% ≥ 80%. With high changes in growth and fire regime, 59% of the districts ≥ 20% of productive area, 20% ≥ 50%, 1% ≥ 80%.

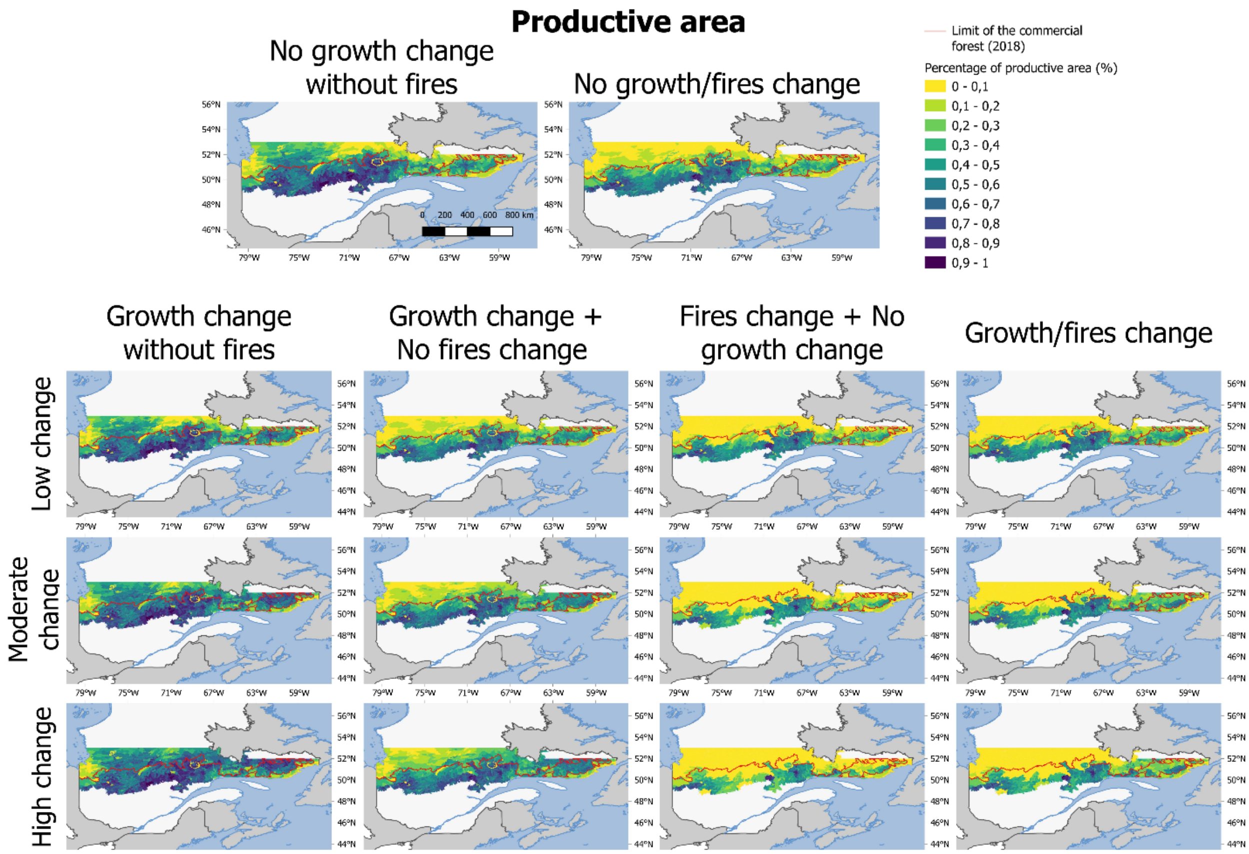

Figure 2.5. Projected percentage of productive area (> 50 m^3/ha and 70 dm^3/stem) for black spruce for four levels of change: no change/current (present), low/minimum (2011-2040 ESM2–RCP 8.5), moderate/medium (2071-2100 ESM2–RCP 4.5) and high/maximum (2071-2100 ESM2–RCP 8.5) in growth/fire activity, and without fires.

Compared with black spruce, with current fire activity and no growth change (present), jack pine merchantable (Figure 2.6 left panels) volume is better than black spruce in the southwest, north-central and east, but worse in the south-central and northwest. With minimum fire activity and low growth change (2011-2040 ESM2–RCP 8.5), a significant decrease in jack pine merchantable volume compared to black spruce can be observed in the central and southern regions. A better jack pine merchantable volume is still observed in the east, west and north central regions. With medium fire activity and moderate growth change (2071-2100 ESM2–RCP 4.5), jack pine merchantable volume is better than black spruce again in the north and east, but worse in the south-central. With maximum fire activity and high growth change (2071-2100 ESM2–RCP 8.5), jack pine merchantable volume is better than black spruce across the northern half of the study area. A worse jack pine merchantable volume can be observed only in a few south-central districts.

For the productive area (Figure 2.6 right panels), there is a northern region where jack pine has a much better productive area than black spruce. This area is the smallest with minimum fire activity and low growth change but widens and moves southward as the level of growth changes and fire activity increases until it covers the entire northern half of our study area. A central region with a lower jack pine productive area than black spruce can also be found in our study area. This area is the largest with minimum fire activity and low growth change but decreases as the level of growth changes and fire activity increases until it almost disappears.

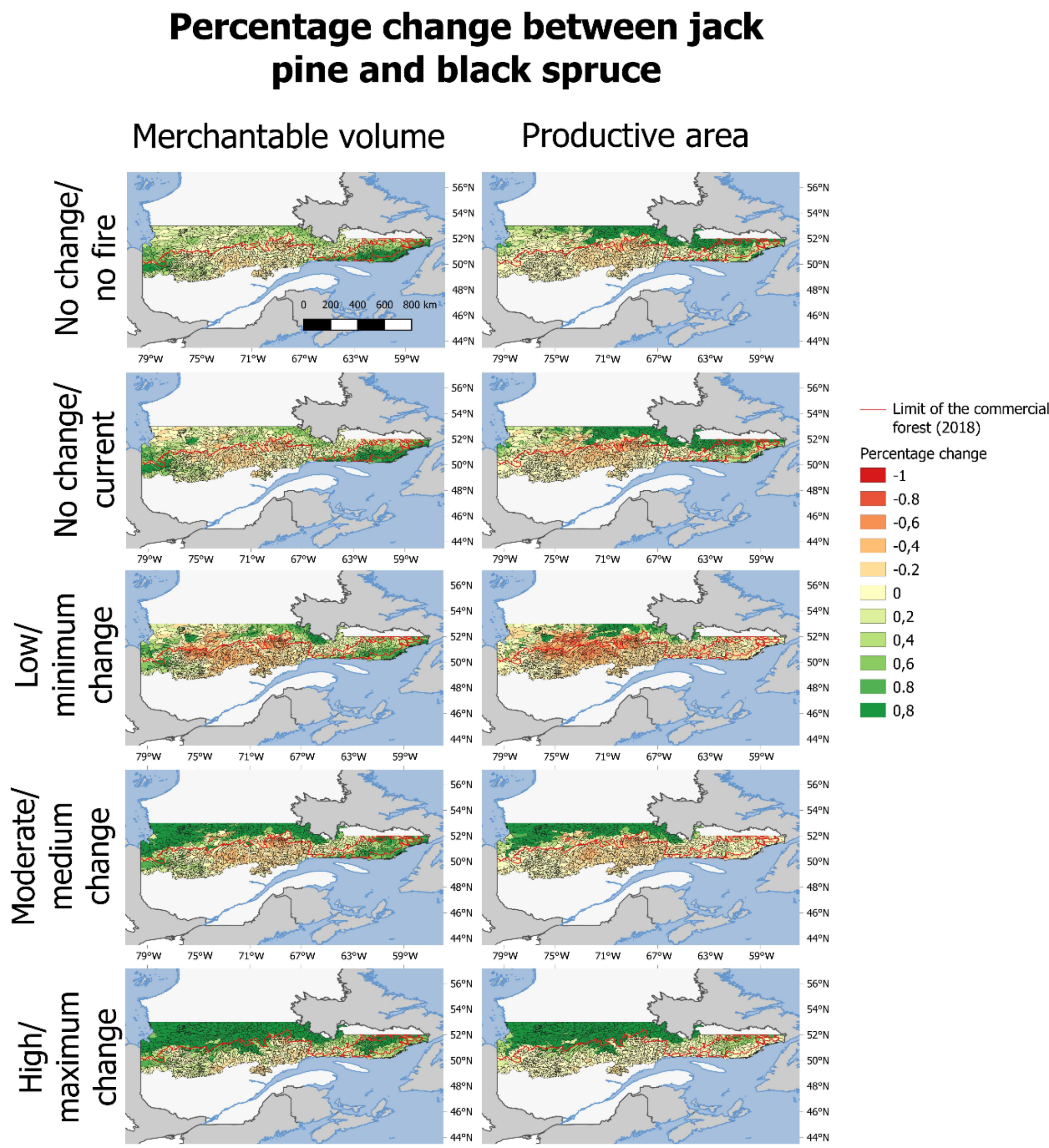

Figure 2.6. Projected change of merchantable volume and productive area (50 m^3/ha and 70 dm^3/stem) between black spruce and jack pine for five levels of change (growth/fire activity): no change/no fire, no change/current (present), low/minimum (2011-2040 ESM2–RCP 8.5), moderate/medium (2071-2100 ESM2–RCP 4.5) and high/maximum (2071-2100 ESM2–RCP 8.5).

2.4 Discussion

Our main goal was to evaluate the cumulative impact of climate change on growth and on fire activity on Quebec's boreal forest timber supply. Our results show that as temperature increases, growth increases, resulting in an increase in total volume. In parallel, fire activity also increases with warming, thereby contributing to reducing total volume. Synergically, as fire activity increases, the positive effect of warming on total volume is reduced: the effect of growth improvement on productivity will fade out as the burned area becomes more extended. Warmer conditions can lead to a longer vegetative season and thus promote growth of trees (Chmielewski et Rötzer, 2001; D'Orangeville *et al.,* 2016, 2018; Hember *et al.,* 2017; Menzel et Fabian, 1999; Messaoud et Chen, 2011; Moreau *et al.,* 2020; Price *et al.,* 2013) but also leads to favorable conditions for fires, which results in increased fire activity (Balshi *et al.,* 2009; Wotton *et al.,* 2010; de Groot *et al.,* 201.3; Boulanger *et al.,* 2014; 2017; Wang *et al.,* 2017).

Our results demonstrate the importance of taking fire into account when projecting future merchantable volume. Taking into account only the effect of a changing climate on tree growth leads to an overestimation of productive areas, resulting in an overestimation of the total volume and thus of the available timber supply for harvesting (Gauthier *et al.,* 2015c; Cyr *et al.,* 2022). Gauthier *et al.,* (2015c) discussed the risk of not considering fire in our study area. Not only does our study support this result, but it also shows that it will be even more necessary to consider fire risk to merchantable volumes in the future under global warming.

Although the effect of fire suppression was not specifically considered, we believe that it would have had limited impact on our results. First, our current fire activity is calculated over a period of time when suppression resources were equivalent to those available today. Regarding fire suppression, our study area is separated into two parts. The southern part corresponds to the full response zone called intensive protection zone. In this area, the Forest Fire Protection Agency of Quebec (Société de protection des forêts contre le feu, SOPFEU) aims to systematically control all fires. The northern part of our study area corresponds to the Northern Protection Zone. Although all fires occurring in this zone are detected, only some of them are fought to ensure the protection of Quebec's communities and strategic infrastructures (SOPFEU, 2018). For the southern part of our study area, Cardil *et al.*, (2019) showed that despite a good fire suppression system, fires in this area are more rarely controlled and result in large areas burned. As fires tend to occur simultaneously, they often create overflow situations (Gillett *et al.*, 2004). During extreme weather conditions, these overflows are then responsible for large areas burned despite suppression efforts (Danneyrolles *et al.*, 2021). With the prediction of increased fire activity due to climate change (Boulanger *et al.*, 2014), more situations leading to large fires will occur, particularly in the boreal regions (Wotton *et al*., 2010). Hence the importance of including fires in all management phases to ensure sustainable forest management, especially under climate change.

One unforeseen outcome of the study is that, although the productive area would be greatly reduced with changes in the fire regime, there is an increase in the merchantable volume in the areas that remain productive. In the future, therefore, harvestable areas would decrease, but the productive areas should have a higher merchantable volume with larger stems and/or higher tree density. This unexpected result indicates that by not taking into account growth change due to climate change and only fire activity under climate change, we can also underestimate the merchantable volume, and accordingly the available timber supply in productive areas.

In terms of productive areas, our results show that the study area is divided in two, with a productive area in the south and an unproductive area in the north. As the level of change in fire regime increases, unproductive areas increase and move southward. As the level of change in growth increases, the merchantable volume of productive areas increases in the south. Even without fire and with improved growth, the south remains much more productive than the northern ones with areas in the south reaching up to 200 m^3/ha and the northern area not exceeding 90 m^3/ha. These results are in agreement with those of Gauthier *et al.,* (2015c) who found this same contrast between the south and the north. This zone with low productivity, and particularly vulnerable to fire and climate change, stretches from west to east along the northern shore of Lake Mistassini and a portion of the east side of the Gulf of St. Lawrence. The boreal forest in the northern part of our study area is thus exposed to arid climatic conditions and grows on low productivity surface deposits (like organic plains of Abitibi and rock deposits of the North Shore) (Gauthier *et al.,* 2015c).

Our results also suggest an advantage of jack pine over black spruce, especially in the northern half of our study area. Black spruce is a competitive species and tends to dominate on mesic sites, whereas jack pine is fast growing and can establish more easily on poor sites, especially following fire (Burns et Honkala, 1990). In the southern areas where an increase in black spruce merchantable volume is observed, there would be limited gain in adding jack pine. However, in the northern half of our study area, characterized by low productivity and high vulnerability to fire and climate change, it might be interesting to consider jack pine over spruce in forest management, e.g. for plantations. Though, as this area is not easily accessible, potential gains in merchantable volume and productive area would depend on considerable financial investment that could be at risk notably when considering regeneration failure. Indeed, the northern half of our study area, characterized by low productivity and high vulnerability to increased fires due to climate change could also be particularly vulnerable to regeneration failure. Natural disturbances such as fire are the dominant cause of stand opening and thus of decreased productivity (Rapanoela *et al.,* 2016; Splawinski *et al.,* 2019; Cyr *et al.,* 2022, Baltzer *et al.,* 2021). However, the impact of loss of stem density produced by regeneration failure was not considered in this study.

