UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ÉVALUATION DU MÉLÈZE LARICIN COMME ESSENCE AMÉLIORANTE DES CONDITIONS DE CROISSANCE ET DU RENDEMENT DE LA FORÊT BORÉALE

THÈSE

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PAR

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AVANT-PROPOS

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Chapitre 1. Roy Proulx, S., Leduc, A., Thiffault, N., et Ameztegui, A., (2023). Tree size drives growth interactions in mixed mature stands of black spruce (Picea mariana) and tamarack (Larix laricina). *Forest Ecology and Management*, 543, 121150. https://doi.org/10.1016/j.foreco.2023.121150.

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

Analysis of variance / Analyse de variance	ANOVA
Akaike information criterion corrected	AIC_c
Basal area	BA
Basal area increment	BAI
Bayesian information criterion	BIC
Climate Moisture Index	CMI
Diameter at breast height / Diamètre à hauteur de poitrine	DBH
Degree Days above 5°C	DD5
Épinette noire (*Picea mariana* (Mill.) B.S.P.)	EPN
Generalized additive model	GAM
Ground-level diameter	GLD
Leaf area index	LAI
Mean annual Temperature	MAT
Mélèze laricin (*Larix laricina* [Du Roi] K. Koch)	MEL
Mean seasonal precipitation	MSP
Neighbourhood competition index	NCI
Potential basal area increment	PBAI
Summer Heat moisture index	SHM
Variance inflation factors / Facteurs d’inflation de la variance	VIF

RÉSUMÉ

Résumé

Les forêts boréales nordiques sont généralement peu productives en raison des conditions de croissance difficiles et de la courte saison de croissance. Un moyen de maintenir ou d'augmenter leur productivité pourrait d'aménager des peuplements mixtes. Cependant, pour tirer un gain en productivité, il faut que les essences soient compatibles ou que les interactions de croissance positives surpassent les interactions négatives. L'épinette noire (*Picea mariana* (Mill.) B.S.P.) et le mélèze laricin (*Larix laricina* [Du Roi] K. Koch) sont deux essences bien adaptées aux conditions de croissance de ce territoire et ayant un fort potentiel pour leur compatibilité de croissance. Cette étude proposait de tester les interactions de croissance sous différents scénarios entre l'épinette et le mélèze et ainsi vérifier si cette dernière essence peut maintenir ou augmenter le rendement des peuplements boréaux. Pour y parvenir, trois mécanismes seront à l'étude : la facilitation de la croissance, la complémentarité des niches écologiques et le rendement des peuplements mixtes. Ces mécanismes ont été investigués à deux échelles différentes : l'arbre et le peuplement sur l'ensemble de la forêt boréale québécoise. Suivant ces échelles, le premier volet concernait l'étude des interactions de croissance à l'échelle de l'arbre en forêt mature mixte (épinette/mélèze). Par la suite, l'étude de jeunes arbres dans des plantations expérimentales mixtes et d'épinette noire monospécifique, âgées de 8 ans ont été échantillonnées. Enfin, nous avons utilisés des données d'inventaires du ministère des Forêts, de la Faune et des Parcs du Québec récoltées à l'échelle de la forêt boréale québécoise, afin de vérifier à quelles proportions, les peuplements mixtes d'épinettes et de mélèzes sont plus productifs.

Ces investigations ont permis d'établir une partie du potentiel du mélèze laricin à d'augmenter la productivité des peuplements de la forêt boréale. Notamment, l'effet positif du mélèze sur les dimensions des jeunes épinettes en plantation, la production élevée des peuplements mixtes de la forêt boréale québécoise lorsque l'épinette et le mélèze étaient à des ratios respectifs de 70 et 30 % ainsi que la bonne complémentarité de leur niche de croissance tout au long de notre étude.

Mots clés : Complémentarité niche de croissance, Dynamique forestière, Contrôle biologique, Aménagement forestier, Indice de compétition, Plantation mixte

ABSTRACT

Abstract

The boreal forest stands have low productivity due to challenging growth conditions and a short growing season. A way to maintain or increase their productivity could be to establish mixed stands instead of monoculture. However, to achieve productivity gains, the assembled tree species must be compatible, or their interactions should be less detrimental for growth than intraspecific interactions. Black spruce (Picea mariana (Mill.) B.S.P.) and tamarack larch (Larix laricina [Du Roi] K. Koch) are two well-suited tree species for the growth conditions of this area and potentially have good growth compatibility. This study aimed to test growth interactions under different scenarios between spruce and tamarack to determine if tamarack can maintain or increase yields in boreal stands. To do so, three processes were examined: growth facilitation, ecological niche complementarity, and mixed stand over-yielding. These processes have been investigated at two different scales: the tree and the stand level throughout the Québec boreal forest. Following these scales, the first part will focus on the study of growth interactions at the tree scale in mature mixed forests (spruce/tamarack). Subsequently, the study of young trees in experimental mixed and single-species spruce plantations, 8 years of age, were sampled. Finally, we used the inventory data from the Quebec Forest ministry collected at the scale of the Quebec boreal forest to verify if mixed stands of spruce and tamarack are more productive than their single species stand counterparts.

These investigations have helped establish part of the potential of tamarack to increase the productivity of boreal forest stands. Specifically, the positive effect of tamarack on the growth of young spruce in plantations, the high productivity of mixed stands in Quebec's boreal forest when spruce and tamarack were at respective ratios of 70% and 30%, as well as the strong complementarity of their growth niches throughout the study.

Keywords: growth complementarity, Forest dynamic, Forest management, Competition indexes, Mixed plantation

INTRODUCTION GÉNÉRALE

Comme en témoignent plusieurs études, les peuplements mixtes offrent de nombreux avantages par rapport aux monocultures (Knoke et al., 2008; Jactel et al., 2009; Morin et al., 2011; Paquette & Messier 2011; Jucker et al., 2020; Messier et al., 2021). Ces études indiquent, entres autres, des gains potentiels en productivité, une amélioration de la résilience et/ou de la résistance aux perturbations, ainsi qu'une augmentation de la biodiversité avec le nombre d'essences dans les peuplements (Jactel et al., 2009; Morin et al., 2011; Paquette & Messier 2011; Felton et al., 2010; Felton et al., 2016). Les conditions climatiques, les caractéristiques du site, la structure, la densité de tiges et le mélange d'essences en présence peuvent avoir des impacts significatifs sur les relations de croissance en peuplement mixte (Forrester 2013; Danescu et al., 2016; Aussanac et al., 2017; Jactel et al., 2018; Brunner & Forrester 2020). La recherche d'essences ayant une bonne compatibilité de croissance peut être complexe, mais elle est essentielle pour un aménagement forestier mixte durable (Coll et al. 2018). L'aménagement de peuplement mixtes permettrait de conserve les fonctions écologiques essentielles, des groupes taxonomiques différents, tout en fournissant un apport en ressource ligneuse (Franklin et al., 2000). L'identification d'essences compatibles se base sur les différences ontogéniques, et lorsque ces différences sont observées entre deux essences, elles ont de fortes chances de présenter une bonne complémentarité des niches de croissance (Boyden et al., 2009). Les différences les plus importantes à considérer sont : la persistance du feuillage, la tolérance à l'ombre, la forme du houppier, la structure du système racinaire et le mode d'acquisition des ressources (Schmid & Kazda 2002; Pretzsch, 2014; Cordonnier et al., 2018). Cependant, il n'est pas possible d'identifier une ou deux différences qui assurent une bonne complémentarité des niches, mais l'addition du nombre de différences entre deux essences augmente les chances de compatibilité des niches de croissance (Prezsch, 2014; Cordonnier et al., 2018). Une combinaison d'essences favorisant la productivité des peuplements mixtes peut s'observer selon divers mécanismes tels que la réduction de la compétition, une meilleure utilisation des ressources disponibles ou l'amélioration des conditions de croissance par une essence (Aakala et al., 2013; Pretzsch, 2014, Ma et al., 2019). La productivité d'un peuplement change naturellement avec le temps, alors que de vieux peuplements seront moins productifs que des jeunes, mais la productivité est aussi modulée par l'environnement de croissance (Ammer, 2018).

Par la suite, lorsque l'on examine les effets des perturbations naturelles et des changements globaux sur les forêts, on constate que l'aménagement de peuplements mixtes peut contribuer à disperser et à atténuer le ou les risques faces à diverses perturbations telles que des épidémies d'insectes, des épisodes de sécheresse et de fort vents (Jactel & Brockerhoff 2007; Grossiord, 2019; Steckel et al., 2020; Chavardès et al., 2021). Cette stratégie d'aménagement repose sur l'adaptation et sur la dispersion du risque face aux perturbations engendrées par les changements globaux en augmentant la diversité des essences plantées sur un même site (Felton et al., 2010). Jactel & Brockerhoff (2007) ont observé une réduction globale de l'herbivorie par les insectes avec l'augmentation du nombre d'essences dans le peuplement. Grossiord (2019) souligne la complexité et la multitude de réactions de croissance possibles dans les peuplements mixtes face aux épisodes de sécheresses. Ainsi, l'augmentation du nombre d'essences dans un peuplement ne garantit pas nécessairement l'augmentation de la résistance aux perturbations (Grossiord, 2019; Steckel et al., 2020).

Les principales interactions de croissance ayant un impact sur la productivité des peuplements sont la compétition, la facilitation et la neutralité (Callaway & Walker 1997; Stachowicz, 2001; Bruno et al. 2003; Kelty, 2006; Larocque et al., 2013). La compétition peut être interspécifique ou intraspécifique, et toutes deux doivent être prises en compte dans la recherche d'essences ayant des compatibilités de croissance (Van de Peer et al., 2017). Certaines essences exercent une forte compétition intraspécifique, ce qui réduit considérablement la croissance des arbres d'une même espèce dans un peuplement (Forrester et al., 2006; Pretzsch et al., 2013). Il peut être avantageux pour la croissance de ces essences qui compétitionnent fortement pour les ressources, de réduire leur proportion au profit d'une autre essence compatible. La neutralité est l'absence d'interaction entre espèces, elle est rarement observée en forêt (Larocque et al. 2013). Enfin, la facilitation augmente la production totale par la réduction de la compétition entre espèces (Loreau & Hector 2001). Le mélange d'essences nécessite une connaissance approfondie des relations de croissance des essences ciblées autant pour les interactions intraspécifiques qu'interspécifiques, pour l'établissement de plantations mixtes.

L'étude des interactions de croissance se déroule à trois échelles distinctes, soient celle de l'arbre, du peuplement et de la région. À l'échelle de l'arbre, les données recueillies sont plus fines, telles que le nombre, l'orientation et la distance des arbres voisins, la hauteur et la taille des arbres, ainsi que la largeur et la forme du houppier des voisins (Canham et al., 2004; Canham & Uriarte 2006; Boivin et al., 2010; Pretzsch, 2014). Bien que chacun de ces effets individuels agissant sur les interactions de croissance soit difficile à mesurer, il est possible de modéliser le poids de chacun de ces effets à l'aide des modèles développés par Canham et al., (2004) et Canham & Uriarte (2006). Cette approche, à plus fine échelle, peut parfois être généralisée à plus grande échelle, mais pour faire une généralisation cohérente, elle doit couvrir un large gradient d'âges, de climats, de structures et de types de sols (Forrester, 2013; Jucker et al., 2014; Jucker et al., 2020; Searle & Chen 2020). Au niveau du peuplement, les éléments étudiés incluent le nombre de tiges à l'hectare, les proportions de chaque essence, le type de dépôt de surface, le drainage, l'âge et la structure du peuplement (Forrester, 2017). À cette échelle, l'intégration des résultats est plus facile et directe avec l'aménagement forestier. Enfin, à l'échelle régionale, l'inclusion des facteurs climatiques et des perturbations naturelles de grandes ampleurs permettent d'ajouter un autre niveau d'explication des relations de croissance (Jucker et al., 2016).

En forêt boréale, plusieurs études ont montré les avantages des forêts mixtes par rapport aux monocultures pour leurs services écosystémiques (Felton et al., 2016; Huuskonen et al., 2021) et pour l'augmentation de leur résilience face aux perturbations (Chavardès et al., 2021). Des gains en productivité en peuplements mixtes pourraient être bénéfiques à la forêt boréale (Paquette & Messier, 2011), qui rencontre plusieurs défis en matière d'aménagement (Price et al., 2013). Dans ce biome où les ressources sont souvent limitées, les interactions de croissance pourraient jouer un rôle prépondérant dans l'augmentation de la productivité, comparativement à d'autres biomes où les ressources sont moins contraignantes comme la forêt tempérée (Paquette & Messier, 2011). La saison de croissance y est courte, la vitesse de décomposition de la matière organique y est lente et les températures de l'air et des sols y sont basses (Saucier et al., 2015). De plus, le climat et les perturbations influencent la productivité de la forêt boréale qui varie considérablement géographiquement, du domaine bioclimatique de la sapinière à bouleau blanc à la pessière à lichens (Payette, 1992; Lord & Robitaille, 2013; Beaudoin et al., 2014).

Pour contribuer à l'augmentation de la productivité de la forêt boréale, nous proposons d'explorer les relations de croissance entre deux essences, l'épinette noire (*Picea mariana* (Mill.) B.S.P.) et le mélèze laricin (*Larix laricina* [Du Roi] K. Koch). L'épinette noire (EPN) est l'essence la plus utilisée pour le reboisement au Québec, représentant une proportion de plus de 56,9% de tous les résineux plantés dans la province entre 2010 et 2016 (Salmon 2017). Le mélèze laricin (MEL) est, pour sa part, très peu utilisé en reboisement, représentant 1,1% des résineux plantés au Québec pour la même période (Salmon, 2017). Dans ce contexte de sous-utilisation du MEL, je me suis questionné sur la pertinence d'une utilisation plus soutenue du MEL sur la croissance et la productivité des peuplements/plantations de la forêt boréale. Les différences ontogéniques entre le MEL et l'EPN laissent croire qu'ils pourraient avoir une bonne compatibilité de croissance (Strong & Roi 1983; Johnston, 1990; Boyden et al., 2009). En effet, une plus grande utilisation du MEL pourrait être bénéfique à la croissance des EPN notamment par une complémentarité de leur niche de croissance et par une augmentation générale de la productivité des peuplements de la forêt boréale, puisque le MEL a un taux de croissance élevé que celui de l'EPN (Strong & Roi 1983; Johnston, 1990; Moroni et al., 2009). De plus, la croissance du MEL est moins affectée que celle de l'EPN par les plantes concurrentes souvent rencontrées en forêt boréale (Thiffault et al., 2013; Thiffault et al., 2017). À ce jour, peu d'études se sont intéressées aux relations de croissance entre ces deux essences même si elles peuvent croître sur des sites similaires (Strong & Roi, 1983). Ainsi, nous avons investigué la croissance des arbres en peuplements mixtes à différents moments de leur développement, à plusieurs échelles (arbre et régionale). Nous passerons en revue les mécanismes les plus susceptibles d'améliorer la croissance des arbres en peuplement mixte EPN-MEL et les caractéristiques physiologiques et morphologiques laissant croire que l'EPN et le MEL sont compatibles.

1.1 Caractéristiques du mélèze laricin et de l'épinette noire

L'EPN et le MEL présentent plusieurs différences morphologiques et physiologiques, bien qu'ils aient la capacité de croître sous des conditions climatiques similaires dans l'ensemble de la forêt boréale canadienne. Ces deux essences se retrouvent fréquemment ensemble sur des sols organiques, des tourbières et des sites à drainage imparfait (Strong & Roi, 1983; Viereck et al., 1990). Pour que des interactions de croissance positives soient observées, deux essences doivent occuper des niches de croissance distinctes lorsqu'elles cohabitent sur de mêmes sites (Kelty, 1992; Man & Lieffers, 1999). Leurs différences morphologiques et physiologiques telles que leur système racinaire, leur taux de croissance, leur tolérance à l'ombre, la forme de leur houppier et la persistance leur feuillage (Strong & Roi 1983; Burns & Honkala, 1990; Pretzsch, 2014; Fichtner et al., 2017; Coll et al., 2018; Cordonnier et al., 2018) laissent croire que l'EPN et MEL pourraient occuper des niches de croissance assez distinctes pour avoir une bonne complémentarité. L'effet de ces différences morphologiques et physiologiques sur la croissance ont très peu été étudiées (Boyden et al., 2009) et elles soutiennent la pertinence d'explorer leur compatibilité de croissance.

Le système racinaire du MEL s'implante à des profondeurs de 0-40 cm, tandis que celui l'EPN s'étend de 0-30 cm (Strong & Roi, 1983). Bien que les deux essences aient des systèmes racinaires superficiels et donc qu'elles acquièrent les ressources peu profondément dans le sol, le rayon de propagation radiale du MEL est beaucoup plus grand que celui de l'EPN (9 m de rayon comparativement à 3 m pour l'EPN) (Strong & Roi, 1983). Ce rayon de propagation radiale confère au MEL une plus grande aptitude à acquérir les ressources disponibles dans le sol et lui donne un plus grand rayon d'influence sur les arbres qui l'entourent. Ce plus grand rayon d'influence du MEL sur les arbres voisins est à investiguer pour savoir s'il a la capacité de réduire l'eau sur les sites à mauvais drainage dans lesquels on le retrouve principalement avec l'EPN (Strong & Roi, 1983). De plus, le MEL a une évapotranspiration moyenne plus élevée que l'EPN (Schulze et al., 1985), ce qui lui confère un plus grand potentiel d'influence sur la quantité d'eau dans le sol. Cependant, les démonstrations de cet effet de réduction d'eau restent parcellaires et plusieurs éléments demeurent à être clarifiés (Jutras et al., 2006). Dans ce type de milieu, une réduction du contenu en eau dans des sols est positive puisqu'elle est non limitante pour la croissance des arbres (Lavoie et al., 2005). En fait, les sols organiques gorgés d'eau ont de faibles taux de décomposition et ce phénomène ralenti la croissance des arbres (Lavoie et al., 2007; Simard et al., 2007). Cependant, Stelling et al. (2023) n'ont pas observé de différence entre la transpiration de l'EPN et du MEL. Enfin, même si les deux essences peuvent croître sur des sols hydromorphes, le système racinaire du MEL est mieux adapté physiologiquement et morphologiquement à ce type de sol (Islam et al., 2003; Islam & Macdonald, 2004) : lorsque son système racinaire est immergé, le MEL peut croître plus rapidement et maintenir un plus grand taux d'assimilation des nutriments que celui de l'EPN (Islam et al., 2003; Islam & Macdonald, 2004). Ces adaptions physiologiques permettent au MEL de dominer les peuplements sur sol organique (Strong & Roi, 1983). Même si ce potentiel effet de réduction de la teneur en eau du sol est prometteur et intéressant, nous ne l'étudierons pas directement dans le cadre de cet étude puisqu'une investigation directe requière trop de ressources matérielles.

L'EPN affiche des taux de croissance en hauteur plus faibles que ceux du MEL (Stanek, 1977; Strong & Roi, 1983). Cependant, l'EPN possède une grande tolérance à l'ombre, alors que le MEL est intolérant (Strong & Roi, 1983). Cette combinaison de taux de croissance et de tolérance à l'ombre entre les deux espèces permet une utilisation plus optimale de l'espace et de la lumière en peuplement mixte par rapport aux monocultures. Les peuplements mixtes, avec une combinaison d'essences tolérantes et intolérantes ayant des taux de croissance différents, sont idéaux pour réduire la compétition pour la lumière, ce qui se traduit souvent par un meilleur rendement et une plus forte densité de tige (Sapijanskas et al., 2014; Pretzsch & Schütze, 2015; Williams et al., 2017; Kunz et al., 2019; Searle & Chen, 2020). Pour le MEL et l'EPN, cette utilisation de l'espace pourrait s'observer à court et à moyen termes (< 50 ans), lorsque le peuplement serait bi-étagé. Par la suite, à l'atteinte de l'EPN dans la canopée, la différence de hauteur maximale entre les deux essences est minime avec seulement quelques mètres de différence (Gower & Richards, 1990). Il n’est pas attendu que leur différence en hauteur en peuplement mature ait un grand impact positif sur leur croissance respective.

En plus d’une différence du taux de croissance en hauteur, la complémentarité de la forme des houppiers entre les essences est un élément important de la complémentarité des niches de croissance (Pretzsch, 2014). Le houppier de l’EPN est mince (quelques mètres de large), presque cylindrique, avec la majorité de son appareil photosynthétique à son sommet (Gower & Richard, 1990). Le MEL à un houppier plus large et de forme conique (Gower & Richard, 1990). Une parfaite complémentarité des houppiers en peuplement mixte est décrite comme pouvant déclencher des capacités d’expansion et d’emboîtement de ceux-ci et elle est habituellement le résultat d’une coévolution des essences (Forrester, 2013; Pretzsch, 2014). Cet emboîtement des houppiers de deux essences différentes provoque une forte complémentarité des niches de croissance entre les essences (Pretzsch, 2014). Bien que l’investigation de la complémentarité de la forme des houppiers de MEL et d’EPN n’ait jamais été réalisée, elles semblent au moins compatibles. La densité de feuillage du MEL est plus faible que celle de l’EPN (Lambert et al., 2005), permettant le passage de plus de lumière dans le peuplement. De plus, même si le houppier du MEL est plus large, il produit une faible obstruction au printemps jusqu’au moment où ses aiguilles sortent complètement de leurs bourgeons. Ces éléments laissent penser que le MEL n’exerce pas une trop forte compétition pour la lumière compagnie de l’EPN, malgré sa tendance à dominer l’EPN en hauteur.

Des différences physiologiques importantes entre les arbres à feuillage persistant et caduc peuvent influencer les réactions compétitives notamment à cause de stratégies différentes de translocation et d’allocation des ressources (Fichtner et al., 2017; Li et al., 2022; Urgoiti et al., 2023). Des essences avec des différences de persistance de feuillage ont une asynchronie dans leurs besoins en ressources lors de la sortie de la dormance au printemps. Cette asynchronie peut augmenter la complémentarité des niches de croissance (Del Rìo et al., 2017; Jucker et al., 2015). Boyden et al. (2009) parlent de différence l’ontogénique entre le MEL et l’EPN (différence dans le développement des individus) menant à une complémentarité des niches de croissance. L’EPN est un conifère à feuillage persistant qui renouvelle son appareil photosynthétique tous les 7 à 10 ans (Bégin, 1999), tandis que le MEL perd et renouvelle ses aiguilles annuellement (Strong & Roi, 1983). La chute annuelle de feuillage peut avoir un impact positif sur le cycle des nutriments du sol (Kelty, 1992). Dans le cas du MEL, ses aiguilles ont un ratio d’azote sur phosphore (N/P) élevé, permettant un largage d’azote lors de la décomposition de la litière (Dijkstra et al., 2009; Moore et al., 2010). De plus, les aiguilles de MEL peuvent modifier le contenu en macronutriments et la communauté microbienne du sol (Grayston & Campbell, 1996; Dijkstra et al., 2009). Ces changements pourraient potentiellement améliorer la croissance des arbres en augmentant la disponibilité des macronutriments (Forrester et al., 2006; Laganière et al., 2017).

La végétation sous couvert est influencée par la composition et la structure des essences de la canopée puisqu'elles modifient la disponibilité des principales ressources (lumière, nutriments et eau) (Barbier et al., 2008). La présence du MEL sur sol organique exerce une influence sur la composition des espèces végétales sous couvert, favorisant l'établissement des plantes vasculaires au détriment des bryophytes (Garant et al., 2022). Les bryophytes sont plus sensibles à l'effet physique de la chute de la litière, alors que les plantes vasculaires sont plus impactées par la quantité de lumière au sol (Hill, 1979). Ces caractéristiques laissent croire que la chute annuelle de litière de MEL et une plus grande quantité de lumière au sol créent un environnement plus favorable pour les plantes vasculaires. Enfin, toutes ses différences ontogéniques entre le MEL et l'EPN portent à croire qu'ils ont un bon potentiel de complémentarité dans leur niche de croissance respective, justifiant des investigations plus exhaustives et ciblées (Boyden et al., 2009; Searle & Chen, 2020).

1.2 Compétition intraspécifique et interspécifique

La compétition entre les arbres voisins s'exerce sur l'acquisition des ressources, à savoir la lumière, l'eau, l'espace et les nutriments (Vandermeer, 1989). La compétition entre les individus d'une même espèce (intraspécifique) peut grandement diminuer la croissance individuelle, surtout lorsque cette espèce à de grands besoins en ressources (Fichtner et al., 2017; Forrester, 2017). Cette diminution de la productivité est engendrée par une compétition directe pour les ressources au même moment de la saison de croissance et de la même manière (Forrester, 2017). La compétition intraspécifique varie d'une essence à l'autre en fonction des besoins en ressources de l'essence, de l'obstruction qu'une espèce produit sur ses voisins et de la quantité de ressources disponibles (Fichtner et al., 2017). L'effet de la compétition entre espèces (interspécifique) est généralement observé comme moins néfaste sur la croissance individuelle des arbres, peu importe la complémentarité des niches entre les espèces (Kelty, 2006; Van de Peer et al., 2017). Cette réduction de la compétition est habituellement due à une exploitation différente des ressources et à des différences dans les besoins en ressources entre les espèces profitant à leur croissance (Kelty, 2006). Toutefois, il existe des exceptions pour les essences qui compétitionnent fortement pour les ressources, puisqu'elles peuvent grandement réduire la croissance de leurs voisins (Urgoiti et al., 2023). Ces essences ne doivent pas être plantées avec d'autres essences qui ont des niches écologiques similaires et qui ne peuvent soutenir les intenses effets compétitifs de leur voisin, car cela peut mener à l'exclusion d'une des essences du peuplement (Morin et al., 2011; Pretzsch et al., 2012).

Certaines essences voient leur croissance presque systématiquement réduite par la compétition intraspécifique, comme le sapin commun (*Abies alba* (Mill.)) qui présente des réductions de croissance en peuplement mixte avec quatre essences fréquemment retrouvées en Europe centrale (Mina et al., 2017). Les peuplements mixtes sont plus productifs lorsque l'effet de la compétition interspécifique sur la croissance des arbres est plus faible que l'effet de la compétition intraspécifique. Il existe plusieurs exemples d'arbres en peuplement mixte ayant une meilleure croissance qu'en peuplement monospécifique (Kelty, 2006; Pretzsch et al. 2012; Van de Peer et al., 2017). Pretzsch et al. (2012) ont observé une surproductivité des peuplements mixtes de peupliers européen (*Fagus sylvatica* [L.]) et d'épinettes de Norvège (*Picea abies* [L.] Karst.) par rapport aux peuplements de peupliers purs. Cette différence est attribuée à la réduction de la compétition intraspécifique intense observée dans les peuplements de peupliers européen purs. Cette surproductivité était absente sur les sites riches, suggérant un effet de facilitation uniquement lorsque les ressources sont limitantes (Pretzsch et al., 2012). Les relations de croissance de l'EPN ont été étudiées selon plusieurs conditions de sites et avec différentes essences voisines (Légaré et al., 2004; Oboite & Comeau, 2019; Chavadès et al., 2022). L'EPN a des réactions de croissance différentes selon les essences constituant son voisinage, alors qu'elle est souvent positivement impactée par des essences à feuillage caduc et négativement par des essences à feuillage persistant (Légaré et al., 2004; Oboite & Comeau, 2019). Même si l'EPN a été passablement étudiée, aucune investigation des relations avec le MEL n'a été produite à ce jour. De son côté, le MEL reste très peu étudié et aucune étude ne fait l'objet de ces relations à notre connaissance.

1.3 De la complémentarité des niches à la facilitation

Cette section est dédiée à la complémentarité interspécifique des niches de croissance comme nous avons déjà traité des interactions intra et interspécifiques. La complémentarité des niches de croissance entre les différentes essences forestières est un mécanisme central dans l'étude des interactions entre les arbres (Vandermeer, 1989; Pretzsch, 2022). La complémentarité des niches n'est pas statique dans le temps et elle est aussi influencée par le climat, les sols, la composition en essences et la structure du peuplement (Forrester, 2013; Toïgo et al., 2015; Jucker et al., 2016; Ratcliffe et al., 2016; Mina et al., 2017). Une bonne complémentarité des niches de croissance mène à la facilitation qui augmente la croissance des essences et elle se définit par des interactions globalement positives (Vandermeer, 1989). La facilitation peut être directe (création d'un environnement favorable) ou indirecte (agit sur les autres compétiteurs, les prédateurs et les pathogènes) (Kelty, 2006; Bruno et al., 2003). La facilitation a aussi des effets sur les aptitudes individuelles, la distribution des populations, le taux de croissance et sur la composition des espèces à l'échelle du peuplement et du paysage (Callaway, 1995; Stachowicz, 2001).

Certaines caractéristiques des essences sont de plus hautes priorités dans la considération d'essences ayant potentiellement des niches de croissance complémentaires, incluant la tolérance à l'ombre, la forme du houppier et des différences dans l'acquisitions des ressources (Morin et al., 2011; Pretzsch, 2014; Sapijanskas et al., 2014; Jucker et al., 2015; Kunz et al., 2019). Lorsqu'une ou plusieurs de ces caractéristiques sont complémentaires, une surproductivité des peuplements mixtes par rapport aux monocultures peut être attendue (Reich et al., 2012; Zuppinger-Dingley et al., 2014; Jucker et al., 2020). Il y a deux principaux termes désignant les différences de productivité entres peuplements mixtes et monospécifiques, soit la surproductivité ordinaire ou celle dite transgressive (Pretzsch & Schütze, 2009). La surproductivité ordinaire d'un peuplement mixte correspond à une augmentation de la productivité par rapport à la somme des productivités moyennes des peuplements monospécifiques correspondant aux essences dans le peuplement mixte (Pretzsch & Schütze, 2009). De son côté, la surproductivité transgressive (en anglais "transgressive overyielding") correspond à une augmentation de la productivité en comparaison avec la productivité de tous les peuplements monospécifiques des essences en présence (Pretzsch & Schütze, 2009). Pour comprendre les mécanismes sous-jacents menant à la surproductivité au niveau du peuplement, il est souhaitable d'investiguer dans un premier temps les relations de croissance au niveau de l'arbre avec des modèles spatialement explicites (Canham et al., 2004; Canham & Uriarte 2006). Ces modèles aident à comprendre l'importance des effets de la distance, de l'ombrage, de l'espèce, du positionnement (nord, sud, est, ouest) et de la taille des voisins sur la croissance des arbres (Canham et al., 2004; Canham & Uriarte 2006; Boivin et al. 2010). Explorer l'effet de la position des arbres voisins permet de mieux saisir l'effet de la tolérance à l'ombre mais aussi des effets de différence en hauteur et de différences de la forme du houppier des essences dans le peuplement (Boivin et al. 2010).

Les mécanismes menant à la facilitation en peuplement mixte incluent le relargage de nutriments au sol (Forrester et al., 2006), la réduction de la compétition intraspécifique (Justes et al., 2014) et l'optimisation de la captation de la lumière et de l'eau (Forrester et al., 2010; Pretzsch et al., 2013; Steckel et al., 2020). Cependant, ces interactions de croissance sont complexes à mesurer en milieu naturel et peuvent grandement changer d'une année à l'autre selon les variations climatiques (Del Rìo et al., 2013; Jactel et al., 2018). Fichtner et al. (2017) ont observé que les essences ayant de plus grands besoins en ressources (eau et nutriments) vont avoir des gains en croissance par la réduction de la compétition en peuplement mixte. À l'opposé, les essences à faibles besoins en ressources vont réagir positivement uniquement lorsqu'un mécanisme de facilitation actif à lieu dans les peuplements mixtes (relargage nutriments, meilleure captation de la lumière, etc.) (Fichtner et al., 2017). L'utilisation de l'eau est un enjeu pouvant conduire à un effet de facilitation lorsque celle-ci est limitante (Forrester et al., 2010; Steckel et al., 2020). Forrester et al. (2010) montrent que 2 essences captant l'eau à différentes profondeurs dans le sol peuvent améliorer l'utilisation de l'eau disponible pour la croissance en peuplements mixtes. Cette utilisation plus optimale de l'eau à différentes profondeurs du sol réduit la susceptibilité des peuplements mixtes aux sécheresses (Steckel et al., 2020). Cependant, le MEL et l'EPN se trouvent souvent sur des sols où l'eau est en excès ralentissant les processus de décompositions du sol et limitant la productivité des peuplements (Saucier et al., 2015). De ce fait, une réduction de l'eau sur ce type de sol en peuplements mixtes pourrait améliorer le taux de décomposition et le rendement des peuplements (Jutras et al., 2006).

