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

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ABSTRACT

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.

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 overyielding (Pretzsch and Schütze, 2009; Pretzsch et al., 2015), enhanced growth stability over time (Bauhus et al., 2017; Del Río et al., 2017; Aussenac et al., 2019), 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 and 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

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Table A
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	190 ± 29	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	243 ± 36	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	137 ± 16	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	184 ± 38	141	19.2 ± 3.0	17.8 ± 9.2	31.3	65 ± 11	17.3 ± 1.5	79 ± 4	19.0 ± 1.8

(Del Río et al., 2013; Forrester, 2017). Intraspecific and interspecific interactions with neighbouring trees are modulated by their relative abundance and their spatial pattern (Silander and Pacala, 1985; Wagner and Radosevich, 1991; Stoll and 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, 2019). 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 and 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 and 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.

2. Materials and methods

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 and 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 °C at the closest weather station (48°47′00″ N; 79°13′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*).

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). 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) based on several studies showing a peak in growth interactions following the canopy closure (Angelstam and 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.

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) [cm2 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 and Qeadan, 2008).

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 and 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 cm^2 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.

$$YBAI = PBAI \times Crowding\ effect \tag{1}$$

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

$$Crowding\ effect = \exp[-\mathrm{C}^*(\mathrm{NCI})^{D}] \tag{2}$$

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))

$$C = \left(\frac{Cprim}{100}\right)^* target\ dbh^{\gamma} \tag{3}$$

where gamma (γ) informs on the sensitivity of crowding effect to target tree size. When γ values are below zero, the crowding impact on growth declines as the dbh of the target tree increases. 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))

$$NCI = \sum_{i=1}^{s}\sum_{j=1}^{n}\lambda_{i,z}\frac{(DBH_{ij})^{\alpha}}{(distance_{ij})^{\beta}} \tag{4}$$

where $j = 1, \ldots, n$ neighbour tree of $i = 1, \ldots, s$ 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 $\beta \sim 0.5$ 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. (7)] and the neighbouring species contributions to the plot basal area.

$$Hegyi\ competition\ index = \sum_{j=1\ j\neq i}^{n}\frac{d_j}{d_i L_{ij}} \tag{7}$$

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.

2.3. Estimation of model parameter

Competition models defined in Eq. 2, 3, 4, and 5 were adjusted with maximum likelihood methods (Canham and 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 and 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 R^2 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 (Fig. A, Appendix A). 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, 1998). 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.

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 (Table A Appendix B). Thus, both crowding models

Table B

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. Maximum likelihood and parameter estimates are separated for the crowding effect (lambda black spruce [λBS], lambda tamarack [λTA], beta [β], alpha [α], *Cprim* parameter [CP], gamma [γ] and *D* parameter [D]).

Parameter estimates	PBAI (cm^2 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