Our combination of different methods projecting tree growth, fire activity and stand productivity, is a valuable strategic method for evaluating how vulnerable a region may be to climate change. In addition, it allows the estimation of the potential timber supply in each district. This is helpful to guide current and future forest management at the northern limit of current commercial forestry. In the northern part of our study area, even without taking fire risk into account, it is quite unlikely that the forest could be managed sustainably and this becomes less and less probable in the future as suggested by our projections. Indeed, these districts already have a very low proportion of productive areas. In contrast, the southern portion of our study area has the potential to be sustainably managed. Not only is the productive area portion of this zone minimally affected by increased fire, but its merchantable volume will likely be also favorably affected by improved growth. This area in the south, easier to access, shows favorable conditions for a timber supply increase, and seems interesting for reforestation programs.

As we are mostly in a northern environment, it is possible that the growth model used (Pau *et al.,* 2022), which is based on an observed temperature range of -2.7°C to 3.2°C, is not wide enough to include the 4°C threshold at which warming becomes detrimental to growth, as observed by other studies (Pedlar et McKenney, 2017). However, the combination of different levels of potential change in growth and fire allows us to forecast scenarios where fire or growth projections would be over or underestimated. Our study did not take into account the local adaptations of black spruce populations to climate. A recent study conducted on black spruce populations from different geographic provenances established in a common garden near Chibougamau provided indications that local black spruce populations were poorly adapted to the changing climate (Girardin *et al.,* 2021b). This was demonstrated by lower productivity of local populations in comparison with populations originating from southern provenance locations. It is therefore likely that it would be possible to increase black spruce productivity by selecting more efficient and resilient provenances in the face of a changing climate. However, our productivity threshold (50 m3/ha and 70 dm3/stem) also remains a minimum threshold since the absolute harvestable age, which ensures maximum wood production per stand, is on average 21 years older in our study area than the minimum age for reaching the productivity threshold (Raulier et al., 2013). In a management context, aiming for harvest at absolute harvestable age would therefore increase vulnerability to fire even further as exposure time would be prolonged. SI could be overestimated due to the selection of dominant or co-dominant trees which could also lead to an underestimation of the vulnerability to fire since a smaller site index would also increase the exposure time. Finally, post-disturbance densification of hardwood species such as poplar or birch was also not considered and may contribute to merchantable walking volume (Baltzer *et al.,* 2021; Augustin *et al.,* 2022).

2.5 Conclusion

Our study shows the importance of incorporating both fire and growth in strategic forest management planning (Savage *et al.,* 2010; Leduc *et al.,* 2015; Gauthier *et al.,* 2015c). It is even more important when considering the extreme impacts of climate change. Not integrating fires leads to an overestimation of the productive area, creating a sharp contrast between timber volume projections and real volumes that incorporate fire activity under climate change, that can lead to a decline of the Quebec boreal forest (Paradis *et al.,* 2013; Gauthier *et al.,* 2015c; Cyr *et al.,* 2022). In light of our results, the forest area that can be sustainably managed is thus likely to decrease with climate change. As unproductive areas increase and move southward with projected changes, it is very unlikely that sustainable forest management could be extended northward of the current commercial forestry limit in the future. However, opportunities in relation to increased productivity in some areas south of the northern limit would benefit to be explored. Finally, future work should be devoted to evaluate the impact of regeneration failures on our results.

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CHAPITRE 3

CURRENT AND FUTURE IMPACTS OF REGENERATION FAILURES ON BOREAL FOREST PRODUCTIVITY

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En préparation pour une prochaine soumission.

Résumé

Avec les augmentations prévues des températures mondiales, de la fréquence et de l'intensité des sécheresses, le biome boréal devrait être l'un des plus fortement touchés par le changement climatique. Des études récentes indiquent que le réchauffement climatique entraînerait une augmentation de la croissance des arbres à sa limite nord la plus froide, dans l'est du Canada, mais aussi une augmentation de l'activité des incendies. Les deux principales espèces de la forêt boréale, l'épinette noire (Picea mariana [Mill.] BSP) et le pin gris (Pinus banksiana Lamb.), sont particulièrement bien adaptées au feu en raison de leurs cônes semi-sérotineux et sérotineux qui contiennent les banques aériennes de graines favorables à leur régénération après feu. Cependant, la résilience de ces deux espèces au feu est limitée par leur fréquence. Ces derniers peuvent avoir des effets sur l'aménagement durable des forêts de deux façons : 1) soit en brulant les peuplements avant qu'ils puissent être récoltés ; 2) soit en brulant les peuplements avant qu'ils aient pu reconstituer un stock de graines suffisant pour se régénérer adéquatement, résultant ainsi en un accident de régénération. Les augmentations prévues de la fréquence et de l'intensité des feux ainsi que de la superficie brûlée en raison du changement climatique pourraient donc entraîner une augmentation des accidents de régénération et, par extension, de la proportion de peuplements ouverts à l'échelle du paysage. Dans cette étude, nous évaluons l'impact des accidents de régénération sur la productivité de la forêt boréale du Québec, Canada, pour l'épinette noire et le pin gris, en tenant compte des variations projetées de croissance, de densité de tiges et de taux de brûlage dues au changement climatique. Nous utilisons le modèle de croissance de Pau *et al.* (2022), les fonctions de prédiction de la densité de régénération de Cyr *et al.* (2022) et le modèle de feu de Boulanger *et al.* (2014), afin de projeter les effets du changement climatique sur la croissance des arbres, la densité des peuplements et le régime de feu. Pour estimer la superficie forestière productive, nous avons calculé le temps d'exposition au feu tandis que pour estimer le risque d'accident de régénération, nous avons utilisé le temps jusqu'à la maturité reproductive ajusté en fonction des changements de croissance. Nos projections qui tiennent compte du risque d'accident de régénération dû au feu sont beaucoup plus inquiétantes et indiquent une possible surestimation de la superficie forestière commerciale disponible de la forêt boréale québécoise. Il y a donc un besoin pressant de mieux suivre la régénération après une perturbation naturelle.

Mots-clés : Accidents de régénération, changement climatique, croissance, taux de brûlage, forêt boréale

Abstract

With projected increases in global temperatures and drought frequency and intensity, the boreal biome is expected to be one of the most strongly affected by climate changes. Recent studies on global warming point to an increase in tree growth at its coldest northern boundary in eastern Canada but also result in higher fire activity. The two major boreal forest species, black spruce (*Picea mariana* [Mill.] BSP) and jack pine (*Pinus banksiana* Lamb.), particularly well-adapted to fire due to their semi-serotinous and serotinous cones, see their resilience restricted by higher fire frequency. Indeed, fires can impact sustainable forest management in two ways: 1) either by burning stands before they can be harvested; or 2) by burning stands before they can restock with enough seeds to regenerate adequately resulting in a regeneration failure. Projected increases in fire frequency, intensity, and area burned due to climate change could therefore lead to an increase in regeneration failure events and, by extension, in the proportion of open stands at the landscape level. In this study, we investigate the impact of regeneration failures on the productivity of the boreal forest of Quebec, Canada, for black spruce and jack pine, taking into account projected changes in growth, stem density and burn rate due to climate change. We use Pau *et al.* (2022) growth model, Cyr *et al.* (2022) regeneration density prediction functions, and Boulanger *et al.* (2014) fire model, to project the effects of climate change on tree growth, stand density and fire regime. To estimate productive forest area, we calculated the exposure time, and to estimate the risk of regeneration failure, we used the time to reproductive maturity adjusted for growth change. Our projections on the risk of regeneration failure due to fire clearly show that current merchantable projections are strongly overestimated and that our forecast on regeneration failure will reduce the available area for commercial harvesting in Québec's boreal forest. There is therefore a pressing need to better monitor post-natural disturbance regeneration, and to consider this risk in forest management planning.

Keywords: Regeneration failures, climate change, growth, fire disturbance rate, boreal forest

3.1 Introduction

With projected increases in global temperatures and drought frequency and intensity, the boreal biome is expected to be one of the most strongly affected by climate changes (Price *et al.*, 2013). On top of an already observed increase of 1.7°C over the past century (Bush et Lemmen, 2019), an increase in mean annual temperature ranging from 4° to 11°C has been projected across the boreal forest by the end of this century (Gauthier *et al.*, 2015b; IPCC, 2013; Price *et al.*, 2013). Continued warming can significantly impact the structure, composition, and function of the boreal forest, particularly in Canada, modulating both tree growth and forest disturbances (Gauthier *et al.*, 2015a; Kurz *et al.*, 2013).

Recent studies on global warming point to an increase in tree growth at its coldest northern boundary in eastern Canada (Price *et al.,* 2013; Girardin *et al.*, 2016; D'Orangeville *et al.*, 2016; Hember *et al.*, 2017; Chaste *et al.*, 2019; Pau *et al.*, 2021). Low temperatures are related to a limited growing season and nutrient-deficient soil conditions, which restrict growth (Jarvis et Linder, 2000). By extending the growing season and improving photosynthetic rates, temperature increases may have a beneficial impact on growth (Menzel et Fabian, 1999; Chmielewski et Rötzer, 2001; Menzel *et al.*, 2006; Ibáñez *et al.*, 2010; Price *et al.*, 2013). Conversely, along the warmer southern edges and in low-moisture areas, where tree growth is frequently constrained by soil moisture availability, warming and decreased water availability could result in forest losses (D'Orangeville *et al.*, 2016; Chaste *et al.*, 2019; Girardin *et al.*, 2021a).

Wildfire is a major disturbance in Canada’s boreal forest (Stocks *et al.*, 2003). Climate change is expected to result in more fire activity in Canada's boreal forests (Balshi *et al.*, 2009; Wotton *et al.*, 2010; de Groot *et al.*, 2013; Boulanger *et al.*, 2014; 2017; Wang *et al.*, 2017) This could offset any potential gain in forest stock caused by climate change (Gauthier *et al.*, 2015b; Rapanoela *et al.*, 2015; Beaudoin *et al.*, 2017; Chaste *et al.*, 2019). Indeed, fires can impact forest productivity in two ways: 1) either by burning stands before they can be harvested; or 2) by burning stands before they can restock with enough seeds to adequately regenerate a closed-forest stand. The two major boreal forest species, black spruce (*Picea mariana* [Mill.] BSP) and jack pine (*Pinus banksiana* Lamb.), are particularly well-adapted to fire due to their semi-serotinous and serotinous cones (Burns et Honkala, 1990). However, their resilience is restricted by fire frequency (Brown et Johnstone, 2012; Baltzer *et al.*, 2021; Pinno *et al.*, 2013), preventing them from reaching the age necessary to produce a seed supply considered adequate to regenerate a stand, leading to a regeneration failure (Girard *et al.*, 2009; Johnstone *et al.*, 2010; Brown et Johnstone, 2012; Whitman *et al.*, 2018). In mature stands, elevated fire intensity may limit recruitment by reducing or eliminating existing aerial seedbanks. Fire can therefore have a significant impact on forest density, and as such, seedling recruitment in the early years after fire is a crucial factor determining the fate of a disturbed boreal forest stand (Johnstone *et al.,* 2004). Indeed, many studies have shown that natural disturbances occurring at short interval, including fire, are a principal cause of stand opening (Payette *et al.,* 2000; Simard *et al.,* 2007; Girard *et al.,* 2008; Rapanoela *et al.,* 2016). Projected increases in fire frequency, intensity, and area burned due to climate change could therefore lead to an increase in regeneration failure events and, by extension, in the proportion of open stands at the landscape level (Rapanoela *et al.,* 2016; Augustin *et al.*, 2022). These negative impacts will be particularly salient in regions with a high proportion of dry surface deposits and drainage. Trees exhibit lower resilience to fire on dry sites (Bogaert *et al.* 2015), their growth would be more limited under climate change in dry areas (Liang *et al.* 2011), and they burn more frequently in dry regions (Mansuy *et al.,* 2010). However, the impacts of regeneration failure on the boreal forest and its productivity are still uncertain, especially in a climate change context. Increased growth associated with climate change (Pau *et al.*, 2022) may mitigate the projected impact of increased fire activity (Splawinski *et al.*, 2019; Cyr *et al.*, 2021; Augustin *et al.*, 2022). However, the few studies that have investigated the impacts of regeneration failures have considered the effect of climate change on fire activity, but not on change in tree growth.

In this study, we investigate the impact of regeneration failures on the productivity of the boreal forest of Quebec, Canada, for black spruce and jack pine, taking into account projected variations in growth, stem density and burn rate due to climate change. Specifically, we identify areas that are likely to be the most sensitive to regeneration failure due to climate change, and then assess the importance of consistently including fire and climate change in strategic forest management planning. Productivity, that we herein define as the stock of merchantable stems available for harvesting, depends both on stem volume, which will be influenced by tree species growth rate, and on productive area, which will be influenced by disturbance rate. Indeed, a stand can burn before reaching commercial maturity but also before reaching reproductive maturity, leading to a regeneration failure. To achieve this goal, we use the Pau *et al.* (2021) growth model, the Cyr *et al.* (2021) regeneration density prediction functions, and the Boulanger *et al.* (2014) fire model, to project the effects of climate change on tree growth, stand density and fire regime. To estimate productive forest area, as Pau *et al.* (submitted), we used the Gauthier *et al.* (2015c) exposure time method with an industry relevant threshold for standing merchantable volumes and mean stem diameter; to estimate the risk of regeneration failure, we used an innovative method inspired by the Gauthier *et al.* (2015c) exposure time method, which is also adjusted to consider growth change.

3.2 Material and methods

3.2.1 Study Area

Our study area extends from ~49°–53°N and ~79°–57° W in the province of Québec, Canada. This area is located at the transition between the spruce-feather moss and the southern portion of the spruce-lichen bioclimatic domains. Black spruce and jack pine are the main tree species in the area, and dominant surficial deposits are organic in western regions, deep till in central and northeastern regions, and rock in the south (Gauthier *et al.*, 2015c; Jobidon *et al.*, 2015; Robitaille *et al.*, 2015). Mean annual temperature decreases from south to north (from –4.9 to 1.6 °C) and total annual precipitation increases from west to east and north to south (from 651 to 1236 mm) (Gauthier *et al.*, 2015c). Our study area is divided into 1113 districts, defined as "an area of land characterized by a unique pattern of relief, geology, geomorphology, and regional vegetation" (Jurdant *et al.,* 1977).

As black spruce largely dominates throughout the study area, the species' timber supply was the main focus of our work. However, since jack pine is a species better adapted to dry conditions than black spruce due to its deeper root system and relatively faster growth (Burns et Honkala, 1990), we also wanted to determine if any advantages could be conferred by the management of jack pine in a context of long-term exposure to increased risks of moisture deficit and wildfires.