En forêt boréale, les relations de facilitation ont été étudiées entre l'EPN et plusieurs autres essences telles que le peuplier faux-tremble (*Populus tremuloides* Michx.), le bouleau d'Alaska (*Betula neoalaskana* Sarg.), le pin gris (*Pinus banksiana* Lamb) et le sapin baumier (*Abies balsamea* (L.) Mill.) (Légaré et al., 2004; Oboite & Comeau, 2019). Parmi ces essences compagnes, le bouleau d'Alaska et le peuplier faux-tremble ont des effets positifs sur la croissance de l'EPN (Légaré et al., 2004; Oboite & Comeau, 2019). Légaré et al. (2004) ont observé un effet positif du peuplier faux-tremble sur le diamètre et la hauteur de l'EPN uniquement lorsqu'il occupe 40 % et moins de la surface terrière dans des peuplements âgés entre 23 et 75 ans. Les auteurs suggèrent qu'il s'agit d'un effet positif du peuplier sur la fertilité des sols par l'apport annuel de litière, lequel augmente la disponibilité des nutriments pour l'EPN. Ils proposent également que les deux essences auraient des niches écologiques distinctes expliquant cet effet positif et qu'elles exploitent les ressources différemment (Légaré et al., 2004). Cependant, on observe une augmentation de la compétition pour la lumière et pour les nutriments sur l'EPN lorsque le peuplier est présent à plus de 40 % (Légaré et al., 2004). Les proportions de chacune des essences à l'échelle de l'arbre et du peuplement sont ainsi importantes dans l'étude des relations de croissance. L'importance de l'échelle, qu'elle soit spatiale ou temporelle, est soulevée par Cavard et al. (2011) qui étudient les mêmes essences que Légaré et al. (2004), mais ils montrent que les interactions changent au fil du temps et selon le type de sol. On remarque également que la croissance de l'EPN est impactée négativement par le peuplier en jeune âge. Toutefois, cette tendance est inversée passer l'âge de 37 ans (Cavard et al., 2011).

Dans le contexte d’une étude des relations de croissance entre MEL—EPN, il est important d’examiner l’effet des proportions des essences à plusieurs échelles spatiales et temporelles. Une interaction de croissance semblable à celle entre l’EPN et le peuplier pourrait être observée entre l’EPN et le MEL pour leurs similitudes sur la persistance du feuillage et quant à son taux de croissance plus élevé que celui de l’EPN (Gower & Richards, 1990; Johnston, 1990). Le MEL a aussi une plus grande capacité à capter et à utiliser l’azote que l’EPN lorsqu’il croît sur des sols organiques (Macdonald & Lieffers, 1990). Cependant, le lien n’est pas nécessairement direct entre la perte annuelle des aiguilles et l’augmentation des nutriments disponibles dans les sols puisque le MEL est très efficace pour récupérer les nutriments avant de perdre ses aiguilles (Chapin & Kedrowski, 1983; Carlyle & Malcolm, 1986). De plus, le relargage de nutriments peut être indisponible à la captation racinaire en raison d’autres phénomènes comme la formation de complexe avec la lignine de la litière de l’EPN (Reich et al., 1998). Ce phénomène a été noté par Dijkstra et al. (2009) qui ont observé la formation d’un complexe résistant à la dégradation microbienne en jeune plantation mixte EPN-MEL, entraînant une réduction du taux de minéralisation de l’azote. Néanmoins, Dijkstra et al. (2009) ont observé une augmentation de la biomasse aérienne, dix ans après l’établissement de la plantation mixte dans un ratio de 1,42 par rapport aux EPN en monoculture. Ces effets hâtifs sont intéressants, mais ils doivent être réévalués au fil du temps, car ils peuvent changer rapidement avec l’augmentation de la taille des arbres, bien qu’ils puissent théoriquement diminuer le temps nécessaire pour atteindre le diamètre marchand (≥ 9 cm à 1,3 m du sol). Nous avons déjà établi les multiples différences morphologiques entre le MEL et l’EPN, mais il reste à savoir si elles sont suffisantes pour engendrer une complémentarité de leur niche de croissance menant à des effets positifs sur la croissance ou à une surproductivité des peuplements mixtes.

1.4 Interactions de croissance au fil du développement du peuplement

Les interactions de croissance varient fortement tout au long du développement des peuplements (Del Rìo et al., 2013; Forrester, 2017; Sterba et al., 2018) et elles atteignent un sommet au stade de fermeture de la canopée (Angelstam & Kuuluvainen, 2004; Shorohova et al., 2009; Jucker et al., 2020), soit habituellement entre 20 et 40 ans en forêt tempérée et boréale (Forrester, 2014; Feng et al., 2022). Les paramètres influençant la croissance des arbres varient avec le temps, la dispersion spatiale des tiges, leur rayon d’influence et les particularités physiologiques des espèces (Silander & Pacala, 1985; Wagner & Radosevich, 1991; Stoll et Newbery, 2005). Urgoiti et al. (2023) ont observé une forte compétition des essences à feuillage caduc sur les essences à feuillage persistant dans de jeunes plantations (11 premières années de croissance). Cependant, Oboite & Comeau (2019) ont observé un renversement de cette tendance alors que la croissance de l'EPN était positivement impactée par le compagnonnage d'essences à feuillage caduc pour des arbres âgés de 25 ans et plus.

L'espace individuel de croissance nécessaire pour chaque tige devient limitant lorsque les appareils photosynthétiques des arbres se chevauchent (entre 20 et 40 ans) et cette réduction d'espace disponible mène à l'auto-éclaircie du peuplement (Kenkel et al., 1997; Harper et al., 2005). La diminution du nombre de tiges après l'auto-éclaircie ou une coupe partielle explique pourquoi on observe une augmentation de la croissance des tiges résiduelles à la suite ces événements (Kneeshaw et al., 2002; Thorpe et al., 2007). Certaines caractéristiques spécifiques des arbres ont des effets changeants au fil du temps, comme le relargage de nutriments aux sols par l'apport de litière (Reich et al., 1998; Forrester et al., 2006; Dijkastra et al., 2009). Par exemple, les essences fixatrices d'azote (qui est un élément limitant dans les sols) ont le potentiel d'augmenter l'azote disponible dans le sol, mais ce mécanisme n'est pas toujours un effet immédiat sur la croissance des arbres (Reich et al., 1998). En effet, le relargage de nutriments varie fortement avec l'âge des arbres du peuplement, le type d'essence produisant la litière, le type de sol et les propriétés de la litière (Reich et al., 1998; Forrester et al., 2006; Dijkastra et al., 2009). L'impact de ce relargage sur la croissance peut survenir tôt (< 10 ans), seulement si les essences produisent une grande quantité de litières, comme c'est le cas pour les espèces *d'Acacias* fixateurs d'azote (Forrester et al., 2006). De plus, le MEL récupère une grande quantité de nutriments présents dans son feuillage avant qu'il ne tombe au sol (Reich et al., 1998). Ainsi, il convient d'explorer les contextes où ce complexe résistant à la dégradation influence la disponibilité des nutriments du sol et la quantité de nutriments relargués au sol en peuplement mixte EPN—MEL.

Au stade juvénile, les peuplements boréaux montrent rarement des interactions de croissance ayant un impact significatif, alors que le climat, le type de sol et la végétation concurrente exercent un grand impact négatif sur leur croissance à ce stade (Verheyen et al., 2016; Grossman et al., 2018; Kambach et al., 2019; Jucker et al. 2020). Le rendement des jeunes peuplements est en effet fortement influencé par la présence des plantes concurrentes (Thiffault & Roy, 2011; Thiffault et al., 2013), dont les plantes éricacées comme le Kalmia (*Kalmia angustifolia* L.). Ces dernières sont très présentes dans la partie ouest de la forêt boréale québécoise, réduisant grandement la productivité des peuplements (Thiffault et al., 2013; Thiffault et al., 2015). La croissance du MEL est moins affectée que l'EPN par l'interférence qu'exerce le *Kalmia* sur les processus nutritionnels (Thiffault et al., 2013; Thiffault et al., 2017). De plus, Moroni et al. (2009) indiquent que le MEL a une plus grande aptitude à fermer le couvert rapidement que l'EPN. Ainsi, la proximité du

MEL pourrait faciliter la croissance de l'EPN en fermant plus rapidement le couvert et en limitant la végétation concurrente. Cependant, la fermeture hâtive du couvert pourrait aussi avoir un effet négatif sur la croissance de l'EPN, tel qu'observé par Urgoiti et al. (2023) par le voisinage d'essences à feuillage caduc.

1.5 Aménagement des peuplements mixtes en forêt boréale

L'aménagement et la sylviculture des forêts mixtes peut poser plusieurs défis, de sa mise en place (patron de reboisement), aux travaux d'éclaircie, jusqu'à l'optimisation du prélèvement de matière ligneuse (utilisation d'une machinerie petite et adaptée, taux de prélèvement, etc.) (Parkatti & Tahvonen, 2020). Le reboisement avec 2 essences et plus pose des défis dans l'optimisation du positionnement des essences et dans le respect des ratios recommandés (si ces indications existent pour les essences plantées) pour optimiser le rendement ou l'atteinte des autres buts désirés par l'établissement de peuplements mixtes. Le respect des proportions peut être un élément crucial de la complémentarité des niches entre deux essences (Légaré et al., 2004, Cavard et al. 2011, Sterba et al., 2018). Sterba et al. (2018) ont montré que les ratios optimaux pour la productivité entre l'épinette de Norvège et le mélèze européen (*Larix decidua* Mill.) sont de 40 et 60% respectivement. Ces essences ont des caractéristiques et physiologies similaires à l'EPN et au MEL. Cette investigation offre les meilleures indications des proportions les plus prometteuses à investiguer pour notre étude.

Par la suite, les décisions d'éclaircies pré-commerciales et commerciales dans les peuplements mixtes doivent être adaptées et elles sont différentes à celles prises en peuplement monospécifique (Parkatti & Tahvonen, 2020). Les décisions de prélèvement sont modulées par les taux de croissance des essences, leur tolérance à l'ombre et les réactions de croissance à la suite d'une coupe (Thorpe et al., 2007; Bose et al., 2015; Bose et al., 2021). Les essences à feuilles caduques vont plus rapidement prendre l'espace disponible et atteindre la canopée plus rapidement que les essences aux feuillages persistants (Fahlvik & Nystrom, 2006; Kaila et al., 2006). Un prélèvement plus hâtif ou une éclaircie plus grande des essences à croissance rapide est donc à prévoir pour qu'elles n'excluent pas leur essence compagne (Huuskonen et al., 2021). Les projections de croissance et les travaux sylvicoles dans les peuplements mixtes se basent presque toujours sur leur croissance en peuplement monospécifique (Pretzsch & Zenner, 2017). Cependant, les peuplements mixtes ont des relations de croissance plus complexes, pouvant, par exemple, augmenter la densité maximale de tiges et augmenter la croissance individuelle des tiges (Légaré et al., 2004; Pretzsch & Biber, 2016). Ces éléments sont importants à connaître et à prendre en compte dans les décisions d'éclaircies pré-commerciales et commerciales. Très peu de littérature est disponible sur les interactions de croissance et sur la récolte de la matière ligneuse dans les peuplements de MEL et d'EPN. Cependant, le MEL devrait atteindre plus rapidement sa maturité pour la récolte que l'EPN (Gower & Richards, 1990; Boyden et al., 2009) et un prélèvement hâtif des MEL pourrait être anticipé selon le but d'aménagement et l'état du peuplement. Les opérations de coupe partielle sont délicates sur sol organique et peuvent être difficiles selon la disposition des essences dans le peuplement (Thorpe et al., 2008). Donc, même si une bonne complémentarité des niches de croissance est anticipée entre le MEL et l'EPN, la planification du reboisement, des travaux d'éducation et de récoltes partielles restent un défi.

Si la présence du MEL améliore la croissance de l'EPN ou la productivité générale des peuplements mixtes, un effet concomitant intéressant à investiguer serait l'atteinte plus hâtive de la maturité sexuelle du MEL et l'EPN. Ce lien vient du fait que la taille des arbres est positivement associée avec l'atteinte de la maturité sexuelle (Viglas et al., 2013). Le temps pour atteindre la maturité sexuelle chez l'EPN varie de 30 à 90 ans selon les différentes situations de croissance (Viglas et al., 2013; Splawinski et al., 2019). En forêt boréale nordique, une atteinte hâtive de la maturité sexuelle diminue le risque d'accident de régénération à la suite d'une perturbation naturelle à grande échelle comme le feu (Payette, 1992; Splawinski et al., 2019). L'atteinte hâtive de la maturité sexuelle est un élément critique du maintien de la productivité et de la résilience des forêts nordiques (Splawinski et al., 2019). De plus, cet élément est d'autant plus important dans un contexte de changements climatiques, augmentant les épisodes de sécheresse et le risque de feu dans les forêts canadiennes (Girardin et al., 2016). Certains peuplements mixtes sont plus résilients aux épisodes de sécheresse que les monospécifiques (Aussenac et al., 2018; Vacek et al., 2021; Chavardès et al., 2022). Cette augmentation de la résilience a été observée par une croissance moyenne plus stable et des moins grands déclins de croissance face aux variations climatiques (Aussenac et al., 2018; Chavardès et al., 2022). Cependant, comme l'amplitude du réchauffement climatique ne peut être précisément prédite et que la résilience des peuplements mixtes dépendra de cette amplitude (Jactel et al., 2018), rien ne garantit le succès des peuplements mixtes face à cette incertitude. L'établissement d'une plus grande proportion de peuplements mixtes n'est pas une panacée dans la lutte aux changements climatiques, mais elle montre des signaux encourageants dans son ensemble (Jucker et al., 2014; Aussenac et al., 2018, Vacek et al., 2021; Chavardès et al., 2022). Pour revenir à nos essences, le MEL n'est pas adapté aux passages du feu puisqu'il a une écorce mince et des cônes non sérotineux (Johnston, 1990). Cependant, il est moins impacté par les feux puisqu'il se trouve majoritairement sur des sols hydromorphes augmentant ainsi sa survie au feu de faible et de moyenne intensité (Busque & Arseneault, 2005). De son côté, l'EPN est bien adapté au passage du feu, (Viereck & Johnston, 1990) ce qui augmente les probabilités de régénération en peuplement mixte avec l'EPN. Le risque d'aménager ce type de peuplement mixte face au feu est donc modérée à faible selon l'emplacement.

Enfin, même si les deux essences ont une désirabilité commerciale, le MEL est sous-utilisé avec seulement 1.5 % du reboisement à l'échelle nationale (CCFM, 2020) et il pourrait aider à diversifier les essences utilisées pour le reboisement (Thiffault et al., 2010). D'un autre côté, l'EPN est actuellement largement utilisée représentant 44.3 % du reboisement à l'échelle canadienne (CCFM, 2020) et 56.9 % à l'échelle québécoise (Salmon, 2017). Plusieurs actions sont nécessaires pour maintenir la productivité des peuplements commerciaux de la forêt boréale et l'utilisation du MEL pourrait être l'une des solutions de par sa capacité à croître et à fermer le couvert rapidement (Moroni et al., 2009). Comme il a déjà été mentionné, le reboisement mixte peut s'insérer dans une stratégie globale visant à augmenter la résilience des peuplements face aux aléas climatiques et aux changements globaux (Jucker et al., 2014). La création de ces connaissances sur les plantations mixtes de MEL et d'EPN est nécessaire et elle pourrait s'avérer un moyen efficace pour maintenir ou augmenter le rendement des peuplements nordiques en forêt boréale canadienne, mais aussi, pour augmenter la résilience et engendrer d'autres bénéfices pour la biodiversité (Felton et al., 2010; Aussenac et al., 2018).

1.6 Objectifs et perspectives du projet

Cette étude a pour but d'évaluer le potentiel du MEL comme essence améliorant le rendement des peuplements mixtes en combinaison spécifique avec l'EPN à différents moments de leur développement et d'investiguer par quels mécanismes comme la complémentarité des niches, facilitation, réduction de la compétition intraspécifique. Le **chapitre 1** s'est concentré sur l'étude de l'effet d'un gradient de mixité MEL—EPN sur la croissance radiale des deux essences à l'échelle de l'arbre dans des peuplements matures de la région de l'Abitibi. La croissance radiale des deux essences durant les 10 dernières années a été utilisée pour investiguer les processus impliqués dans la compétition intra et interspécifique et de complémentarité des niches de croissance. Nous avons étudié la variation des relations de croissance selon la distance, la taille et l'identité du voisinage avec les indices de voisinage développées par Canham et al. (2004). Nous voulions mesurer l'impact du voisinage de chacune des essences ainsi que leur croissance respective et connaître leur sensibilité à l'effet du voisinage en peuplement mature équien. Dans le **chapitre 2**, des plantations d'EPN monospécifiques et mixtes à 50% de MEL—EPN ont été étudiées afin de savoir si elles présentent des disparités de conditions de croissances. Cette question a été abordée par l’étude des dimensions d’EPN dans des plantations âgées de 8 ans localisées dans la région de l’Abitibi dans le domaine bioclimatique de la sapinière à bouleau blanc. Les mécanismes à l’étude étaient le potentiel du MEL comme outil de contrôle biologique des plantes concurrentes, l’effet de sa litière sur les nutriments du sol et son potentiel hâtif de complémentarité des niches de croissance avec l’EPN. La proximité du MEL pourrait accélérer la fermeture du couvert et son apport annuel de litière au sol pourrait créer un environnement plus favorable pour la croissance des arbres plantés. Nous avons mesuré le volume des gaules d’EPN pour déterminer si des différences de taille étaient observées entre les types de voisinages. Finalement, le **chapitre 3** a porté sur le rendement des peuplements mixtes MEL—EPN de la forêt boréale québécoise dans les domaines bioclimatiques de la pessière à mousses et la sapinière à bouleau blanc. Nous avons utilisé un gradient de mixité allant des peuplements dominés par l’EPN (≤ 90%) à dominés par MEL (≤ 75%) selon les facteurs climatiques et édaphiques. L’étude visait à investiguer s’il existe des proportions optimales entre les deux essences maximisant la surface terrière du peuplement. De plus, nous voulions analyser l’impact de l’augmentation de MEL sur la taille et le nombre de tiges d’EPN. Les données des placettes-échantillons temporaires du ministère des Forêts, de la Faune et des Parcs du Québec ont permis d’aborder ces questions à l’échelle de la forêt boréale du Québec. Dans son ensemble, notre projet vise à poser des bases dans l’exploration des relations de croissance entre l’EPN et le MEL à différentes échelles spatiales et temporelles. Nous avons étudié les relations de croissance à l’échelle de l’arbre en peuplements matures (chapitre 1), en jeunes plantations (chapitre 2) et à l’échelle régionale sur l’ensemble de la forêt commerciale boréale québécoise (chapitre 3).

CHAPITRE 1

Tree size drives growth interactions in mixed mature stands of black spruce (*Picea mariana*) and tamarack (*Larix laricina*)

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Little is known about the growth interactions of black spruce (*Picea mariana*) and tamarack (*Larix laricina*), two important commercial tree species of the Canadian boreal forest. We investigated growth relations between black spruce and tamarack in mature mixed stands. We sampled tree-rings of 223 black spruce and 103 tamaracks to analyze their basal area increment over 10 years. We mapped, identified the species, and measured the diameter at breast height of each neighbouring tree in 112 circular plots of 400 m^2 to analyze basal area increments through spatially explicit models. The model estimating crowding effect of neighbouring tree was adjusted with 4 parameters expressing the effect of distance, size of neighbours, size of target tree and species. Our models suggested that the size of neighbouring trees was the main parameter influencing competition between the studied species. Black spruce basal area increments over 10 years declined up to 22 cm^2 when surrounded by large neighbours. Tamarack basal area increments declined by 48 cm^2 due to competition by large neighbours. However, the overall crowding effect showed that tamarack was more sensitive to competition than black spruce and the intraspecific and interspecific competition had similar effect. Our research provides insight on growth relations between two important commercial species of the Canadian boreal forest.

Keywords: intraspecific competition, interspecific competition, spatially explicit models, boreal forest, growth complementarity

1.1 Introduction

Managing for mixed stands is proposed as an alternative to monocultures due to their potential to provide a better combination of timber production, ecological functions, and other forest ecosystem services (Forrester, 2017; Jonsson et al., 2018). Mixed stands can exhibit over-yielding (Pretzsch & Schütze, 2009; Pretzsch et al., 2015), enhanced growth stability over time (Bauhus et al., 2017; Del Rìo et al., 2017; Aussenac et al., 2018), and increased resistance and resilience to biotic stressors (Hantsch et al., 2014; Poeydebat et al., 2021) compared to single species stands. However, not all species mixtures can improve stand resilience to drought (Grossiord, 2019; Steckel et al., 2020), and some mixtures can lead to a decline in productivity compared to monospecific stands (Aussenac et al., 2017). Therefore, identifying compatible species combinations is crucial for the sustainable management of forests (Coll et al., 2018).

Environmental conditions strongly dictate stand productivity, but competition for resources and growing space can also be a major driver of individual tree growth (Aakala et al., 2013; Aussenac et al., 2017; Ma et al., 2019). Moreover, both processes are interrelated, and the interaction between two or more species can vary along environmental gradients, even ranging from negative (competition) to positive (facilitation) interactions depending on the characteristics of the environment and the tree neighborhood (Maestre et al., 2009; Fichtner et al., 2017). Competition for light, soil nutrients and space can be intense in monospecific stands and reduce individual tree growth (Forrester et al., 2006; Pretzsch et al., 2013). Species mixtures can reduce the competition for resources and space or facilitate the growth of one or both species (Klein et al., 2016; Ratcliffe et al., 2015). These interactions arise mainly through the reduction of abiotic stress and/or an increase availability of a limiting resource (McIntire & Fajardo, 2014; Klein et al., 2016). Trees species with marked physiologic differences and able to grow in the same environment are often the best candidates for positive growth interactions (Fichtner et al., 2017).

Moreover, growth interactions are a continuous long-term mechanism, and their outcome is highly dependent on the defined time frame (Del Rìo et al., 2013; Forrester, 2017). Intraspecific and interspecific interactions with neighbouring trees are modulated by their relative abundance and their spatial pattern (Silander & Pacala, 1985; Wagner & Radosevich, 1991; Stoll & Newbery, 2005). Investigating the growth interaction at the tree level is key since facilitation and competition processes can occur at small spatial scale. The outcome of the interaction can rapidly change within each stand where competition intensity varies (Fichtner et al., 2017). Furthermore, the individual tree growing space changes over time, notably with stand self-thinning and artificial thinning through harvest (Kenkel et al., 1997; Harper et al., 2005). Variations in the competition relations between trees through stand development complexify management decisions.

Spatially explicit growth models at the tree level can quantify the competitive interactions between subject trees and their neighbours and have proven useful in studying growth interactions (Canham et al., 2006; Coates et al., 2009; Larocque, 2018). Spatially explicit models are based on competition indices, which are a robust and flexible way to understand how growth is affected by neighbours' position, distance, height, species, and size (Porté & Bartelink, 2002; Canham et al., 2006). These models based on individual tree growth can provide managers with key information for adapting silviculture and increase management sustainability (Liu et al., 2011; Goetz et al., 2012; Zhou et al., 2013).

In Canada's boreal forest, tamarack (*Larix laricina* [Du Roi] K. Koch) and black spruce (*Picea mariana* [Mill.] B.S.P.) are two species that can grow on thick organic soil, a common soil type. Black spruce is a slow growth evergreen shade tolerant conifer while tamarack is a fast growth deciduous shade intolerant conifer (Strong and Roi 1983). Furthermore, tamarack growth is more sensitive to environmental changes than black spruce (Stelling et al., 2023). Deciduous and evergreen have different responses to competition because of difference in resources translocation and management within the plant itself during the growing season (Fichtner et al. 2017; Li et al., 2022), thus highlighting some of their physiologic differences. These fundamental physiological differences increase the chance of exhibiting growth complementarity (Burns & Honkala, 1990; Fichtner et al. 2017). It is important to investigate mixed stand growth interactions in the boreal forest where the productivity is very variable (Beaudoin et al., 2014). However, information about the growth interactions between these two important commercial species is critically lacking.

Thus, we studied the growth interactions between tamarack and black spruce in boreal eastern Canada. Our objective was to investigate the effects of competitive interactions between the two species on tree basal area increment along a gradient of mixture in the boreal forest. We studied four mature mixed stands exclusively composed of black spruce and/or tamarack established on organic soils in the boreal forest of Québec, Canada. We hypothesized that (1) Interspecific competition will be asymmetric where black spruce will exert more competition (2) Intraspecific competition effect of black spruce will be higher than competition from tamarack (3) Black spruce basal area increment over 10 years will be less sensitive to crowding than tamarack basal area increment (4) Distance from neighbouring trees will not impact basal area increment over 10 years for both species.

1.2 Materials and Methods

1.2.1 Study sites and sampling design

The experimental sites are located within the northwestern boreal forest of Québec (Canada) between latitudes 49°00’65” N and 48°47’40” N, and longitudes 79°14’36” W and 79°03’54” W. This region belongs to the black spruce–feathermoss bioclimatic domain, within the Claybelt of northwestern Quebec (Saucier et al., 2009). Topography is flat and soils are mainly composed of fine clay deposits due to the sedimentation of proglacial Lake Barlow-Ojibway (Vincent & Hardy, 1977). The region is dominated by poorly drained soils and organic matter accumulation associated with paludification from low decomposition rate and high sphagnum growth (Fenton et al., 2005). The average annual precipitation is 909 mm, mean temperature is 0.0 ºC at the closest weather station (48º47’00” N; 79º13’00” W) and mean growing degree days vary between 1200 and 1400 (Environment Canada, 2021). Fire is the main natural disturbance, followed by defoliating insect outbreaks, mainly the eastern spruce budworm (*Choristoneura fumiferana* Clemences).

In the study region, the most common tree species are black spruce, white birch (*Betula papyrifera* Marsh), trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), tamarack, and jack pine (*Pinus banksiana* Lamb.). We sampled two stands where black spruce was the dominant species (named *St-Helene* [48° 47' 54" N; -79° 14' 10" W] [~ 40 ha] and *RYAM* [48° 48' 31" N; -79° 14' 13" W] [~ 15 ha]) and two where tamarack was dominant (named *Beaucanton* [49° 0' 36" N; -79° 9' 22" W] [~ 2.1 ha] and *Turgeon* [49° 0' 36" N; -79° 3' 55" W] [~ 9 ha]) based on basal area (Table 1.1). The stand selection was based on three criteria: (i) they had to be mature forests and even-aged stands with exclusive presence of black spruce and tamarack in the canopy; (ii) established on organic soil deposits (40 cm + organic layer); and (iii) have a canopy closure > 60% (Table 1.1) based on several studies showing a peak in growth interactions following the canopy closure (Angelstam & Kuuluvainen, 2004; Shorohova et al., 2009; Jucker et al., 2020). These criteria in stand selection and the geographic proximity implies little environmental and climatic variation between stands. Data for the number of years since fire and canopy closure were obtained from the most recent governmental forest inventory (Ministère des Forêts, de la Faune et des Parcs, 2020). Two stands were burned in a fire in 1775. Based on tree ages 76 to 114 years, we can assume that they were harvested around 1900. General information about each stand is presented in Table 1.1.

One hundred and twelve circular plots (11.28 m radius) were randomly distributed in the four stands. In each plot, we mapped all trees, measured their diameter at breast height (dbh, 1.3 m) and noted their species. Black spruce represented 71% of the 8209 mapped trees, with the remaining being exclusively tamarack (29%, 2380 trees), while other species presence was anecdotic (0.53% of neighbours). The azimuth of each tree relative to magnetic north was measured with a compass in the plot centre. We used a Vertex III digital hypsometer (Haglöf, Langsele, Sweden) at height 1.3 m with a precision of 0.1 m to measure the distance of each tree to the plot centre. The relative positions between trees were calculated using the distance to the plot centre and azimuth using trigonometric relations. In each plot, we selected one to three dominant or codominant target trees located near the centre to be considered as target trees. Target trees had to be devoid of visible damages to the stem and crown. Target trees (n = 326) were black spruce (n = 223) and tamarack (n = 103). We took two increment cores at orthogonal angles at breast height on each target tree with a Pressler's borer and measured their height with the Vertex III digital hypsometer. A total of 652 increment cores were collected for radial growth analyses. Radial growth was measured for each increment core with a VELMEX UniSlide measuring system (Velmex Inc., Bloomfield, New York) with the accuracy of 0.001 mm. As the response was variable at the tree level, cumulative basal area increment (BAI) [cm^2 $years^{-1}$] over 10 years (2008 to 2017) was calculated using the R package "dplr" (Bunn, 2008). We used BAI over ten years to capture a sufficient period of growth interactions to average annual fluctuations of climatic conditions. Using the basal area rather than annual ring width reduced bias, as it is more closely related to volume growth (Biondi & Qeadan, 2008).

Table 1.1. Location and dendrometric description of each sampled stand used to study the growth interactions between black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in boreal eastern Canada. dbh = diameter at breast height (1.3 m); BA = basal area; mean proportion of tamarack % (mean number of stem). Values are presented as mean ± SD.

Stand name	Canopy closure (%)	Stem ha^{-1}	Number of target trees (N)	Target tree dbh (cm)	Mean BA (m^2 ha^{-1})	Mean proportion of tamarack (%)	Black spruce		Tamarack	
							Age (year)	Target tree height (m)	Age (year)	Target tree height (m)
St-Helene	75 to 85	1852 ± 292	154	17.9 ± 3.8	14.9 ± 10.1	21.5	98 ± 16	15.4 ± 1.9	76 ± 16	19.3 ± 2.6
Beaucanton	65	2372 ± 392	21	15.4 ± 3.4	19.2 ± 8.5	52.9	95 ± 5	12.1 ± 1.9	79 ± 23	15.1 ± 3.0
Turgeon	60 to 79	1757 ± 392	10	17.0 ± 4.7	13.9 ± 8.5	63.7	57 ± 2	11.2 ± 1.2	52 ± 7	16.6 ± 3.2
RYAM	85	1345 ± 197	141	19.2 ± 3.0	17.8 ± 9.2	31.3	65 ± 11	17.3 ± 1.5	79 ± 4	19.0 ± 1.8

1.2.2 Neighbourhood competition analysis

We conducted a spatially explicit analysis of neighbourhood competition based on the approach of Canham et al. (2004) and Canham & Uriarte (2006), which has demonstrated its parsimony, efficacy, and adaptability to a wide range of forest ecosystems (Uriarte et al., 2004; Canham et al., 2006). Furthermore, the formulation of Canham et al. (2006) does not assume certain functional forms or prior relationships between each of the previously mentioned components and growth. The full model expresses the cumulative BAI over 10 years (YBAI) of target trees as a function of potential basal area increment (PBAI), and crowding by neighbours (Crowding effect, spatially explicit) [Eq. 1]. We used BAI as a response variable because it incorporates the size effect on growth, as opposed to one-dimensional radial growth. The PBAI corresponds to the growth of a hypothetical “free-growing” tree (i.e., the optimal growth of the target tree when competition is minimal) when crowding effect is at its lowest (Eq.1) [Canham et al., 2006]. The PBAI is expressed in cm² 10 years^{-1}, and it is a parameter estimated by the model based on observed growth (Coates et al., 2009). This potential growth is then multiplied by one scalar that represents the various competition factors that can constrain growth, and its values are ranging from 0 to 1.

$$YBAI = PBAI \times Crowding\ effect \qquad \text{Eq. 1}$$

The crowding effect is defined as a negative exponential equation (Eq. 2)

$$Crowding\ effect = \exp\left[-\mathrm{C} * (\mathrm{NCI})^{D}\right] \qquad \text{Eq. 2}$$

where *C* controls the sensitivity of the neighbourhood competition index effect (NCI) and parameter *D* controls the magnitude of the effect. In turn, the *C* parameter can depend on target tree size (Eq. 3)

$$C = \left(\frac{Cprim}{100}\right) * target\ dbh^{\mathrm{Y}} \qquad \text{Eq. 3}$$

where gamma (γ) and *Cprim* informs on the sensitivity of crowding effect for target tree size. When γ values are below zero, the crowding impact on growth declines as the dbh of the target tree increases. High values for the *Cprim* express higher crowding sensitivity of the species regardless of it size. The formulation of Eq. 3 assesses the sensitivity of target tree size to competition and consider the growth rate difference between small and large target tree subject to the same competitive environment.