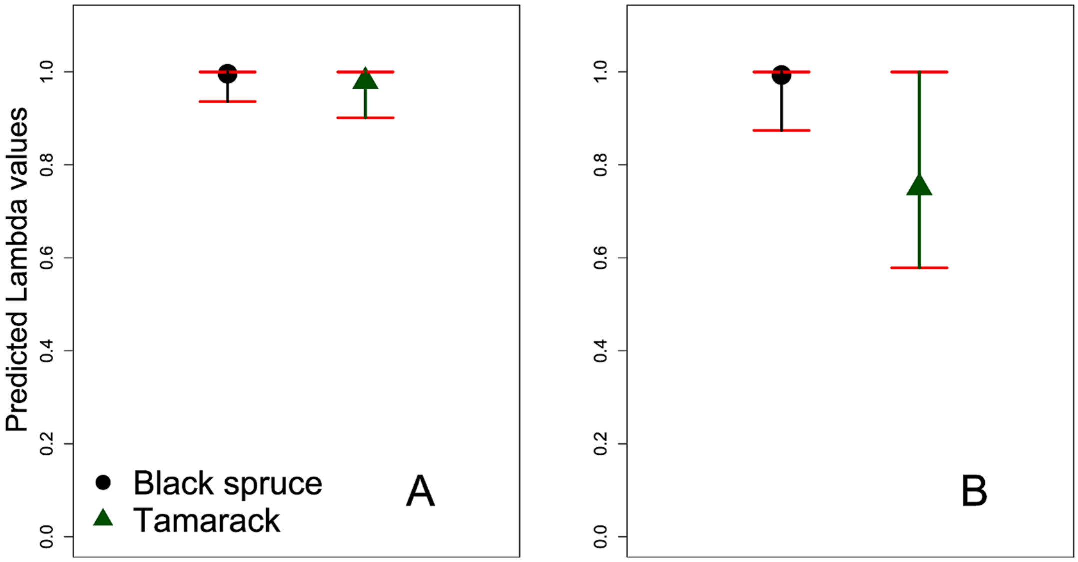

Fig. 1. Predicted lambda values for neighbouring species (black spruce, *Picea mariana* [Mill.] B.S.P. and tamarack, *Larix laricina* [Du Roi] K. Koch) for each models A) black spruce crowding; B) tamarack crowding models in boreal stands of eastern Canada. Circles represent the effect of black spruce neighbours on target trees; triangle represents the effect of tamarack neighbours on target trees. Data are shown as model-averaged predictions and 95% CI.

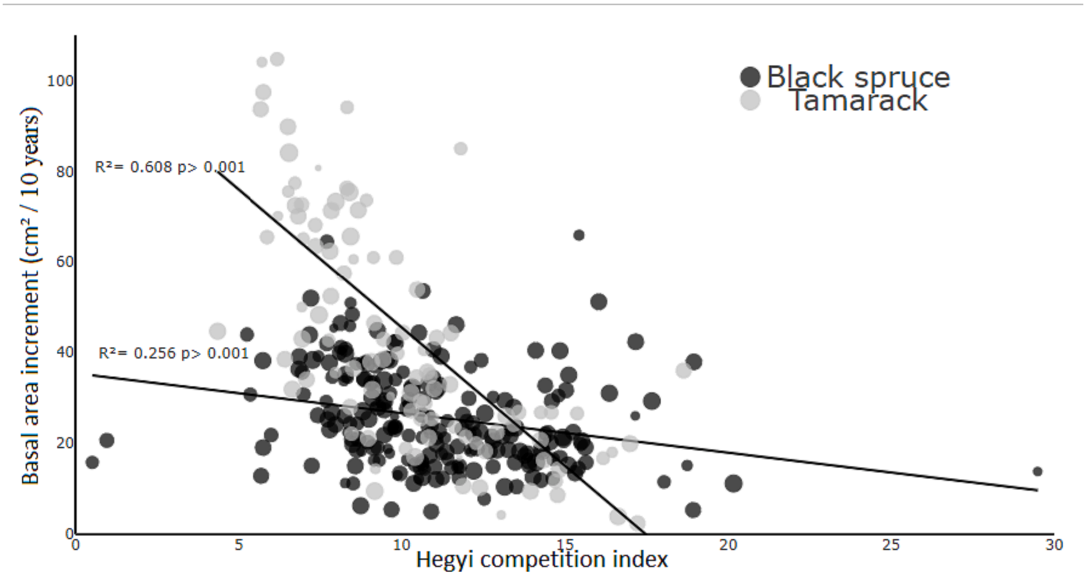

Fig. 2. Basal area increments over 10 years of black spruce (*Picea mariana* [Mill.] B.S.P.) and tamarack (*Larix laricina* [Du Roi] K. Koch) as a function of Hegyi values in boreal stands of eastern Canada. The size of the points is modulated by the black spruce basal area on each plot. Each line shows the linear correlation between the basal area increment and the Hegyi values for black spruce (black) and tamarack (grey). R^2 is the square of the correlation between the basal area increment and the Hegyi values.

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. A). However, for black spruce, models tended to underestimate large BAI values, which was not the case for tamarack (Appendix A; Fig. A).