3.2.2 Establishing present growth, stand density and burn rate

To characterize growth, we used the Gauthier *et al.* (2015c) method using site index (SI) and to characterize stand density and the relative density index at 100 years (RDI_{100}). The SI, or the height at 50 years, is a commonly used temporal indicator of growth in forestry. Growth in height reflects site fertility and consequently the potential productivity of a forest stand (Monserud, 1984). Given that height growth is negligibly affected by stand density (Skovsgaard et Vanclay 2008), SI mostly depends on site quality and climate, being less affected by surrounding competition compared to diameter at breast height (DBH 1.3 m above ground) (Spurr et Barnes, 1973). The RDI_{100} corresponds to the density of a stand relative to that of a very dense stand in which all the trees are assumed to be of the same mean diameter size, normalized to 100 years (Drew et Flewelling, 1979). Our current (1981-2010) SI and RDI_{100} are derived from dendrometric characteristics from 9884 black spruce sample plots and 619 jack pine sample plots distributed over the entire study area. This dataset is composed in the south of sample plots from the regular Gouvernement du Québec forest survey conducted between 1990 and 2001 and in the north and east, of northern ecodendrometric northern plots surveys conducted by the Gouvernement du Québec annually from 2006 to 2009. This dataset also contains a wide variety of information on environmental and forest stands variables, such as slope exposure, elevation, surficial deposit, hydrologic regime, partial disturbance, ecological type, forest cover, height class, understory vegetation, and development stage.

Having SI and RDI100 values only for our 9884 black spruce plots and 619 jack pine plots, the second step was to spatialize productivity and estimate regional growth and density for each district of our study area. As Gautier *et al.* (2015c), we used the Gouvernement du Québec detailed integrated map of forest polygons (an average of 2700 polygons larger than 4 ha for each 1113 districts over the study area). In the south, this map is composed of information obtained with aerial photographs taken from 1990 to 2001 as part of the third decennial forest inventory program, while in the north, an approach based on the analysis of Landsat satellite images confirmed by the use of aerial photographs (between 2005 and 2008) was used (Robitaille et al. 2015).

In order to assign an SI and RDI100 to each of the forest polygons from those of the plots, the non-parametric k-NN matching method, repeated 100 times, from Gauthier et al. (2015c) which consists of estimating the indices of a given polygon with the weighted mean of the indices of the k most similar plots (k=13 for black spruce and k=14 for jack pine) was used. Climatic, environmental, and forest stand variables were used to characterize the similarity between sites (See Gauthier et al., 2015c for more details). The weighting of a reference plot of a target polygon is based on the inverse of the distance computed from these variables (Raulier et al., 2013). To include the uncertainty in the estimation of the SI and RDI100 of the polygons, a bootstrap resampling was applied to k plots from the k plots used for each of the polygons which is repeated 10 times. Then the weighted mean of the SI and RDI100 by stand area was calculated for each of the 1113 districts.

Under the current climate, we used the fire regime from Gauthier *et al.* (2015c). In that work, the fire map from Gouvernement du Québec, based on data from aerial surveys and satellite images, was used. As data from 1972 are complete and have been subject to quality control, only the period between 1972 and 2009 was used to define the territory's current regional fire activity. The study area was divided into 10 homogeneous fire regime (HFR) zones from Gauthier *et al.* (2015c) where burn rate varies between 2.272% HFR y^{-1} and 0.12% HFR y^{-1}. Indeed, HFR reflects the spatial heterogeneity of the fire regime unlike other ecological classifications (Boulanger *et al.,* 2012). The fire regime defines the patterns of fire seasonality, frequency, size, spatial continuity, intensity, type and severity. Therefore, using a model based on HFR allows a more accurate spatial estimate of climate effects on burn rate and thus a better projection of the future burn rate (Boulanger *et al.*, 2014).

3.2.3 Effects of climate change on tree growth, stem density and burn rates

In order to evaluate the influence of climate change on our study area in the future, we vary the climate, which in turn varied the future fire regime, the growth and the density of 9884 black spruce plots and 619 jack pine plots. Having SI and RDI100 values only for our 9884 black spruce plots and 619 jack pine plots for each time period, we used the same method as Gauthier et al. (2015c) described above, to spatialize productivity and estimate regional growth and density for each district and each time period of our study area.

3.2.3.1 Future climate projection

We selected 3 future periods: 2011-2040, 2041-2070, and 2071-2100 (Table 3.1). We used the period 1981–2010 for our present climate (baseline). For the Global Climate Model (GCM), we used 2003–2017 adjusted weather station observations from the fourth generation Canadian Regional Climate Model (CanRCM4) and driven by the second-generation Canadian Earth System Model (CanESM2)/fourth generation coupled GCM (CGCM4) to mimic 1981–2010 normals (Dunne *et al.*, 2012). For the Representative Concentration Pathway (RCP), we used the high (RCP 8.5) emission scenarios (Meinshausen *et al.*, 2011). We then calculated normals for all climate variables used by Pau *et al.* (2021) and Boulanger *et al.* (2014) models to project future tree growth and fire disturbance rates, for each of our 4 periods. All climate data have been calculated with BioSim 11 (Régnière *et al.*, 2017).

3.2.3.2 Climate effects on growth

To project growth change in response to climate change, we used the black spruce and jack pine growth models developed by Pau *et al.* (2021). Originally calibrated using data from 2591 black spruces and 890 jack pines, this Generalized Additive Models (GAM) implements height growth based on climate normals corresponding to the growth period of each stem, and site type (as a function of texture, stoniness and drainage). With this model, we can forecast trends in height growth for our 9884 sample plots and our future periods (Table 3.1). We then estimated percent changes in height growth between future and baseline as follows:

(1) $$Percent\ change\ between\ future\ and\ baseline\ (Height\ growth_{Future-baseline}) = \left(\frac{Height\ growth_{future} - Height\ growth_{baseline}}{Height\ growth_{baseline}}\right) \times 100$$

These percentages of height growth changes were then applied to our plots SI, giving us a future SI for each plot and period. In order to avoid incoherent projected SI and according to observed values and production tables of Pothier and Savard (1998), we have limited SI to a maximum value of 22 for both species.

Table 3.1. Projected temperature, growth and burn rate for their corresponding periods (ESM2–RCP 8.5).

Periods	Present	2011-2040	2041-2070	2071-2100
Increase in mean temperature	T= 0^{o}C	+1.3^{o}C	+3.7^{o}C	+6.6^{o}C
Black spruce growth change (Pau *et al.* 2021)	SI = 12.82m	+10.5%	+27.3%	+59.7%
Jack pine growth change (Pau *et al.* 2021)	SI= 13.38m	+4%	+17%	+82.1%
Fire activity	Burn rates = 0. 79% y^{-1}	+84%	+326%	+620%

3.2.3.3 Climate effects on stand density

In order to vary stand density in response to climate change, we used a transfer function that translated seedling density predictions, calculated from SI (projected according to the climate as described above) and basal area at a period p (e.g., 2011-2040), into an updated RDI100 for the next period p + 1 (e.g., 2041-2070). The post-fire seedling densities were projected using empirically-based relationships (Splawinski *et al.*, 2014, Viglas *et al.,* 2013; Briand *et al.*, 2015), that consider SI, species, and basal area. Then, following the approach used by Cyr *et al.* (2021), we translated post-fire seedling density predictions into RDI100 values using a quantile mapping (Maraun, 2016) between the distribution of seedling density predictions and observed distribution of RDI100 values at period p = 0, using the 'qmap' R package (Gudmundsson, 2016). This approach is based on the assumption that the distribution of RDI100 at period p = 0 for a given population of stands is directly linked with the distribution of the post-fire seedling density that these same stands would have produced if they had burned.

3.2.3.4 Climate effects on fire regime

To project burn rate change in response to climate change, we used an updated version of the multivariate adaptive regression splines (MARS) produced by Boulanger *et al.* (2014), based on HFR zones for Canada. HFR reflects the spatial heterogeneity of the fire regime unlike other ecological classifications (Boulanger *et al.,* 2012). Five HFR from Boulanger *et al.* (2014) are located in our study area. With this model, we forecasted trends in area burned for our 4 periods (Table 3.1). It was then determined which Boulanger *et al.* (2014) 5 HFR zones matched our 10 HFR zones from Gauthier *et al.* (2015c). We then estimated percent change in area burned between future and baseline as follows:

$$(2) \qquad Percent\ change\ between\ future\ and\ baseline\ (Area\ burned_{Future-baseline}) = \left(\frac{Area\ burned_{future} - Area\ burned_{baseline}}{Area\ burned_{baseline}}\right) \times 100$$

These percentage increases in burned area were then applied to our annual average burn rates, giving us a future annual average burn rate for each plot and period/RCP. Due to the overlap of the Boulanger *et al.* (2014) HFR zones with our 10 HFR zones (Supplementary information S1), we therefore had multiple percent increases for each HFR zone. Therefore, we weighted the percent increases by the area occupied.

3.2.4 Productivity estimation

3.2.4.1 Production classes and exposure times

In order to derive the productivity threshold, we applied the exposure time equation of Gauthier *et al.* (2015c). Briefly, we used the minimum age at which black spruce stands of a given SI and RDI100 exceed a double productivity threshold (50 m^3/ha and 70 dm^3/stem) as calculated by Gauthier *et al.* (2015c) based on the production tables of Pothier et Savard (1998). We used the same method to derive the exposure time of jack pine. The exposure time table for black spruce and jack pine is available in supplementary material (S1).

3.2.4.2 Probability of exceeding the double productivity threshold taking into account fires

Based on the burn rate calculated before and as Gauthier *et al.* (2015c), we computed the probability that a stand with a given SI and RDI100 exceed the productivity thresholds for standing merchantable volume and mean stem diameter, while accounting for fire, using the equation of Johnson et Gutsell (1994) (Gauthier *et al.*, 2013):

$$(3) \qquad Probability\ of\ exceeding\ the\ double\ productivity\ threshold\ taking\ into\ account\ fires = exp(-exposure\ time\ x\ burn\ rate)$$

This procedure was repeated 10 times to include variability in the computed burn rate. This gives a frequency distribution of the probability of reaching the double threshold against fire for each polygon. Then, the weighted by stand area mean of the probabilities of exceeding the double productivity threshold taking into account fire were calculated for each district.

3.2.4.3 Productive area

From the SI and RDI100 and using the equations of Pothier et Savard (1998), we calculated merchantable volume (m^3/ha) at 100 years by district and by exposure time for each time period. We were also able to calculate the post-fire productive area as well as the total pre-fire volume and the total productive volume for each district and for each exposure time:

$$(4) \qquad Post\ fire\ productive\ area = Suitable\ areas\ for\ management\ before\ fire\ x\ Probability\ of\ exceeding\ the\ two\ parameter\ productivity\ threshold\ taking\ into\ account\ fires$$

(5) $Total\ volume\ before\ fire\ = Volume\ x\ suitable\ areas\ for\ management\ before\ fire$

(6) $Total\ productive\ volume\ = Volume\ x\ \ post\ fire\ productive\ area$

Suitable areas for management exclude areas with high physical limitations, without vegetation or considered unproductive (SI too low or negative RDI100).

3.2.5 Regeneration failures estimation

To estimate the risk of regeneration failure, we used an innovative method inspired by the exposure time method of Gauthier *et al.* (2015c) described above.

3.2.5.1 Time to reproductive maturity

In order to assess the stand sensitivity to regeneration failure, we calculated the minimum age at which stands of a given SI and RDI100 exceeded the age at which a stand produces a sufficient amount of seed to regenerate (Table 3.2), using SI and RDI100 and the empirically-based relationships to calculate post-fire seedling density from Cyr *et al.* (2021) and Splawinski *et al.* (2014). We considered two seedling thresholds: (1) a maximum threshold of $1/m^2$ required to fully re-stock a stand (Greene et al., 2002), and (2) a critical threshold of $0.25/m^2$ required to prevent a stand opening.

3.2.5.2 Probability to be safe from regeneration failures

In the same way of Gauthier et al. (2015c), we then calculated the probability that a stand with a given SI and RDI100 would exceed the seedling threshold while accounting for fire, using the equation of Johnson et Gutsell (1994) (Gauthier *et al.*, 2013):

(7) $$Probability\ of\ exceeding\ the\ seedling\ threshold\ taking\ into\ account\ fires \\ = exp(-Minimum\ age\ for\ exceeding\ the\ seedling\ thresholds\ x\ burn\ rate)$$

This gives a frequency distribution of the probability to be safe from regeneration failures against fire for each polygon. This procedure was repeated 10 times. Then, the weighted by stand area mean of the probabilities to be safe from regeneration failures taking into account fire were calculated for each district, species and seedling threshold.

Table 3.2. Minimum age at which a stand of given site index (SI, height in m at 50 years) and relative density index at 100 years (RDI100) exceeds the seedling thresholds (> 1/m^2 or > 0.25/m^2).

			SI											
			Seedling > 1/m^2 (maximum threshold)						Seedling > 0.25/m^2 (critical threshold)					
			12	**14**	**16**	**18**	**20**	**22**	**12**	**14**	**16**	**18**	**20**	**22**
RDI100	Black spruce	**0.1**	231	216	215	224	241	264	95	90	89	90	94	100
		0.3	193	175	173	184	206	236	76	72	70	70	72	76
		0.5	140	125	123	130	149	188	57	53	51	50	50	52
		0.7	89	79	75	77	84	104	37	34	32	31	30	29
		0.9	43	35	31	27	25	25	25	25	25	25	25	25
	Jack pine	**0.1**	187	171	168	170	179	/	63	61	60	59	60	60
		0.3	143	133	130	132	139	150	50	48	47	46	46	46
		0.5	95	86	82	82	85	92	37	35	34	33	33	33
		0.7	54	49	47	45	44	45	25	25	25	25	25	25
		0.9	25	25	25	25	25	25	25	25	25	25	25	25

3.2.5.3 Area safe from regeneration failures

We were then able to calculate the area and the total volume at 100 years safe from regeneration failures for each district and for both thresholds:

$$(8) \qquad Area\ safe\ from\ regeneration\ failures \\ = Suitable\ areas\ for\ management\ before\ fire\ x \\ Probability\ of\ exceeding\ the\ seedling\ threshold\ taking\ into\ account\ fires$$

$$(9) \qquad Total\ volume\ safe\ from\ regeneration\ failures\ = Volume\ x \\ Area\ safe\ from\ regeneration\ failures$$

Suitable areas for management exclude areas with high physical limitations, without vegetation or considered unproductive (SI too low or negative RDI100).

3.3 Results

Currently (1981-2010), the area considered suitable for management if fires are not taken into account would be 20.3 M ha for black spruce and 24.5 M ha for jack pine. As the climate becomes warmer, forest areas suitable for management are projected to increase for both species. Compared to the current (1981-2010) period, for black spruce, an increase of +16% is expected over 2011-2040, +23% over 2041-2070 and +22% over 2071-2100. For jack pine, a slight decrease of -4% is predicted over 2011-2040, then an increase of +10% over 2041-2070 and +17% over 2071-2100. The area suitable for management is also always higher for jack pine than for black spruce (the whole bar; Figure 3.1).

However, despite this increase of forest areas suitable for management, a decrease of productive areas can be observed with climate change. Compared to the current (1981-2010) period, for black spruce, -5% of productive areas has been projected over 2011-2040, -25% over 2041-2070 and -32% over 2071-2100. For jack pine, -22% of productive areas is expected over 2011-2040, -28% over 2041-2070 and -32% over 2071-2100 (the dark green, light green and yellow parts of the bar; Figure 3.1).