We characterized the neighbourhood of each target tree via the neighbourhood competition index (*NCI*) developed by Canham et al. (2004) to quantify the competition pressure exerted on target trees (Eq. 4)

$$NCI = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_{i,z} \frac{\left(DBH_{ij}\right)^{\alpha}}{(distance_{ij})^{\beta}} \qquad \text{Eq. 4}$$

where *j*= 1, …, *n* neighbour tree of *i* = 1, …, *s* species on target tree *z,* and alpha (α) and beta (β) are parameters estimated by the analyses and modulate the shape of neighbour size and distance, respectively.

When the α parameter is around 1, the effect of the neighbours is proportional to their size. A value of zero indicates no effect as a result of neighbour size on competition. α values > 2 evidence a disproportionate effect of size on the *NCI* (Canham et al., 2006). The β parameter regulates the effect of distance from neighbouring trees on a given target tree. Values of β ~ 0.5 indicate that the competitive effect declines as a square root of the distance (Canham et al., 2006). In our study, the longest distance measured between neighbours and target trees was 11.24 m (plot radius). The λ parameter is a per capita competition coefficient that ranges from 0 (no competition) to 1 (high competition) and quantifies differences between species in their competitive effect on a target tree.

To further investigate the competition relationships and the species interactions, we calculated Hegyi competition index (Hegyi, 1974) [Eq. 5] and the neighbouring species contributions to the plot basal area.

$$Hegyi\ competition\ index\ = \sum_{j=1\ j\neq i}^{n} \frac{d_j}{d_i L_{ij}} \qquad \text{Eq.5}$$

where d_j and d_i are respectively the diameters of neighbouring competitors and target trees and L_{ij} is the distance between neighbouring and target trees. The Hegyi competition index effect on BAI was calculated with the neighbouring species basal area on each plot and compared through graphical interpretation.

1.2.3 Estimation of model parameter

Competition models defined in Eq. 2, 3, 4 were adjusted with maximum likelihood methods (Canham & Uriarte, 2006) using the *anneal* function in the "likelihood" package (Murphy, 2015) within the R program (R Core Development Team, 2022). To assess the strength of parameter estimates by maximum likelihood, we used asymptotic two-unit support intervals (Edwards, 1992). The two-unit support interval is comparable to a 95% support limit employing a likelihood ratio test (Burnham & Anderson, 2002). A regression slope between observed BAI and predicted BAI was used to measure bias (an unbiased model has a slope of 1). The R2 of the regression was used to measure the goodness-of-fit as the marginal R^2 is the measure of the overall variance explain by the model including the error term (Appendix A, Fig. 1.5). Calculation of the neighbourhood competition was performed with the "neighbourhood" package (Ameztegui, 2020).

We compared the crowding model to a null model (a model that includes no predictors, and therefore predicted growth is the average observed growth) for black spruce and tamarack using the second-order Akaike information criterion corrected for small sample size (AIC_c) [Akaike, 1971]. We also test the variance of BAI over 10 years correlated with the crowding model with ANOVA. Normality of residuals was verified visually to ensure they met model assumptions. The bias of the models was investigated by the slopes of predicted vs. observed BAI.

1.3 Results

The black spruce crowding model explained 42.4 % (Marginal R^2) of BAI over 10 years and the tamarack crowding model explained 65.9 % of BAI over 10 years (Appendix B; Table 1.3). Thus, both crowding models explained a high proportion of the variation of BAI over 10 years. The bias was minimal as investigated between predicted and observed BAI and it was strongly correlated for each model (Appendix A; Fig. 1.5). However, for black spruce, models tended to underestimate large BAI values, which was not the case for tamarack (Appendix A; Fig. 1.5).

1.3.1 Species effect

The crowding models estimated the species effect through λ values, and they were close to 1, expressing a similar and strong negative effect of intraspecific and interspecific competition (Table 1.2; Fig. 1.1A and 1.1B). The λ estimate for black spruce in the tamarack crowding model was higher ($\lambda BS = 0.993$; $\lambda TA = 0.751$), which suggests a larger influence of interspecific competition on tamarack (Fig. 1.1B).

Table 1.2 : Parameter estimates for black spruce (*Picea mariana* [Mill.] B.S.P.) and tamarack (*Larix laricina* [Du Roi] K. Koch) basal area increment over 10 years for each model and their potential basal area increment (PBAI) in boreal stands of eastern Canada. Parameter estimates are separated for the crowding effect (lambda black spruce [λBS], lambda tamarack [λTA], beta [β], alpha [α]. Theses parameters are scaling the effects of inter and intraspecific competition, distance and size respectively on NCI (Eq.4). *Cprim* parameter [CP], gamma [γ] scaling C parameter effect on NCI (Eq.3) and *D* parameter [D] determine the sensitivity to NCI in the crowding effect (Eq. 2).

Parameter estimates	PBAI (cm² 10 years^{-1})	Crowding						
		λ BS	λ TA	β	α	CP	γ	D
Black spruce BAI~Crowding	58.4	0.996	0.979	0.08	3.74	304.3	-2.25	0.35
Tamarack BAI~Crowding	186.7	0.993	0.751	0.49	1.81	494.4	-1.91	0.55

However, when we isolated the species effect of black spruce and tamarack on PBAI over 10 years in each model, they had no effects on PBAI (Fig. not shown). When examining the confidence intervals (CI = 95%) for each species, they were overlapping, suggesting no differences in species competitive effect (Fig. 1.1).

Overall, black spruce seemed to be consistently a stronger competitor than tamarack, with higher λ and fewer variations in the λ estimates than the tamarack effect (Table 1.4, Appendix B; Fig. 1.1A and 1.1B). Furthermore, black spruce did not differently perceive the intra and interspecific competition (Fig. 1.1A), but neighbouring species identity had no effect on black spruce PBAI (Fig. not shown).

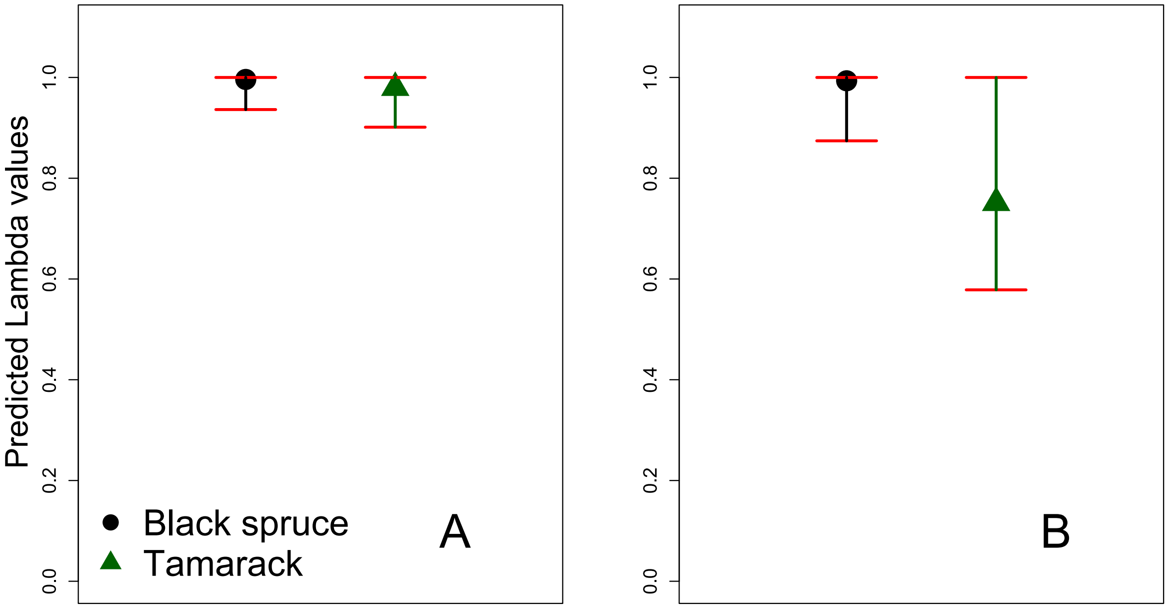

Figure 1.1 : Predicted lambda values for neighbouring species (black spruce, *Picea mariana* [Mill.] B.S.P. and tamarack, *Larix laricina* [Du Roi] K. Koch) for each models A) black spruce crowding; B) tamarack crowding models in boreal stands of eastern Canada. Circles represent the effect of black spruce neighbours on target trees; triangle represents the effect of tamarack neighbours on target trees. Data are shown as model-averaged predictions and 95% CI.

Competition based on Hegyi's equation was negatively correlated with the basal area increment over 10 years for both species (Fig. 1.2). Tamarack's BAI was more sensitive and more strongly correlated to competition ($R^2 = 0.608$, $p < 0.001$) than black spruce's BAI ($R^2 = 0.256$, $p < 0.001$) (Fig. 1.2). Black spruce is the species mainly responsible for high competition values (Hegyi's > 15), the black spruce BAI was mainly impacted by intraspecific competition, as the size of each point is modulated by black spruce basal area around target tree (Fig. 1.2). We observed no particular pattern between competition based on Hegyi and the species competition on tamarack BAI over 10 years (Fig. 1.2).

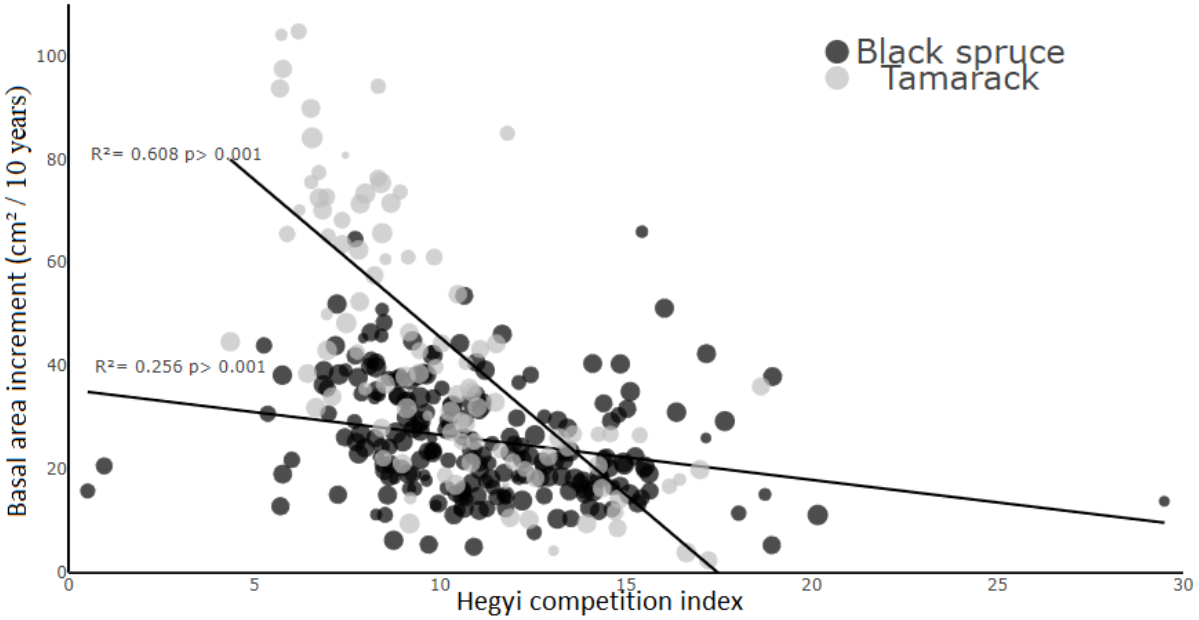

Figure 1.2: Basal area increments over 10 years of black spruce (*Picea mariana* [Mill.] B.S.P.) and tamarack (*Larix laricina* [Du Roi] K. Koch) as a function of Hegyi values in boreal stands of eastern Canada. The size of the points is modulated by the black spruce basal area on each plot. Each line shows the linear correlation between the basal area increment and the Hegyi values for black spruce (black) and tamarack (grey). R² is the square of the correlation between the basal area increment and the Hegyi values.

The dbh of neighbours had a linear, negative effect on potential growth (PBAI) for both species. Trees surrounded by the largest neighbours (dbh ~ 45 cm) exhibited about half the growth of trees surrounded by the smallest neighbours (dbh ~ 9 cm) [Fig. 1.3]. Black spruce PBAI was more sensitive to the size of the neighbours (Fig. 1.3) than tamarack (Fig. 1.3), as indicated by parameter α (3.74 for black spruce vs. 1.81 for tamarack; Table 1.2).

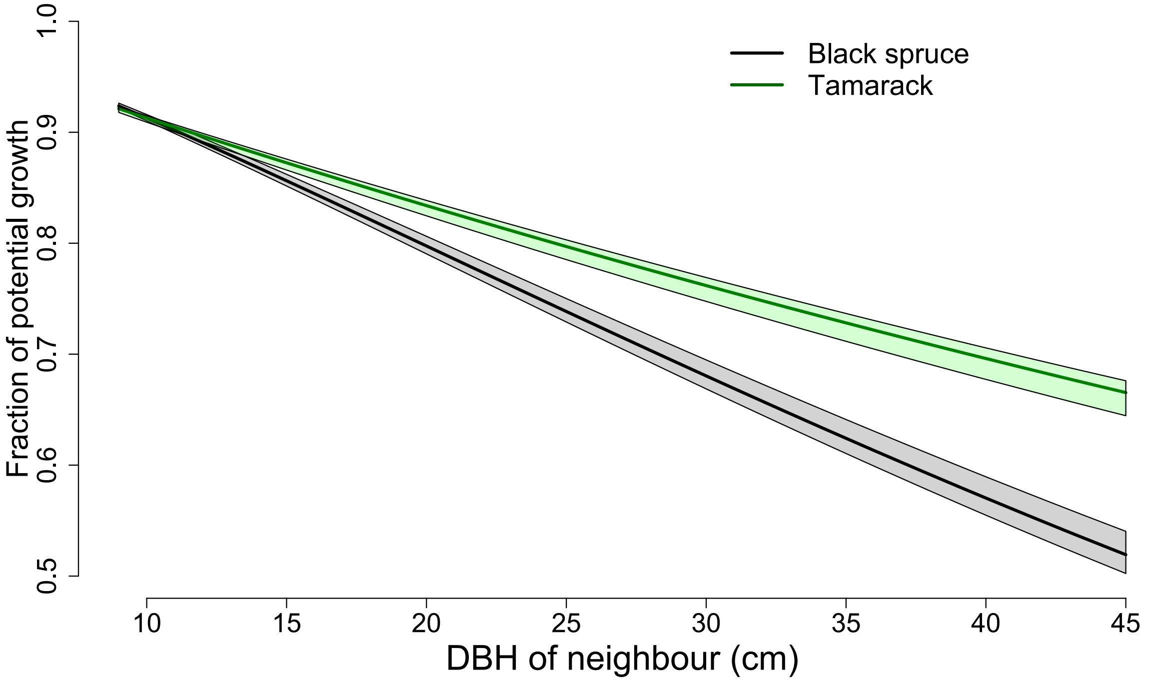

Figure 1.3: Fraction of potential growth as a function of the neighbour diameter at breast height (dbh; 1.3 m) for each model black spruce (*Picea mariana* [Mill.] B.S.P.) crowding (black); tamarack (*Larix laricina* [Du Roi] K. Koch) crowding models (green) in boreal stands of eastern Canada. We used alpha parameter predictions to produce these figures and their 95% CI and model-averaged predictions for all other parameters in the equations.

The effect of neighbour's size was strong and negative for black spruce BAI, for which the decline was 22 cm² 10 years^{-1} (40 % decline) when neighboured by large trees. The relative growth decline for tamarack was lower than black spruce because of growth rate difference (27.7% decline). However, the potential growth decline for tamarack was higher estimated at 48 cm² 10 years^{-1} as the dbh of neighbouring trees increase (Fig.1.3). Even if black spruce was more sensitive to neighbouring dbh, the absolute potential growth decline is higher for tamarack because of its higher growth rate.

1.3.2 Target tree size effect

Both species growth sensitive to crowding thus affected by target tree size through logarithmic relation (Fig. 1.4). The growth was at the lowest when target tree was small sized (Fig. 1.4). Both species small target trees (dbh = 9 cm) were more sensitive to crowding and expressing 40 % of their potential growth as predicted by the gamma parameter (black spruce γ = - 2.25; tamarack γ = - 1.91) [Fig. 1.4; Table 1.2]. This sensitivity to crowding declined rapidly between dbh 9 to 20 cm and then plateaued at higher dbh (20 to 39 cm) [Fig. 1.4]. As the dbh of target tree increase to ≥ 25 cm, black spruce growth was less sensitive to crowding than tamarack (Fig. 1.4). At maximum observed dbh (~ 39 cm), tamarack was still more sensitive to crowding than black spruce, recovered 95 % of its potential growth from crowding (Fig. 1.4) compared to 97 % for black spruce (Fig. 1.4).

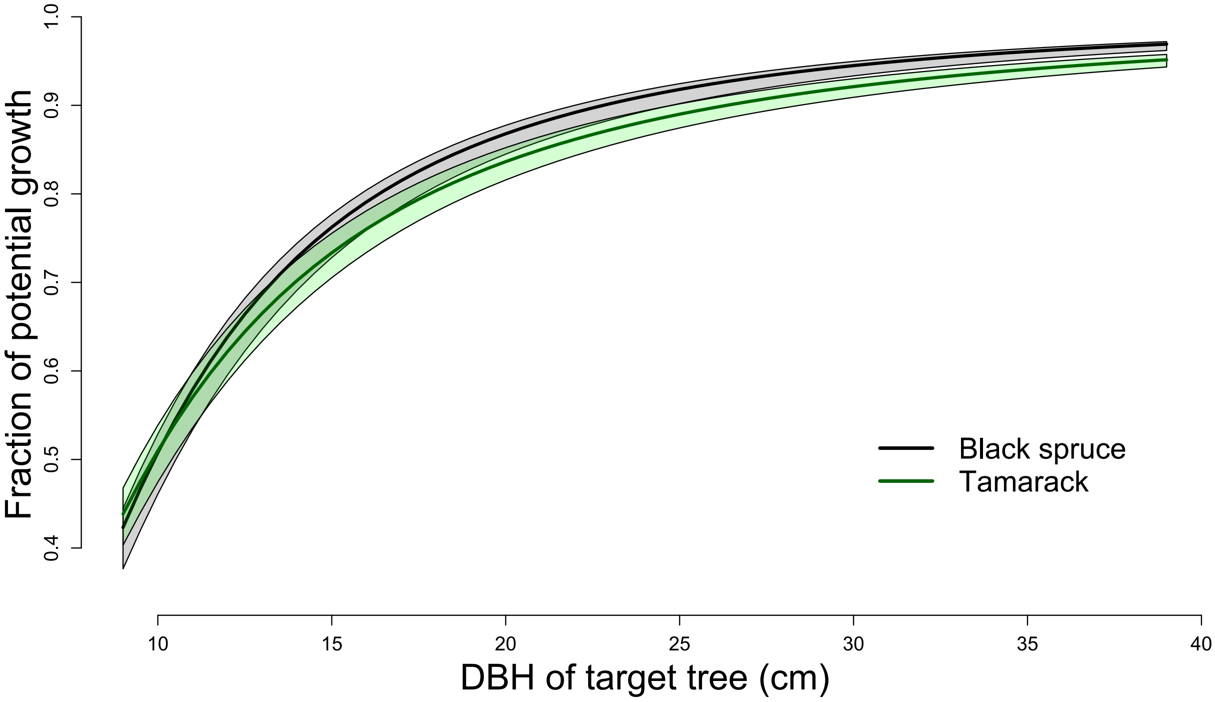

Figure 1.4 : Fraction of potential growth as a function of the diameter at breast height (dbh; 1.3 m) of target trees for each model black spruce (*Picea mariana* [Mill.] B.S.P.) crowding (Black); tamarack (*Larix laricina* [Du Roi] K. Koch) crowding (green) in boreal stands of eastern Canada. We used the gamma parameter predictions to produce these figures and their 95% CI and model-averaged predictions for all other parameters in the equations.

1.3.3 Distance effect

The distance between neighbouring trees and target trees, controlled by the β parameter in the NCI equation (Eq. 4), did not impact BAI over 10 years, as indicated by the low estimated values of the β parameter (close to 0 for spruce and ~ 0.5 for tamarack, Table 1.2). The β value (0.49) for tamarack could have influenced the PBAI, but we tested the effect of neighbour tree distance on PBAI and it did not influenced BAI (figure not shown). This β value (~ 0.5) for tamarack indicated that competition of neighbours declined according to a square root function of distance. For black spruce, the β estimate was low (0.08) which indicated no effect on BAI over 10 years. The small 2-unit support interval for the estimation of β indicates that the model correctly estimated this parameter. The low values corresponded to a true lack of effect on neighbour position, rather than to a poor estimation of the effect (Table 1.3, Appendix B).

1.4 Discussion

Our study is the first to explore growth interactions between black spruce and tamarack in mature stands of the Canadian boreal forest. We wanted to isolate the competitive interactions between trees, and we kept constant the environment and stand structure variability effect on growth. We identified target tree size and neighbouring tree size as the main factors influencing growth interactions. Using the crowding model developed by Canham and Uriarte (2006), we observed variations in basal area increment (BAI) due to competition among trees. Contrary to our initial hypothesis, the impact of interspecific and intraspecific competition on crowding was symmetric and did not significantly affect BAI over a period of 10 years for both species. Intraspecific competition among black spruce was equal to interspecific competition from tamarack, but black spruce competitive effect was consistently higher than that of tamarack based on lambda values. Tamarack was more sensitive to competition than black spruce, except when surrounded by large neighbours (with a diameter at breast height ~ 45 cm). We cannot totally exclude shading effect only on the lack of distance effect on BAI since shading is also part of crowding effect. However, we tested the cardinal direction effect in the crowding model from Boivin et al., (2010) formulation and we did not detect a conclusive effect of the cardinal direction from the model selection. The high shade tolerance of black spruce (Humbert et al., 2007) and the homogeneous vertical structure of the sampled stands likely explain this result. Although tamarack is shade intolerant, we did not detect a shading effect on its growth, which may be attributed to its higher average height compared to black spruce (as shown in Table 1.1) that creates a two-storey stand structure. Finally, the geographic proximity of the sampled stands – within a 25 km – distance reduces the possibility of interactions between growth and climate.

1.4.1 Species effect on competition

Although we did not detect a strong species-specific competitive effect on BAI over 10 years (from either black spruce or tamarack), we observed a tendency for tamarack to exert less competition on surrounding trees. This trend was also apparent for the Hegyi competition index where black spruce intraspecific competition mainly contributed to its growth decline. Chavardès et al. (2022) also observed that black spruce's growth was more impacted by intraspecific than interspecific competition when mixed with jack pine, trembling aspen, balsam fir, or paper birch, whereas balsam fir and black spruce have a strong negative competitive effect on black spruce growth (Oboite & Comeau, 2019). In our case, intraspecific and interspecific competition were similar for black spruce, but they had limited effect on BAI over 10 years. Tamarack was more sensitive to competition than black spruce and equally affected by intraspecific and interspecific competition.

A niche partitioning effect on growth could be significant only at specific proportions of black spruce and tamarack (Justes et al., 2014). Légaré et al. (2004) observed a positive effect of trembling aspen on black spruce size and height. However, this only occurred when aspen represented ≤ 41% of the stand basal area. Légaré et al. (2004) attributed this positive effect on stand growth to an overall strong growth complementarity between trembling aspen and black spruce, but also to a reduction of the intraspecific competition of black spruce. Our sampling effort covered all the mixture gradient from plot dominated by tamarack to dominated by black spruce (> 90% of the total basal area), but there was no monospecific plot of either species. Our sample is representative of regenerated stands on organic soil but does not allow direct comparison with strict monospecific stands. Other growth parameters can be influenced by niche partitioning, such as average growth or the growth baseline (Chavardès et al., 2021). Furthermore, the positive effect of niche partitioning is more likely to occur at a different stage of the stand development (e.g., before the self-thinning stage) [Schupp, 1995]. Niche partitioning between two species can lead to higher stand-level productivity than a monospecific stand (Chavardès et al., 2021). There are growth interactions in mature mixed stand of black spruce and tamarack as seen from the variance of BAI over 10 years explained by the crowding model, However, these growth interactions were less influenced by the species effect than predicted.

There was little height stratification in the canopy between the studied species (Table 1.1) even if black spruce reached lower maximal height compared to tamarack (~15 m vs. ~20 m) [Gower and Richards, 1990]. Height stratification in mixed stands creates a better occupation of the canopy space and can enhance the light interception, thus increasing stand yield (Pretzsch, 2014; Pretzsch & Schütze, 2015; Shanin et al., 2019; Aldea et al., 2021). In mixed stands, a good height stratification and a complementarity in crown morphology increase the possibility of observing less negative growth interactions between species and they are a key feature in niche partitioning optimizing light interception (Pretzsch, 2014; Pretzsch et al., 2020). In our case, the complementarity for height and crown morphology between mature black spruce and tamarack seems good and had neutral effect on BAI. Otherwise, we would have detected a negative distance and higher weight of the cardinal direction effect on BAI over 10 years (Boivin et al. 2010).

1.4.2 Size effect on competition

Both species BAI were negatively impacted by crowding when target tree size was small (dbh 9 to 20 cm). This size effect was higher when the neighbouring trees dbh was > 25 cm. Our results suggest that black spruce potential growth is more impacted than tamarack by larger neighbours. However, the absolute growth decline of tamarack BAI over 10 years attributed to neighbour size was larger because of its higher growth rates than black spruce (Fig. 1.2). Furthermore, as the dbh of target tree increase, the PBAI of tamarack is slower to recover its PBAI than black spruce (Fig. 1.4). This slower recovery from tamarack indicates that black spruce was less sensitive to crowding as their dbh increase. The figure 1.2 illustrates the combined influence of both target tree size and neighbouring tree size effects on growth for each species. These influences of size explained why tamarack is overall more sensitive to crowding than black spruce. The only scenario where black spruce was more impacted by competition than tamarack was when surrounded by large neighbours (dbh ≥ 45 cm). Other studies have shown similar important impact of neighbouring tree size and target tree size on growth (Coates et al., 2009; Baribault & Kobe, 2011). The growth of smaller stems is often more impacted by neighbouring trees than the crowding effect they exert on larger neighbours (Canham et al., 2006). The observed size effect could be associated with the distribution of dbh in the sampled plots, which was mainly comprised of medium to large stems (20 to 35 cm dbh), as well as the stand structure (even-aged), past self-thinning stage and the age (mature). As a result, target trees dbh were > 20 cm, like most of their neighbours, and small stems were underrepresented in the dataset.

1.4.3 Distance effect on competition

The lack of a distance effect was probably a result of the development stage of the sampled stands, which was past the self-thinning stage (Oliver & Larson, 1996). Intermediate and overtopped trees growing close to dominant and codominant trees have already been excluded from stands. The remaining trees have enough space to take their place in the canopy without major growth limitations due to a shading effect. Svetlik et al. (2021) showed that the available area around trees was not a good predictor of the radial growth in mature Norway spruce (*Picea abies* [L.] Karst.) stands. Coates et al. (2009) found comparable results for the distance effect with hybrid spruce trees, such as the complex of white (*Picea glauca* [Moench] Voss), Sitka (*P. sitchensis* [Bong.] Carr.), and Engelmann (*P. engelmannii* Parry ex Engelm.) mixed with multiple shade-intolerant species. However, they were not able to capture the total distance in which the crowding effect occurred for hybrid spruce (> 15 m). The hybrid spruce studied by Coates et al. (2009) have superior maximal size and height than black spruce, and therefore have a larger radius of competitive influence. Based on our β estimates, we can conclude that the effect of distance on crowding was fully captured within 11.24 m for black spruce and tamarack. The mean distance between target trees and their neighbours was high and not variable (7.69 ± 2.49 m), which can explain the lack of distance effect on crowding. Furthermore, the stem density was similar across all studied stands (Table 1.1) because the studied stands are at the same development stage and have the same structure (mature and even-aged). Finally, we also tested the cardinal direction effect of neighbouring trees in the crowding model from Boivin et al. (2010) without detecting an effect on BAI.

1.4.4 Management implications

Our study results indicated that both black spruce and tamarack trees with small diameters at breast height (dbh) of 9 to 20 cm were greatly impacted by crowding. However, larger trees with dbh > 20 cm were less affected by crowding and exerted more competition on smaller trees. Commercial thinning could remove the larger merchantable stems (> 20 cm) of both species to enhance the growth of small stems suppressed by larger neighbours. Furthermore, smaller stems are less vulnerable to windthrow after harvest (Lavoie et al., 2012). We would recommend keeping the species mixture in each harvest stand.

Our results suggest that larger trees, especially black spruce, can be retained after harvest and still exhibit good growth rates. This finding is supported by Thorpe et al. (2007), who observed enhanced growth rates for black spruce after partial harvest in a similar environment in northern Ontario. Our results provide flexibility in management based on stem size, where larger stems could still exhibit good growth rates and smaller stems could benefit from the removal of large neighbors. However, we acknowledge that the size effect needs to be unbiased because partial harvests should focus on removing trees with less potential for growth based on their size (Coates et al., 2009). The size effect on competition can be biased by sampling criteria or other confounding factors interacting with size. Our stand selection criteria give us confidence in the absence of such factors.

We did not detect a strong negative interspecific growth interaction between black spruce and tamarack, suggesting that more mixed stands could be established in the boreal forest. Since tamarack has a superior growth rate than black spruce and black spruce was overall less sensitive to competition, this species mixture shows good potential to observe overyielding in mixed stands compared to monoculture (Pretzsch et al., 2015).

1.5 Conclusion

To our knowledge, our investigation of growth relationship between these two important commercial species of trees in the Canadian boreal forest is the first of its kind. Our competition models explained a large proportion of tree BAI variance for tamarack and black spruce, reflecting the importance of individual tree growth interactions in mature stands of the boreal forest. The main parameter influencing competitive interaction was the size of neighbouring trees and black spruce was less sensitive to competition than tamarack. The intraspecific and interspecific competition effect were limited and similar, suggesting black spruce and tamarack as a good species mixture. These competition results between trees are attributed to the stand state (mature and past self-thinning), thus reducing certain competitive interactions (Angelstam & Kuuluvainen, 2004; Shorohova et al., 2009; Jucker et al., 2020). Our findings should help enhance management of mixed stands based on individual tree growth approaches. Future research on black spruce and tamarack growth relations should test a wider range of site conditions, stand development stages, mixture ratio and environmental conditions.