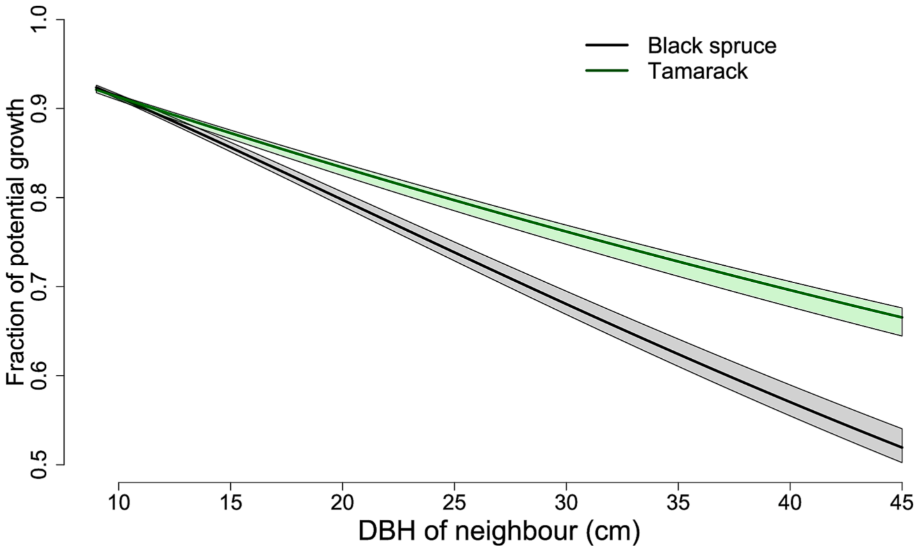

Fig. 3. Fraction of potential growth as a function of the neighbour diameter at breast height (dbh; 1.3 m) for each model black spruce (*Picea mariana* [Mill.] B.S.P.) crowding (black); tamarack (*Larix laricina* [Du Roi] K. Koch) crowding models (green) in boreal stands of eastern Canada. We used alpha parameter predictions to produce these figures and their 95% CI and model-averaged predictions for all other parameters in the equations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

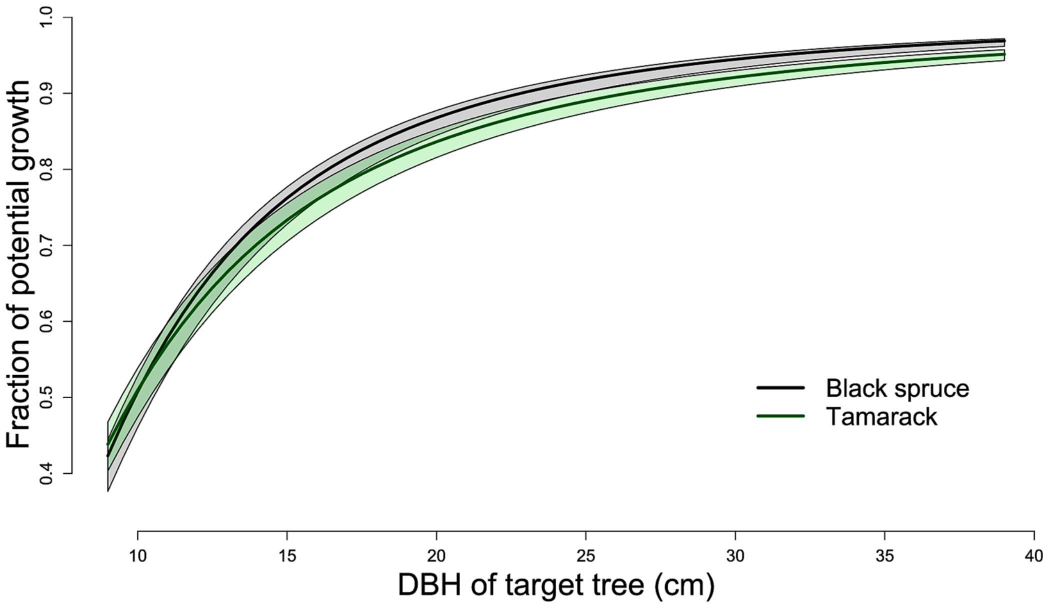

Fig. 4. Fraction of potential growth as a function of the diameter at breast height (dbh; 1.3 m) of target trees for each model black spruce (*Picea mariana* [Mill.] B.S.P.) crowding (Black); tamarack (*Larix laricina* [Du Roi] K. Koch) crowding (green) in boreal stands of eastern Canada. We used the gamma parameter predictions to produce these figures and their 95% CI and model-averaged predictions for all other parameters in the equations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 2; Fig. 1A and B). 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. 1B).

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).

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 B, Appendix B; Fig. 1A and B). Furthermore, black spruce did not differently perceive the intra and interspecific competition (Fig. 1A), but they had no effect on black spruce PBAI (Fig. not shown).

Competition based on Hegyi's equation was negatively correlated with the basal area increment over 10 years for both species (Fig. 2). Tamarack's BAI was more sensitive and more strongly correlated to competition ($R2 = 0.608$, $p < 0.001$) than black spruce's BAI ($R2 = 0.256$, $p < 0.001$) (Fig. 2). Black spruce is the species mainly responsible for high competition values (>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. 2). We observed no particular pattern between competition based on Hegyi and the species competition on tamarack BAI over 10 years (Fig. 2).