Furthermore, a large proportion of the areas that remain productive despite climate change may not reach the maximum seedling threshold ($1/m^2$) required to fully re-stock a stand, and may therefore experience a decline in density. This portion of productive areas with a risk (maximum threshold of $1/m^2$) of regeneration failure increases with climate change. For black spruce, 83% of productive areas exceed the maximum seedling threshold ($1/m^2$) over 1981-2010, 76% over 2011-2040, 68% over 2041-2070 and only 54% over 2071-2100. For jack pine, this portion of productive areas exceeding the maximum seedling threshold ($1/m^2$) is higher for jack pine than for black spruce, with 99.6% over 1981-2010, but is still predicted to decrease in the future with 97% over 2011-2040, 84% over 2041-2070 and 70% over 2071-2100 (the dark green section of the bar; Figure 3.1).

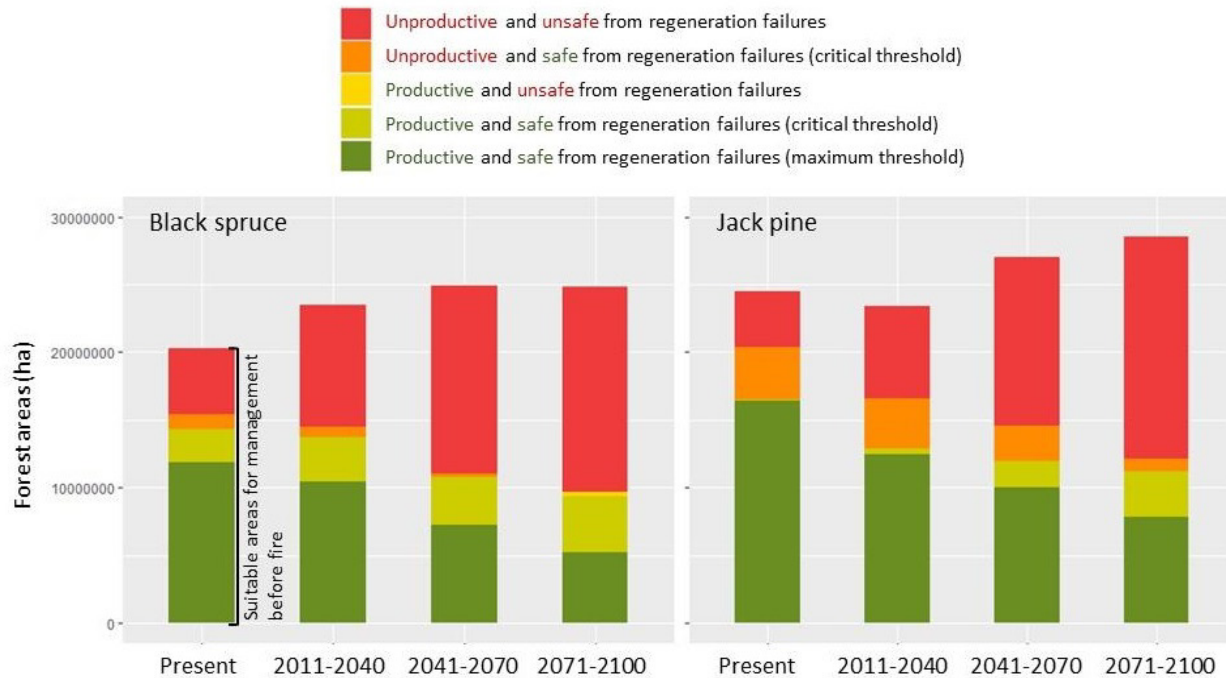


Figure 3.1. Projected forest areas (ha) unproductive/productive and unsafe/safe from regeneration failures (for a critical seedling threshold of 0.25/m^2 and a maximum seedling threshold of 1/m^2) for black spruce and jack pine for four periods: present, 2011-2040 ESM2–RCP 8.5, 2041-2070 ESM2–RCP 8.5 and 2071-2100 ESM2–RCP 8.5.

As climate change impacts become more severe, a decrease in area safe from regeneration failures for both seedling thresholds is expected, increasing the risk of density loss and more importantly stand opening. For the critical threshold (0.25/m^2), compared to the current (1981-2010) period and for black spruce, -6% of area safe from regeneration failures has been observed for the 2011-2040 period, -29% over 2041-2070 and -39% over 2071-2100. For jack pine, although the areas safe from regeneration failures are greater than for black spruce, a significant decline is still observed with -19% over 2011-2040 compared to the current (1981-2010) period, -29% over 2041-2070 and -40% over 2071-2100 (the dark green, light green and orange parts of the bar; Figure 3.1).

If we look at the total volume, the volume currently (1981-2010) obtained from areas suitable for management when not accounting for fire would be 1.7 B m^3 for black spruce and 2.6 B m^3 for jack pine. As the climate becomes warmer and as for the area, this volume is expected to increase for both species and is also always higher for jack pine than for black spruce (the whole bar; Figure 3.2).

However, the amount of this total volume impacted by fire (both in terms of preventing commercial and reproductive maturity from being reached) is increasing over time. For black spruce, 21% of volume suitable for management is affected by fire over 1981-2010, 33% over 2011-2040, 49% over 2041-2070 and 55% over 2071-2100. For jack pine, 14% over 1981-2010, 25% over 2011-2040, 40% over 2041-2070 and 53% over 2071-2100 (the red section of the bar; Figure 3.2). This indicates the importance to take fire into account a priori.

What differs from the area results of Figure 3.1 is that, for black spruce, the total volume productive and the total volume exceeding the critical seedling threshold (0.25/m^2) remains fairly stable over time. Compared to the current (1981-2010) period, for black spruce, +9% of total productive volume has been projected for the 2011-2040 period, +2% over 2041-2070 and +2% over 2071-2100. For jack pine, a decrease of -18% is predicted over 2011-2040, and of -13% over 2041-2070 and then an increase of +16% over 2071-2100 (the dark green, light green and yellow parts of the bar; Figure 3.2).

Although the productive total volume remains quite constant with climate change, a large part of this productive volume may not reach the maximum seedling threshold (1/m^2) and as for the area results. This proportion is also expected to increase with climate change (the light green section of the bar; Figure 3.1).

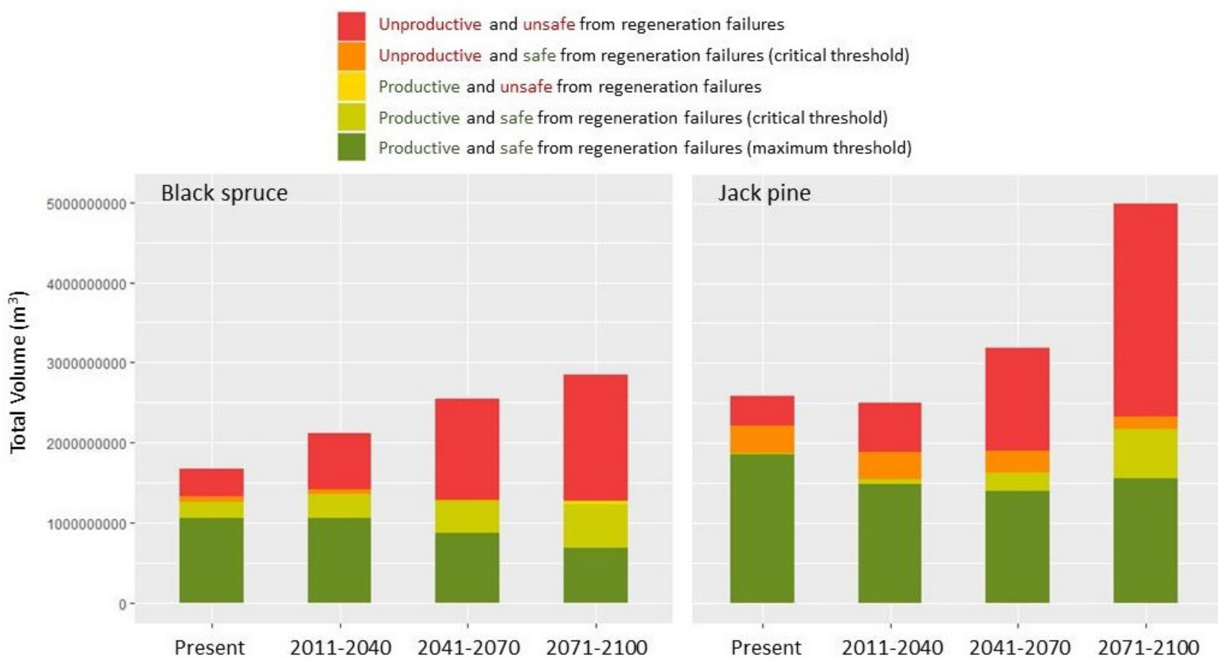


Figure 3.2. Projected total volume unproductive/productive and unsafe/safe from regeneration failures (for a critical seedling threshold of 0.25/m^2 and a maximum seedling threshold of 1/m^2) for black spruce and jack pine for four periods: present, 2011-2040 ESM2–RCP 8.5, 2041-2070 ESM2–RCP 8.5 and 2071-2100 ESM2–RCP 8.5.

If we take a closer look at which part of our study area does not exceed the critical seedling threshold ($0.25/m^2$) and is therefore likely to be impacted by a stand opening, for the current (1981–2010) climate and for black spruce, the northwest part of the study area has a very low percentage of area safe from regeneration failures (≤ 30%) and the east and south has a medium to high percentage of area safe from regeneration failures. For jack pine, the amount of safe area is greater with 97% of districts having a percentage of areas safe from regeneration failures ≥ 50%, over 1981–2010 (Figure 3.3).

As climate change impacts become more severe, areas with a low percentage of area safe from regeneration failures (critical seedling threshold of $0.25/m^2$) increase and move southward and eastward, with a decrease up to -100% of areas safe from regeneration failure and stand opening compared to current period (1981–2010).

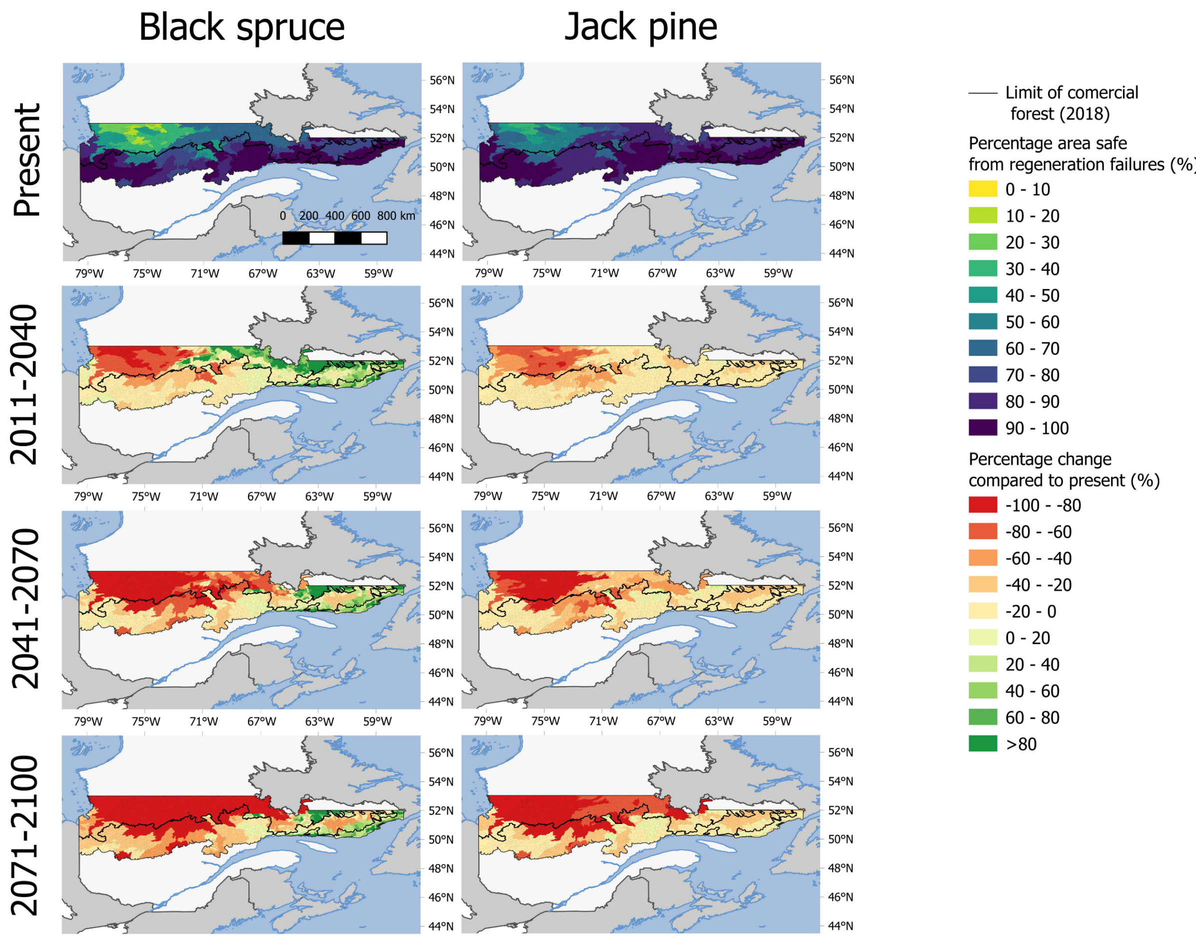


Figure 3.3. Projected percentage of area safe from regeneration failures (critical seedling threshold of $0.25/m^2$) over 1981-2010 (present) and projected percentage change of area safe from regeneration failures compared to present, for black spruce and jack pine for three periods: 2011-2040 ESM2–RCP 8.5, 2041-2070 ESM2–RCP 8.5 and 2071-2100 ESM2–RCP 8.5.

3.4 Discussion

Our results highlight the risk of not taking fire into account in productivity studies or in strategic forest management planning (Gauthier *et al.*, 2015c; Leduc *et al.,* 2015; Cyr *et al.*, 2021). Indeed, fewer stands reach commercial maturity because of increased fire activity, which leads to a strong overestimation of the future areas of productive forest areas. There is also a high risk in not taking into account post-fire regeneration. In Canada, a monitoring of post-fire regeneration is not necessary for strategic forest management planning (Cyr *et al.*, 2021). Ignoring regeneration failure also leads to a strong overestimation of the available productive forest area.