1.6 Acknowledgements

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1.7 Author contributions

AL and NT acquired funding. SRP, NT and AL conceptualized the project. SRP wrote the original draft. SRP collected data. SRP and AA conducted analyses. AA, NT and AL read, commented and approved the final manuscript.

1.8 Conflicts of Interest

The authors declare that they have no competing interests.

1.9 Appendix A: Goodness-of-fit for selected models

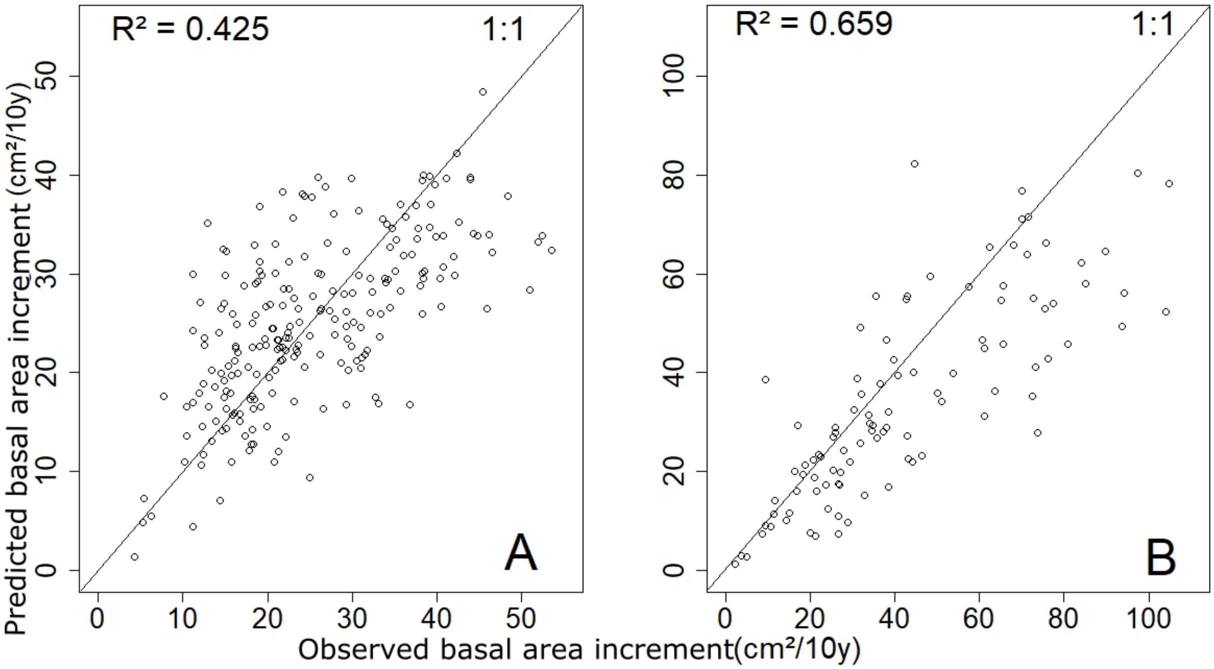

Figure 1.5 : Predicted BAI (cm² 10 years^{-1}) as function of observed BAI (cm² 10 years^{-1}) for each model (black spruce crowding A, and tamarack crowding model B). Model-averaged predictions were used to produce each part of the figure. The diagonal line represents the one-to-one relationship.

1.10 Appendix B: Table 1.3: Tested models explaining BAI; Table 1.4: Minimum and maximum estimate parameters by the crowding model

Table 1.3 : Tested models explaining black spruce (*Picea mariana* [Mill.] B.S.P.) and tamarack (*Larix laricina* [Du Roi] K. Koch) basal area increment over 10 years (BAI) in boreal stands of eastern Canada. K = number of parameters; AIC_c = Akaike's information criterion for small sample size; marginal R^2 = predictive power and p value = ANOVA significance test.

Candidate Models	K	AIC_c	Marginal R^2	p value
Black spruce BAI ~ Crowding	8	1611	0.424	< 0.001
Null model	1	2170	< 0.01	-
Tamarack BAI ~ Crowding	8	901.4	0.659	< 0.001
Null model	1	1273	< 0.01	-

Table 1.4 : Maximum and minimum likelihood parameter estimates for black spruce and tamarack basal area increment over 10 years (BAI) for each model and their potential basal area increment (PBAI). Parameter estimates are separated for the crowding effect (CROW), lambda black spruce (λBS), lambda tamarack (λTA), beta (β), alpha (α), *Cprim* parameter (CP), gamma (γ) and *D* parameter (D)).

Parameter estimates		PBAI (cm² 10 years^{-1})	Crowding						
			λBLS	λTAM	β	α	Cprim	γ	D
Black spruce									
BAI~CROW	Min	56.1	0.936	0.901	0.07	3.7	301.3	-2.28	0.350
	Max	60.2	1	1	0.09	3.78	315.0	-2.20	0.354
Tamarack									
BAI~CROW	Min	173.6	0.874	0.578	0.43	1.79	469.7	-1.95	0.54
	Max	187	1.00	1.00	0.50	1.85	495.0	-1.87	0.56

CHAPITRE 2

Early influences of tamarack (*Larix laricina*) on black spruce (*Picea mariana*) and its immediate environment in plantations

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Mixed plantations are garnering increased attention due to their potential to provide a broader array of benefits compared to monocultures. Although numerous studies have indicated promising complementarity between black spruce (*Picea mariana*) and tamarack (*Larix laricina*), few have delved into individual tree growth interactions to thoroughly assess early growth complementarity. We sampled 119 planted black spruce and their immediate environment to quantify and qualify any differences between two conditions in young plantations: mixed tamarack ("mixtures") and black spruce monocultures ("monocultures") within young plantations. We investigated the effect of neighbouring under four perspectives: tree competition, microenvironment, foliar nutrients, and soil nutrients. Our results showed increased values for black spruce foliar nitrogen total concentration, soil pH and canopy closure in mixtures compared to monocultures. Furthermore, black spruce stem volume was bigger by 38.1% in mixture compared to monoculture. Black spruce stem volume was negatively affected (86% decrease) by the combined effect of shrubs and non-crop trees under high competition pressure, despite the plantation being mechanically released in 2017. Collectively, our results suggest that black spruce growing in mixtures holds a greater growth potential than black spruce in monocultures.

Keywords: mixed plantation, early growth interactions, neighbouring tree effect, boreal forest, non-crop competition

2.1 Introduction

Sustainable forest management encompasses diverse benefits for social, economic, and ecological purposes, achieved in part by using reforestation with multiple tree species and initiating mixed stands (Bolte et al., 2009; Felton et al., 2016). Mixed stands can exhibit an increased resilience and stabilize yields in the face of extreme climate, provide additional protection against insect defoliation and increase biodiversity (Jactel & Brockerhoff 2007; Bielak et al., 2014; Felton et al., 2016). Notably, trees in mixed stands often demonstrate better resource use (soil and light) than in monoculture (Liang et al. 2016, Pretzsch & Schütze, 2016), potentially leading to over-yielding of mixed stands (Zhang et al., 2012; Lu et al., 2016). However, managing mixed stands is more complex than monocultures, requiring more planning for harvesting and adapted machinery (Yilmaz & Akay, 2008). Interactions in multi-species plantations can be complex, and when the mixing ratio, site conditions, and/or tree spacing are sub-optimal, under-yielding can occur (Toïgo et al., 2015; Drossler et al., 2018). Therefore, identifying compatible tree species should be a primary focus of forest management, followed by studying growth relationships to determine adequate species combinations and under which circumstances.

Studying planted trees during early years provides insights on individual growth trajectories and the future productivity of plantations (Bianchi et al., 2021). Positive growth interactions can emerge in the early stages (10-15 years) of mixed plantations, enhancing the growth of one or both species compared to monoculture (Dijkstra et al., 2009; Nord-Larsen & Meilby, 2016). Mixing shade tolerant with shade intolerant species often lead to good growth complementarity and potentially to over-yielding (Cordonnier et al., 2018). However, early positive effects don’t guarantee over-yielding over a whole rotation, as this situation can reverse during subsequent stages of stand development (Drossler et al., 2018). Moreover, interactions between crop trees, shrubs, and non-crop trees can have lasting impacts on individual tree growth and alter stand structure, particularly if the affected crop tree is shade intolerant (Bell & Pitt, 2005).

The Canadian boreal forest is characterized by a cold climate and relatively low productivity (Saucier et al. 2015), but also serves as the primary source of wood fibre for the forest industry (Beaudoin et al., 2014). Multiple actions are needed to ensure plantation productivity in the boreal forest, such as mechanical release of competing vegetation (Wiensczyk et al., 2011), and mixed plantations could help ensure productivity, through better space and resources acquisitions (Forrester, 2014; Pretzsch, 2014). The selection of compatible species should be based on different shade tolerance, resource requirements and root system depth, as well as compatible crown architecture (Pretzsch, 2014; Coll et al., 2018).

Furthermore, growth compatibility between species could be modulated by site conditions such as water and/or nutrient availability (Laganière et al., 2015; Toïgo et al., 2015). Diversifying the species chosen for reforestation in the boreal forest could possibly enhance plantation productivity (Thiffault et al., 2010). Currently, spruces dominate reforestation in Canada, constituting 44.3% of all planted species (CCFM, 2020). In the boreal forest, black spruce (*Picea mariana* [Mill.] B.S.P.) is the most used spruce species in plantations. In contrast, tamarack (*Larix laricina* [Du Roi] K. Koch) is a marginal species in reforestation programs, accounting for only 1.5% of planted trees nationwide (CCFM, 2020). Yet numerous studies highlight physiological complementarity between black spruce and tamarack (Islam & Macdonald, 2004; Boyden et al., 2009). Tamarack is a fast-growing, shade-intolerant and deciduous conifer, while black spruce is a slow-growing, shade-tolerant evergreen conifer (Strong & Roi, 1983). The annual litter input from tamarack is rich in nitrogen which could benefit soil fertility (Moore et al., 2010). This annual litter input can change soil macronutrient content, microbial communities, and pH (Dijkstra et al., 2009; Prescott & Grayston, 2013), potentially enhancing neighbouring tree growth and overall stand yield by increasing macronutrient availability (Forrester et al., 2006; Laganière et al., 2017). Only a few studies have reported about the early growth relations between tamarack and black spruce (Boyden et al., 2009). Assessing the microenvironment is valuable to untangle the effects of shrubs, soil composition and neighbouring species on crop tree growth (Baraloto et al., 2005). Furthermore, examining tree leaf nutritional status is useful to better predict crop tree long-term growth trajectory (Alva et al., 2006).

Our objective was to compare the neighbouring effects of tamarack and black spruce on soil characteristics (macronutrient concentration and pH), competing vegetation, and the stem volume of black spruce, eight years after planting in the Canadian boreal forest. Our specific aims were to (1) detect differences in microenvironment associated with the neighbouring of tamarack or black spruce, (2) assess the effects of neighbouring crop tree species and competing vegetation on black spruce dimensions after 8 years, (3) identify potential changes in early canopy closure driven by tamarack and black spruce neighbours, and (4) investigate the influence of neighbouring species effect on soil and black spruce foliar nutrient concentrations. We hypothesized that the presence of tamarack as a neighbouring species would significantly alter soil macronutrient concentrations and pH levels, compared to areas dominated exclusively by black spruce. We anticipated that the stem volume of black spruce would be differently influenced by the proximity of tamarack versus black spruce, owing to variations in their microenvironmental effects. We predicted that early canopy closure will be distinctly affected by tamarack and black spruce, potentially leading to varied competitive dynamics among plant species. Finally, we expected that the neighbouring species, be it tamarack or black spruce, would have a measurable yet distinct impact on both soil and foliar nutrient concentrations in black spruce.

2.2 Materials and methods

2.2.1 Site description and experimental design

The experimental site was in the Lake Duparquet Research and Teaching Forest (LDRTF) in the northwestern boreal forest of Québec, Canada (48º29’7” N – 48º29’5” N; 79º25’5” W – 79º26’0” W), within the balsam fir (*Abies balsamea* (L.) Mill.) – white birch (*Betula papyrifera* Marsh) bioclimatic domain (Saucier et al., 2009). This region is known for extensive clay deposits left by the proglacial Lake Barlow-Ojibway (Vincent & Hardy, 1977). The climate is cold and continental with average temperatures of 0 °C and mean annual precipitation of 900 mm (Environment Canada, 2019). The tree species dominating early succession are trembling aspen (*Populus tremuloides* Michx.), white birch, and jack pine (*Pinus banksiana* Lamb.). Late successional stands are typically dominated by balsam fir, white spruce (*Picea glauca* [Moench] Voss), black spruce, and eastern white cedar (*Thuja occidentalis* L.) (Bergeron, 2000). The understory composition is generally characterized by ericaceous shrubs (Thiffault et al., 2015), along with species such as *Gaultheria hispidula*, *Coptis groenlandica*, *Cornus canadensis*, and *Dryopteris spinulosa* depending on soil fertility and overstory dominance (Légaré et al., 2001). Soils in this area are generally classified as Luvisols that originated from silty clay deposits from proglacial Lakes Barlow and Ojibway, with a mor humus layer ranging from 0 to 50 cm in thickness. In natural stands of this region, tamarack and black spruce usually co-occur on peatlands or on thick organic soils with complex drainage (Perala, 1971; Viereck et al., 1990).

The site was clearcut during the winter of 2011–2012. In spring 2013, the site was mechanically prepared using a double-pass forest harrow. The experimental design included two blocks, each measuring 5000 m² (100 m × 50 m). The blocks were divided into two different treatments: black spruce monospecific and 50/50 mixture covering 2500 m² (50 m × 50 m) each. All treatments were established with a density of 2500 stems/ha, with seedlings planted at an approximate spacing of 2 m x 2 m. The mixed plantation treatment involved alternating rows of planted tamarack and black spruce (Fig. 2.1). This design allowed us to investigate the effects of neighbouring tree species and competing vegetation on black spruce growth.

In 2017, the plantation underwent mechanical vegetation control using motor-manual brushsaws to remove competing vegetation, leaving only black spruce and tamarack. At the time of sampling, the competing vegetation had resprouted and was primarily composed of willow (*Salix* spp.), pin cherry (*Prunus pennsylvanica* L.f.), trembling aspen and red raspberry (*Rubus idaeus* L.).

2.2.2 Tree measurements

In June and July 2021 (8 years after planting), we selected 121 planted black spruce as target trees, 69 neighboured only by other black spruce saplings and 52 neighboured by tamarack and black spruce sapling (Fig. 2.1). The target trees were randomly distributed across all experimental units, irrespective of the treatment applied (Fig. 2.1). Our selection criteria focused on height (equal or superior to other crop tree height), absence of scars or injuries, and overall healthy foliage excluding chlorotic trees. This approach aimed to target the trees most likely to become dominant or codominant in the future (Jobidon, 2000). To assess the neighbouring tree effects, we established 40 m² circular plots (radius = 3.57 m) centred on each target black spruce tree. Within these plots, we recorded and measured all planted trees present (Fig 2.1). In the mixed planting environment, this allowed us to investigate the effect of neighbouring trees at a ratio of 2 black spruce trees for 6 tamarack trees, as the plot is centred on target black spruce (Fig. 2.1, Table 5).

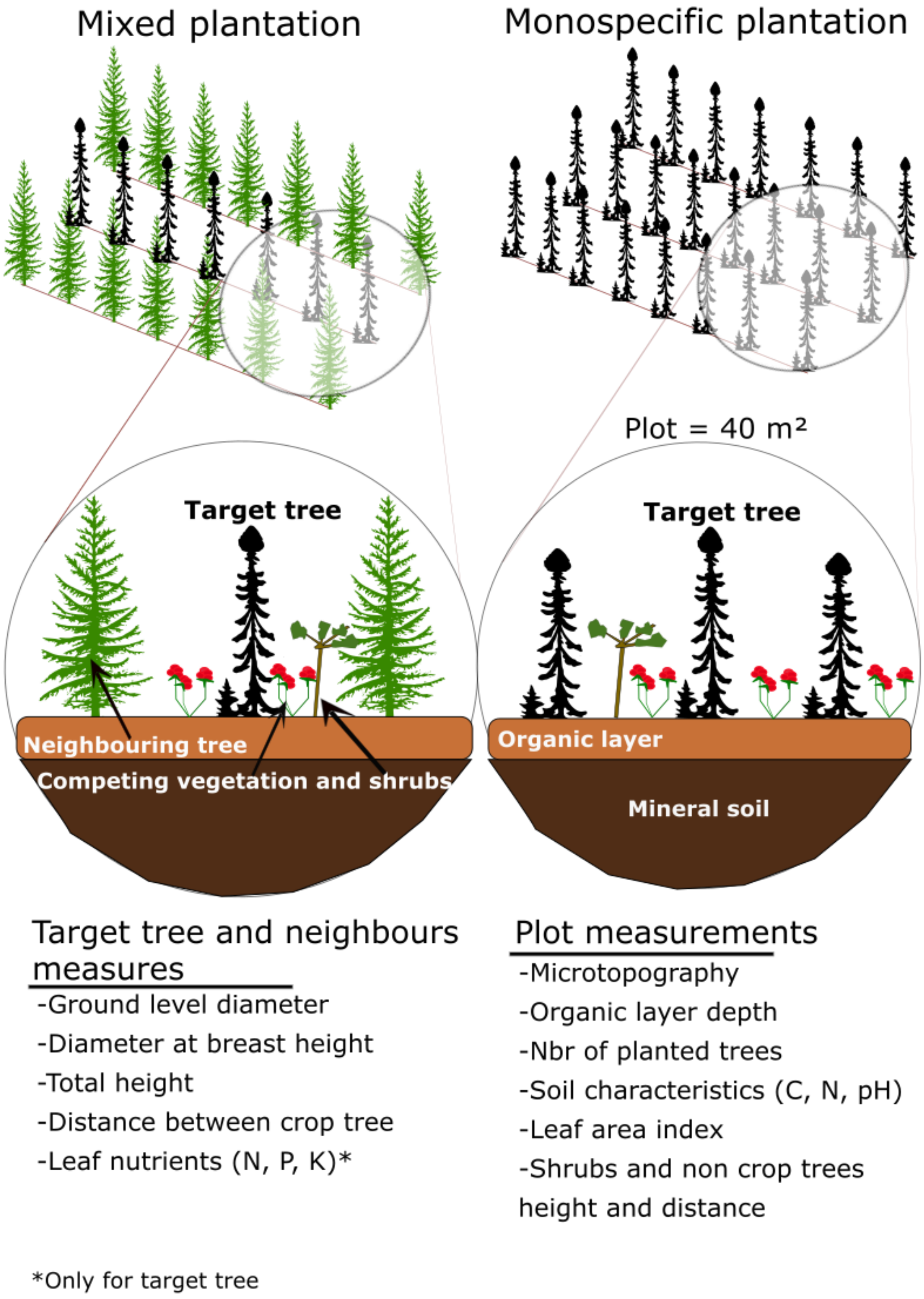

Figure 2.1: Schematic representation of the plantation design in pure and mixed plots, with the list of variables assessed.

Target trees and neighbouring crop tree competitors were measured for total height, ground-level diameter (GLD), and diameter at breast height (DBH, measured at 130 cm above the ground level) (Table 2.1). All target trees had a height greater than 1.3 m; we therefore calculated stem volume index during the 8th growing year as:

$$Vol_8 = \frac{13\,\pi}{1200} \times (GLD^2 + GLD \times DBH + DBH^2) + \frac{\pi(DBH)^2(H-130)}{12000} \qquad \text{Eq. 1}$$

where Vol_8 is the stem volume index (dm^3) based on the volume of a cylinder from 0 m to 1.3 m in height and the volume of a cone from 1.3 m up, GLD, DBH and total tree height (H) are all measured in centimetres.

Table 2.1 : Plot characteristics as a function of competing neighbours (black spruce or tamarack). DBH = diameter at breast height (130 cm), GLD = ground-level diameter, BA = basal area, LAI = leaf area index, ATT = above target tree, BCNT = between closest neighbouring tree. Values are presented as mean ± standard deviation.

Soil characteristics	**Black spruce neighbour**	**Tamarack neighbour**
Organic layer depth (cm)	8.7 ± 5.8	9.2 ± 4.9
C/N mineral	15.0 ± 2.4	14.7 ± 2.3
C/N organic	27.6 ± 7.4	25.2 ± 7.1
pH mineral	5.00 ± 0.42	5.17 ± 0.62
pH organic	5.52 ± 0.42	5.81 ± 0.59
Plot level characteristics		
Tamarack BA (m^2 / ha)	0.02 ± 0.05	0.80±0.48
Black spruce BA (m^2 / ha)	0.17 ± 0.19	0.003 ± 0.028
LAI ATT	0.15 ± 0.34	0.34 ± 0.32
LAI BCNT	0.79 ± 0.48	1.07 ± 0.45
Number of crop trees	7.5 ± 1.8	6.3 ± 1.8

Black spruce dimensions and foliar nutrition		
DBH (cm)	2.53 ± 0.64	2.47 ± 0.67
GLD (cm)	5.17 ± 0.88	4.91 ± 1.06
Height (cm)	239.1 ± 30.8	241.4 ± 36.3
Stem volume index (dm^3)	35.7 ± 21.6	33.8 ± 23.6
C/N	60.7 ± 5.9	56.7 ± 5.6
Total N (%)	0.86 ± 0.10	0.91 ± 0.09
Total P (%)	2.28 ± 1.72	2.68 ± 1.81
Total K (%)	8.06 ± 6.51	9.14 ± 6.52

2.2.3 Plot characteristics measurements

To determine the leaf area index (LAI) of the canopy in each plot, we captured images with a fisheye camera (CI-110 Plant canopy Imager, CID Bio-Science, Inc. Camas, WA, USA) at the beginning of July 2021, during cloudy days. The first image was taken perpendicular to the ground at mid-height of the target black spruce trees, achieved by bending down the tree. This measurement is referred to as ‘LAI above target tree’. A second image was taken 45 cm above the ground, at the midpoint between the target tree and the neighbouring nearest competitor crop tree. This measurement is referred to as ‘LAI between closest neighbouring tree’. The images were analyzed with CID Bio-Science software (Camas, WA, USA) to compute the LAI. Microtopography at the base of each target tree was classified into three categories: flat, mound, and pit. This visual estimation considers the surrounding microtopography to estimate if the water would accumulate or not at the base of each tree during the snow melt period or after a prolonged rain event.

2.2.4 Soil and leaf sampling and processing

From June 21-25, 2021, we collected soil samples from both organic and mineral layers using a trowel to analyze their C/N ratio and measure their pH. The sampling was conducted 1 m south from each target tree trunk, at a maximum depth of 20 cm as the root system of black spruce is shallow with roots from mature trees rarely exceeding 30 cm depth (Strong & Roi, 1983). If the organic horizon exceeded a thickness of 20 cm, we did not collect mineral soil samples since tree roots are not reaching the mineral soil. The depth of the organic layer was recorded at the sampling location. All samples were frozen within 8 hours. In the lab, soil samples were cleaned of any impurity (stone, root, etc.), air-dried for 2-week, oven-dried at 50 °C for 1 week and sieved on a 2 mm mesh screen. Total C and total N (%) were determined by dry combustion on a LECO CNS 928 (LECO Corporation, St-Joseph, MI, USA). Soil pH was determined using a 1:2 soil:water ratio for mineral soil samples and a 1:10 ratio for organic samples (Fisher Scientific Accumet 50; Denver Instrument, Bohemia, New York).

Between June 20-26, 2021, we collected foliar samples from each target black spruce tree. The samples consisted of 1-year-old twigs (from 2020) located in the upper third of the trees and facing South. After collection, the samples were kept in a cooler and frozen within 8 hours. The foliar samples were dried using the same method as the soil samples. Needles were separated from the twigs and then ground using a Retsch cutting mill SM 200 (Verder scientific, Vleuten, Netherlands) operating at 10,000 rpm. Total N concentration was determined by dry combustion as above; P and K concentrations were measured following the method outlined by Yash (1998) using a Perkin-Elmer Optima 7300DV (PerkinElmer, Inc. Waltham, MA, USA).

2.2.5 Competition indices

We calculated the Hegyi competition index (Hegyi, 1974) to estimate the effects of neighbouring crop tree competitors on target trees as follows:

$$Hegyi\ competition\ index\ = \sum_{j=1\ j\neq i}^{n} \frac{d_j}{d_i L_{ij}} \qquad \text{Eq.2}$$

where d_j and d_i are respectively the diameters of the neighbouring competitors and of target trees, and L_{ij} is the distance between neighbouring competitors and target trees. We considered any planted tree with a height equal to or greater than the target trees and located within a 3.57 m radius as significant neighbouring competitors (White et al., 2014).

We identified and measured the height of all competing woody shrubs and non-crop trees reaching at least two thirds of the height of the target trees and located within a 1.2-meter radius from the target trees (White et al., 2014). We used the sum of competing vegetation angles (Prévosto, 2005) as a competition index to quantify the competition of shrubs and non-crop trees on target trees (Eq. 3). The angles of each shrub and non-crop tree were taken from the base of the target tree to the top of each competing shrubs. This competition index is distance dependent, influenced by the height of competing vegetation, independent from the target tree height, and calculated as:

$$Sum\ of\ competing\ vegetation\ angles = \sum_{j=1\ j\neq i}^{n} \Phi_i \qquad \text{Eq. 3}$$

where Φ_i is th angle from the base of the target tree to the top of each neighbour.

2.2.6 Statistical analysis

2.2.6.1 Supervised forward model selection

We used a supervised forward model selection approach with the linear model function *lm* in the 'stats' package (R Core team Development Team, 2022) [Objective 1]. This analysis allowed us to explore the relationships between the stem volume of black spruce at age 8 and various environmental variables. The variables included in our analysis were the number of crop trees per plot, depth of the organic layer, microtopography, Hegyi competition index and the sum of competing vegetation angles around the target trees. We used the linear model:

$$\mathrm{Vol}^{8th}{}_{k} = \beta_0 + \beta_1(x1) + \dots + \beta k(xk) \qquad \text{Eq. 4}$$

where β is a vector of k fixed effects.

We included a global model and a null model as part of our candidate models to test for the lack of effect of all variables and the null hypothesis, respectively. We checked the homoscedasticity and normality of residuals to ensure that the linear model assumptions were met. We initially used generalized linear model to test the spatial autocorrelation with treatments nested within blocks as random factors, but since these factors did not explain any variance of black spruce stem volume, we excluded them from further analysis and used linear models instead (Bates et al., 2015). With the list of environmental variables (i.e. number of crop trees, depth of the organic layer, microtopography, Hegyi competition index and the sum of competing vegetation angles around the target trees), we conducted the supervised forward model selection based on the Akaike Information Criterion corrected for small samples (*AICc*) (Akaike, 1998) and *ΔAICc* (the difference in *AICc* score from the top model) to determine the inclusion or exclusion of models. The *AICc* score for each model was calculated using the *AICcmodavg* function in the 'AICcmodavg' package (Mazerolle, 2023). The *AICc* threshold value and the model selection process at each step followed the approach of Portier et al. (2016). In the first step, we built univariate models to test each variable individually. We retained each model with a *ΔAICc* < 6 of the first model (Symonds & Moussali, 2011). In the second step, we added a second variable to each selected model and performed *AICc* model selection. If the model with two variables showed a lower *AICc* score of 2 or less compared to the related univariate model, we kept the model with two variables and discarded the univariate model. We repeated the process of adding variables until the model could no longer be improved by additional variables. At the end of this procedure, each model with a *ΔAICc* distance of 2 or more from the best model was considered less parsimonious and discarded (Anderson & Burnham, 2002). Furthermore, each added variable in the model had to be uncorrelated with each other (Pearson coefficient < 0.7) and have a significant effect ($p < 0.05$) on black spruce stem volume to avoid overfitting the model. Finally, we compared the *AICc* of the selected model to a null model to ensure the improvement of the model. The model parameter estimates and unconditional 95% confidence intervals, excluding 0, were considered influential of the 8th-year stem volume of black spruce. The QR decomposition matrix was used to estimate the parameters for each model and the adjusted R^2 was calculated with the ‘performance’ package (Lüdecke et al., 2021).

2.2.6.2 Neighbouring species impact on black spruce volume

To evaluate the neighbouring species effect of tamarack and black spruce [Objective 2], we included the neighbouring species as a factor (black spruce or tamarack) into the best model selected from the supervised forward model selection for predicting the 8th-year stem volume of black spruce. We then compared the best model with and without the neighbouring species effect to examine its impact on black spruce stem volume using AIC_c. We verified the normality of residuals and checked for homogeneity of variances for each model using Levene’s test (Gastwirth et al., 2009).

All statistical analyses were performed within the R programming environment (R Core team Development Team, 2022). We conducted analyses of variance (ANOVA) to examine the effects of neighbouring tree species on both measured LAI, foliar nutrient concentrations (N, P and K), soil nutrients (C/N ratio) and soil pH (organic and mineral) [Objectives 1, 3 and 4]. We assessed the normality of residuals and checked for homogeneity of variances using Levene's test (Gastwirth et al., 2009). In order to meet the assumption of normality for LAI above target trees, we applied a log transformation to the response variable. Analyses were conducted on transformed data, but we present values (and differences) on their original scale for the sake of clarity. We used $\alpha = 0.05$ as a threshold of statistical significance.

2.3 Results

2.3.1 Effects of environmental variables on black spruce volume

The supervised forward model selection, using only environmental variables, resulted in the selection of a single model comprising microtopography, the sum of competing vegetation angles, and the Hegyi competition index by the Akaike criterion (Table 2.2). The second-ranked model was composed of competing vegetation angles, and the Hegyi competition index (Table 2.2). With 58% of *AICc* weight and explaining 22.9% of the variance, the first-ranked model was deemed the best fit for the data as no other model was best fitting for black spruce stem volume (Table 2.2). None of the other candidate models had a ΔAIC_c within 2; they were not kept for further analysis.

Table 2.2 : Most parsimonious models explaining black spruce 8th-year stem volume, including the number of parameters (K), delta AIC_c compared to the highest-ranked model (ΔAIC_c), model weight (AIC_cWt), and model predictive power (Adjusted R^2). The second half of the table shows parameters influencing black spruce 8th years stem volume and 95% confidence intervals excluding 0. For microtopography, mound was used as the reference level. Model in bold indicate retained model ($\Delta AIC_c < 2$). We included the null model as a reference level for *AICc* score.

Candidate Models	*K*	ΔAIC_c	AIC_cWt	Adjusted R^2
8th-year stem volume ~ microtopography + Hegyi competition index + Sum of competing vegetation angles	**6**	**0**	**0.58**	**0.229**

8th-year stem volume ~ Hegyi competition index + Sum of competing vegetation angles	4	2.24	0.19	0.197
8th years stem volume ~ 1	2	24.3	< 0.001	-

Parameters	Lower 95% CI	Averaged estimate (β)	Upper 95% CI	Adjusted R^2
Microtopography				
Pit	0.84	14.1	27.36	0.06
Flat	2.05	11.87	21.68	
Sum of competing vegetation angles	-0.06	-0.04	-0.02	0.138
Hegyi competition index	-9.30	-5.67	-2.05	0.07

The largest effect on black spruce stem volume was observed from the competition of surrounding shrubs and no-crop trees (Sum of competing vegetation angles) (Fig. 2.2A, Table 2.2). Competing vegetation detrimentally impacted black spruce at maximum observed competition (sum of angles > 600°) reducing predicted stem volume of black spruce by 86% (-26.9 dm^3) relative to conditions where competing vegetation was absent (Fig. 2.2A). The predicted size decline associate with intermediate competition values (200 to 400 °) ranged between -8 and -16 dm^3 respectively (Fig. 2.2A). The explained variance of the competing vegetation was the highest among tested parameters at 13.8% (Table 2.2). The main contributors to this competing vegetation were willow, pin cherry and trembling aspen, in order of abundance. When competition from other crop-trees was high (Hegyi > 4), our model predicted stem volume that were 25 m^3 lower than the highest predicted mean stem volume under low competition (44 dm^3) (Fig. 2.2B). This corresponded to a 43.2% decrease of stem volume. However, there were a limited number of observations for high values of Hegyi competition index, which resulted in wider confidence intervals at these extreme values (Fig. 2.2B).