3.2. *Neighbour tree size effect*

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. 3). Black spruce PBAI was more sensitive to the size of the neighbours (Fig. 3) than tamarack (Fig. 3), as indicated by parameter α (3.74 for black spruce vs.

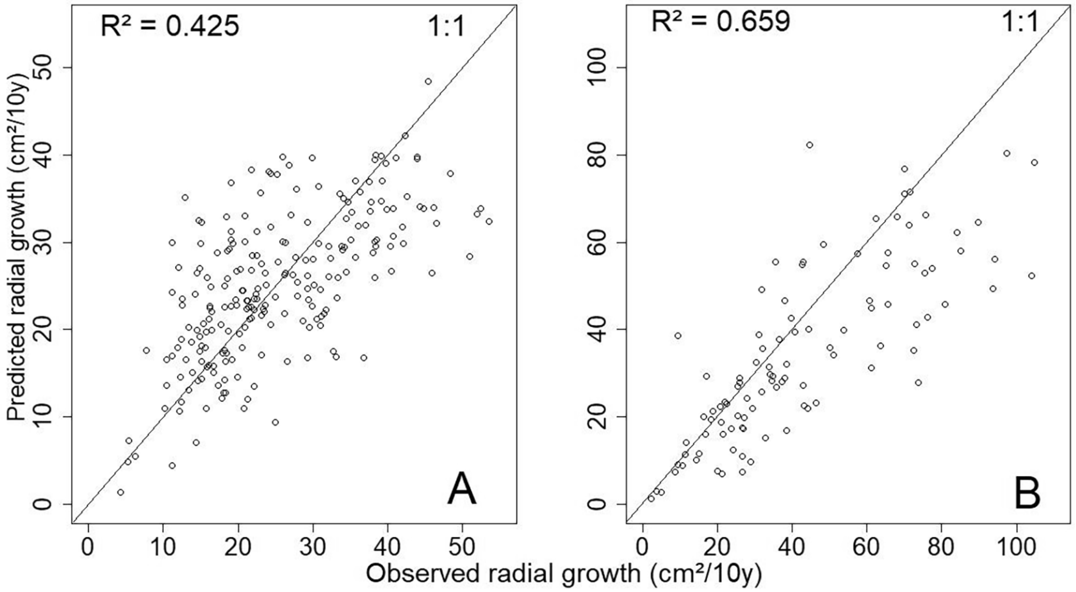

Fig. A. Predicted BAI (cm^2 10 years^{-1}) as function of observed BAI (cm^2 10 years^{-1}) for each model (black spruce crowding A, and tamarack crowding model B). Model-averaged predictions were used to produce each part of the figure. The diagonal line represents the one-to-one relationship.

Table 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	-

1.81 for tamarack; Table 2).

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 cm^2 10 years^{-1} as the dbh of neighbouring trees increase (Fig. 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.

3.3. *Target tree size effect*

Both species growth sensitive to crowding thus affected by target tree size through logarithmic relation (Fig. 4). The growth was at the lowest when target tree was small sized (Fig. 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 $\gamma = -2.25$; tamarack $\gamma = -1.91$) (Fig. 4; Table 2). This sensitivity to crowding declined rapidly between dbh 9 to 20 cm and then plateaued at higher dbh (20 to 39 cm) (Fig. 4). As the dbh of target tree increase to ≥ 25 cm, black spruce growth was less sensitive to crowding than tamarack (Fig. 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. 4) compared to 97 % for black spruce (Fig. 4).

3.4. *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 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

Table 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 (cm^2 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

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 B, Appendix B).

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. 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) 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.

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 than black spruce. 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 and 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 and up to plot dominated by tamarack or 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 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) 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 and 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 was good and had neutral effect on BAI. Otherwise, we would have detected a negative distance and cardinal direction effect mainly linked with shading on BAI over 10 years.

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 bigger 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. 2). Furthermore, as the dbh of target tree increase, the PBAI of tamarack is recovering slower than PBAI of black spruce (Fig. 4). This slower recovery from tamarack indicates that black spruce was less sensitive to crowding as their dbh increase. The Fig. 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 and 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 mainly comprised 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 were > 20 cm, like most of their neighbours, and small stems were underrepresented in the dataset.

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 et al., 1996). Intermediate and overtopped trees that were growing close to dominant and codominant trees have already been excluded. 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 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) mainly 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.

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 during 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).

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 and 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.

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.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A Goodness-of-fit for selected models

Appendix B. Table A: Tested models explaining BAI; Table B: Minimum and maximum estimate parameters by the crowding model

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