Despite an increase in potential growth productive areas, productive areas are expected to decrease under the most extreme climate change scenario due to projected burn rate increase over time. Not only are productive areas expected to decrease, but all of the areas that have become unproductive are also at risk of stand opening since they do not reach the critical threshold ($0.25/m^2$). In addition, among the areas that remain productive despite climate change, a large proportion are at risk of density loss since they do not reach the maximum threshold ($1/m^2$). A large part of Quebec's boreal forest is therefore subject to a risk of regeneration failure and thus to a decrease in stand density or even a total stand opening. This risk increases with climate change and extends towards the south. These results are in agreement with previous studies in the region (Girard *et al.,* 2009; Rapanoela *et al.,* 2016; Chaste *et al.*, 2019; Splawinski *et al.,* 2019; Baltzer *et al.,* 2021; Cyr *et al.,* 2021; Augustin *et al.*, 2022). Surprisingly, the risk increases even if tree growth is projected to improve. The potential positive effect of climate change on tree growth therefore does not adequately compensate for increases in fire frequency.

The total volume of the study area is less affected by climate change than the extent of productive areas. Productive total volume remains relatively constant due to an increase in the average merchantable volume within areas that remain productive. Trees in these areas will therefore grow faster. However, a significant part of the total productive volume could still be affected by regeneration failures at the maximum threshold.

Our results also suggest an advantage of jack pine over black spruce. Jack pine (Pinus banksiana Lamb.) is a species better adapted to dry conditions than black spruce (Marchand *et al.*, 2021; Pau *et al.*, 2021). It grows faster and has a deeper root system (Burns et Honkala, 1990). Jack pine has a faster time to reproductive maturity than black spruce (Viglas *et al.,* 2013; Briand *et al.,* 2014), which allows it to disperse seeds even with higher burn rates.

The use of two thresholds (critical and maximum) allows us to identify a range of values whose boundaries are defined with areas that will completely open up and become non forested, and with those that will not be able to restock fully and may be subject to density loss. However, the risk of present and future regeneration failures and their impact on boreal forest productivity may still be underestimated, since other disturbances such as insects and pathogens outbreaks and anthropogenic disturbances such as harvesting are not considered in this study. Indeed, a succession of disturbances can increase this risk and change the structure and composition of forests. For example, because of their higher proportion of regenerating stands following harvesting, managed forests may be more susceptible to regeneration failure. In addition, the large areas affected by outbreaks may represent a build-up of fuel that could increase the risk of large, severe fires in some areas (Le Goff *et al.*, 2008; Fleming *et al.*, 2002). Moreover, these disturbances often target productive stands.

The effects of increases in fire intensity and severity, which have the capacity to lead to regeneration failure in well stocked and mature stands where seed availability is not a limiting factor needs to be studied further. Indeed, severe fires can reduce or eliminate existing aerial seedbanks. This is currently a large knowledge gap and may play a large role in the opening of boreal forest stands and declines in productivity.

Our double productivity threshold (50 m^3/ha and 70 dm^3/stem) is also very minimal since the exploitability age that ensures maximum wood production per stand is on average 21 years higher in our study area than our minimum age for reaching our double productivity threshold (Raulier *et al.*, 2013). In a management context, by aiming to harvest at the exploitability age, vulnerability to fire would be even more important because the exposure time would be extended. It is therefore also possible that the impact of climate change via fires on the productivity of the boreal forest is underestimated compared to reality.

The exclusive use of the high emissions scenario RCP 8.5 (Representative Concentration Pathway) (Meinshausen *et al.*, 2011) causes a possible underestimation of future productivity when considering fires. Indeed, RCP 8.5 corresponds to the most extreme emission scenario and therefore induces a very large increase in fires. We made this choice in order to have the largest possible future climate range.

In order to evaluate the possible impacts of regeneration failure on the boreal forest productivity, we simulated a hypothetical area safe from regeneration failure considering that all stands could reach reproductive maturity. Our study allows for a relative comparison of even-state landscapes. However, a non-dynamic simulation of the Quebec boreal forest territory does not allow us to project the future evolution of the landscape, which could be quite different from what we have now. Indeed, fire, along with climate and physical characteristics of the territory, influences the age structure of stands as well as their composition (Chabot *et al.*, 2009). In Quebec's boreal forest, fires are generally stand-replacing, intense, not very frequent, and affect large areas. They cause the mortality of the majority of trees and could therefore cause a change in stand composition (Chabot *et al.*, 2009). As mentioned above, we also did not consider other natural disturbances, such as outbreaks, or anthropogenic disturbances that target productive stands (Cyr *et al.*, 2021). Increased and more intensive disturbances could greatly alter the landscape of Quebec's boreal forest. The major innovation of our study, in addition to taking into account the effects of climate change on fire and its impacts on the Quebec boreal forest, is that we also integrated the effects on growth and density, which affects the time to reproductive maturity and therefore the regeneration failure risk.

3.5 Conclusion

Projections that take into account the risk of regeneration failure due to fire are much more worrying and indicate a possible overestimation of the available forest area for management of Quebec's boreal forest. The risk of regeneration failure was not taken into account during the creation of the northern limit of commercial forest and the results of this study add to and reinforce those of our previous study which aimed to evaluate the impact of climate change on forest management in Quebec. There is therefore a pressing need to better monitor post-natural disturbance regeneration. It would also be particularly interesting to compare our scenarios in a dynamic model to see what impact the dynamic evolution of the landscape has on these results.

3.6 Acknowledgements

We thank Ouranos for providing an internship opportunity to M. Pau, and especially D. Houle for his guidance during the internship. We thank the Ministry of Forests, Wildlife and Parks of Québec for providing the data. We are grateful to R. Saint-Amant for help with the BioSIM 11 software. The project was funded by a NRSERC strategic grant to Y. Bergeron and collaborators.

CONCLUSION

4.1 Faits saillants et contributions à l'avancée des connaissances

Cette thèse, dont les trois chapitres sont liés les uns aux autres dans une suite logique, nous a ainsi permis, lors du chapitre 1, d'établir les relations entre le climat et la croissance en hauteur de l'épinette noire (*Picea mariana* [Mill.] BSP) et du pin gris (*Pinus banksiana* Lamb.) au Québec. Nous avons ensuite pu utiliser ces résultats dans le chapitre 2 pour déterminer les impacts combinés des changements de croissance (chapitre 1) et de régime de feux dus au changement climatique sur la productivité de la forêt boréale québécoise. Enfin, le chapitre 3 a permis d'évaluer l'importance des impacts des accidents de régénération sur la productivité de la forêt boréale (chapitre 2) toujours en tenant compte des impacts projetés sur la croissance (chapitre 1), sur le régime des feux ainsi que sur la densité de tiges.

Pour rappel, le premier chapitre avait pour but d'évaluer l'influence de la température, des précipitations et de la sécheresse sur la croissance en hauteur des arbres des deux espèces précédemment citées. Ce chapitre innove par l'utilisation de l'indice de qualité de station (IQS ou SI en anglais), c'est-à-dire la hauteur à 30 ans, associé aux normales climatiques (sur 30 ans) correspondant à la période de croissance de chaque tige. Cela nous a permis d'avoir un climat unique pour chaque arbre et de pouvoir évaluer la réponse au climat des arbres à un même stade de vie. Nous nous sommes aussi intéressés à une période relativement précoce dans la vie de l'arbre : de l'année où l'arbre atteint 1 m jusqu'à l'année à 1 m + 30 ans. Cette période, où la courbe de croissance est l'une des plus rapide chez les deux espèces, est tout particulièrement intéressante mais peu étudiée. Ainsi, les résultats de ce chapitre, pour l'épinette noire, montrent un effet positif de l'augmentation des températures sur la croissance en hauteur, qui est cependant atténué quand le sol s'assèche. À des températures élevées, la disponibilité en eau du sol devient alors un facteur limitant la croissance en hauteur de l'épinette. Nos résultats montrent que la demande atmosphérique en eau a aussi un effet positif sur la croissance en hauteur des deux espèces, bien que cet effet atteigne un plateau à partir d'un certain seuil pour l'épinette noire. Nous avons également montré que la croissance en hauteur des épinettes était plus importante sur les sites mésiques et sablonneux que sur les sites rocheux, plus pauvres en nutriments, ou subhydriques, peu drainés. Nos résultats révèlent que le pin gris est quant à lui plus sensible à la demande atmosphérique en eau qu'à la température et à la disponibilité en eau du sol, puisqu'il va chercher plus profondément les ressources dans le sol par rapport à l'épinette noire. Il semble donc se rétablir plus rapidement après une sécheresse et est donc moins sensible au réchauffement climatique. Les modèles issus de ces analyses rétrospectives nous ont permis de projeter les tendances de croissance en hauteur des deux espèces jusqu'en 2100 pour la forêt boréale québécoise. Ces projections suggèrent des effets globalement positifs sur la croissance des deux espèces. La principale contribution de ce chapitre réside donc dans ces deux nouveaux modèles, l'un pour l'épinette noire et l'autre pour le pin gris, ayant tous deux de bonnes capacités prédictives qui pourront être facilement transposables à l'aménagement forestier où l'IQS est d'ailleurs souvent utilisé. Nous avons cependant émis l'hypothèse que les effets positifs du changement climatique sur la croissance de ces espèces risquent d'être annulés par l'augmentation de la fréquence des feux. C'est ce que nous avons cherché à vérifier dans le chapitre 2 grâce aux modèles issus du chapitre 1.

L'objectif du chapitre 2 était donc d'évaluer la réponse de la réserve de bois de la forêt boréale du Québec pour l'épinette noire, en termes de volume marchand et de superficie productive, aux changements de croissance et de taux de brûlage dus au changement climatique. L'innovation de ce chapitre se trouve dans l'utilisation de trois méthodes complémentaires, dont les modèles du chapitre 1, afin de pouvoir établir l'impact cumulatif des changements de taux de croissance et de taux de brulage induits par le changement climatique sur la productivité de la forêt boréale du Québec. Nous avons aussi utilisé une combinaison de différents niveaux de changement potentiel de la croissance et de taux de brûlage afin d'établir des scénarios dans lesquels les projections de feux ou de croissance pourraient être sur ou sous-estimées. Cela a permis de déterminer la vulnérabilité d'une région face à l'accroissement des taux de brulage induits par le changement climatique en termes de productivité, ainsi que d'estimer l'offre potentielle de bois dans chaque district une fois ces deux facteurs intégrés dans les projections. Comme attendu suite aux résultats du chapitre précédent, lorsque la température augmente, la croissance augmente, et en conséquence la réserve de bois également. En parallèle, l'activité des feux augmente aussi avec le changement climatique, réduisant ainsi la réserve de bois. Synergiquement, et à mesure que le taux de brûlage augmente, l'impact positif de l'amélioration de la croissance sur la productivité s'atténue. Les effets positifs du changement climatique sur la croissance de l'épinette noire observés lors du chapitre 1 sont donc bien contrebalancés par les effets négatifs de l'augmentation de la fréquence des feux qui réduisent drastiquement les zones productives. Cependant, pour certaines zones qui restent productives malgré l'accroissement du taux de brulage, une augmentation du volume marchand estimé a pu être observée. Nos résultats suggèrent également un avantage du pin gris sur l'épinette noire, surtout dans la moitié nord de notre zone d'étude. Les résultats de ce deuxième chapitre vont contribuer à l'aménagement forestier actuel et futur de la forêt boréale québécoise et plus précisément au niveau de la limite nordique d'attribution des forêts. Toutefois, en territoire aménagé, le risque liés aux feux demeure : non seulement le peuplement risque de brûler avant d'avoir été récolté mais il est aussi à craindre qu'il brûle avant d'avoir atteint l'âge nécessaire pour pouvoir se régénérer, provoquant des accidents de régénération qui ne sont pas pris en compte dans l'aménagement de la forêt boréale québécoise.

Pour le troisième et dernier chapitre, le but était donc d'évaluer l'impact des accidents de régénération sur la productivité de la forêt boréale québécoise, pour l'épinette noire et le pin gris, en tenant compte des variations projetées de croissance, de densité de tiges et de taux de brûlage dues au changement climatique. Nous avons utilisé la méthode du chapitre 2 pour projeter la productivité présente et future en tenant compte des effets directs (via la croissance) et indirects (via les feux) du changement climatique. Le modèle du chapitre 1 a aussi été utilisé pour projeter les changements de croissance induits par le changement climatique. L'innovation de ce chapitre est l'utilisation du temps jusqu'à maturité reproductive, pour estimer le risque d'accident de la régénération tout en l'ajustant pour le changement de croissance, ainsi que l'utilisation de deux seuils de semis : un maximal et un critique, nous permettant d'évaluer les risques minimes à extrêmes, allant d'une simple perte de densité à une ouverture totale du peuplement qui deviendra non forestier. Nos résultats montrent que non seulement les zones productives vont diminuer avec le changement climatique, mais toutes les zones devenues improductives vont également être exposées à un risque d'ouverture du peuplement puisqu'elles n'atteignent pas le seuil critique. De plus, parmi les superficies qui demeurent productives malgré le changement climatique, une grande proportion est à risque de perte de densité puisqu'elle n'atteint pas le seuil maximal. Une grande partie de la forêt boréale québécoise est donc soumise à un risque d'accident de régénération qui s'aggravera avec le changement climatique et ce, malgré les effets positifs sur la croissance. En outre, nos résultats suggèrent encore une fois un avantage du pin gris sur l'épinette noire. Nos projections tenant compte des risques d'accident de régénération sont encore plus alarmistes et contribuent à la mise en garde sur l'importance des accidents de régénération qui restent encore grandement sous-estimés dans la planification stratégique forestière au Québec.

4.2 Le devenir de la limite nordique d'attribution des forêts

Afin de synthétiser les résultats de cette thèse et de faciliter la comparaison avec la limite nordique d'attribution des forêts actuelle, nous avons résumé nos résultats en utilisant des critères proches de ceux utilisés pour la création de la limite nordique (Figure 4.1). Nous avons donc classé les districts en 3 catégories : (1) peu vulnérable au feu (et donc aménageable) si ses peuplements ont en moyenne plus de 66% de probabilité de dépasser les seuils (productivité ou maturité reproductive), (2) vulnérable au feu (à risque mais toujours aménageable) si ses peuplements ont en moyenne plus de 33% mais moins de 66% de probabilité de dépasser les seuils, et enfin (3) très vulnérable (et donc non aménageable) si ses peuplements ont en moyenne moins de 33% de probabilité de dépasser les seuils (Gauthier *et al.*, 2013).

Pour le présent, on observe que notre zone d'étude est divisée en deux parties, avec une zone peu vulnérable aux feux au sud et une zone vulnérable, voire très vulnérable, sur toute la portion nord. Ces résultats sont très proches de ceux de la limite nordique où l'on peut aussi retrouver cette même division entre le sud et le nord (Gauthier *et al.*, 2015c). Cette zone à faible productivité, particulièrement vulnérable aux incendies et au changement climatique, s'étend d'ouest en est le long de la rive nord du lac Mistassini et d'une partie de la rive est du golfe du Saint-Laurent. La forêt boréale de la partie nord de notre zone d'étude est exposée à des conditions climatiques arides et se développe sur des dépôts de surface à faible productivité (comme les plaines organiques de l'Abitibi et les dépôts rocheux de la Côte-Nord) (Gauthier *et al.*, 2015c).