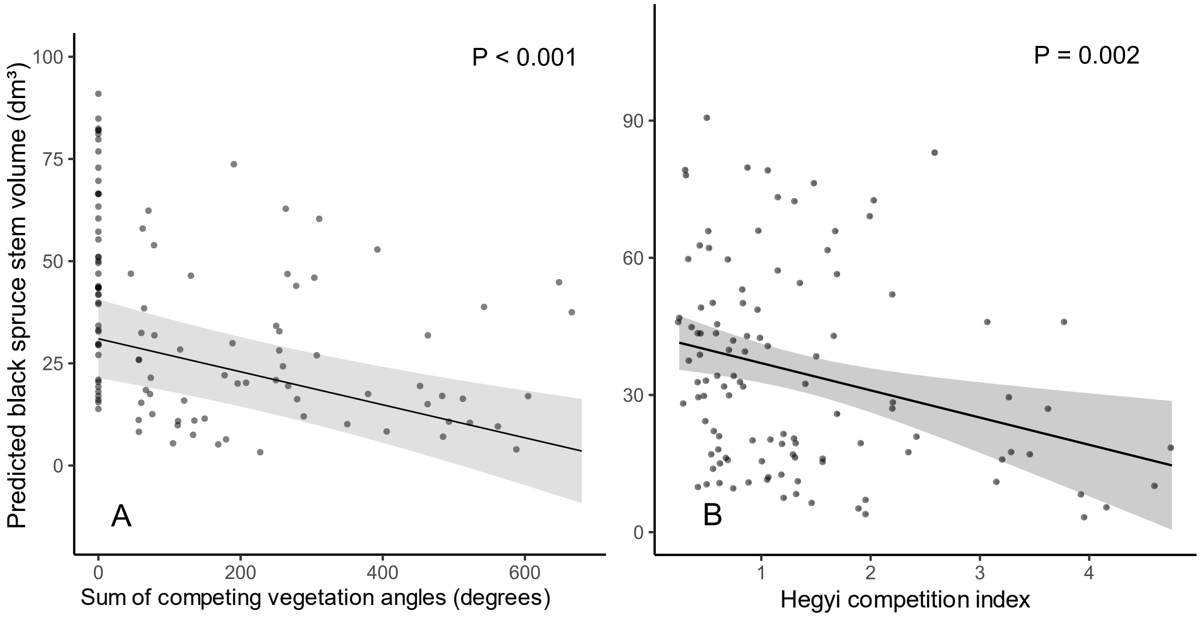

Figure 2.2 : Predicted black spruce stem volume at the 8th years (dm^3) based on sum of competing vegetation angles (°) (A) and Hegyi competition index (B). Averaged predictions using the retained model are included with 95% CI. The p-values shows the level of significance and grey circles correspond to the original observations.

The flat microtopography exhibited a positive effect on black spruce stem volume compared to mounds (Table 2.2; Appendix A, Fig. 2.6). In contrast, the presence of a pit at the base of crop trees had a similar effect as mound and flat microtopography, with no significant increase or reduction in the predicted stem volume (Fig. 2.6).

2.3.2 Effects of neighbouring species on black spruce volume

With the inclusion of the neighbouring species effect in the best and most parsimonious environmental model, the explained variance of black spruce stem volume increased from 22.9 to 25.4% (adjusted R^2). The model, incorporating the neighbouring species effect, retained 76% of the AIC_cWt compared to the model without the neighbouring species effect with ΔAIC_c greater than 2, which indicate the latter was less parsimonious than the model with the neighbouring species effect (Table 2.3).

Table 2.3 : Most parsimonious models explaining black spruce 8th-year stem volume with and without the neighbouring species effect, including the number of parameters (K), delta AIC_c compared to the highest-ranked model (ΔAIC_c), model weight (AIC_cWt), and model predictive power (adjusted R^2). Model in bold indicate retained

model ($\Delta AIC_{c} < 2$). The second half of the table shows parameters influencing black spruce 8th years stem volume and 95% confidence intervals excluding 0.

Candidate Models	*K*	ΔAIC_c	AIC_cWt	Adjusted R^2
8th year stem volume ~ microtopography + Hegyi competition index + Sum of competing vegetation angles + neighbouring species	**7**	**0**	**0.76**	**0.254**
8th year stem volume ~ microtopography + Hegyi competition index + Sum of competing vegetation angles	6	2.3	0.24	0.229

Parameters	Lower 95% CI	Averaged estimate (β)	Upper 95% CI	Adjusted R^2
Neighbouring species (Tamarack)	0.58	9.72	18.86	0.008

The predicted stem volume of black spruce exhibited a 38.1% bigger (31.5 dm^3) in mixed neighbouring situation compared to monospecific situation (predicted stem volume was = 19.5 dm^3; Fig. 2.3). However, this positive effect of tamarack was weak as the variance explained by the neighbouring species variable alone was low ($R^2 = 0.008$). The neighbouring species effect alone would not predict a significant portion of stem volume variance. The observed effect, though significant ($p = 0.037$), was not particularly strong, as the upper confidence interval for black spruce neighbours and mean prediction estimate for tamarack neighbours nearly overlapped (30.4 dm^3 and 31.5 dm^3, respectively) (Fig. 2.3).

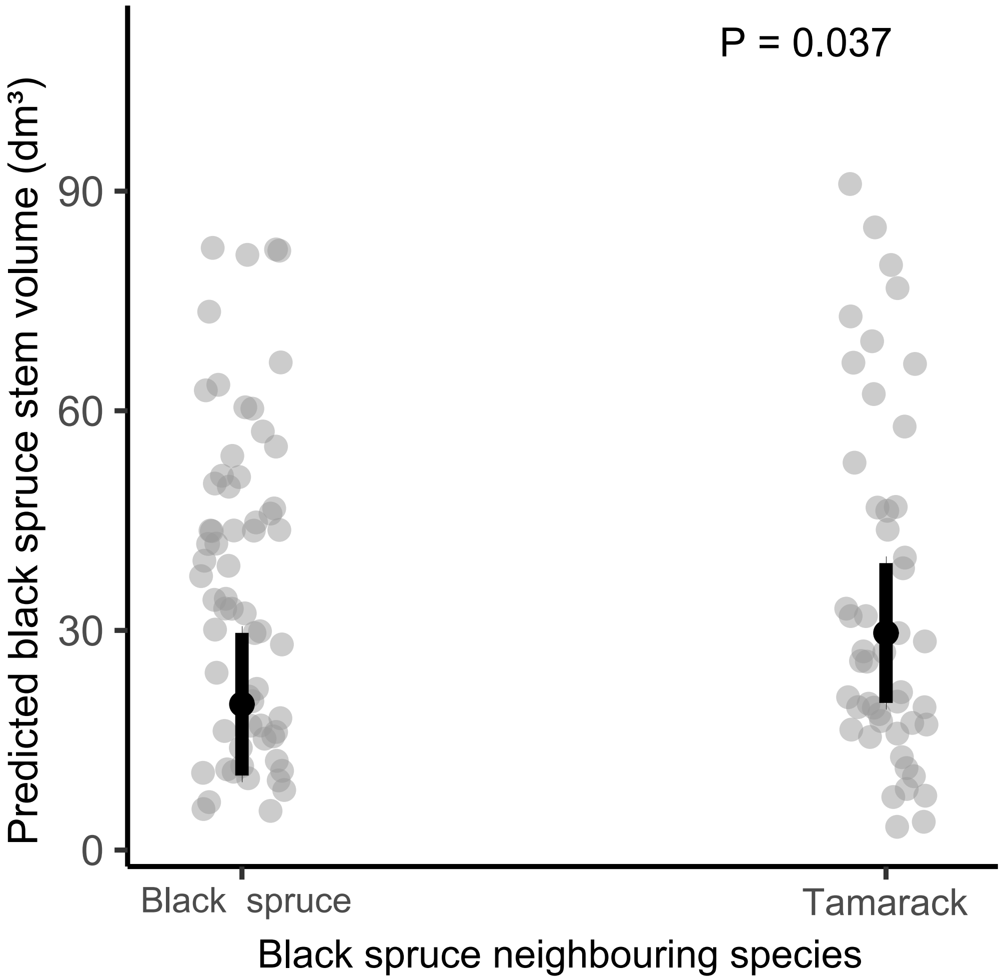

Figure 2.3 : Predicted black spruce stem volume (dm^3) based upon neighbouring species effect (black spruce or tamarack). Averaged predictions using the retained model are included with 95% CI. Grey circles correspond to the original observations, and the p-value shows the level of significance between groups.

2.3.3 Effects of neighbouring species on immediate growing environment

The ANOVA revealed significant differences between tamarack and only black spruce neighbouring for both measured leaf area indices, total foliar N concentration, and pH of mineral and organic layers (Appendix A; Table 2.4), with *p-values* ≤ 0.02 (Table 2.4). However, neighbouring tree species did not have an impact on the other tested variables, i.e., P and K total foliar concentration, C/N ratio of organic and mineral layers (Appendix A; Table 2.4).

Having tamarack as a neighbour resulted in a 25.6 % increase in LAI between closest neighbouring tree (Fig. 2.4A). The LAI above target trees increased by 55 % (Fig. 2.4B). These increases in canopy closure were consistently observed across both measurements, and the effect of tamarack was highly significant, with *p-values* of 0.002 and < 0.001 (Fig. 2.4). Furthermore, there was no difference in the mean competing vegetation cover and the number of planted crop trees (p = 0.15; p = 0.08 respectively) between plots testing the effect of neighbouring species, which enhances our confidence in the observed effect of tamarack on canopy closure (Table 2.1).

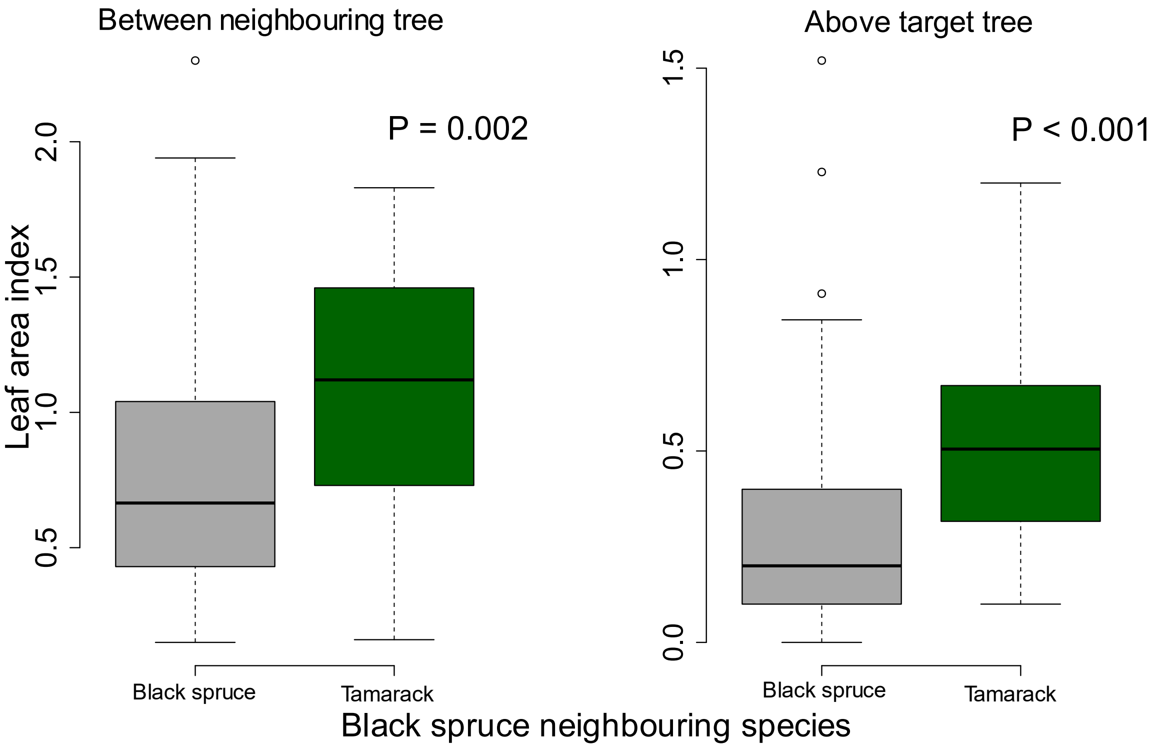

Figure 2.4 : Effect of neighbouring species for leaf area index at mid distance between the closest crop tree at 45 cm from ground level and above target tree at its mid height. The p-values shows the differences between groups.

Tamarack neighbours slightly increased pH of both soil layers, thereby reducing soil acidity (Fig. 2.5). Specifically, tamarack raised pH from 5.53 to 5.81 and from 5.00 to 5.17 for the mineral and organic layers, respectively (Fig. 2.5, Appendix A; Table 2.4).

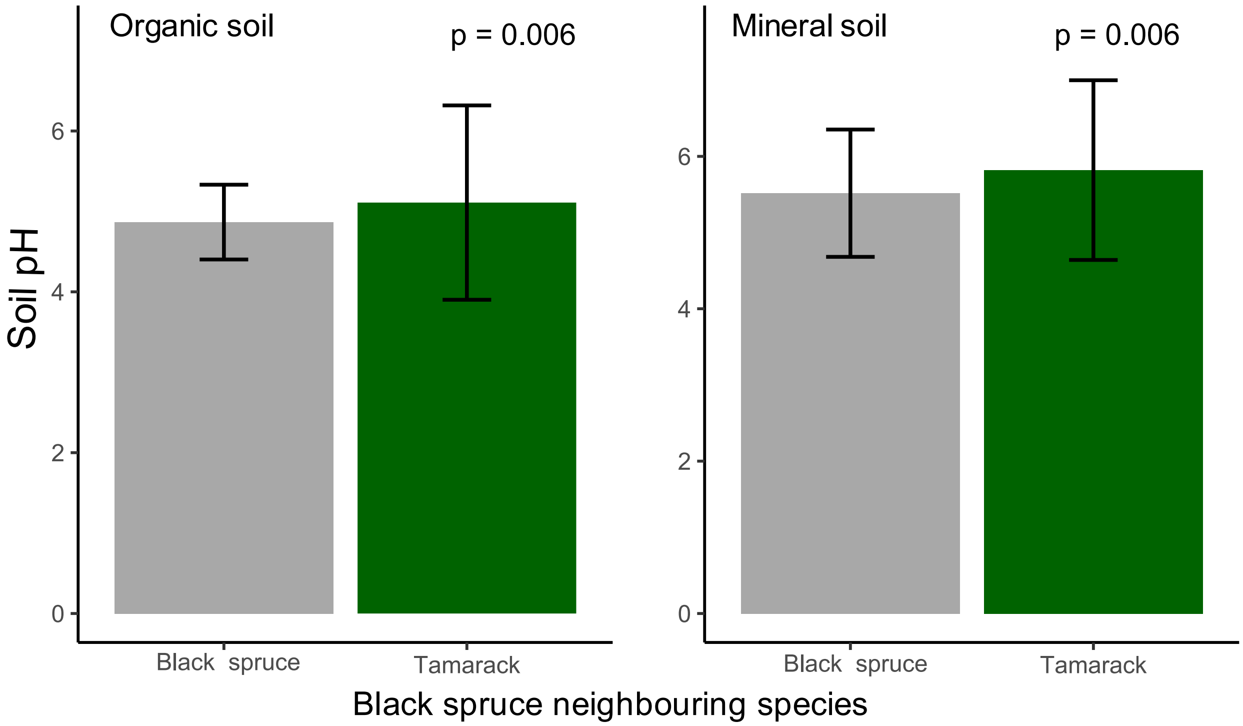

Figure 2.5 : Effect of black spruce neighbouring species on the pH of organic and mineral soil. The p-values show the differences between groups.

Lastly, we observed a very slight difference in the total foliar N concentration of black spruce when neighbouring tamarack versus black spruce (Appendix A; Table 2.4). The variation in total foliar N concentration in black spruce was 0.91% with tamarack neighbouring, compared to 0.87% with black spruce neighbouring.

2.4 Discussion

We detected bigger black spruce stem volume on the 8th-year from the effect of mixed neighbouring. It is unusual to perceive such an effect at this stage of stand development since significant effects of neighbouring species usually occur at later stages, under closed canopy (Forrester, 2014; Feng et al., 2022). The less negative effect of tamarack on black spruce stem volume can be attributed to growth complementarity for resource acquisition and minimal interference. This effect could be the result of additive effects of tamarack on pH and total N foliar concentrations enhancing soil conditions. Furthermore, the candidate model without the neighbouring species term was still plausible with a ΔAIC_c

just over 2 (Table 2.3). Despite the modest strength of tamarack effect, the predicted difference in black spruce stem volume was ecologically meaningful (mean prediction of 19.5 dm^3 for black spruce neighbours vs 31.5 dm^3 for tamarack neighbours). This shows an early high potential of mixed plantations of black spruce and tamarack to achieve over-yielding through the stand rotation. Our results are in agreement with Boyden et al. (2009), who observed higher tree volume after 11 years for both tamarack and black spruce mixed plantations compared to monocultures of both species. They attributed this over-yielding to a better resource acquisition through optimal canopy stratification. In our case, the higher stem volume of black spruce in mixed stands could be explained by low competitive interactions during the early years of plantation due to the mechanical release and black spruce's shade tolerance, even with tamarack creating higher canopy closure. The light and space availability were not constraining resources, as larger black spruce trees were observed in mixture, even though LAI measurements suggest that tamarack intercepted more sun light than black spruce neighbouring trees. Other work suggests overall foliage density is probably lower for tamarack than for black spruce (Lambert et al., 2005). On the other hand, we observed only a few black spruce trees facing high competition intensity from both shrubs and crop trees (Fig. 2.2). Even if tamarack grows faster and has a larger crown than black spruce (Lambert et al., 2005), it is a deciduous conifer filtering more light in spring to its neighbours than other conifer species. This can explain why we did not detect less negative shading effects on black spruce in the sampled plots even if the canopy was more closed in the mixtures. However, light and space will become less available in the future and the potential for over-yielding should be assessed at this time. Moreover, yield is measured at the stand level, whereas our study focuses on the individual tree level. While our study shows good potential for mixed stand, we can't extrapolate on mixed plantation yield, but only on individual tree growth 8 years after planting. Finally, we sampled the dominant black spruce as they are likely to be a part of the mature stand, as the oppressed trees will probably die (Cyr and Thiffault 2009). The direct upscaling of our results to the stand level must be done with caution.

In mixed stands, the net positive effect of mixture on growth typically occurs later, peaking between 20 and 40 years (Forrester, 2014; Feng et al., 2022). The growth relation effect mainly arises during canopy closure, which increases competition for resources, thus accentuating the growth differences between monoculture and mixed plantations (Jucker et al., 2020). When a species mixture results in an overall lower level of competition for resources between different tree species, the stand yield is usually enhanced (Ratcliffe et al., 2015). The early effect observed in this study could be the beginning of a clear positive difference between monoculture and mixed plantations or could be reversed at canopy closure when competition becomes more intense (Drossler et al., 2018). Tamarack, being fast-growing and shade intolerant, exhibits good growth complementarity for space occupancy when mixed with black spruce (slow-growing shade tolerant) (Strong & Roi 1983; Jucker et al., 2015; Lu et al., 2018). Slow-growing shade tolerant mixed with shade intolerant fast-growing trees can lead to over-yielding (Cordonnier et al. 2018). Furthermore, tamarack growth can be enhanced by neighbouring black spruce, as shown by Dijkstra et al. (2009). Although our study only focused on black spruce size and did not sample pure tamarack plantations, it is worth noting the possible neighbouring positive effect in the other direction. Mixed stands can enhance stand yield (Pretzsch et al., 2015), but also improve growth stability through stand rotation (Del Rìo et al., 2017; Aussenac et al., 2018). While our study focuses on early stand development, future research should investigate how increasing stand density affects interspecific competition and growth dynamics in mixed planted boreal forests.

Higher canopy closure surrounding young crop trees offers some benefits, including protection from extreme temperature variations, increased soil moisture retention; it could also help to outcompete other vegetation (Balandier et al., 2009; Pitt et al., 2009; Swanson et al., 2011; Martinez Pastur et al., 2023). Additionally, canopy cover protects from frost damage during leaf out in spring (Marquis et al., 2021). Our results suggest that this difference in canopy closure is a result of the tamarack effect, as we measured competing vegetation cover and height differences and did not observe differences between black spruce monoculture and mixture plots (data not shown). However, there is a delicate balance between the positive effects of canopy closure and the negative effects of competition for soils resources and light. As trees become bigger, competition for light intensifies, leading to self-thinning if left unmanaged (Drossler et al., 2018). Furthermore, during the canopy closure process, competition between trees can influence the architecture of both fast and slow-growing, and shade tolerant and intolerant trees (Van de Peer et al., 2017). In our study, we observed that intense competition from crop trees and shrubs resulted in a significant reduction in black spruce stem volume. Despite the mechanical release of the plantation in 2017, we still observed a negative effect of shrubs, indicating the high potential of shrubs and non-crop trees to influence crop tree growth. The main groups forming competing vegetation were tall shrubs and intolerant hardwoods (willow, pin cherry and aspen), which can be effectively managed with mechanical release as they mainly compete for light (Balandier et al., 2006; Thiffault et al., 2014). It is possible that we mainly observed the effect of past competition conditions from competing vegetation on black spruce, which continues to influence its current growth. Early mechanical release from non-crop species in black spruce plantations is essential for productivity since the basal area of crop trees linearly decreases as the basal area of non-crop species increases (Jobidon et al., 2004; Sharma et al., 2010). Thiffault et al. (2014) highlighted the importance of early mechanical release to prevent the overtopping of competing vegetation on crop trees, as overtopped trees may experience up to 96% decline in growth and face reduced survival. Our results corroborate this, but also highlight the negative competitive effect from other crop trees. Furthermore, the competitive effect differed when black spruce was neighboured by tamarack or black spruces. The combine results of all vegetation effect on black spruce allow us to create a gradient of competitive effects on black spruce stem volume. This gradient starts with non-crop tree having the strongest negative effect, followed by other black spruce trees with an intermediate negative effect and tamarack neighbouring with the least negative effect. Thus, a combination of mechanical release and mixed planting would maximize black spruce individual growth.

In the sampled mixed stand, the presence of tamarack slightly reduced soil acidity; higher soil pH can promote macronutrient cycling and increase their availability in soils (Binkley & Fisher, 2019). However, pH difference of 0.3 and 0.5 units are common and generally have a minimal ecological impact on tree growth (Binkley & Fisher, 2019), which is in the range of the pH difference we observed. Additionally, we did not observe any difference in soil C/N ratio associated with the neighbouring species effect. Therefore, it is surprising to detect a difference in total foliar N concentration associated with the presence of tamarack. However, the difference is minimal and probably not biologically significant for black spruce. The relations between soil macronutrients and leaf nutrient concentrations can be complex and take longer than 8 years to be biologically significant after plantation establishment. For instance, Dijkstra et al. (2009) observed a reduction in N mineralization when black spruce was mixed with tamarack compared to black spruce monoculture, ten years after planting. This reduction was attributed to the interaction between tamarack's N-rich litter and black spruce's lignin-rich litter (Reich et al., 1998), forming a resistant complex to microbial degradation (Dijkstra et al., 2009). Despite this litter interaction, the above-ground biomass of mixed plantations equalled the monocultures for both tamarack and black spruce (Dijkstra et al., 2009). Tamarack litter is known for its high N content (Reich et al., 1998), which enhance the N mineralization rate compared to litter in black spruce monoculture (Moroni et al., 2009). Finding the optimal species ratio and spacing between trees can help balance the acceleration of N mineralization from tamarack litter while reducing the input of lignin-rich black spruce litter. In our study, we tested a 50-50% mixture ratio with 2 m spacing, while Dijkstra et al. (2009) also tested a 50% ratio, but with three densities (0.25, 0.5 and 1 m spacing) without observing enhanced N mineralization by tamarack compared to black spruce monoculture. We did not measure N mineralization, but we observed a slight increase in total N foliar from black spruce in mixtures. It could be the spacing which was higher in our study preventing the formation of the lignin-rich and microbial-resistant complex, but this would need to be formally measured and followed on a longer time period. Under an optimal ratio, tamarack litter could act as nutrient pumps beneficial for neighbouring trees, but this has yet to be demonstrated. An improved nutrient cycling in mixed stands compared to monoculture can be a key mechanism to improve growth and potentially stand yield (Forrester et al., 2006).

The mean density of crop trees observed was 1850/ha, despite the initial density being 2500/ha, with a maximum sampled density of 2325/ha and a minimum of 1125/ha (Table 2.1). These variations could be attributed to mortality or the removal of smaller crop trees during mechanical release. However, as the plantation ages, the radius of influence will expand, changing the number of trees and the species ratio that have a competitive effect on black spruce. The observed species ratio is due to the plot being centred on target black spruce and to the competitive radius of influence only being 3.57 m considering equal or taller neighbouring trees (White et al., 2014). Furthermore, the mixed plantation was established with alternating rows of each species, thus limiting the number of crop tree influencing growth at the time of the study. Exploring various plantation densities and patterns could evidence other early interactions that influence the growth trajectory of the plantation. Boyden et al. (2009) demonstrated that high-density planting (64000/ha; 64 trees m^{-2}) was beneficial for tamarack – black spruce mixture during the 10th year of growth, surpassing both monospecific plantation of tamarack and black spruce. However, this density will lead to very high stand self-thinning and is not a viable option for forest management. Finally, mixed plantations with alternating species rows are easy to carry out, but as more complex plantation patterns can be difficult to consistently achieve. Although our study was conducted at a single location, the mixed-species plantation exhibited numerous encouraging signs for individual tree productivity when compared to black spruce monoculture. Further investigation should therefore aim to include more sites and locations with different competing vegetation to test our hypotheses in a larger context.

2.5 Conclusion

Our study offers valuable insights into the drivers of black spruce growth and soil characteristics during early plantation establishment and highlights the potential of tamarack as neighbouring species to improve black spruce growth. We observed less negative impacts of tamarack neighbours on black spruce attributes as well as on soil characteristics, though to a lesser extent. Even if these effects were not all ecologically significant, the emergence of numerous early differences between neighbouring species eight years after planting is both encouraging and surprising (Boyden et al. 2009). Black spruce and tamarack mixture showed great potential to be a viable management option for wood production through the positive effect of tamarack on black spruce stem volume. However, our results showed the importance of at least one mechanical release, as shrubs and non-crop trees have shown considerable negative impacts on black spruce growth, even if the studied plantation was released in 2017.

Assessing if mixed stand of black spruce – tamarack support greater biodiversity compared to their respective monocultures could add substantial weight to the case for this forest management strategy. Other associated advantages of mixed stands, such as heightened resistance and resilience to disturbances, drought, insects, and diseases (Kelty, 2006; Jactel & Brockerhoff 2007; Poeydebat et al., 2021), should also be assessed for tamarack-black spruce stands. To ascertain the inference potential and extent of our results, we recommended that our study design be replicated in other bioclimatic domains, including diverse soil conditions, and monitored over the long-term. Such studies would strengthen the knowledge and validate, or possibly challenges, our findings regarding the mixed stand of tamarack and black spruce.

2.6 Acknowledgements

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2.7 Author contributions

AL and NT acquired funding. SRP, NT and AL conceptualized the project. SRP wrote the original draft. SRP collected data. SRP, NT, AL and JL conducted the analyses. NT, AL and JL read, commented, edited and approved the final manuscript.

2.8 Data availability

Data will be made available on request.

2.9 Supporting information

The details on the supporting information are presented in Appendix A

2.10 Conflicts of interest

The authors declare that they have no competing interests.

2.11 Appendix A: Table 2.4 and Figure 2.6

Table 2.4 : ANOVA results (p-values) testing the neighbouring tree species effect between black spruce (Picea mariana) and tamarack (Larix laricina), significant effects are presented in bold.

Tested variables	Residual degree of freedom	Mean value as function of the neighbour		*p*-values
		Black spruce	Tamarack	
Leaf area index				
Above target	**118**	**0.15**	**0.34**	**<0.001*****
Between target tree and nearest neighbour	**112**	**0.79**	**1.07**	**0.002****
Black spruce foliar nutrients				
N total (%)	**111**	**0.87**	**0.91**	**0.02***
P total (%)	112	2.25	2.70	0.19
K total (%)	112	7.88	9.04	0.31
Soil nutrients				
C/N total mineral	104	15.0	14.74	0.589
C/N total organic	95	27.60	25.22	0.122
pH mineral	**104**	**5.53**	**5.81**	**0.006****
pH organic	**104**	**5.00**	**5.17**	**0.006****

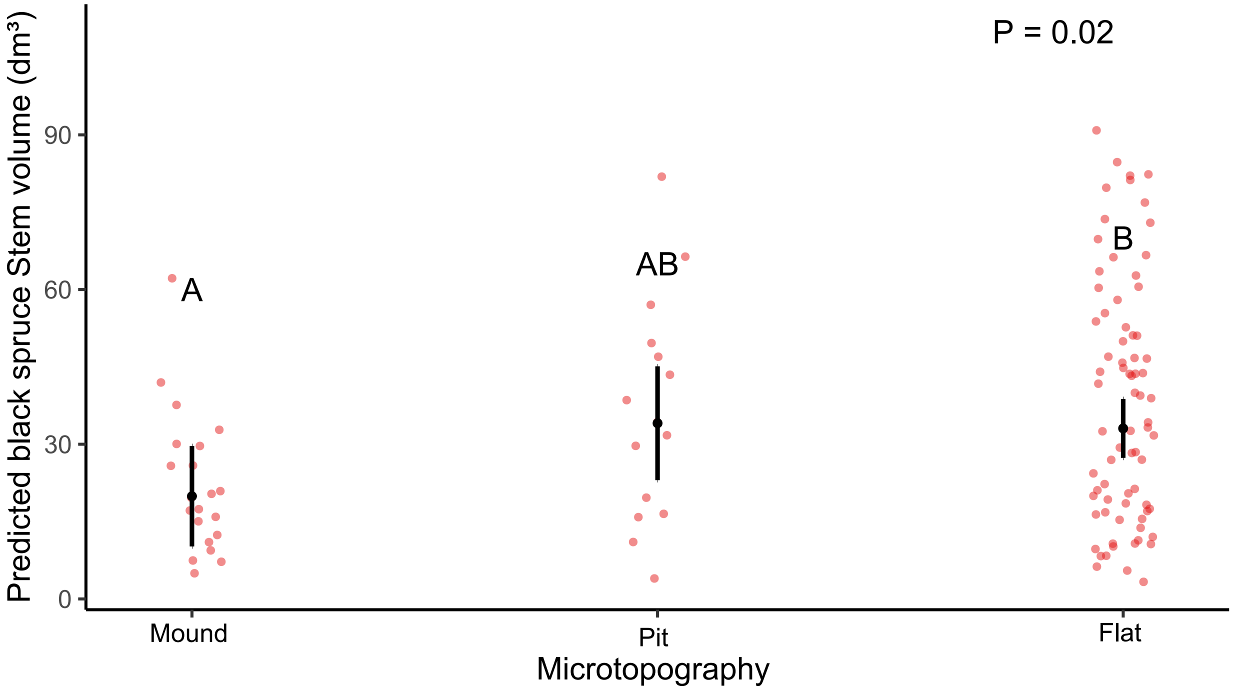

Figure 2.6 : Predicted black spruce stem volume at the 8th years (dm^3) based upon average microtopography effect (Mound, Pit and Flat). Averaged predictions using the retained model are included with 95% CI. Red open circles correspond to the original observations. The p value and letters show the differences between groups.

CHAPITRE 3

Mixed stands of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) offer high secondary growth in eastern boreal forests of Canada

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The Canadian boreal forest is still lacking investigation into compatible species mixtures that can lead to higher growth rates than monospecific or pure stands. The effect of species mixtures on stand productivity can vary with stem density, species proportion, site characteristics, and climate variation. We investigated mixed stands of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) in eastern Canadian boreal forests. Using modern forest survey data, we analyzed stand basal area variation in 756 mature stands exclusively composed of these two species over a study area spanning 535,000 km². We generated a linear relationship between mixed stand basal area and stem density, and the residual of this relation was used as response variable named 'residual basal area'. Positive and negative deviations of residual basal area were analysed with generalized additive models and quantile regressions with tamarack basal area, climate, and site characteristics as explanatory variables. The selected model included tamarack basal area, mean seasonal precipitation, degree days, mean annual temperature, stand age, latitude, longitude, and the type of surficial deposit. Tamarack exhibited a linear positive effect on predicted residual basal area. The most significant effect was observed from the interaction between tamarack basal area and stand age, predicting positive residual basal area of 16 m^2 ha^{-1} when stand aged was 150 years old and tamarack basal area was between 12 and 17 m^2 ha^{-1}. Quantile regressions revealed that tamarack could enhance basal area while increasing black spruce stem size and density. Landscape managers may consider the establishment of mixed black spruce and tamarack stands to favor secondary growth in eastern Canadian boreal forests.

Keywords: Basal area variations, Mixed species stands, Generalized additive models, Mixed stands management, niche complementarity

3.1 Introduction

The investigation of growth compatibility between tree species, to manage mixed forests stands, is a long-lasting research topic as mixed stands can offer numerous advantages over monospecific or pure stands (Assmann 1970, Hooper et al. 2005, Paquette and Messier, 2011). Mixed forests stand can reach higher productivity (Kelty 1992, Paquette and Messier, 2011; Jucker et al., 2020) and greater resilience and resistance to global change impacts on tree growth compared to monospecific stands (Poeydebat et al., 2021; Vacek et al., 2021). Additional benefits of mixed stands include increased biodiversity, and reduced risk from pathogens and windthrow (Hartley, 2002; Felton et al., 2016). Mixed stands also offer key advantages towards forest management such as improved regeneration, increased financial security, and greater adaptive capacity (Felton et al., 2016). Some research proposes converting monospecific stands to mixed stands to ensure sustainable forest management facing future growth projections (Felton et al., 2016; Hilmers et al., 2020; Reventlow et al., 2021). However, large-scale conversion may not be realistic due to obstacles like increased management complexity and uncertainty concerning economic return (Felton et al., 2016). Increasing the ratio of mixed stands over the landscape is more widely accepted and advocated (Schuler et al., 2017; Reventlow et al., 2021; Feng et al., 2022). Further investigation is needed to better understand the dynamics of mixed stands before being able to model precisely on a large-scale mixed forest growth and integrate it into management practices (Pretzsch and Zenner, 2017; Oboite and Comeau, 2019).

Assessing growth interactions in mixed stands should consider stand density, site conditions, and species proportions (Condès et al., 2013; Forrester et al., 2013; Huber et al., 2014; Sterba et al., 2014). Productivity in mixed stands is strongly linked to stand stem density (Forrester, 2014; Forrester and Bauhus, 2016), with maximum stand density influenced by site quality (Ducey and Knapp, 2010; Condès et al., 2017). Several studies highlighted the significant impact of stand density on growth interactions in mixed stands

(Condès et al., 2013; Pretzsch and Biber, 2005; Brunner and Forrester, 2020). Strong negative interactions tend to occur at high densities, although species proportion and ontogeny can modulate these interactions (Boyden et al. 2009, Forrester et al., 2013; Brunner and Forrester, 2020). For example, maximum stand density can be increased in mixed stands compared to monospecific stands (Pretzsch and Biber, 2016). Density partially incorporates the effect of stand structure on growth, which is not often measured although it can impact productivity (Pretzsch and Biber, 2005; Pretzsch and Del Río, 2020). Structurally, tree position in the canopy changes the species competition effect on its neighbor (Canham et al., 2006; Coates et al., 2009; D'Amato and Puettmann, 2004). Thus, considering stem density alongside species interaction is warranted to investigate mixed stands with a wide range of tree ages and stand structure. Site conditions often modulate interspecific growth interactions (Del Río and Sterba, 2009; Pretzsch et al., 2013). Productive sites tend to reduce both positive and negative interactions, while less productive sites tend to maximize positive interactions between compatible tree species (Del Río and Sterba, 2009; Pretzsch et al., 2013).

Deciduous and evergreen tree species mixed are often considered when investigating overyielding (Fichtner et al., 2017). However, deciduous trees can suppress neighboring evergreen tree growth and achieve overyielding from their unique productivity in mixed stands (Urgoiti et al., 2023). Species ontogeny and proportion both play a key role in species complementary leading to enhanced stand productivity (Boyden et al., 2009, Sterba et al., 2014; Pretzsch and Zenner, 2017; Sterba et al., 2018). Proportion can be measured with different tree characteristics such as basal area, stem number, stem volume, and total biomass (Bravo-Oviedo et al., 2014). Basal area is often used as a proxy because it accurately describes species proportion in even-aged stands (Groot et al., 2014).

In the boreal forest, black spruce (*Picea mariana* [Mill.] B.S.P.) has already shown growth complementarity with trembling aspen (*Populus tremuloides* Michx.) and birch (*Betula neoalaskana* Sarg.) (Légaré et al., 2004; Oboite and Comeau, 2019), making it a well studied species from a growth relation perspective especially in the Canadian boreal forest. However, other companion species still require growth complementarity investigation with black spruce as it is an economically important species in North America (Viereck and Johnston, 1990). Increasing the ratio of mixed stands in the boreal forest is a holistic approach to enhance the resilience and the resistance of managed stands to disturbances (Poeydebat et al., 2021; Vacek et al., 2021). Tamarack (*Larix laricina* [Du Roi] K. Koch) and black spruce as a mixture showed promising growth complementarity signs from an ontogenetic perspective (Boyden et al. 2009; Dijkstra et al., 2009) and at the juvenile stage (Roy Proulx et al., 2024). Furthermore, mature black spruce growth is not negatively impacted by neighboring tamarack (Roy Proulx et al., 2023). Black spruce is a slow growing evergreen and shade tolerant species, whereas tamarack is a fast growing deciduous and shade intolerant species (Viereck and Johnston, 1990; Johnston, 1990). This combination of tree species with distinct shade tolerances and growth rates has often showed a positive effect on stand productivity (Fichtner et al., 2017; Sterba et al., 2018). Norway spruce (*Picea abies* L. Karst) and European larch (*Larix decidua* Mill.), two species physiologically similar to black spruce and tamarack, showed good growth complementarity at mid species proportions in mature stands (110 to 170 years) (Sterba et al., 2018). They observed an overyielding peak at 50-50% species proportions and declines when either species occupied higher proportions in the stand (Sterba et al., 2018). The growth dynamic between these European species can guide the investigation on black spruce and tamarack on the stand scale. However, black spruce and tamarack are growing in a different context in Canada as they are often found together on organic surficial deposits or on soils with complex drainage (Johnston, 1990). Organic surficial deposits are unproductive sites and difficult to manage (Simard et al., 2007). Investigating tamarack and black spruce mixed stands to maintain or enhance stand productivity could add an interesting management option in the Canadian boreal forest.

In this study, the objective was to detect and study basal area variation in boreal mixed stands composed of black spruce and tamarack in northern Québec, Canada. Furthermore, we investigated if basal area variation in mixed stands was modulated by climate, site characteristics, species proportion, or interactions between these variables. We studied these effects using data covering the balsam fir (*Abies balsamea* [L.] Mill.)–white birch (*Betula papyrifera* Marsh) and the black spruce–feathermoss bioclimatic domains of Québec (Saucier et al., 2009) (Fig. 1). We hypothesized that: (1) the highest basal area in tamarack and black spruce mixed stands will be observed at mid-species proportions, similar to findings by Sterba et al. (2018), (2) tamarack dominated stands (>50% of the total basal area) will not reduce black spruce productivity based on Roy Proulx et al. (2023), (3) climatic variables will modulate black spruce and tamarack growth interactions as observed in other mixed stands (Condès et al., 2017; Forrester, 2014), and (4) site conditions interacting with species proportion will influence mixed stand basal area (Del Río and Sterba, 2009; Pretzsch et al., 2013).

3.2 Methods

3.2.1 Dataset and plot selection criteria

Our study area extended from 46.66–52.01°N and 79.51–61.86°W, corresponding to the boreal forest of Québec, Canada (Fig. 3.1). A climatic gradient exists between the eastern and western parts of the Québec boreal forest: the eastern part experiences more precipitation and colder temperatures than the western part. Mean annual temperatures are cold, averaging 0°C (Table 3.1), and annual precipitation increases from West (808 mm) to East (1,359 mm) [based on 1981-2010 observed values; Environment Canada, 2024]. To represent forests in the study area, we used the latest forest survey dataset available and collected by the provincial government, between 2010 and 2018 (MRNF, 2017). This forest survey was based on circular plots of 11.28 m radius (400 m^2) in which all merchantable trees (≥9 cm diameter at breast height, DBH) were tallied for DBH and identified by species. Stand age was estimated by collecting increment cores from four trees in each plot.

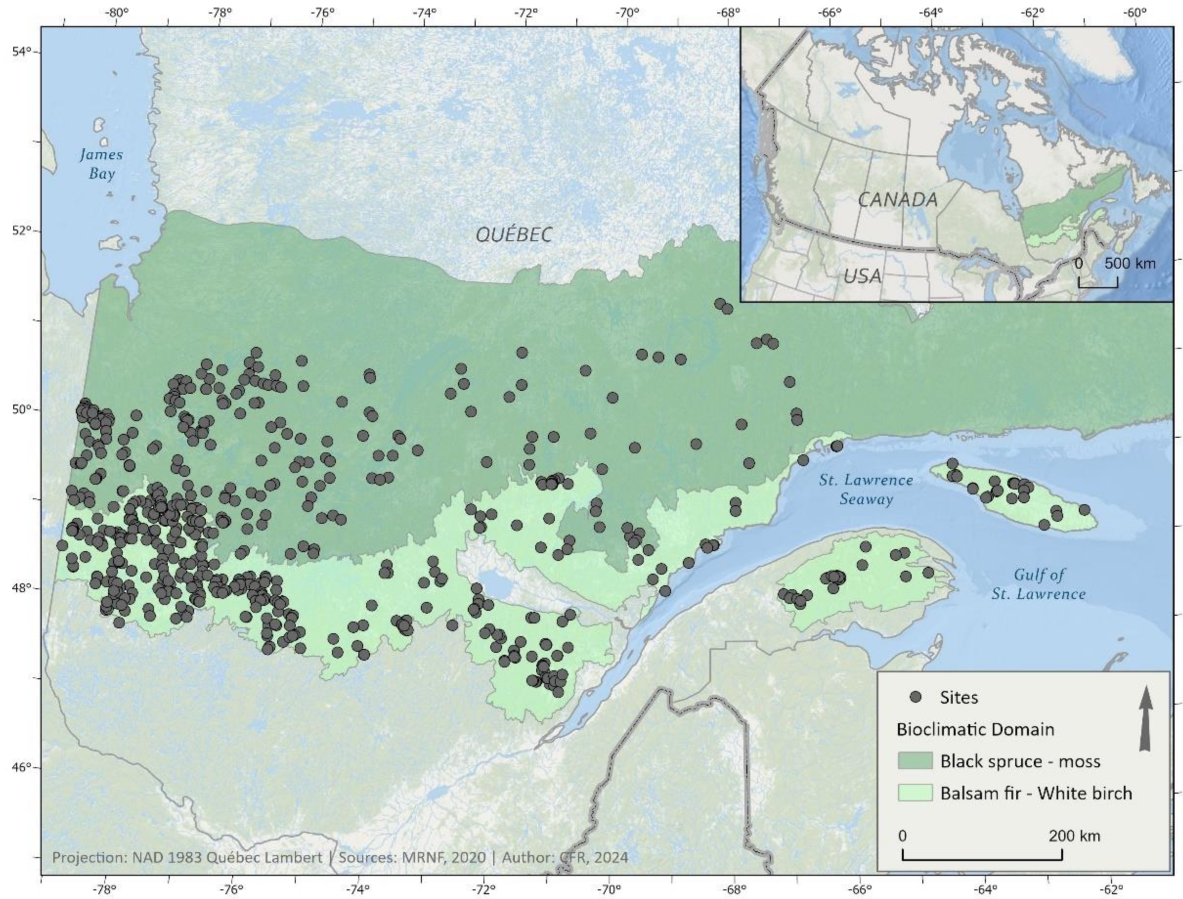

Figure 3.1 : Locations of plots (N = 756) in mixed stands of the Black spruce- feathermoss and Balsam-fir white birch bioclimatic domains.

From the original dataset comprising 36,846 plots, we selected a subset of plots within the Balsam fir – white birch and the Black spruce – feathermoss bioclimatic domains (Saucier et al., 2009) and in which black spruce and tamarack composed ≥75% of the basal area. Following the selection, we excluded plots that had <10% of their basal area composed by either of the two species, and those in which black spruce and tamarack composed >90% and >75% of the basal area, respectively. The number of plots dominated by tamarack was low, and since our focus was on mixed stands, we ended up with 756 plots meeting our criteria.

Table 3.1 : Site and climate characteristics of the 756 selected plots, based on data from the provincial survey dataset (MRNF, 2017) and 1981-2010 Climate Normal (Environment Canada, 2024). Data are presented as mean ± SD.

Basal area ($m^2 ha^{-1}$)	13.78 ± 8.73
Density (stems ha^{-1})	909 ± 489
Mean Annual Temperature (ºC)	0.85 ± 0.91
Summer Heat Moisture Index	33.73 ± 3.01
Mean Seasonal Precipitation (mm)	485.9 ± 38.8
Degree Days >5°C	1,263 ± 131
Hogg's Climate Moisture Index	54.1 ± 14.9
Stand age (years)	78 ± 39
Surficial deposit (number of plots)	
Clay	153
Organic	295
Till	118
Other types	190
Number of plots (N)	756

3.2.2 Climate and soil data

Historic climate data for each of the 756 plot locations were generated using the ClimateNA software package v7.42 (Wang et al., 2016). Given that the forest survey was conducted from 2010 to 2018, we generated 30-year annual and seasonal normal between 1981 and 2010. The climate variables considered in the analysis were Mean Annual Temperature (°C; MAT), Mean Seasonal Precipitation (mm; MSP), Hogg's

Climate Moisture Index (mm; CMI) (Hogg, 1997), Degree Days > 5°C (DD5), and Summer Heat Moisture Index (SHM). SHM was calculated as the (mean warmest month temperature) / (MSP/1000).

Site surficial deposits were predominantly composed of organic soils, undifferentiated tills, and clay soils (Table 3.1). Other surficial deposits, including undifferentiated till with rare outcrops, outwash plains, juxta-glacial deposits and glaciolacustrine shallow-waters were grouped because they were uncommon. We adapted the soil classification developed by Mansuy et al. (2010) based on surficial deposit and drainage. This classification, designed for the boreal forest, categorizes soils based on their drying potential, facilitating the study of interactions between tree growth, soils, and climate (Pau et al., 2021). The classification comprises four classes of surficial deposit drainage (SDD) (see Supporting information A3, Table 3.5). Our adaptation of the classification resulted in high occurrence of tamarack and black spruce on organic, clay soils, and till to a lesser extent.

3.2.3 Statistical analyses

3.2.3.1 Residual Basal area

We investigated mixed stand secondary growth (radial growth) with the proxy variable named 'residual basal area', which is the deviation of the linear relationship between total basal area ($m^2\ ha^{-1}$) and stem density (stems ha^{-1}) (see Appendix A1, Fig A). This provided an expected basal area value for each stem density based on the relationship in the sampled mixed stands. The resulting linear equation for mixed stands was as follows:

$$Total\ basal\ area = 0.0151 * (stem\ density) \qquad \text{Eq. 1}$$

The relationship was proved robust between basal area and stem density ($R^2 = 0.920$, see Appendix A1, Fig A). Throughout this manuscript, the term 'residual basal area' designated the basal area deviation from the linear relationship between mixed stand total basal area and stem density. The difference between observed and predicted values generated by this linear model quantifies the potential effect of environmental conditions influencing forest productivity and it was used as response variable in subsequent analyses.

3.2.3.2 Quantile regression on residual basal area

To quantify secondary growth of tamarack and black spruce in the selected mixed stands, we applied quantile regressions on residual basal area. Quantile regression corrects the maximum likelihood estimation of linear models based on least squares (Cade and Noon, 2003). For our study, we applied 90th quantile regression to provide information about the “ideal” or “maximum” response between two stand characteristics, as other limiting factors are unmeasured (Cade and Noon, 2003, Linares et al., 2009; Halpern and Lutz, 2013). The boreal forest is an ecosystem with many factors influencing its productivity (Martin et al., 2023). In this context, percentile regressions are practical because they can reveal the highest potential of yield increases if densities and site conditions are optimal. Thus, we used 90th quantile regression as an approach to estimate the maximum effect of tamarack on mixed stand basal area variation without measuring all restraining and enhancing factors (Linares et al., 2009; Halpern and Lutz, 2013). We aimed to investigate the optimal growth conditions between tamarack and black spruce with the 90th quantile regression controlling for the effects of other unmeasured variables influencing growth in mixed stands. We used the 90th quantile regression on basal area and residual basal area with the function *rq* in the ‘quantreg’ package (Koenker et al., 2018) to test our first hypothesis (the positive effect of tamarack in mixed stands is maximized at intermediate proportions with black spruce). To smooth the regression curve, we categorized tamarack basal area into six increasing classes divided in 2 m² ha^{-1} increments (0.16–1.99, 2–3.99, 4–5.99, 6–7.99, 8–9.99, ≥10 m² ha^{-1}). Each class contained roughly the same number of mixed stands while keeping the same tamarack basal area increment between classes. We produced boxplots associating each tamarack and black spruce basal area class to their percentage of stand total basal area but, only for productive stands (>50 m³ ha^{-1}) (Cyr et al., 2022) (see Appendix A2, Figs. A2, A2.1). These boxplots help associate each species’ basal area class to specific proportion in mixed stand and it was done in a management perspective. We also investigated the black spruce quadratic mean diameter and mean stem number using a 90th quantile regression with the same tamarack basal area classes. To test the second hypothesis (in mixed stands, tamarack increases the overall stand productivity without reducing black spruce productivity), we examined the effect of each basal area class, which is the addition of 2 m² ha^{-1} of tamarack, on black spruce stem density and mean size. We used the smoothing spline method to determine the 90th quantiles for each tamarack class. To ensure compliance with model assumptions of residual deviance, we assessed observed vs predicted residuals and the distribution of residuals.

3.2.3.3 Generalized additive model (GAM)

We tested the additive effect of climatic variables, site characteristics, and stand species proportion on residual basal area using a Generalized Additive Model (GAM) with the *gam* function from the 'mgcv' package (Wood, 2015). We used GAM because the relationships between residual basal area and the explanatory variables were not linear. Using the residual basal area in the GAM remove the density effect in non-managed situations; in contrast, that effect is controlled in plantations of thinned stands. To verify the first and third hypotheses (the positive effect of tamarack in mixed stands is maximized at mid proportions with black spruce, and basal area is modulated by climate), we formulated a base model composed of the single effects of all uncorrelated climatic and site variables (surficial deposit, mean seasonal precipitation, mean annual temperature, tamarack basal area, stand age, latitude, longitude and degree days >5°C) (see Supporting information A2, Table A2). Variable selection for the base model involved a Pearson correlation test, ensuring the exclusion of highly correlated variables (<-0.7 and >0.7) within the same model. The test was performed with the function *correlate* in the 'corrr' package (Kuhn et al., 2020). Multicollinearity was further examined with R^2 and Variance Inflation Factors (VIF) using the *multicol* function in the 'fuzzySim' R package (Barbosa, 2015) (see Supporting information A4, Table A4). Following these procedures, we removed Hogg's CMI and SHM due to high correlations with other variables (see Supporting information A1, Table A1). We included each uncorrelated variable in the base model, and we assessed the interaction effect of each variable with tamarack basal area. Initially, the model included the density effect, but the effect was so dominant that the model retained this variable only and struggled to adjust the other variables. By working on residual basal area, the model allowed us to focus on the other effects.

The selection of GAM was based on the Bayesian Information Criterion (*BIC*), the score distance from the best model (*ΔBIC*), and model parsimony (Brewer et., 2016). To test our fourth hypothesis (basal area is influenced by site conditions interacting with tamarack basal area), we built a base model (comprised of each uncorrelated explanatory variables) and we added an interaction of each explanatory variable with the basal area of tamarack (Supporting information A2). We tested one interaction at a time in each candidate model and we selected the best model along with models with *ΔBIC* scores <2. Interactions were tested with the *ti* term in the *gam* function, and we produced smoothing parameters for each variable in the interaction and for the single variable effect on residual basal area. We tested spatial autocorrelation in the base model with the latitude and longitude; yet the individual effects of both parameters explained more variance. Our statistical approach with 90th quantile regression and GAM, supported the analysis of complex forest inventory data where many factors are not controlled. All statistical analyses were conducted within the R programming environment (R Core Development Team, 2022) and we used $\alpha = 0.05$ as a significance threshold for all analyses.

3.3 Results

3.3.1 Tamarack effect on mixed stand basal area

Total basal area doubled from 11.9 m^2 ha^{-1} to 24.8 m^2 ha^{-}1 across the first and second class of tamarack basal area (0.16–1.99 and 2–3.99 m^2 ha^{-1}, respectively) under the best growing conditions based on the 90th quantile regressions (Fig. 2a). Furthermore, the regression passed from 11.9 to 34.4 m^2 ha^{-1} for total basal area between the first and the last tamarack class (≥10 m^2 ha^{-1}) (Fig. 2a). The residual basal area difference was 14.2 m^2 ha^{-1} from the first class to the highest class of tamarack basal area (Fig. 2b). The regression slope was steepest between the first and second class as the addition of 2 m^2 ha^{-1} of tamarack between these classes resulted in a potential difference of 6.97 m^2 ha^{-1} in residual basal area (Fig. 2b). Furthermore, black spruce quadratic mean diameter and mean number of black spruce stems per ha showed a positive relation with tamarack basal area (Fig. 2c, 2d).

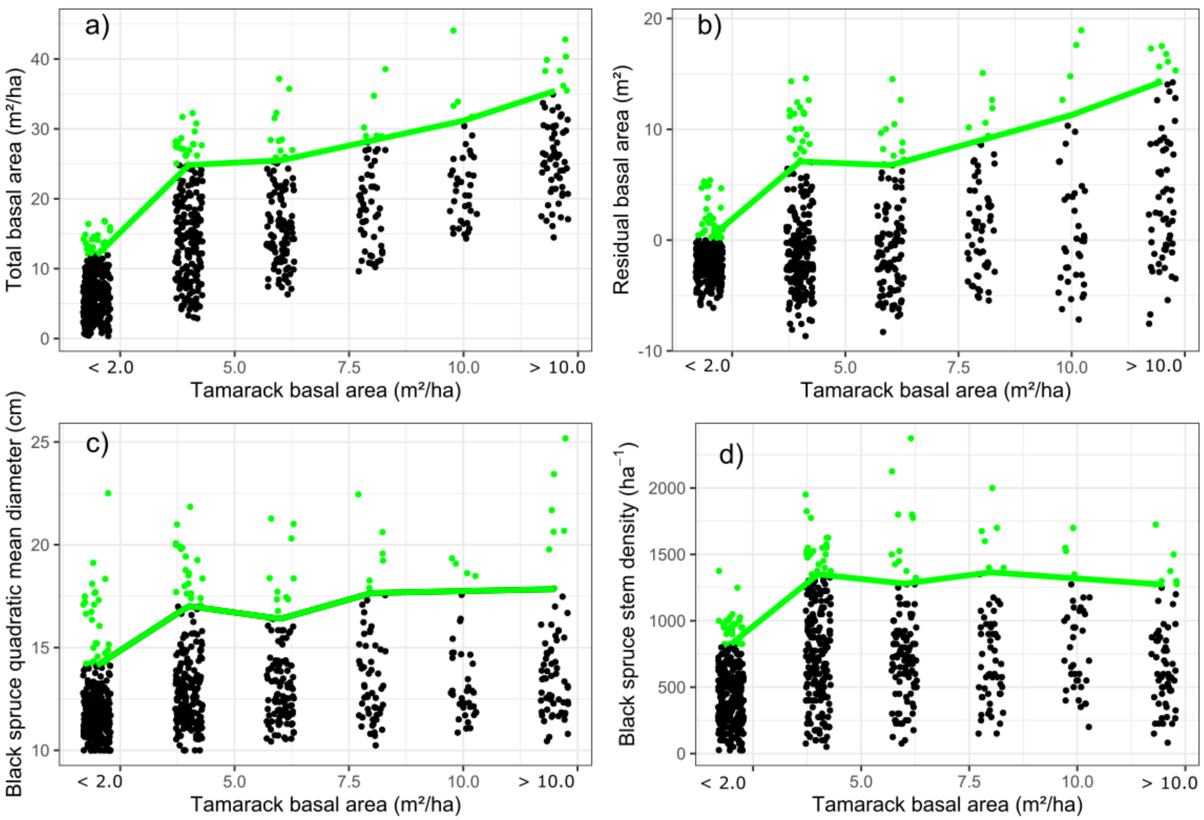

Figure 3.2: Quantile regressions showing the relationship between tamarack basal area classes and response variables. Panels (a) and (b) show the 90th quantile regression of total basal area and residual basal area, respectively. Panels (c) and (d) show the 50th quantile regression of black spruce quadratic mean diameter and stem density, respectively. Tamarack basal area classes were 0.16–1.99, 2–3.99, 4–5.99, 6–7.99, 8–9.99 and ≥10 m^2 ha^{-1}.

The four last tamarack class (4–5.99, 6-7.99, 8-9.99 and ≥10 m^2 ha^{-1}) creates a linear positive relation with total basal area and residual basal area (Fig. 2a, 2b). Black spruce quadratic mean diameter and stem density relation with tamarack basal area remained stable throughout class after the initial increase (Fig. 2c, 2d). The highest observed value for black spruce quadratic mean diameter at the 90th quantile was 17.8 cm in tamarack dominated conditions (≥10 m^2 ha^{-1}) (Fig. 2c). The 90th regression with the number of black spruce stem was stable around 1300 (stems ha^{-1}) after the initial increase (Fig. 2d).

3.3.2 Climate, site and species proportion effects

We only selected the first GAM based on the *BIC* score, which was composed of all uncorrelated variables (base model) and the interaction between stand age and tamarack basal area (Appendix A1, Table A1). All other candidate models scored >2 *ΔBIC* from the best-ranked model with the closest, with a *ΔBIC* of 60 (Appendix A1, Table A1). The selected model showed good predictive power, explaining 46.4%

of the residual basal area variance (Table 2). The selected model bias was minimal, as observed from the predicted vs observed correlation, but the model tended to slightly overestimate higher residual basal area values (see Supporting information A5, Fig. A5).

Table 3.2 Effect of each variable in the selected generalized additive models (GAM) to explain residual basal area. Regression slopes (β), standard deviations (Std. dev), t-value, p-value for categorical variables. The reference level for surficial deposits was Clay. Estimated degrees of freedom (EDF), F-value, and p-value for each smooth term in the GAM. Adjusted R², deviance explained and the number of observations (N) for the entire model. Bold values are significant at α = 0.05.

Parametric coefficients					
	β	Std. dev	*t*-value		*p*-value
Intercept	0.837	0.319	2.63		0.009
Surficial deposit					
Organic	**-1.62**	**0.38**	**-4.19**		**<0.001**
Other	-0.27	0.46	-0.58		0.560
Till	-0.23	0.47	-0.50		0.619
Smooth terms			EDF	*F*-value	*p*-value
Mean Seasonal Precipitation			2.06	2.47	0.091
Day Degrees >5°C			1.70	0.59	0.514
Mean Annual Temperature			3.56	2.05	0.081
Tamarack basal area			**7.21**	**31.1**	**<0.001**
Stand age			**3.21**	**51.7**	**<0.001**
Latitude			3.78	2.21	0.067
Longitude			**3.41**	**4.65**	**<0.001**

Tamarack basal area × Stand age	**6.87**	**14.6**	**<0.001**
Adjusted $R^2 = 0.464$	Deviance explained = 48.8%		N = 756

In the selected model, six of the nine variables significantly influenced residual basal area deviation (Table 2) with all effects being highly significant ($p < 0.001$). Organic surficial deposits had lower predicted residual basal area compared to other deposits, which all exhibited a positive effect (Table 2, Fig 3d).

The single effect of tamarack basal area on residual basal area was positive, with the highest predicted residual basal area observed when tamarack was totalling ≥20 $m^2 ha^{-1}$ in mixed stands (Fig. 3a). The steepest increase of predicted residual basal area was between tamarack basal area values of 0.16 and 5 $m^2 ha^{-1}$ (Fig. 3a). The predicted effect of stand age followed a bell-shaped curve, peaking around 90 years enhancing residual basal area by 4.56 $m^2 ha^{-1}$ and decreasing afterward (Fig. 3b). We observed higher predicted residual basal area in the western part of the boreal forest (longitude 79.51–70.00°W) than in the eastern part, where residual basal area deviation reached zero (Fig. 3c).

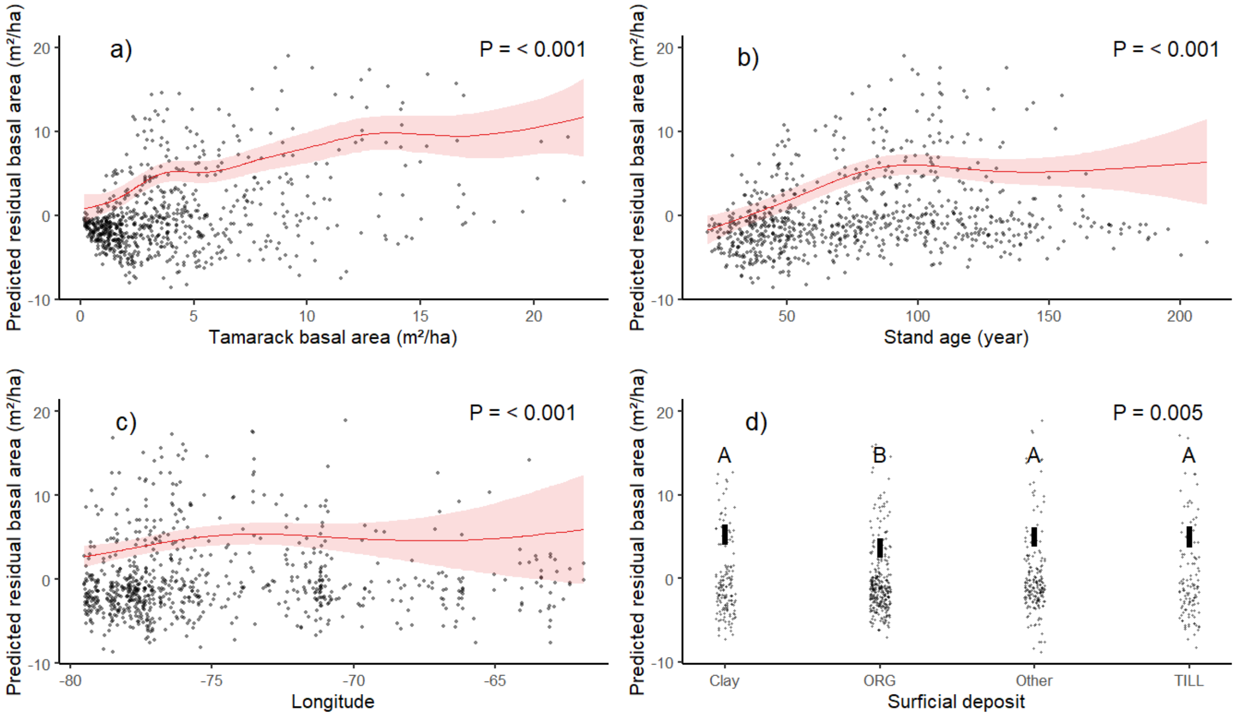

Figure 3.3 : Significant predicted effect on residual basal area. a) Effect of tamarack basal area (observations between 0.16 and 22.21 m² ha^{-1}). b) Effect of stand age (observations between 19 and 210 years). c) Effect of longitude (observations between -79.51 and -61.88 W). d) Effect of the surficial deposit where Clay is the reference level relative to all other surficial deposits and black rectangles represent 95% confidence bands. In panels a), b), c) red colored shading represents the 95% confidence intervals and grey circles are original observations.