Avec le changement climatique, la zone très vulnérable et vulnérable aux feux s'élargit et s'étend vers l'est et le sud jusqu'à dépasser la limite nordique d'attribution des forêts de 2018 et atteindre la bordure sud de notre zone d'étude.

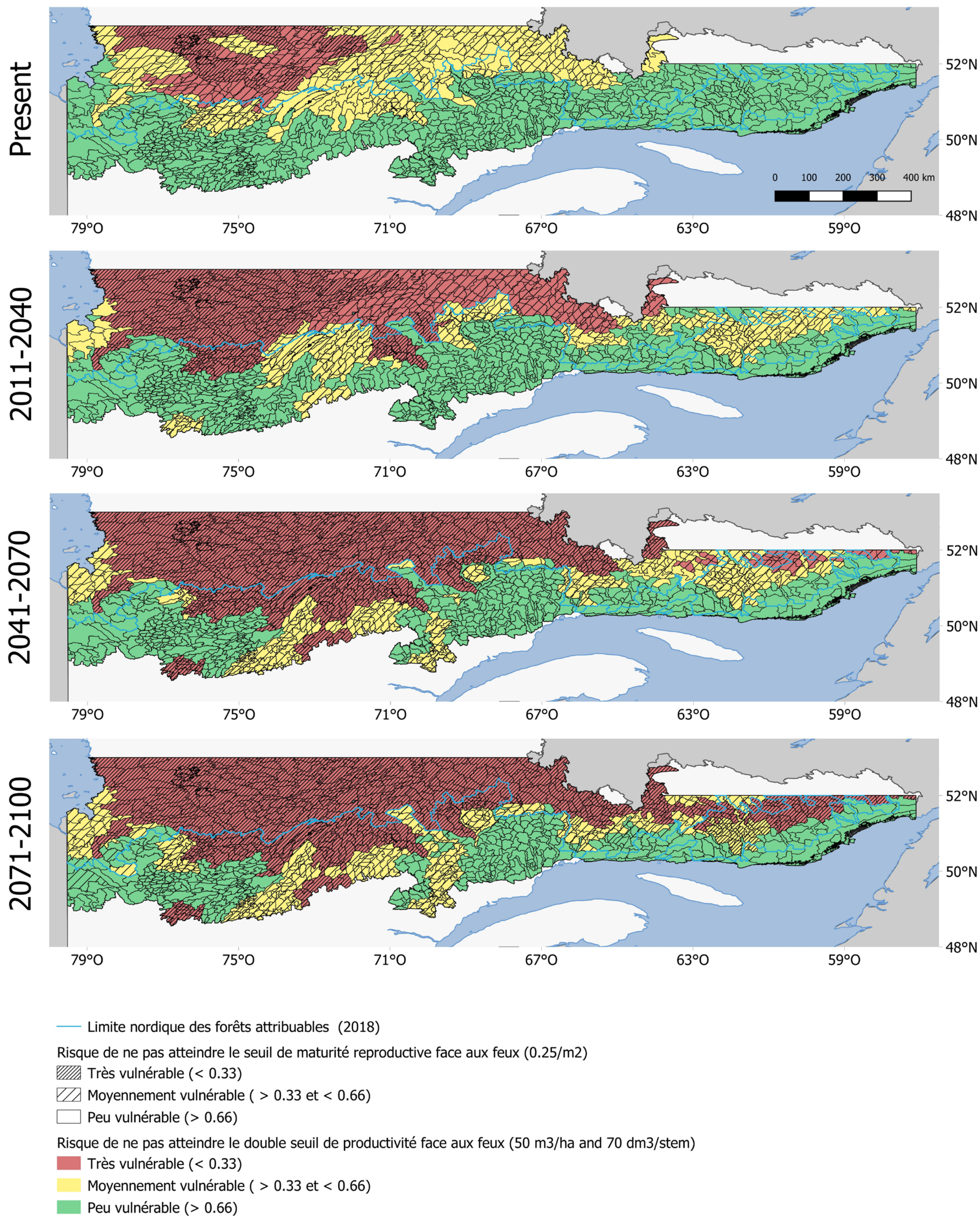


Figure 4.1. Vulnérabilité face aux feux pour l'épinette noire et pour quatre périodes : présent (1981-2010), 2011–2040 ESM2–RCP 8.5, 2041–2070 ESM2–RCP 8.5 et 2071–2100 ESM2–RCP 8.5.

4.3 Implications pour l'aménagement forestier

Nos résultats soulignent donc le risque de ne pas prendre en compte les feux, la régénération naturelle post-perturbation ainsi que le changement climatique, dans les études de productivité ou dans la planification stratégique de l'aménagement forestier. Au Québec, ces critères ne sont pourtant pas obligatoires et ne sont donc pas toujours intégrés à la planification stratégique de l'aménagement des forêts. Comme le montrent les résultats de cette thèse, ne pas inclure les feux, que ce soit pour les risques de perte de productivité ou pour les risques d'accidents de régénération, pourrait conduire à une forte surestimation des réserves de bois disponibles pour la récolte, créant un écart entre la productivité planifiée et la productivité réelle, pouvant conduire à un déclin de la forêt boréale québécoise (Paradis *et al.*, 2013; Gauthier *et al.*, 2015c; Cyr *et al.*, 2022). À l'inverse, ne pas tenir compte des possibles effets positifs du changement climatique sur la croissance entraînerait une sous-estimation du volume marchand et, par conséquent, de la réserve en bois disponible dans certaines zones productives du sud.

À la lumière de nos résultats, les zones présentant un risque très élevé de ne pas atteindre le seuil de maturité commerciale et/ou celui de maturité reproductive augmentent et descendent vers le sud avec le changement climatique (Figure 4.1). Comme la superficie forestière, qui peut être gérée de façon durable, tend à diminuer, il semble peu probable qu'à l'avenir un aménagement durable des forêts puisse être étendue au nord de la limite actuelle. Cette limite nordique d'attribution des forêts devrait au contraire être relocalisée vers le sud, notamment au niveau de la zone centrale qui semble particulièrement frappée par le changement climatique, jusqu'à devenir très vulnérable aux feux (Figure 4.1).

En revanche, les parties sud-est et sud-ouest de notre zone d'étude ont le potentiel d'être gérées de manière durable et pourraient présenter des opportunités pour l'aménagement forestier. Ces zones semblent peu affectées par l'augmentation des feux et leur volume marchand pourrait être aussi favorablement influencé par une meilleure croissance. Les possibilités d'accroître la productivité dans certaines zones au sud de la limite nordique d'attribution des forêts gagneraient donc à être explorées.

Dans ces zones au sud, qui devraient rester productives et où une augmentation du volume marchand de l'épinette noire avec le changement climatique est espérée, l'ajout de pins gris n'apporterait qu'un gain limité. Toutefois, dans les zones caractérisées par une faible productivité et une grande vulnérabilité aux feux et au changement climatique, il pourrait être intéressant de considérer le pin gris plutôt que l'épinette noire, notamment pour les plantations. Une grande partie de ces zones se trouvent néanmoins au nord et ne sont donc pas facilement accessibles. Les gains potentiels en volume marchand et en surface productive dépendraient donc d'un investissement financier considérable qui pourrait être à risque puisque beaucoup de ces zones sont vulnérables aux accidents de régénération. De plus, comme l'ont montré certaines études récentes (Girardin *et al.*, 2021b), les populations locales sont moins adaptées au réchauffement climatique que les populations plus au sud et ont une productivité plus faible. Pour les plantations, il sera donc avantageux de sélectionner des populations du sud, plus résilientes face au changement climatique. Là où le reboisement est trop couteux, l'idéal serait plutôt de favoriser la rétention d'arbres matures dans les coupes pour éviter les accidents de régénération dus à des perturbations successives (Cyr *et al.*, 2022).

4.4 Enjeux des recherches futures

Nous avons vu, lors de cette thèse, que des incertitudes persistent et mériteraient d'être investiguées plus en détail dans des recherches futures.

Premièrement, il est possible que le modèle de croissance de l'épinette noire du chapitre 1 ne soit pas basé sur une plage de température observée (de -2,7°C à 3,2°C) assez large pour inclure le seuil de 4°C observé dans d'autres études (Pedlar et McKenney, 2017), et à partir duquel le réchauffement devient préjudiciable à la croissance. De même, la distribution du pin gris dans l'étendue écologique et climatique de notre zone d'échantillonnage reste limitée par rapport à celle de l'épinette noire. La sensibilité des forêts boréales du nord au changement climatique peut également différer de celle des forêts boréales du sud en raison d'adaptations spécifiques liées à des environnements physiques distincts (Moreau *et al.*, 2020; Klesse *et al.*, 2020; Girardin *et al.*, 2021b). La sensibilité à la sécheresse n'est pas la même sur l'ensemble de la forêt boréale canadienne (Girardin *et al.*, 2021b) et le climat actuel et futur est également plus sec dans le centre et l'ouest du Canada qu'au Québec (Girardin *et al.*, 2016b). Malgré notre zone d'échantillonnage couvrant un large éventail climatique, il serait donc intéressant d'utiliser notre approche dans d'autres régions du Canada pour évaluer l'impact d'un climat plus chaud et plus sec.

D'autres facteurs, comme le mélange d'espèces dans les peuplements, peuvent également influencer l'impact du climat sur la croissance (Oboite & Comeau, 2019; Chavardès *et al.*, 2021). De plus, avec la migration vers le nord des espèces à feuilles caduques associée au changement climatique, les peuplements mixtes caduques-conifères devraient être de plus en plus nombreux (McKenney *et al.*, 2011;

Terrier *et al.*, 2013). D'autres recherches sur la façon dont les différents facteurs environnementaux et locaux influencent la croissance des espèces d'arbres boréales restent encore à mener.

Les autres perturbations naturelles, telles que les épidémies ou les perturbations anthropiques qui ciblent les peuplements particulièrement productifs, (Cyr *et al.*, 2021) n'ont pas été considérées lors de cette thèse. Hors l'augmentation et l'intensification des perturbations pourraient modifier grandement le paysage de la forêt boréale québécoise et les successions de perturbations vont aussi considérablement augmenter les risques d'accident de régénération (Le Goff *et al.*, 2008; Fleming *et al.*, 2002).

Le seuil de productivité (50 m^3/ha et 70 dm^3/tige) reste aussi un seuil minimal puisque l'âge d'exploitabilité absolu, qui assure une production maximale de bois par peuplement, est en moyenne 21 ans plus élevé dans notre zone d'étude que l'âge minimum pour atteindre le seuil de productivité (Raulier *et al.*, 2013). Dans un contexte d'aménagement, en visant une récolte à l'âge d'exploitabilité, la vulnérabilité au feu serait encore plus importante car le temps d'exposition serait prolongé. Comme nous l'avons fait avec les deux seuils de semis, il serait donc intéressant d'utiliser un seuil d'exploitabilité absolu comme deuxième seuil de productivité afin d'avoir une vulnérabilité plus proche de la réalité.

L'utilisation exclusive du scénario d'émissions élevées RCP 8.5 (Representative Concentration Pathway) (Meinshausen *et al.*, 2011) dans le chapitre 3 entraine possiblement une sous-estimation de la productivité future. En effet, le RCP 8.5 correspond au scénario le plus extrême d'émissions de gaz à effets de serre et induit donc une très forte augmentation des feux. Nous avons fait ce choix afin de couvrir l'étendue la plus large possible des conditions climatiques futures. En effet, pour la période 2011-2040 et pour notre zone d'étude, les projections de réchauffement climatique restent plutôt faibles et assez proches du RCP 4.5, alors qu'au contraire pour la période 2071-2100, le réchauffement climatique projeté avec le RCP 8.5 est extrême et beaucoup plus chaud que pour le RCP 4.5. Comme cela a été fait dans le chapitre 1, il serait tout de même intéressant de rajouter le RCP 4.5 pour le chapitre 3 afin de visualiser les résultats pour un scénario d'émissions moyen.

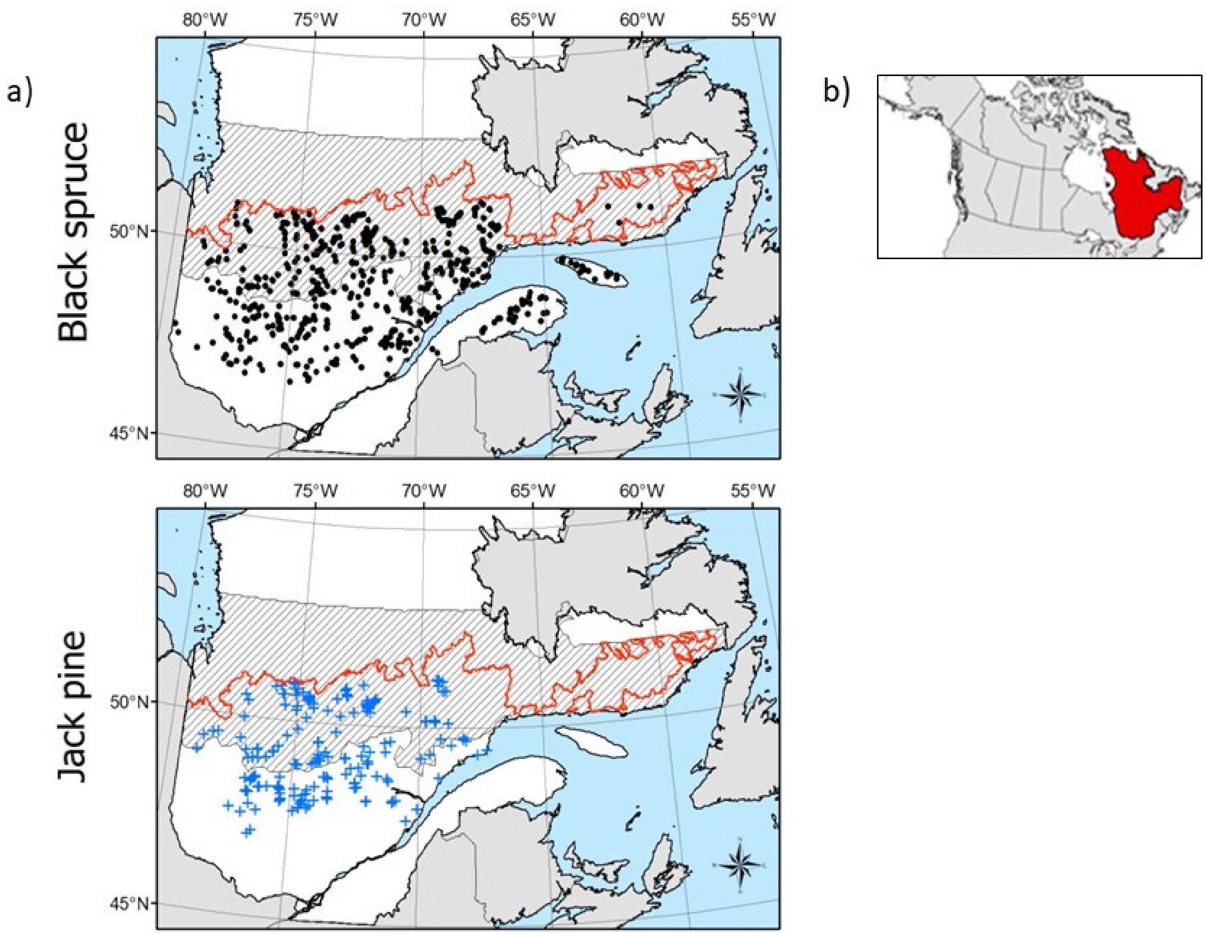
Enfin, dans cette thèse, nous avons réalisé une simulation non dynamique du territoire de la forêt boréale québécoise. Nous ne prenons donc pas en compte l'évolution future du paysage, qui pourrait être très différente de ce que nous connaissons actuellement. En effet, les feux, le climat et les caractéristiques physiques du territoire influencent la structure d'âge des peuplements ainsi que leur composition (Chabot *et al.*, 2009). Il serait donc particulièrement intéressant d'utiliser nos scénarios dans un modèle dynamique pour voir quel impact l'évolution dynamique du paysage pourrait avoir sur ces résultats.

Néanmoins, notre travail apporte un éclairage nouveau et important sur les effets combinés du changement climatique via la croissance des arbres (effets directs) et le régime des feux (effets indirects) sur le potentiel de production de la forêt boréale fermée du Québec. Cette thèse devrait aider à assurer la durabilité de l'aménagement forestier durable, en tenant mieux compte du changement climatique.

ANNEXE A

MATÉRIEL SUPPLÉMENTAIRE DU CHAPITRE 1

Supporting Information S1.1. a) Black spruce and Jack pine plot locations (as black dots and blue crosses, respectively) according to the database developed by the Direction des inventaires forestiers of the Ministry of Forests, Wildlife and Parks of Quebec (Laflèche et al. 2013), b) Location of Quebec within Canada. The red line indicates the 2018 limit for commercial forests (Jobidon et al. 2015), and hatching indicates our study area.

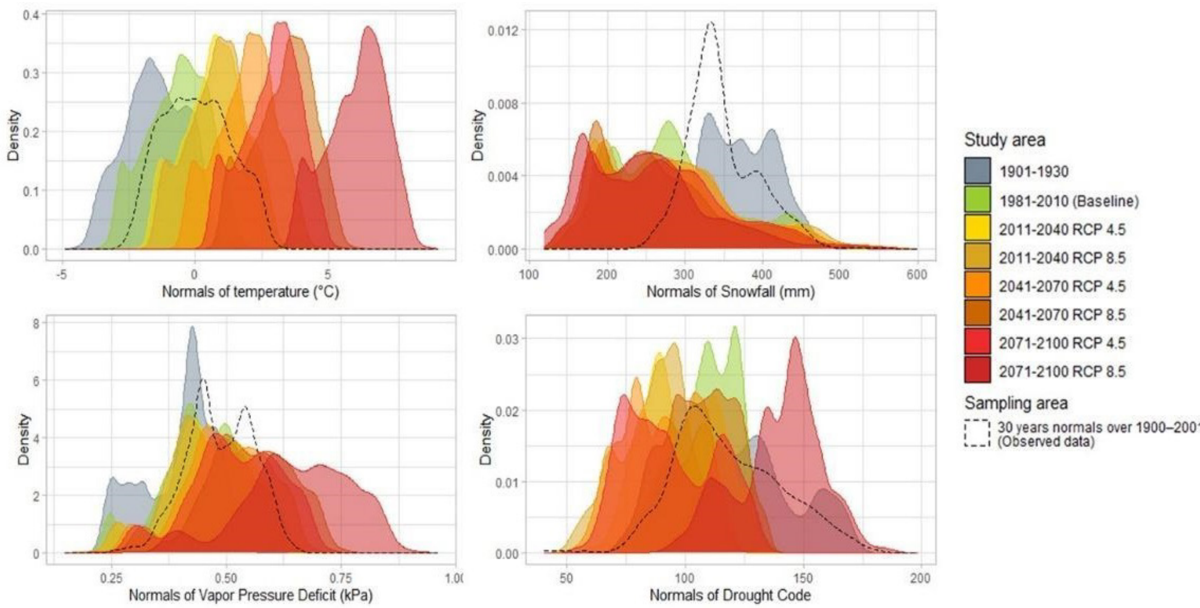


Supporting Information S1.2. Classification of surface deposits in different surficial deposit-drainage (SDD) code from Mansuy et al. (2012) based on their texture, stoniness, drainage and morphology and their proportion in black spruce and jack pine plots (sampling area), and in our study area.

	Surface deposit	SDD	Black spruce	Jack pine	Study area
2A	Juxta-glacial deposits		164 (6%)	140 (16%)	350 (3%)
2AK	Kame		2 (0%)		5 (0%)
2AE	Esker		10 (0%)	5 (0%)	58 (0%)
1AD	Washed Till				22 (0%)
1ACY	Till derived from crystalline rocks > 50 cm to 1 m with rare or very rare outcrops		4 (0%)		
1BP	Dead-ice moraine	VAVC	5 (0%)	5 (0%)	
1AB	Glacial block fields				11 (0%)
1BF2A	Frontal moraine composed of juxta-glacial deposits				6 (0%)
1BF1A	Frontal moraine composed of till				3 (0%)
1BF2BD	Frontal moraine composed of glaciofluvial delta				2 (0%)
1BA	Ablation Till (> 1 m)				197 (2%)
1BC	Rogen moraine, ribbed moraine				151 (1%)
1BG	De Geer moraine				9 (0%)
1BI	Interlobate moraine	AC			7 (0%)
1P	Dead-ice moraine				325 (3%)
1BI2A	Interlobate moraine composed of juxta-glacial deposits				5 (0%)
M1A	Thin till (< 25 cm)		148 (6%)	23 (3%)	
R	Outcrop > 50%		5 (0%)	5 (0%)	1397 (12%)
R1A	Outcrop between 25 and 50%		64 (2%)	23 (3%)	
1AAR	Cochrane till < 50 cm with abundant outcrop	ROC			8 (0%)
1AR	Undifferentiated till < 50 cm with abundant outcrop				2218 (19%)
8E	Scree				3 (0%)
2BD	Glaciofluvial delta		16 (0%)	10 (1%)	5 (0%)
2BE	Outwash plain		329 (13%)	253 (28%)	242 (2%)
4GA	Glaciolacustrine: shallow-water facies (> 1 m)		64 (2%)		366 (3%)
4GS	Glaciolacustrine: shallow-water facies (<25 cm)		48 (2%)	26 (3%)	78 (1%)
4P	Beach	MAC	5 (0%)	5 (0%)	
5S	Shallow-water facies		21 (1%)	17 (2%)	143 (1%)
9S	Stabilized dune		12 (0%)	11 (1%)	16 (0%)
8A	Altered materials		40 (2%)		
8AM	Altered materials > 25 cm to 50 cm with rare or scanty outcrops		22 (1%)		
8AY	Altered materials > 50 cm to 1 m with rare or very rare outcrops		20 (1%)		

3	Fluvial deposits				13 (0%)
3AE	Recent alluvial deposit				10 (0%)
3AN	Ancient alluvial deposit				29 (0%)
4A	Lacustrine plain				1 (0%)
4GAR	Glaciolacustrine: deep-water facies (>25 cm to 1 m)				4 (0%)
5A	Deep-water facies				90 (1%)
5AR	Deep-water facies (> 50 cm to 1 m)				9 (0%)
5SR	Shallow-water facies (> 50 cm to 1 m)				13 (0%)
6	Littoral deposits				41 (0%)
6R	Thin littoral deposits				3 (0%)
6S	Raised beach				5 (0%)
R_6	Littoral deposits < 50 cm with abundant outcrop				1 (0%)
5S_R	Shallow-water facies (> 50 cm to 1 m)				1 (0%)
R_5A	Deep-water facies < 50 cm with abundant outcrop				1 (0%)
1AM	Undifferentiated till > 25 cm to 50 cm with rare or scanty outcrops		131 (5%)	11 (1%)	
1AY	Undifferentiated till > 50 cm to 1 m with rare or very rare outcrops	MAM	410 (16%)	60 (7%)	
1AAY	Cochrane till > 50 cm to 1 m with rare or very rare outcrops		5 (0%)		
1A	Undifferentiated till		969 (37%)	291 (33%)	3483 (30%)
1BF	Frontal moraine		5 (0%)	5 (0%)	4 (0%)
1AA	Cochrane till	MM	2 (0%)		79 (1%)
1BD	Drumlins, drumlinoids, profiled shapes				277 (2%)
7E	Thick organic deposits		71 (3%)		
7T	Thin organic deposits mince		19 (1%)		
7	Organic deposits				1399 (12%)
7BR	Rippled ombrotrophic				54 (0%)
7BS	Structured ombrotrophic				197 (2%)
7BU	Uniform ombrotrophic				210 (2%)
7FS	Structured minerotrophic	ORG			9 (0%)
7FU	Uniform minerotrophic				2 (0%)
7R	Organic deposits < 50 cm with abundant outcrop				7 (0%)
7_R	Organic deposits < 50 cm with abundant outcrop				3 (0%)
R_7	Organic deposits < 50 cm with abundant outcrop				11 (0%)

Supporting Information S1.3. Climate range for our sampling area and for each period of our study area.



Supporting Information S1.4. Equations to calculate monthly Vapor Pressure Deficit (VPD) from Landsberg and Sands (2010).

Eq 1. $VPD_{month} = 0.5 \times (\varepsilon_{Tmax} - \varepsilon_{Tmin})$

where ε_{Tmax} and ε_{Tmin} are saturated vapor pressures at maximum and minimum temperatures, and are calculated as follows:

Eq 2. $\varepsilon_T = 0.61078 \times e^{17.269 \times T/(273.3 + T)}$

Supporting Information S1.5. Classification of surficial deposit-drainage (SDD) code from Mansuy et al. (2012) in our four site types: coarse-sand deposits (SAND), rock outcrops (ROC), mesic undifferentiated till and outwash plains (MT), and sub-hydric undifferentiated till and organic deposits with black spruce (SHT) and their proportion in black spruce and jack pine plots (sampling area), and in our study area.

SDD			Drainage	Site type	Black spruce	Jack pine	Study area
VAVC	Very abundant stoniness and very coarse	Disintegration moraine and juxta-glacial deposits	X	SAND	0	0	57 (0%)
			M	SAND	173 (7%)	145 (16%)	375 (3%)
			S	SAND	5 (0%)	5 (0%)	13 (0%)
			H	SHT	7 (0%)	0	0
AC	Abundant stoniness and coarse	Ablation tills and Rogen moraines	X	SAND	0	0	51 (0%)
			M	SAND	0	0	610 (5%)
			S	SAND	0	0	25 (0%)
			H	SAND	0	0	3 (0%)
ROC	Rock	Rock outcrops	X	ROC	4 (0%)	0	349 (3%)
			M	ROC	213 (8%)	51 (6%)	2549 (22%)
			S	ROC	0	0	104 (1%)
			H	ROC	0	0	7 (0%)
MAC	Moderately abundant stoniness and coarse	Outwash	X	SAND	8 (0%)	8 (0%)	6 (0%)
			M	MT	489 (19%)	301 (34%)	439 (4%)
			S	SHT	71 (3%)	13 (1%)	393 (3%)
			H	SHT	9 (0%)	0	89 (0%)
MAM	Moderately abundant stoniness, Moderately coarse	Undifferentiated thin till	X	SAND	0	0	0
			M	MT	491 (19%)	71 (8%)	0
			S	SHT	55 (2%)	0	0
			H	SHT	0	0	0

			X	/	0	0	5
MM	Moderate stoniness, Moderately coarse	Undifferentiated thick till	M	MT	675 (26%)	279 (31%)	2970 (26%)
			S	SHT	290 (11%)	17 (2%)	713 (6%)
			H	SHT	11 (0%)	0	59 (0%)
ORG	Organic	Organic deposits	H	SHT	90 (3%)	0	1457 (13%)

Supporting Information S1.6. Pearson's correlations between variables for a) black spruce data set, and b) jack pine data set.

a)

	Temperature normals	Drought Code normals	Vapor pressure deficit normals	Snowfall normals	Age at ground level	Latitude	Longitude	Precipitations normals
Temperature normals	/	0.26	0.48	-0.34	-0.30	**-0.82**	-0.13	0.13
Drought Code normals		/	0.16	-0.47	0.54	-0.19	0.02	**-0.83**
Vapor pressure deficit normals			/	-0.53	-0.15	**-0.79**	-0.65	0.04
Snowfall normals				/	-0.05	0.37	0.64	0.60
Age at ground level					/	0.24	0.15	-0.55
Latitude						/	0.42	-0.16
Longitude							/	0.08
Precipitations normals								/

b)

	Temperature normals	Drought Code normals	Vapor pressure deficit normals	Snowfall normals	Age at ground level	Latitude	Longitude	Precipitations normals
Temperature normals	/	0.03	0.65	-0.31	-0.57	**-0.90**	0.11	0.30
Drought Code normals		/	-0.02	-0.53	0.48	0.06	0.24	**-0.88**
Vapor pressure deficit normals			/	-0.39	-0.36	**-0.81**	-0.44	0.24
Snowfall normals				/	0.06	0.31	0.25	0.59
Age at ground level					/	0.51	0.13	-0.34
Latitude						/	0.31	0.20
Longitude							/	-0.52
Precipitations normals								/

Supporting Information S1.7. Variance inflation factor (VIF) for each variable for black spruce and jack pine.

	VIF	
Variables	Black spruce	Jack pine
Age at ground level	2.07	2.61
Temperature normals	1.80	2.73
Drought Code normals	2.46	2.57
Vapor pressure deficit normals	1.68	2.04
Snowfall normals	1.82	1.97

Supporting Information S1.8. Model selection according to the Bayesian Information Criterion (BIC) for a) black spruce, and b) jack pine.

To examine significant interactions, we developed a model composed of our base model that included: *age at ground level, juvenile suppression, latitude and longitude for spatial autocorrelation, sampling plots as a random effect, temperature, the Drought Code (DC), vapor pressure deficit (VPD), snowfall, and site type*; and all possible two-way interactions between climate variables and site type, and among climate variables (*temperature and DC, temperature and VPD, temperature and snowfall, DC and snowfall, DC and VPD, VPD and snowfall, temperature and site type, DC and site type, VPD and site type, and snowfall and site type*). Two interactions were significant for black spruce: *temperature and DC, and snowfall and VPD.* Two interactions were significant for jack pine: *DC and VPD, and snowfall and VPD*. We selected models for each species according to BIC. A model was considered to be better than another one if the former's BIC was lower, and ΔBIC between models was ≥2. To avoid circularity and redundancy among the set of predictors while keeping the models explored as parsimonious as possible, we only kept models that had significant interactions, and for models with similar BIC values (as for jack pine), we preferred the least amount of interaction (base model).