Climate variables had less impact on residual basal area than the other tested variables (Table 2). Little to no residual basal area deviation was observed by Mean Annual Temperature, Mean Seasonal Precipitation, and Degrees Days >5 °C effect (Table 2). However, GAM incorporated their partial additive effect within the best model explaining residual basal area.

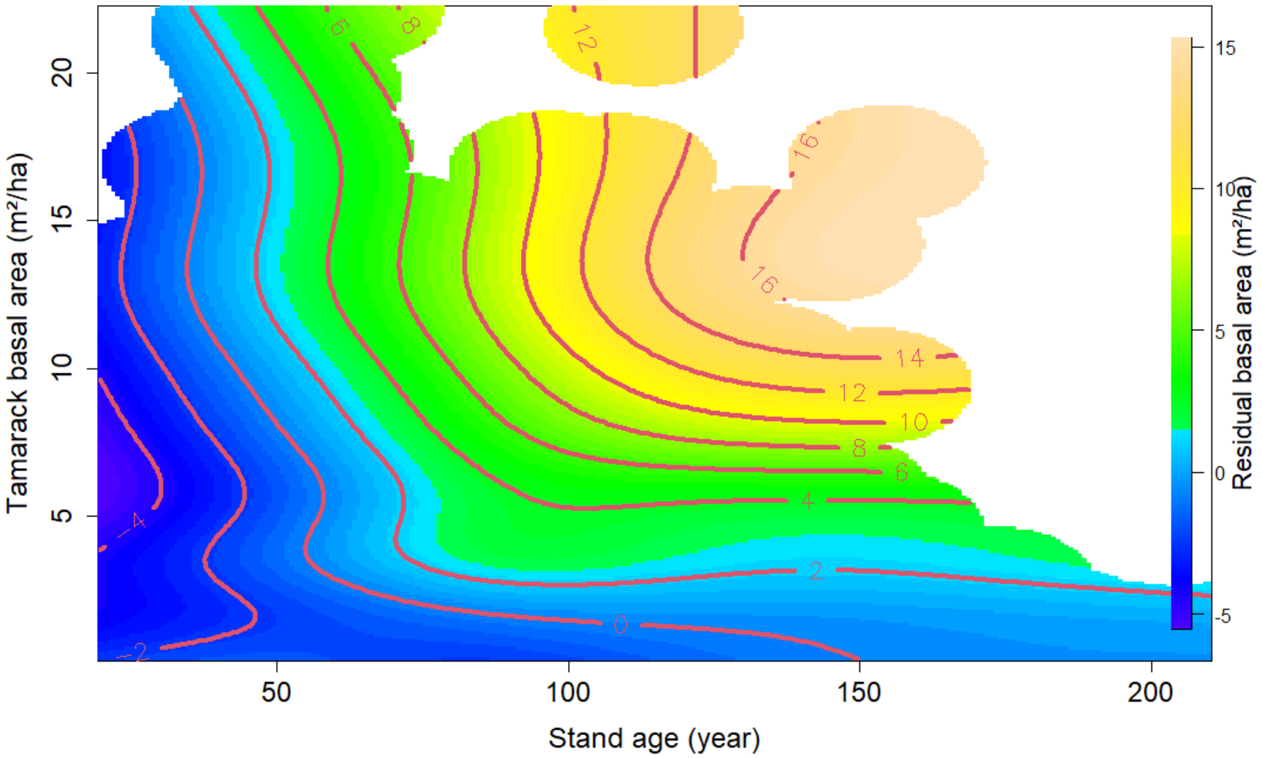

Figure 3.4 : Contour plot of tamarack basal area and stand age interaction effect on residual basal area where the number on each line indicates effect magnitude. Dark blues show negative predicted residual basal area and yellows show positive predicted residual basal area. Tamarack basal area ranged from 0.16 to 22.21 m² ha^{-1}, and stand age ranged from 19 to 210 year. Gaps in the figure indicate predictive model limits.

The interaction between stand age and tamarack basal area modulated residual basal area, thus predicting the largest residual basal area deviation as both variables increased (Fig. 4). The maximum predicted residual basal area was reached (predicted gain of 16 m² ha^{-1}) when tamarack basal area was between 12 and 17 m² ha^{-1} and stand age ranged from 145 to 170 years (Fig. 4). Furthermore, stands with less than 5 m² ha^{-1} of tamarack basal area exhibited small (<4 m² ha^{-1}) or negative predicted residual basal area, regardless of stand age (Fig. 4).

3.4 Discussion

Tamarack had a positive effect on secondary growth in mixed stands as the addition of tamarack basal area linearly increased the residual basal area. The maximal positive effect of tamarack in the best growth conditions was noticeable at high proportion (75%) on both total basal area and residual basal area, as indicated by the 90th quantile regression (Fig. 2a and 2b). Furthermore, these observations were supported by the GAM results where we observed a linear positive effect of tamarack basal area on residual basal area. However, we hypothesized to observe the highest basal area in mixed stands where black spruce and tamarack occupied equal proportion (Sterba et al. 2018). Our second hypothesis was confirmed, tamarack dominated stands did not negatively affect black spruce quadratic mean diameter and black spruce stem density. The third hypothesis was not confirmed as we did not observe a modulation of mixed stand residual basal area from climatic variables. Finally, we detected higher residual basal area deviation from West to East in boreal forests of Québec, and lower deviation in organic soils confirming the influence of site conditions.

3.4.1 Tamarack and black spruce effect on mixed stand basal area

We anticipated a bell-shaped relationship where the residual basal area deviation would peak when tamarack and black spruce occupy equal proportions (50-50%) of the total basal area, as observed with similar European species like Norway spruce and European larch (Sterba et al. 2018). In our study, the highest residual basal area was observed when tamarack proportion was around 75%. Instead of a bell-shaped relationship, we detected a linear effect of tamarack on residual basal area. This observation could suggest the substitution of black spruce stems for tamarack stems, as tamarack has a larger stem size at maturity than black spruce (Viereck and Johnston, 1990; Johnston 1990). However, this was not the case, as black spruce stem density was constant throughout tamarack classes in the quantile analyses. Furthermore, black spruce quadratic mean diameter linearly increased with tamarack basal area, and the largest black spruce stems were recorded in stands with high tamarack basal area (≥10 m^2 ha^{-1}). Black spruce growth is known to be positively influenced by deciduous tree basal area (Oboite and Comeau, 2019). Our results suggested a positive contribution from black spruce stems to residual basal area deviation, even in tamarack-dominated stands. A recent study showed lower growth of evergreen trees caused by deciduous companion trees, which sustain a higher growth rate than in monospecific stands (Urgoiti et al., 2023). Our result suggested no detrimental effect of tamarack on black spruce and possibly a positive effect.

In quasi pure stands of black spruce (<2 m^2 ha^{-1} of tamarack), we observed a lower commercial stem density, which may be due to a high level of intraspecific competition. High intraspecific competition in black spruce monospecific stands was observed by Légaré et al. (2004) and Roy Proulx et al. (2023). The increase in tamarack basal area had a positive effect on black spruce size and stem density, suggesting niche complementarity between species. Also, the studied mixed stands could support higher stem density than in monospecific stands. Several studies documented the significant effect of stand density on species interaction or the lack of interaction when the density is low (Forrester and Bauhus, 2016; Pretzsch and Biber, 2016; Himes and Puettmann, 2020). Norway spruce and European larch have highly compatible crown shapes as the stand density was increased by 29.1% and the mortality was reduced due to less self-thinning compared to monospecific stands (Pretzsch and Biber 2016). In our case, black spruce-dominated stands could have had lower stem density due to high intraspecific competition and a lower maximum stem density than stands with even species proportions. We cannot assess the exact mechanism, but stem density strongly dictates total basal area, possibly through mortality and the modulation of growth interaction (Pretzsch and Forrester, 2017). Under low competition, species with high resource needs show a positive effect of tree diversity, whereas a positive tree diversity effect is observed under higher competition for species with lower resource needs (Fichtner et al., 2017). In addition, the modulation of the competition from the density effect is consistently more detrimental to growth in monospecific than in mixed stands (Forrester et al., 2006; Pretzsch et al., 2013). Tamarack growth is more responsive to climate variation (Tian et al., 2022; Stelling et al., 2023) and to competition (Roy Proulx et al., 2023); thus, it seems to have higher resource needs than black spruce. Our investigation of species proportion suggests higher competition in stands dominated by black spruce, and the inclusion of tamarack reduces competition, as observed from residual basal area deviation and the increases of black spruce stem density and size.

We observed lower residual basal area deviation on organic surficial deposits compared to all other surficial deposits. Mixed stands of black spruce and tamarack are commonly found on organic deposits with slow drainage (See Supporting information A3, Table A3) However, these difficult growth conditions lowered residual basal area and probably the growth of both species. Tamarack is more adapted than black spruce to soil hydromorphic conditions and it can sustain higher growth rates in such slow drainage circumstances (Islam et al. 2003, Islam and Macdonald 2004). Sandy and mesic soil types are better for black spruce growth compared to sub-hydric and rocky sites (Pau et al. 2021). Many of our sampled stands were in western boreal forests of Québec often characterised by organic soils resulting from paludification (Fenton et al., 2005). The observed soil effect could explain the low black spruce stem density in stands without a sufficient proportion of tamarack. Tamarack can have a positive effect on neighboring tree growth due to a higher water uptake in organic soils and probably enhancing soil decomposition rates (Jutras et al. 2006). A positive effect on growth conditions from tamarack may explain the threshold effect observed around 5 m² ha^{-1} in the GAM predictions (Figs. 3a and 4). This threshold was also observed in the 90th quantile regression, where the addition of 2 m² ha^{-1} of tamarack from the first to the second classes resulted in a maximal increment of 6.97 m² ha^{-1} in residual basal area (Fig. 2b). The basal area difference of 3 m² ha^{-1} between these classes is a consequence of black spruce stems. Further investigations are needed on tamarack's potential to reduce water content in organic soils.

3.4.2 Residual basal area, age and overyielding

We only selected stands dominated by black spruce (up to 90% of total basal area) and tamarack (up to 75% of total basal area), therefore we can parsimoniously compare our findings to formal overyielding studies by using both ends of the mixture gradient and deviation from residual basal area. However, we cannot formally assess overyielding in mixed stands compared to monospecific stands because we solely focused on mixed stands (Pretzsch and Schütze, 2009; Pretzsch et al., 2013). We observed a positive interaction between stand age and tamarack, suggesting earlier reach of positive residual basal area starting in stands aged 50 when tamarack basal area > 20m²/ha. This can seem late on a stand rotation perspective, but we studied mixed stand mainly established on less productive sites (Table 1). Positive interaction can be observed as soon as 20 years after seedling establishment in some of Finland's boreal forests (Jucker et al. 2020). Most studies show the interactions peaking around 20 to 40 years, leading to positive or negative growth effects (Forrester, 2014; Feng et al., 2022). The growth interaction can be delayed by poor site conditions or by low stem density. In less productive sites, tamarack may accelerate the attainment of sexual maturity, as size is linked to sexual maturity (Viglas et al., 2013). Black spruce reproductive maturity can be achieved as late as 90 years to produce a sufficient seed supply to regenerate stands after fire (Viereck and Johnston, 1990; Viglas et al. 2013). Therefore, if tamarack enhances its neighbor's size between 50 and 90 years, as suggested by our results, it could benefit black spruce seed supply, reducing risks of regeneration failure with early sexual maturity, which is crucial to maintain yield in boreal forests, where fire is prevalent (Payette, 1992; Splawinski et al., 2019). Further investigations are needed to assess the potential for reducing risks of regeneration failure for mixed stands of black spruce and tamarack, and our results are promising in that regard. Nonetheless, throughout our results (GAM and 90th regression) we observed mixed stands with less than 5 m² ha^{-1} of tamarack were unlikely to achieve positive residual basal area deviation. This last observation seems to highlight the importance of species proportion evaluated a mixture potential to enhance resistance and resilience to disturbances (Grossiord et al., 2014; Knoke, 2017; Metz et al., 2016).

We selected mixed stands with a minimum black spruce proportion of 25%; therefore, we can expect a non-negligible contribution of black spruce stems to all observed effects on residual basal area. The quadratic mean diameter of black spruce was highest (17.8 cm) in stands with tamarack basal area exceeding 10 m^2 ha^{-1}, suggesting larger black spruce stems in tamarack dominated stands. Sterba et al. (2018) recorded the highest overyielding in mixed stands composed of Norway spruce and European larch at mid-proportion mixtures and in 170-year-old stands; however, the same stands exhibited underyielding at age 50. In our case, we only examined the tamarack effect and observed the largest residual basal area deviation in stands dominated by tamaracks aged between 145 and 170 years (Fig. 3a). Therefore, to maximize total basal area, we recommend using silviculture treatments that result in stands dominated by tamarack with 25% of black spruce. Other studies highlight the importance of age and species proportions in yield variation of mixed stands (Sterba et al., 2018; Jucker et al., 2020).

Our approach using residual basal area was designed to observe deviation from expected stem density and explain these deviations with our selected variables. We did not investigate the stem spatial distribution or the relative height of each species in the selected stands, which could provide more insight on stand structure (Sterba et al., 2018; Pretzsch et al., 2015). Stand density partially captures the effect of stand structure on growth interaction in mixed stands (Perot and Picard, 2012), which modulates maximum stand density (Pretzsch and Biber, 2016). The observed deviation in residual basal area can be influenced by changes in maximum stand density with species proportions. Improvement in light interception from structural differentiation in crown and height explains the positive effect on growth observed in mixed stands (Kelty, 1992; Pretzsch, 2014; Vacek et al., 2021). In mature, even-aged mixed stands of black spruce and tamarack, the difference in height between species is marginal (Roy Proulx et al., 2023), reducing bias of not measuring crown width and height.

All climate variables had a limited effect on residual basal area, suggesting a growth stability to climate in mixed stands of tamarack and black spruce (Appendix A1, Table A1). Some studies show an increased resilience of mixed stands to climate variation including drought or heat stress (Steckel et al., 2020; Chavardès et al., 2021), while some species mixtures do not reduce the negative drought effect on growth (Pretzsch et al., 2018). We used mean climatic values and the cumulative Degree Days >5 °C from 1980 to 2010 to characterize the last 30 years conditions, which has less temporal precision compared to yearly climatic variables. However, annual growth is more responsive to yearly climatic variables and provides insightful climate-growth relationships. Interspecific growth interactions of black spruce are modulated by annual climate variables like temperature and precipitations (Oboite and Comeau, 2019). However, the outcome of this interaction between climate and black spruce growth changes with companion species identity and it is positive with deciduous companion species and negative with balsam fir (Oboite and Comeau, 2019). Our results did not indicate a high impact of climate variables, showing encouraging signs for tamarack and black spruce stands in facing regional to global changes in climate. Chavardès et al. (2022) similarly found that companion species could attenuate the impact of heat stress on black spruce in some boreal forests with distinct surficial deposits of eastern Canada, whereas Stelling et al. (2023) showed black spruce growth stability and tamarack sensitivity to climate in monospecific stands. Our study provides some insight that mixing these species could enhance growth stability, but proper comparison with both species in monospecific stands remained to be tested.

3.4.3 Managing tamarack and black spruce stands

To provide clear targets for management, we calculated the percentage of each tamarack basal area class only for stands with sufficient wood volume (≥50 m^3 ha^{-1}) (Cyr et al., 2022) (Appendix A2, Figs. A2 and A2.1). Our results indicated that retaining ~55% of tamarack or more maximizes the total stand basal area, with black spruce proportion comprising ~35 % of the total basal area (Appendix A2). To maximize black spruce basal area while achieving positive residual basal area deviation, the target tamarack basal area to maintain is around 5 m^2 ha^{-1}, which corresponds to approximately 27% of the total basal area in productive stands (Appendix A2, Figs. A2). The mid tamarack classes (>2 to <10 m^2 ha^{-1}) had a positive effect on black spruce size, ranging from 12.5 to 13.1 cm in quadratic mean diameter, while maintaining its stem density around 750 stems ha^{-1}. The percentage of the total basal area occupied by tamarack in these middle classes (>2 to <10 m^2 ha^{-1}) ranged from 15-43%, while black spruce percentage was between 56-79% (See Appendix A2, Figs. A2 and A2.1). These percentages can be targeted by forest managers seeking to maximize black spruce productivity and total basal area at the same time.

Our results provided insights into species proportions that maximize total basal area or black spruce basal area. Research based on large datasets covering a wide spectrum of environmental conditions is useful to understand the main trajectory of interspecific growth relations and to estimate optimal mixture ratios. Yet, individual tree growth models are better suited to untangle the exact mechanisms behind growth interactions to integrate these effects into forest management predictions and planification (Pretzsch, 2022).

3.5 Conclusion

We examined secondary growth (radial growth) of mixed black spruce and tamarack stands in a suite of growing conditions from plots distributed across a vast territory (> 535,000 km²) of Québec. Our results revealed the capacity of black spruce and tamarack to grow together under various climatic and site conditions. Notably, tamarack showed potential to produce positive deviations from the expected relationship between stem density and basal area in mixed stands with black spruce. Tamarack's potential to enhance basal area was achieved in stands with >5 m^2 ha^{-1}, whereas stands with less tamarack basal area showed less potential. The lowest basal area was observed in black spruce-dominated stands when tamarack proportion was near 10 % of the basal area. Tamarack and stand age interaction exhibited the highest positive effect on residual basal area, beyond the respective simple effects. All tested climatic variables had limited effects on residual basal area, suggesting growth stability in the sampled mixed stands.

Our study provided quantitative information for forest managers on the range of black spruce and tamarack mixing proportions that enhance stand basal area. Nonetheless, we advocate for additional research examining overyielding in mixed black spruce and tamarack stands, and the need to control for stem density as well as surficial deposits and drainage as they all impact growth interactions. Black spruce with tamarack is a species combination showing compatibility. Given the importance of sustainable management for future forests (Schuler et al., 2017; Coll et al., 2018; Reventlow et al., 2021), our study provides support for the establishment of mixed stands with studied species.

3.6 Acknowledgments

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3.7 Author contributions

AL and NT acquired funding. SRP, NT, and AL conceptualized the project. SRP wrote the original draft. SRP and RC retrieved and curated data. SRP, NT, and AL conducted the analyses. NT, AL, and RC read, commented, edited and approved the final manuscript.

3.8 Conflicts of Interest

The authors declare that they have no competing interests.

3.9 Appendix A : Linear regression between basal area and stem density in sampled mixed stands and BIC model selection.

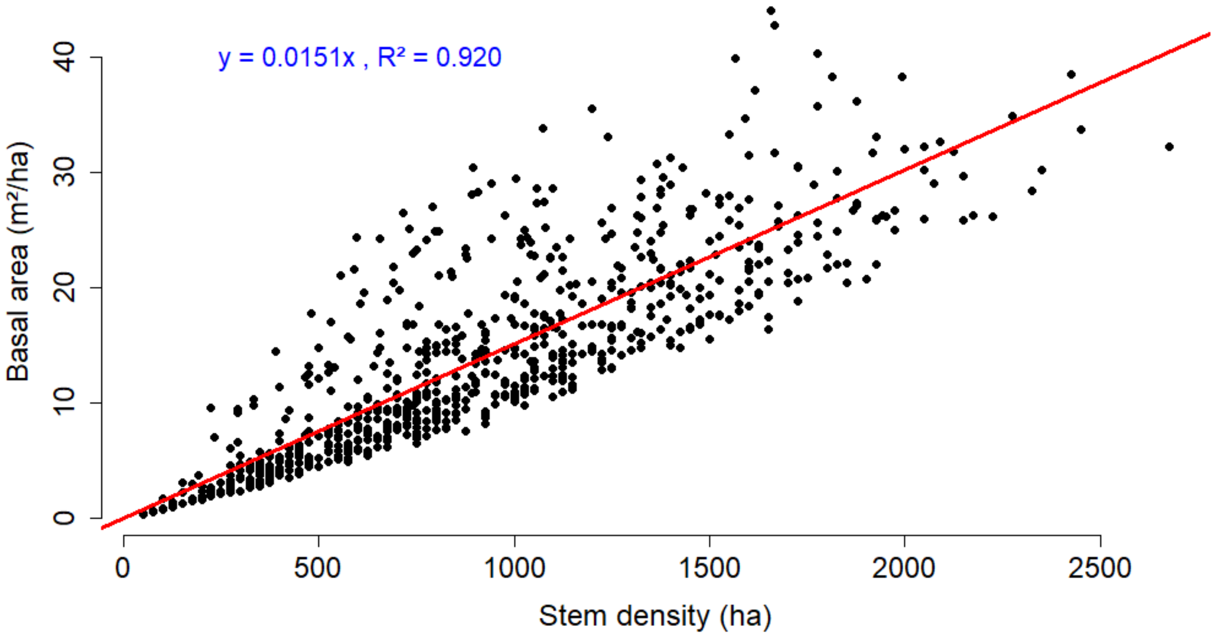

Figure 3.5 : Linear regression between basal area (m² ha^{-1}) and stem density (ha) for black spruce and tamarack mixed stands.

Table 3.3 : Most parsimonious models explaining residual basal area, including the degrees of freedom (df), the BIC score (BIC), the distance from highest-ranked model (ΔBIC), and model predictive power (Adjusted R²). Variables in the generalized additive model base model: SDD: surficial deposit, MSP: Mean Seasonal Precipitation, MAT: Mean Annual Temperature, TAM: tamarack basal area, AGE: stand age, LAT: latitude, LONG: longitude, DD5: Degree Days >5°C.

Candidate model	**df**	**BIC**	**ΔBIC**	**Adjusted R²**
Base model + TAM x AGE	**31.8**	**4210**	**0**	**0.464**
Base model	25.1	4270	60	0.367
Base model + TAM x MSP	32.3	4299	89	0.376

Base model + TAM x LONG	37.4	4308	98	0.392
Base model + LONG x LAT	35.9	4309	99	0.385
Base model + TAM x DD5	37.6	4316	106	0.386
Base model + TAM x LAT	38.1	4317	107	0.388
Base model + TAM x MAT	39.0	4318	108	0.391
Base model + TAM x SDD	53.3	4387	177	0.399

3.10 Appendix B : Tamarack and black spruce percentage as function of tamarack basal area

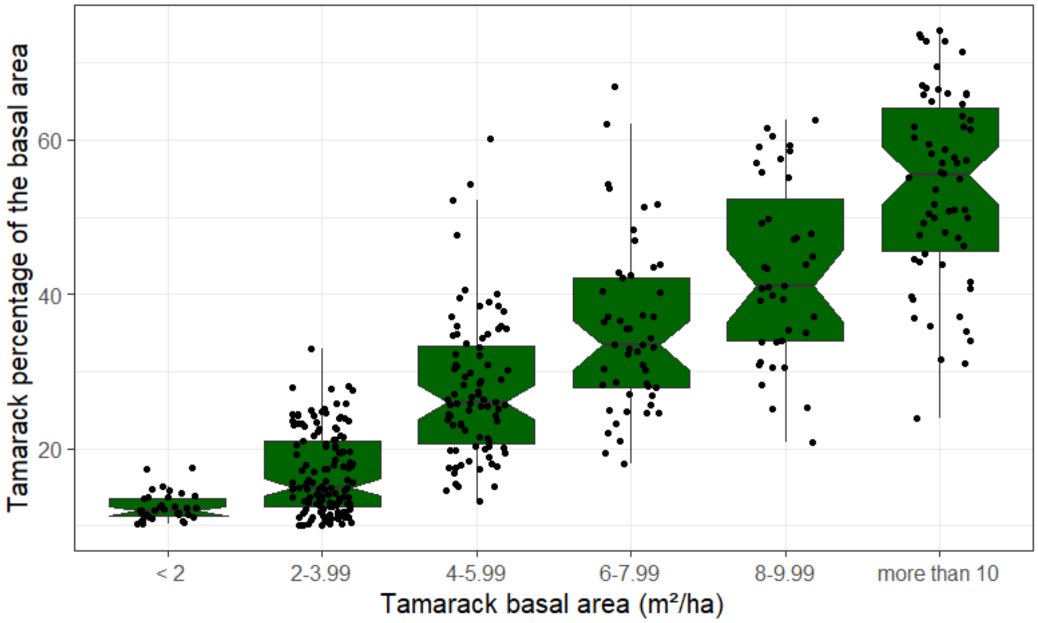

Figure 3.6 : Tamarack percentage of the stand total basal area as a function of tamarack basal area (m²/ha) for stands with ≥50 m³/ha. Box plots represent quantiles (0.025, 0.25, 0.5, 0.75, 0.975).

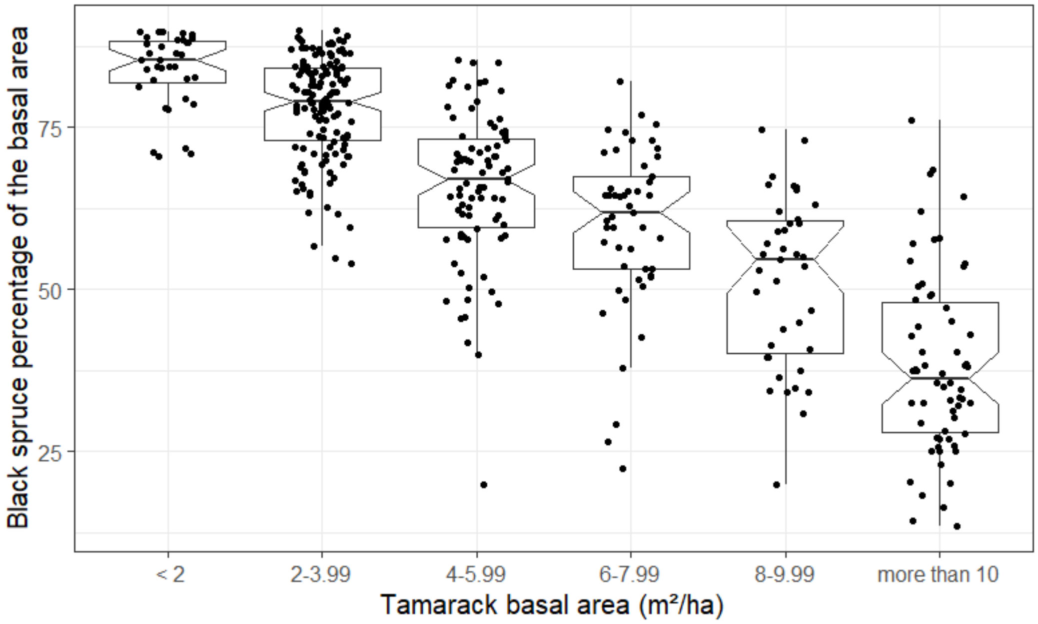

Figure 3.7 : Black spruce percentage of the stand total basal area as a function of tamarack basal area for stands with ≥ 50m³/ha. Boxplots represent quantiles (0.025, 0.25, 0.5, 0.75, 0.975).

3.11 Supporting information A1

Table 3.4 : Pearson’s correlations between variables for the generalized additive model

	Mean Seasonal Precipitation	Summer Heat Moisture	Degree Days >5°C	Hogg’s Climate Moisture Index	Mean annual temperature	Tamarack basal area	Stand age	Longitude	Latitude
Mean Seasonal Precipitation		**-0.87**	-0.27	**0.72**	-0.13	0.08	-0.10	0.27	-0.42
Summer HeatMoisture			0.69	**-0.83**	0.37	-0.03	-0.08	-0.50	0.06
Degree Days >5°C				-0.61	0.64	0.08	-0.36	-0.56	-0.54
Hogg’s Climate Moisture Index					0.01	0.10	0.09	**0.78**	-0.18
Mean Annual Temperature						0.19	-0.31	0.16	-0.64
Tamarack basal area							-0.08	0.06	-0.18
Stand age								0.13	0.37
Longitude									0.03
Latitude									

3.12 Supporting information A2

Table 3.5 : List and formulation of all candidate models summited to BIC model selection, RBA : residual basal area, SDD: surficial deposit, MSP: Mean Seasonal Precipitation, MAT: Mean Annual Temperature, TAM: tamarack basal area, AGE: stand age, LAT: latitude, LONG: longitude, DD5: Degree Days >5°C.

Candidate models	**Model formulation**
Base model	RBA ~ SDD + MSP + DD5 + MAT + TAM + AGE + LAT + LONG
Model 1	RBA ~ BASE MODEL
Model 2	RBA ~ BASE MODEL + TAM x SDD
Model 3	RBA ~ BASE MODEL + TAM x MSP
Model 4	RBA ~ BASE MODEL + TAM x DD5
Model 5	RBA ~ BASE MODEL + TAM x MAT
Model 6	RBA ~ BASE MODEL + TAM x AGE
Model 7	RBA ~ BASE MODEL + TAM x Latitude
Model 8	RBA ~ BASE MODEL + TAM x Longitude
Model 9	RBA ~ BASE MODEL + Latitude x Longitude

3.13 Supporting information A3

Table 3.6 : Classification of surficial deposit-drainage (SDD) based on surficial deposit and drainage (Slow = 50 and 60; moderate = 30 and 40; Rapid = 0, 10 and 20).

	Surficial deposit	SDD	Drainage (number of plot)		N
4GA	Glaciolacustrine: shallow-water facies (> 1 m)	CLAY	Moderate	58	153
			Slow	95	
1A	Undifferentiated till	TILL	Rapid	2	118
1BF	Frontal moraine		Moderate	89	
1AA	Cochrane till		Slow	27	
7E	Thick organic deposits	ORG	Moderate	2	295
7T	Thin organic deposits				
7TY	Thin organic deposits (50 cm to 1 m) with outcrop		Slow	293	
7TM	Thin organic deposits (25 to 50 cm) with outcrop				
1AD	Washed Till	OTHERS	Rapid	40	189
1AM	Undifferentiated till > 25 cm to 50 cm with rare or scanty outcrops				
1AY	Undifferentiated till > 50 cm to 1 m with rare or very rare outcrops				

1BP	Dead-ice moraine	Moderate	119
2A	Juxta-glacial deposits		
2BE	Outwash plain		
3AN	Ancient alluvial deposit		
4A	Lacustrine plain		
4GAR	Glaciolacustrine: deep-water facies (>25 cm to 1 m)		
4GS	Glaciolacustrine: shallow-water facies (<25 cm)		
5S	Shallow-water facies		
6S	Raised beach		
8A	Altered materials	Slow	40
8AM	Altered materials > 25 cm to 50 cm with rare or scanty outcrops		
8AY	Altered materials > 50 cm to 1 m with rare or very rare outcrops		
M1A	Thin till (< 25 cm)		
R1A	Outcrop between 25 and 50%		

Total	756

3.14 Supporting information A4

Table 3.7 : Variance inflation factor for variables in the generalized additive model.