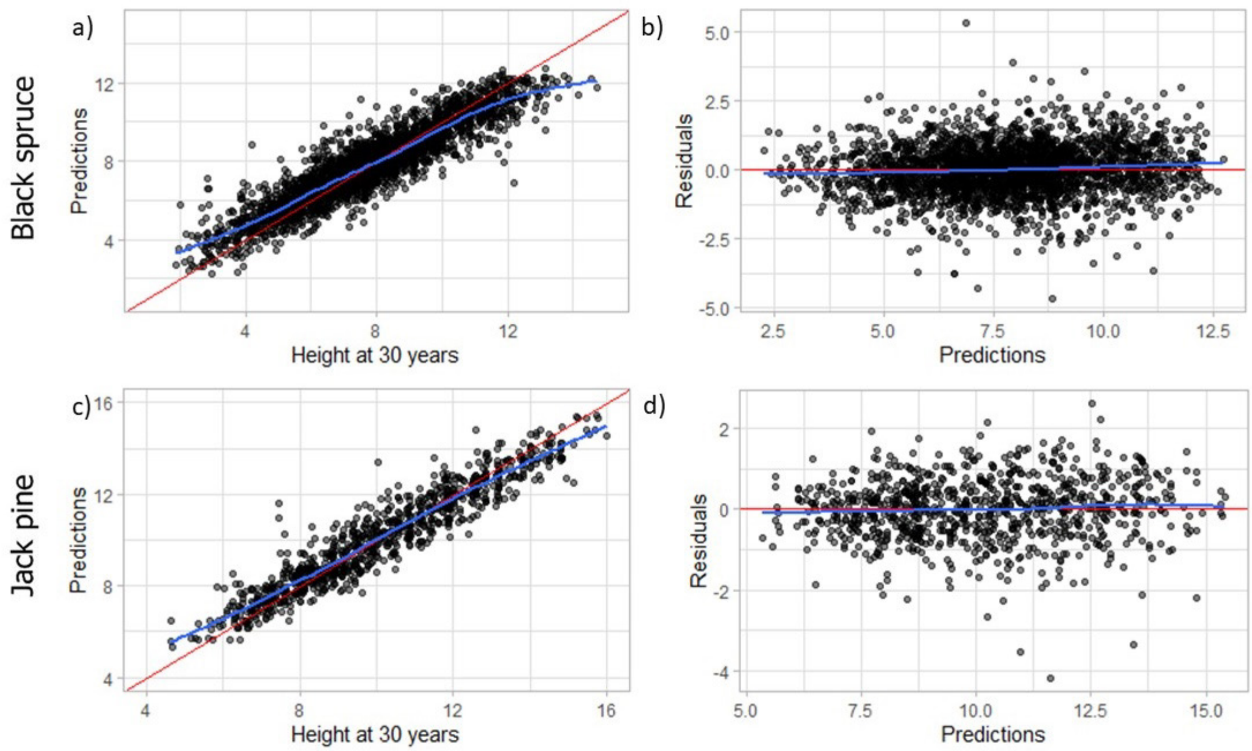
a)

Models	BIC	ΔBIC
Base model + T x DC	**10541**	0
Base model	10558	17
Base model + Snowfall x VPD	10588	47

b)

Models	BIC	ΔBIC
Base model	**3199**	0
Base model + DC x VPD	3199	0
Base model + Snowfall x VPD	3219	20

Supporting Information S1.9. Observed data vs. predictions for a) black spruce and c) jack pine; and residuals vs. prediction for b) black spruce and d) jack pine. Blue lines are smooth lines and red lines are 1:1 lines for a) and c), or y = 0 for b) and d).



Supporting Information S1.10. Root-Mean-Square Error (RMSE) and adjusted R^2 from 10 repeated 10-fold cross-validations. Bold numbers represent mean values.

		Black spruce		Jack pine	
Repetition	Fold	RMSE	Adjusted R^2	RMSE	Adjusted R^2
1	1	1.552	0.804	1.653	0.873
1	2	1.414	0.796	1.547	0.878
1	3	1.254	0.799	1.632	0.873
1	4	1.686	0.797	1.246	0.872
1	5	1.444	0.807	1.325	0.868
1	6	1.424	0.801	1.498	0.873
1	7	1.362	0.805	1.428	0.859
1	8	1.355	0.807	1.632	0.878
1	9	1.471	0.802	1.676	0.874
1	10	1.472	0.803	1.672	0.871
1	**Mean**	**1.443**	**0.802**	**1.531**	**0.872**
2	1	1.357	0.800	1.610	0.875
2	2	1.466	0.809	1.134	0.871
2	3	1.513	0.803	1.629	0.870
2	4	1.452	0.809	1.618	0.867
2	5	1.507	0.812	1.677	0.869
2	6	1.384	0.796	1.600	0.871
2	7	1.289	0.797	1.886	0.878
2	8	1.571	0.796	1.633	0.873
2	9	1.502	0.795	1.544	0.870
2	10	1.358	0.804	1.199	0.878
2	**Mean**	**1.440**	**0.802**	**1.553**	**0.872**
3	1	1.486	0.804	1.228	0.870
3	2	1.426	0.803	1.569	0.859
3	3	1.446	0.798	1.591	0.871
3	4	1.373	0.806	1.658	0.875
3	5	1.611	0.808	1.666	0.877
3	6	1.558	0.800	1.595	0.881
3	7	1.246	0.800	1.543	0.865
3	8	1.381	0.799	1.536	0.875
3	9	1.382	0.802	1.602	0.881
3	10	1.382	0.800	1.482	0.866
3	**Mean**	**1.429**	**0.802**	**1.547**	**0.872**
4	1	1.444	0.801	1.472	0.873

4	2	1.354	0.799	1.711	0.874
4	3	1.455	0.799	1.525	0.869
4	4	1.326	0.804	1.404	0.875
4	5	1.481	0.807	1.519	0.867
4	6	1.576	0.807	1.278	0.874
4	7	1.427	0.796	1.282	0.868
4	8	1.401	0.806	1.479	0.875
4	9	1.441	0.801	1.916	0.866
4	10	1.441	0.800	1.699	0.879
4	**Mean**	**1.435**	**0.802**	**1.528**	**0.872**
5	1	1.583	0.789	1.615	0.876
5	2	1.486	0.804	1.276	0.872
5	3	1.335	0.805	1.543	0.872
5	4	1.425	0.807	1.309	0.874
5	5	1.316	0.796	1.818	0.875
5	6	1.461	0.804	1.756	0.881
5	7	1.483	0.799	1.673	0.869
5	8	1.320	0.801	1.766	0.865
5	9	1.534	0.807	1.457	0.866
5	10	1.475	0.806	1.535	0.872
5	**Mean**	**1.442**	**0.802**	**1.575**	**0.872**
6	1	1.494	0.797	1.642	0.874
6	2	1.436	0.798	1.618	0.868
6	3	1.508	0.804	1.582	0.870
6	4	1.619	0.802	1.565	0.877
6	5	1.534	0.795	1.391	0.875
6	6	1.347	0.802	1.088	0.866
6	7	1.290	0.801	1.190	0.876
6	8	1.376	0.808	1.365	0.870
6	9	1.388	0.807	1.900	0.876
6	10	1.428	0.807	1.595	0.867
6	**Mean**	**1.442**	**0.802**	**1.494**	**0.872**
7	1	1.328	0.798	1.354	0.874
7	2	1.629	0.805	1.739	0.874
7	3	1.476	0.802	1.241	0.875
7	4	1.461	0.799	1.335	0.863
7	5	1.543	0.815	1.261	0.882
7	6	1.309	0.801	2.014	0.867
7	7	1.468	0.796	1.458	0.867
7	8	1.432	0.803	1.480	0.876

7	9	1.379	0.801	1.334	0.866
7	10	1.380	0.800	1.870	0.878
7	**Mean**	**1.440**	**0.802**	**1.509**	**0.872**
8	1	1.579	0.806	1.333	0.874
8	2	1.457	0.805	1.215	0.869
8	3	1.404	0.805	1.535	0.871
8	4	1.526	0.805	1.316	0.869
8	5	1.419	0.791	1.731	0.869
8	6	1.374	0.801	1.684	0.876
8	7	1.370	0.805	1.596	0.867
8	8	1.403	0.801	1.735	0.881
8	9	1.497	0.805	1.482	0.873
8	10	1.310	0.796	1.658	0.873
8	**Mean**	**1.434**	**0.802**	**1.529**	**0.872**
9	1	1.370	0.805	1.765	0.875
9	2	1.342	0.800	1.532	0.871
9	3	1.475	0.799	1.443	0.872
9	4	1.603	0.803	1.336	0.873
9	5	1.342	0.806	1.541	0.868
9	6	1.373	0.804	1.218	0.876
9	7	1.436	0.800	1.539	0.868
9	8	1.598	0.807	1.583	0.869
9	9	1.446	0.799	1.760	0.877
9	10	1.404	0.797	1.405	0.872
9	**Mean**	**1.439**	**0.802**	**1.512**	**0.872**
10	1	1.380	0.800	1.762	0.870
10	2	1.342	0.801	1.373	0.870
10	3	1.520	0.800	1.460	0.872
10	4	1.682	0.801	1.231	0.870
10	5	1.334	0.805	1.634	0.876
10	6	1.450	0.803	1.512	0.863
10	7	1.342	0.803	1.684	0.880
10	8	1.364	0.796	1.455	0.879
10	9	1.408	0.808	1.628	0.867
10	10	1.432	0.803	1.444	0.875
10	**Mean**	**1.425**	**0.802**	**1.518**	**0.872**
Total mean		**1.437**	**0.802**	**1.530**	**0.872**

Supporting Information S1.11. Standard errors (m) percentiles (0%, 5%, 50%, 95%, 100%) for each species and for each period a) for the entire study area and b) for portions of the study areas with projected future climate within the calibration range.

a)

Species		Black spruce					Jack pine				
Percentile		0	0.05	**0.5**	0.95	1	0	0.05	**0.5**	0.95	1
1915		0.21	0.26	**0.52**	1.20	2.09	0.73	0.80	**1.15**	4.55	6.16
1995		0.22	0.30	**0.58**	1.09	2.07	0.75	0.82	**1.21**	4.43	6.08
2025	RCP 4.5	0.25	0.36	**0.68**	1.14	2.07	0.78	0.92	**1.40**	4.17	5.90
	RCP 8.5	0.26	0.39	**0.69**	1.13	2.07	0.78	0.95	**1.40**	4.23	5.92
2055	RCP 4.5	0.37	0.52	**0.83**	1.29	2.12	0.91	1.13	**1.60**	3.96	5.65
	RCP 8.5	0.41	0.68	**1.04**	1.50	2.36	1.17	1.39	**1.94**	3.92	5.51
2085	RCP 4.5	0.46	0.66	**0.99**	1.67	2.49	1.03	1.29	**1.80**	3.95	5.58
	RCP 8.5	0.78	1.15	**1.74**	2.68	5.56	1.70	2.17	**3.41**	5.22	7.38

b)

Species		Black spruce					Jack pine				
Percentile		0	0.05	**0.5**	0.95	1	0	0.05	**0.5**	0.95	1
1915		0.21	0.25	**0.42**	0.85	1.84	0.73	0.78	**0.88**	1.19	1.43
1995		0.22	0.28	**0.45**	0.98	1.60	0.75	0.79	**0.95**	2.89	3.80
2025	RCP 4.5	0.25	0.34	**0.53**	1.16	2.02	0.78	0.87	**1.13**	3.34	3.84
	RCP 8.5	0.26	0.37	**0.58**	1.11	2.02	0.78	0.91	**1.16**	3.29	3.82
2055	RCP 4.5	0.37	0.50	**0.72**	1.27	2.10	0.91	1.07	**1.37**	3.59	3.92
	RCP 8.5	0.41	0.54	**0.84**	1.32	2.19	1.17	1.35	**1.77**	2.88	3.67
2085	RCP 4.5	0.46	0.59	**0.90**	1.41	2.13	1.08	1.20	**1.42**	3.65	3.90
	RCP 8.5	/	/	**/**	/	/	/	/	**/**	/	/

Supporting Information S1.12. Projected H30 (m) percentiles (0%, 5%, 50%, 95%, 100%) for each species and for each period **a)** for the entire study area and **b)** for portions of the study areas with projected future climate within the calibration range.

a)

Species		Black spruce					Jack pine				
Percentile		0	0.05	**0.5**	0.95	1	0	0.05	**0.5**	0.95	1
1915		8.67	9.60	**10.95**	13.20	14.35	5.56	7.22	**10.54**	13.65	14.63
1995		9.13	9.81	**11.62**	13.81	14.52	5.33	7.33	**12.18**	15.33	17.34
2025	RCP 4.5	9.85	10.80	**12.69**	14.73	15.56	5.26	8.74	**13.19**	16.83	19.76
	RCP 8.5	9.91	10.85	**12.74**	15.01	16.01	4.79	8.52	**12.95**	16.15	18.63
2055	RCP 4.5	11.09	11.79	**13.75**	15.70	16.48	6.34	10.15	**14.12**	18.24	21.62
	RCP 8.5	11.17	12.37	**14.71**	16.58	18.28	8.31	12.09	**15.94**	20.85	24.18
2085	RCP 4.5	10.97	12.04	**14.29**	16.28	17.58	7.34	11.08	**14.93**	19.89	23.63
	RCP 8.5	13.29	15.13	**18.03**	20.71	23.22	12.26	15.38	**20.94**	26.73	30.59

b)

Species		Black spruce					Jack pine				
Percentile		0	0.05	**0.5**	0.95	1	0	0.05	**0.5**	0.95	1
1915		9.20	9.63	**11.05**	13.01	13.84	9.32	10.39	**11.93**	13.99	14.63
1995		9.13	9.80	**11.43**	13.55	14.32	8.72	10.30	**12.95**	15.40	16.54
2025	RCP 4.5	9.86	10.68	**12.23**	14.23	15.15	9.64	10.91	**13.25**	15.38	16.54
	RCP 8.5	10.01	10.75	**12.54**	14.81	15.69	9.60	11.32	**13.66**	15.88	16.84
2055	RCP 4.5	11.10	11.82	**13.50**	15.14	15.77	10.22	12.36	**14.11**	16.26	17.04
	RCP 8.5	11.74	12.42	**13.80**	15.02	15.77	10.72	12.68	**14.02**	15.62	16.57
2085	RCP 4.5	11.65	12.31	**13.76**	14.82	15.65	10.54	11.60	**13.66**	15.00	16.16
	RCP 8.5	/	/	**/**	/	/	/	/	**/**	/	/

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