Variables	VIF
Mean Annual Temperature	9.08
Degrees Days >5°C	6.95
Latitude	6.25
Longitude	5.19
Mean Seasonal Precipitation	3.31
Age	1.23
Tamarack basal area	1.07

3.15 Supporting information A5

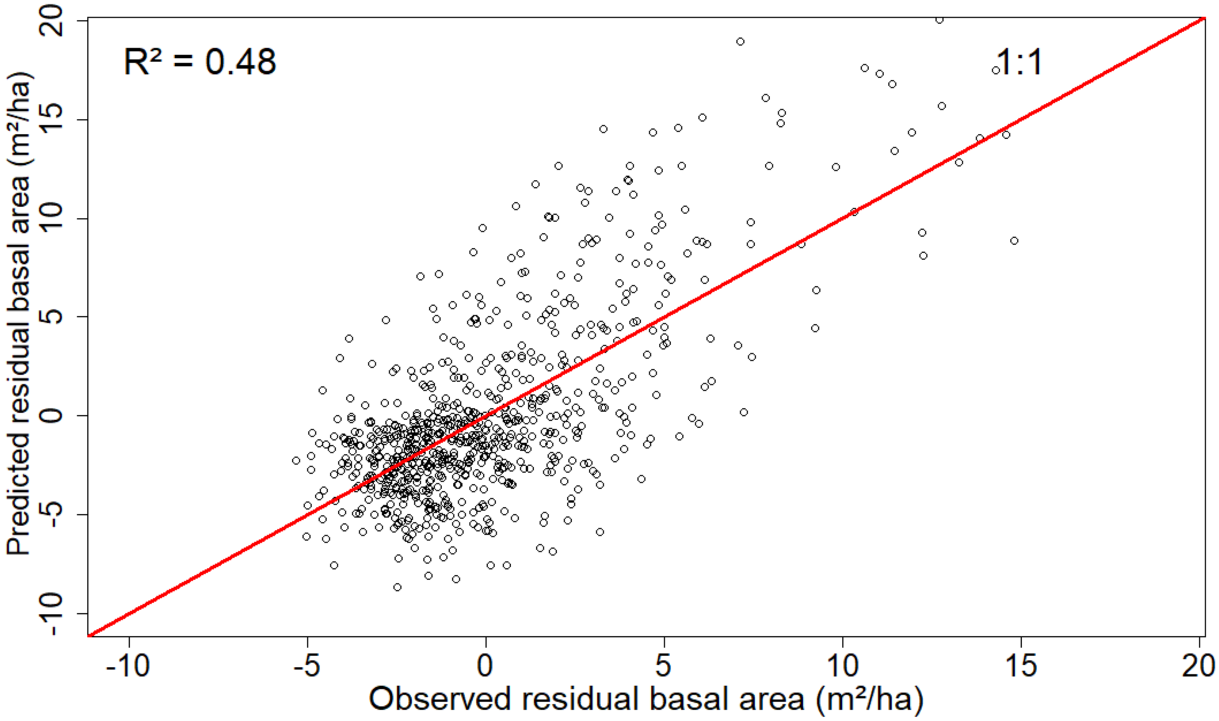

Figure 3.8: Predicted residual basal area (m² ha^{-1}) as a function of observed residual basal area (m² ha^{-1}) for the selected generalized additive model. The diagonal line represents the one-to-one relationship.

CHAPITRE 4 CONCLUSION GÉNÉRALE

En explorant les relations de croissances entre le MEL et l'EPN en forêt boréale à différents moments du développement des peuplements, notre objectif était d'estimer dans quelle mesure et sous quelles circonstances le MEL pouvait être bénéfique pour la croissance de l'EPN et pour la productivité des peuplements mixtes. Notre étude visait à évaluer l'existence de relations de croissance positives (facilitation et niche complémentaire) ou des relations de croissance moins négatives entre les essences choisies, soit le MEL et l'EPN. Ce faisant, le MEL et l'EPN semblent avoir des niches de croissance complémentaires et les plantations mixtes EPN—MEL sont plus susceptibles d'augmenter la productivité que les peuplements monospécifiques d'EPN. Enfin, nous pensons que d'autres approfondissements des connaissances en reboisement mixte sont nécessaires puisque deux chapitres de notre étude portaient sur des forêts mixtes d'origine naturelle ; en effet, les trajectoires de croissance peuvent être très différentes selon l'origine du peuplement (Bergeron et al., 1999; Wu et al., 2022).

Retour sur les volets de notre étude

Notre premier chapitre suggère que les EPN matures sont moins sensibles à la compétition que les MEL, mais ces derniers compensent par des taux de croissance plus élevés. Cette plus grande sensibilité du MEL à la compétition et aux variables climatiques a aussi été observée par Stelling et al. (2023). De plus, nos résultats suggèrent que l'EPN récupère plus rapidement sa croissance radiale opprimée par la compétition produite par ses voisins au fur et à mesure que son diamètre augmente. De son côté, la croissance du MEL est moins affectée que celle de l'EPN par la taille de ses voisins (Fig. 4.1). Ces réactions à la compétition suivent les tolérances à l'ombre des deux essences dans des peuplements matures équiens où la lumière est limitante. Le MEL, intolérant à l'ombre, est désavantagé par rapport à l'EPN, qui lui, la tolère bien lorsque ceux-ci ont des hauteurs similaires (Strong et Roi, 1983). De plus, nous avions testé, sans grand support, l'effet de la direction des voisins dans l'effet du voisinage avec la formulation de Boivin et al. (2010). Il est étonnant de voir que les variations de croissances de nos deux espèces n'étaient pas davantage expliquées par cette formulation de l'effet du voisinage, surtout pour le MEL. Le développement de ce peuplement mixte suggère que le MEL atteint plus rapidement sa hauteur maximale que l'EPN, mais lorsque ce dernier atteint la canopée, sa croissance radiale pourrait être augmentée. Il n'y avait pas de différence entre le voisinage d'EPN et de MEL sur leur croissance radiale alors que l'effet de l'espèce n'impactait pas l'effet global du voisinage. Cependant, l'effet compétitif du MEL sur ses voisins était plus variable et légèrement moins négatif que celui de l'EPN. Dans les peuplements mixtes étudiés, l'effet compétitif prédominant était celui de la taille des voisins plutôt que celui de la distance ou de l'identité de l'essence voisine. L'auto-éclaircie avait déjà eu lieu lorsque la distance moyenne entre les arbres était supérieure à 7 m, expliquant l'absence d'effet de la distance. Il serait intéressant de connaître l'intensité de l'effet de la distance avant l'auto-éclaircie lors de la fermeture de la canopée et ainsi, mieux prévoir des travaux d'éclaircie répliquant cette dynamique naturelle. De plus, les relations de croissance restent à être étudiées dans des peuplements matures à structure irrégulière et sur d'autres types de sols que des sols organiques. Ces questions demeurent en suspens et découlent de notre étude sur les peuplements matures mixtes EPN—MEL. L'investigation des relations de croissance avant l'auto-éclaircie apporterait des réponses sur les ratios optimaux des essences à utiliser en reboisement.

Les résultats de notre deuxième chapitre investiguant les effets compétitifs dans les jeunes peuplements mixtes et monospécifiques d'EPN nous permettent de créer un gradient d'intensité de la compétition subie par l'EPN selon la composition de l'environnement immédiat de croissance (Fig. 4.1). Le plus fort effet négatif sur la taille des EPN était la présence considérable d'arbustes et de plantes concurrentes (Fig. 4.1). Par ailleurs, les EPN dans les plantations mixtes ont une plus grande taille via une réduction de la compétition comparativement aux EPN en plantations monospécifiques (Fig. 4.1). Comme l'EPN est l'essence la plus utilisée pour le reboisement au Québec à 56,9 % (Salmon, 2017), l'identification d'une essence compagne pouvant aider à sa croissance pourrait ajouter une option de reboisement mixte sur ce territoire nordique. L'échelle et la portée de ce volet ne justifient pas la mise en place d'un reboisement mixte à grande échelle, mais certainement une augmentation du nombre de placettes expérimentales sur différents types de sols et dans d'autres régions du Québec. De plus, le suivi du dispositif échantillonné, lorsque celui-ci aura entre 20 et 50 ans, apporterait des indications manquantes et importantes à ce moment charnière, puisque les relations de croissances y atteignent un sommet (Forrester, 2013; Feng et al., 2022). De plus, nous avons observé une plus grande fermeture du couvert dans les plantations mixtes, ce qui pourrait accentuer la compétition pour la lumière (Fig. 4.1). Au moment de notre étude, nous avons même observé un effet positif de la présence du MEL sur la taille des EPN. Une occupation différente en hauteur, une forme complémentaire du houppier et une plus faible densité de feuillage du MEL peuvent expliquer l'effet observé (Lambert et al., 2005; Pretzsch, 2013). Par la suite, lorsque les EPN se trouvaient en voisinage mixte, leurs aiguilles avaient une plus grande concentration en azote et le pH du sol était légèrement moins acide.

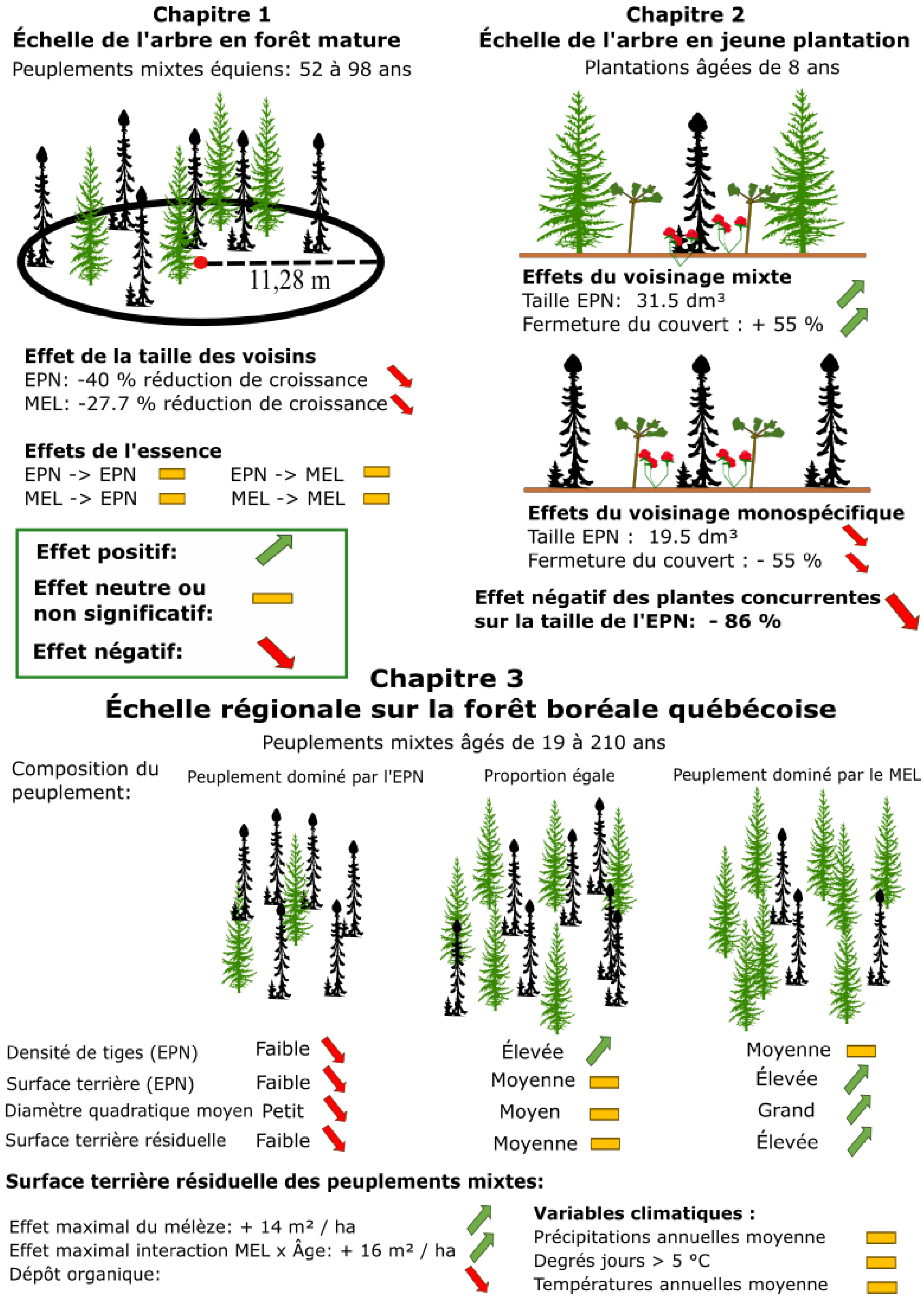

Figure 4.1: Représentations schématiques des principaux résultats pour chacun des chapitres de l'étude. Mélèze laricin (Larix laricina) (MEL), Épinette noire (Picea mariana) (EPN).

Le troisième chapitre, portant sur l'analyse des placettes-échantillons temporaires de la forêt boréale québécoise, apporte plusieurs constats sur la dynamique et l'occurrence des peuplements mixtes d'EPN et de MEL. En effet, les placettes dominées par l'EPN (> 90 % de la surface terrière) sont abondantes (N = > 10000) dans les domaines bioclimatiques de la pessière à mousses et de la sapinière à bouleau blanc du Québec. Les placettes mixtes sont en plus faible quantité (N = 756) et les placettes pures de MEL sont très rares (N = < 40), en plus de se retrouver presque uniquement sur des sites à mauvais drainage et sur les dépôts organiques. Cette association systématique entre le MEL et les sols organiques peut être due à sa grande capacité à pousser sur ce type de sol (Islam et al., 2003). La faible occurrence du MEL pourrait aussi être expliquée par sa faible utilisation en reboisement (Salmon, 2017; CCFM, 2020) et à l'impact négatif des épidémies de tenthrède du mélèze (*Pristiphora erichsonii* (Hartig)) au début du 20^{e} siècle (Turnock, 1972). Ces deux phénomènes expliquent pourquoi nous retrouvons le MEL sur les sites moins productifs. Actuellement, il est difficile d'évaluer le rendement des peuplements mixtes EPN—MEL à l'échelle de la forêt boréale du Québec sur des dépôts plus productifs et ayant un meilleur drainage. L'effet observé par la longitude soutient l'affirmation selon laquelle les peuplements mixtes EPN—MEL se retrouvent majoritairement sur des sols d'argile et organiques, alors qu'une forte abondance de ce type de sol se trouve à l'ouest du Québec. D'autre part, nous avons observé plusieurs effets positifs du MEL sur la surface terrière résiduelle (relation entre le nombre de tiges et la surface terrière), sur le diamètre quadratique moyen et sur la densité de tiges de l'EPN (Fig. 4.1). De plus, l'interaction supportant le mieux les variations de surface terrière résiduelle était formée de l'âge du peuplement en interaction avec la surface terrière du MEL. Ces multitudes d'effets positifs du MEL sont très encourageants pour une utilisation accrue des peuplements EPN—MEL (Fig. 4.1).

Il est à noter que les variables climatiques n'ont pas eu d'effet sur la surface terrière résiduelle. Ainsi, la température moyenne, les précipitations et le nombre de degrés jours > 5°C n'ont pas eu d'effet significatif sur la variable réponse. Cependant, l'utilisation d'un taux de croissance annuel des arbres (biomasse totale, croissance en hauteur/diamètre, etc.) est plus appropriée que la surface terrière à l'hectare dans l'investigation des relations climat—croissance. D'un autre côté, l'utilisation de la surface terrière par placette permet d'inclure une plus grande quantité d'arbres dans nos analyses, d'observer des tendances sur plusieurs décennies et ainsi, d'observer un effet à long terme du climat sur la surface terrière. Nos résultats montrent une stabilité de la surface terrière résiduelle face aux variables climatiques de 1981 à 2010. Notre investigation actuelle sur ces relations suggère un potentiel encouragent des peuplements MEL—EPN à constituer des peuplements mixtes plus résilients faces aux changements climatiques. En effet, certains peuplements mixtes sont moins vulnérables aux perturbations naturelles en plus d'être plus résilients et résistants aux épisodes de sécheresse (Pretzsch et al., 2012; Jactel et al., 2018; Chavardès et al., 2022).

Investigation de la surproductivité des peuplements EPN—MEL

L'approche préconisée par cette thèse était de mettre le MEL comme point central et d'évaluer son potentiel à améliorer la croissance de ses voisins et le rendement des peuplements mixtes. Le choix de l'EPN comme essence compagne provient de son fort intérêt par l'industrie forestière et de ses caractéristiques complémentaires avec le MEL, que nous avons déjà énumérées. Nous avons déjà évoqué les différentes façons de mesurer la surproductivité entre les peuplements mixtes et monospécifiques, mais cette investigation compartimente les peuplements selon leur type et leur composition en essence, alors que notre but était d'examiner les effets du MEL sur ses voisins et son environnement. Dans ce contexte, il n'était pas dans nos objectifs d'examiner les peuplements monospécifiques des deux essences, ceci nous éloignant des effets du MEL comme point central de notre étude, principalement dans l'investigation des effets compétitifs interspécifiques. Par ailleurs, les résultats produits par l'ensemble de cette thèse, notamment lors du troisième chapitre, posent des bases pour de futures études sur la surproductivité. En effet, nous avons investigué les peuplements mixtes allant de dominés par l'EPN (≤ 90 % de la surface terrière) jusqu'à des peuplements dominés par le MEL (≤ 75 %). Une maximisation de la surface terrière était observée lorsque le MEL était présent à près de 75 % de la surface terrière, suggérant qu'un peuplement dominé par le MEL offrirait une plus grande surface terrière. De plus, en étudiant l'augmentation graduelle du MEL dans les peuplements, nos résultats montrent des effets positifs ou de maintien du MEL sur l'EPN, notamment sur sa taille et sa densité de tiges à l'hectare.

Des essences similaires ont déjà été étudiées, donnant d'autres indications sur les proportions prometteuses menant à des augmentations de rendement et sur les conditions requises pour les atteindre (Mina et al., 2017; Oboite & Comeau, 2019). Mina et al. (2017) ont étudié l'épinette de Norvège et le mélèze Européen, montrant qu'ils ont des niches complémentaires, augmentant ainsi la croissance moyenne de 30 % lorsque la compétition est forte dans le peuplement (surface terrière des voisins de 20 à 80 m²). De plus, la complémentarité des niches de croissance était modulée par l'humidité relative (Mina et al., 2017). Il s'agit donc d'un contexte spécifique de surproductivité qui peut aussi se solder par une sous-productivité lorsque ces conditions ne sont pas en place (Mina et al., 2017). Kweon et Comeau (2019) ont listé sept facteurs influençant la surproductivité des jeunes peuplements de la forêt boréale de l'Ouest canadien. Les facteurs étaient très variés, allant des variables climatiques, de compétition et de taille des arbres jusqu'à l'effet de différents traitements sylvicoles (Kweon & Comeau 2019).

Plusieurs études se basent sur les distances phylogénétiques et les traits fonctionnels pour évaluer le potentiel de complémentarité des niches de croissance entre deux essences (Coyle et al., 2014; Paquette et al., 2015; Searle & Chen, 2020). Cependant, dans le cas du MEL et de l'EPN, ceux-ci sont proches phylogénétiquement puisqu'ils font partie de la famille des *Pinaceae* (Wang & Ran, 2014). C'est pour cette raison que nous proposons davantage les différences ontogéniques comme pistes expliquant la complémentarité des niches de croissance observées entre l'EPN et le MEL. Boyden et al. (2009) proposent aussi cette piste pour expliquer la surproductivité en peuplement EPN—MEL, alors qu'ils ont étudié les dix premières années d'interactions de croissance entre ces deux essences. Cette explication semble la plus plausible pour expliquer le fondement de la complémentarité des niches de croissance entre l'EPN et le MEL.

L'étude de la surproductivité est complexe ; celle-ci est influencée par plusieurs facteurs (Kweon & Comeau, 2019) et différentes variables peuvent être utilisées pour la mesurer (Kelty, 2006; Paquette & Messier, 2011; Searle & Chen, 2020). Les différences de productivité peuvent être mesurées sur la biomasse totale, une partie de la biomasse (tronc, branches, racines et biomasse foliaire) ou sur la croissance (radiale ou en hauteur) (Kelty, 2006; Paquette & Messier, 2011). Cependant, l'investigation de la biomasse totale est difficilement réalisable, particulièrement dans la quantification de changements au fil du temps sur le système racinaire ou sur l'appareil photosynthétique. Nous pensons qu'il est maintenant plus opportun de conduire des investigations sur la surproductivité entre l'EPN et le MEL en se basant sur les résultats produits dans cette thèse et en complémentarité avec les autres études sur ces mêmes essences (Boyden et al., 2009; Dijkstra et al., 2009).

Perspectives d'aménagement et de sylviculture des peuplements EPN—MEL

Le premier chapitre nous informe que le MEL et l'EPN sont tous deux principalement affectés par la taille en diamètre de leurs voisins, alors que cette étude portait sur des peuplements matures et équiens. Ces peuplements seraient de bons candidats à une coupe partielle prélevant les plus grosses tiges et laissant aux plus petites tiges marchandes l'opportunité d'augmenter leur croissance. Cependant, le recrutement de nouvelles tiges dans les trouées et la faisabilité d'une coupe partielle sur les sols organiques restent incertains (Thorpe et al., 2007).

Ensuite, les résultats du troisième chapitre soulèvent le fait que les peuplements dominés par le MEL sont ceux avec les plus fortes variations positives de la surface terrière résiduelle. Cependant, même si ces peuplements ont une plus grande surface terrière, nous sommes au fait qu'il s'agit d'une essence moins désirée par l'industrie forestière. Donc, l'établissement de plantations constituées à 25 % d'EPN et à 75 % de MEL reste peu réaliste dans le contexte forestier québécois. Cependant, nous avons aussi observé une forte variation positive de la surface terrière résiduelle lorsque le MEL constituait 27-30 % de la surface terrière totale. De surcroît, à cette proportion de MEL, le diamètre quadratique moyen et le nombre de tiges à l'hectare d'EPN sont augmentés. Donc, une première approche pourrait être d'inclure une plus faible proportion d'une essence moins désirable (27 à 30 % de MEL) pour l'industrie forestière et ainsi, effectuer un premier pas vers l'aménagement d'une plus grande quantité de peuplements mixtes. Cette approche graduelle face à l'industrie forestière pourrait permettre une meilleure acceptation de ces changements, la mise en place de nouvelles stratégies de récolte et l'adaptation à l'augmentation des volumes de bois d'une essence traditionnellement moins désirable.

En plaçant nos travaux en ordre chronologique avec le développement des peuplements, nous avons vu l'effet négatif de la proximité et de la quantité des compétiteurs sur la taille des jeunes EPN âgés de 8 ans (Chap. 2 Fig. 2.2B). Par la suite, le troisième chapitre indique une augmentation linéaire des variations de la surface terrière résiduelle entre l'âge de 20 à 90 ans. Enfin, notre premier chapitre indique l'absence d'effet de la distance pour des peuplements âgés de 52 à 98 ans, montrant ainsi la fin de cette période charnière d'interactions de croissance. L'investigation particulière de la période 20 à 50 ans serait d'intérêt puisqu'il s'agit d'une période de changement des interactions pouvant grandement modifier la trajectoire de croissance et le rendement des peuplements matures (Forrester, 2014; Feng et al. 2022). Une étude sur cette période permettrait de connaître l'effet de la distance sur les relations de croissance EPN—MEL, étant donné qu'aucun des volets de notre étude ne se concentre sur cette période critique des relations de croissance. La période 20 à 50 ans correspond également au moment de l'auto-éclaircie naturelle et pourrait servir de guide aux travaux d'éclaircie pré-commerciale. L'importance d'avoir des informations précises sur la période d'auto-éclaircie est révélée par Pretzsch et Biber (2016), qui ont observé une augmentation de la densité de tiges de 29% en peuplements mixtes et la réduction de la mortalité durant l'auto-éclaircie (Urgoiti et al. 2023b). Nous ne pouvons pas tirer les mêmes conclusions que Pretzsch et Biber (2016) sur les peuplements EPN—MEL, mais nos résultats nous amènent à s'intéresser davantage à cette étape du développement du peuplement.

Une des forces de notre étude est l'investigation à plusieurs échelles spatiales et temporelles des peuplements mixtes EPN—MEL. L'échelle spatiale plus fine (utilisée au 1^{er} et 2^e chapitre) permet de mieux comprendre et maîtriser les mécanismes de croissance ensuite observés à grande échelle dans les peuplements mixtes de la forêt boréale (3^e chapitre). Même si notre prise de données ne permet pas d'investiguer toutes les relations de croissance, elle a permis d'écarter certains effets et de suspecter la présence d'autres mécanismes menant à la complémentarité observée des niches de croissance. L'étude du stade juvénile rend possible l'observation de la mise en place d'une combinaison d'effets positifs pour la productivité pouvant subsister (pH du sol et taille des EPN) tout au long du développement du peuplement. À l'opposé, certains effets ne subsistent pas dans le temps, mais ils sont importants à étudier : l'effet de la distance des voisins et l'impact des plantes et arbustes sur la croissance des gaules. Certaines plantes concurrentes peuvent grandement entraver la productivité, retardant ainsi la fermeture du couvert (Thiffault et al. 2013). Dans le cas de plantations mixtes MEL—EPN, nos résultats se joignent à ceux de Moroni et al. (2009), montrant la bonne capacité du MEL à fermer plus rapidement le couvert et limiter l'influence des plantes concurrentes. Nos résultats montrent aussi que cette fermeture pourrait avoir un effet positif sur les dimensions des EPN. Au stade mature, nous avons analysé l'effet de la compétition à l'échelle de l'arbre (1^{er} chap.) et à l'échelle régionale, soit en examinant les variations de surface terrière (3e chap.). Un des parallèles que nous pouvons faire entre les résultats de ces deux chapitres se porte sur l'effet de la compétition interspécifique légèrement plus faible du MEL observé au premier chapitre. Cet effet semble être concret au troisième chapitre lorsque nous avons observé un effet positif du MEL sur la surface terrière sans impacter négativement l'EPN. Notre plus grande unité d'échantillonnage au troisième chapitre permet d'extraire cet effet qui n'était pas concluant lors du premier chapitre.

L'examen de la résilience et de la résistance des peuplements mixtes EPN—MEL face aux perturbations naturelles est un élément important à considérer, particulièrement à l'égard des épidémies d'insectes et des feux. Des études ont montré une réduction des dommages causés par les insectes défoliateurs en peuplements mixtes (Jactel & Brockerhoff, 2007). Le principal insecte défoliateur affectant l'EPN est la tordeuse des bourgeons d'épinette (*Choristoneura fumiferana* Clemences), alors que des défoliations annuelles répétées peuvent aller de la réduction de la croissance à la mort des individus (Blais, 1957). Cependant, Chavardès et al. (2021) ont montré une augmentation de la vulnérabilité de l'EPN à la tordeuse en peuplements mixtes avec le peuplier faux-tremble. De son côté, le MEL est affecté par la tenthrède du mélèze, celle-ci provoquant la mort des MEL fortement touché et accélérant la dynamique d'exclusion de cette essence pionnière des peuplements (Girardin et al. 2002). Notre étude ne permet pas d'apporter des réponses sur la vulnérabilité aux épidémies de tordeuses des bourgeons d'épinette et de tenthrède du mélèze en peuplements EPN—MEL. Deux éléments intéressants sont soulevés lors du troisième chapitre, apportant des réponses sur la vulnérabilité aux feux des peuplements mixtes EPN—MEL. Le premier réside en l'absence d'effet des variables climatiques sur la surface terrière résiduelle, plus particulièrement pour les variables suivantes : précipitations saisonnières, température annuelle moyenne et de degrés jours au-dessus de 5°C. L'absence d'effet négatif ou positif de ces variables représente un signe encouragent, voire même une potentielle amélioration de la résistance des peuplements mixtes face aux variations climatiques. Cette observation est d'autant plus intéressante puisqu'on sait déjà que la croissance l'EPN est vulnérable aux hautes températures (Girardin et al., 2016). Le deuxième élément est l'augmentation des variations positives en surface terrière résiduelle entre 50 et 90 ans avec l'accroissement de la surface terrière de MEL dans le peuplement. Cet effet suggère une réduction du temps nécessaire pour atteindre des variations positives de surface terrière résiduelle causée par la présence du MEL. Cette accélération pourrait augmenter la taille moyenne des EPN, réduire le temps nécessaire pour atteindre leur maturité sexuelle et donc réduire leur vulnérabilité aux feux des peuplements mixtes (Viglas et al., 2013).

Notre étude sur un type de peuplement mixte à deux essences pose plusieurs défis et diverge du contexte traditionnel d'aménagement des forêts pour la production de fibre qui homogénéise les forêts pour augmenter l'efficacité de la production (Puettmann et al. 2009). Par ailleurs, les peuplements à deux essences sont une première démarche réaliste et intéressante dans l'aménagement mixte des forêts, alors que d'autres travaux en Europe portent sur l'investigation de relations de croissance de peuplements à trois essences (Mina et al., 2017; Pretzsch, 2017). Des peuplements à trois essences complexifient encore davantage les relations de croissance et les connaissances nécessaires pour faire un aménagement durable. Paquette et Messier (2010) montrent un effet linéaire positif de la diversité en essence sur la productivité des peuplements de la forêt boréale. Leurs investigations exposent la tendance globale dans ce biome, sans pointer de combinaison d'essences en particulier. Cependant, ils montrent le lien positif entre la diversité en espèces et la diversité fonctionnelle, venant ensuite affecter positivement la productivité de la forêt boréale (Paquette et Messier 2010). De plus, il peut être souhaitable de mettre en place des peuplements mixtes simplement pour obtenir des augmentations de résilience et de résistance face aux perturbations ou encore pour les divers services écosystémiques qu'ils peuvent offrir (Jactel & Brockerhoff, 2007; Knoke et al., 2008; Gamfeldt et al., 2013; Seidl et al., 2016; Chavardès et al., 2021). Il restera toujours des angles morts, des hypothèses inexplorées, des incertitudes et des situations de croissance sur lesquelles nous avons peu d’information ou encore de la difficulté à prédire les dynamiques de croissance. Ces raisons ne doivent pas être un prétexte pour l’inaction face aux défis que pose les changements climatiques sur les modes d’aménagement de la forêt (Achim et al., 2021).

Nous pensons avoir fourni des contributions plaidant pour l’établissement d’une plus grande quantité de peuplements MEL-EPN ainsi qu’une poursuite des investigations dans ces peuplements. D’une manière plus large, notre étude correspond à un désir de mieux documenter les peuplements mixtes en général afin d’éventuellement diversifier les essences plantées en forêt boréale canadienne. D’autre part, un nombre considérablement plus grand d’études a été produit en Europe sur les peuplements mixtes (Del Rìo et al., 2017; Bauhus et al., 2017; Pretzsch et al., 2017; Pretzsch, 2022), aidant à la compréhension de ces systèmes et à la diversification des possibilités d’aménagements (Pretzsch & Zenner, 2017). Une augmentation des recherches conduites sur les peuplements mixtes aurait avantage à voir le jour en Amérique du Nord, celles-ci pouvant éventuellement mener à l’augmentation du nombre de peuplements mixtes agissant ainsi comme une stratégie globale d’atténuation des effets négatifs des changements climatiques sur les forêts aménagées (Hisano et al., 2018).

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