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

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Abstract

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 increased 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.

Key words: mixed plantation, young plantation, neighbouring tree effect, boreal forest, non-crop competition

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). Eventually, 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 and 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 and 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 and 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 and 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 do not 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 (Pitt and Bell 2005).

The Canadian boreal forest is not only 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). 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 and 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 and Roi 1983). The annual litter input from tamarack is rich in nitrogen and phosphorus, which could benefit soil fertility (Moore et al. 2011). This annual litter input can change soil macronutrient content, microbial communities, and pH (Dijkstra et al. 2009; Prescott and 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, 8 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.

Materials and methods

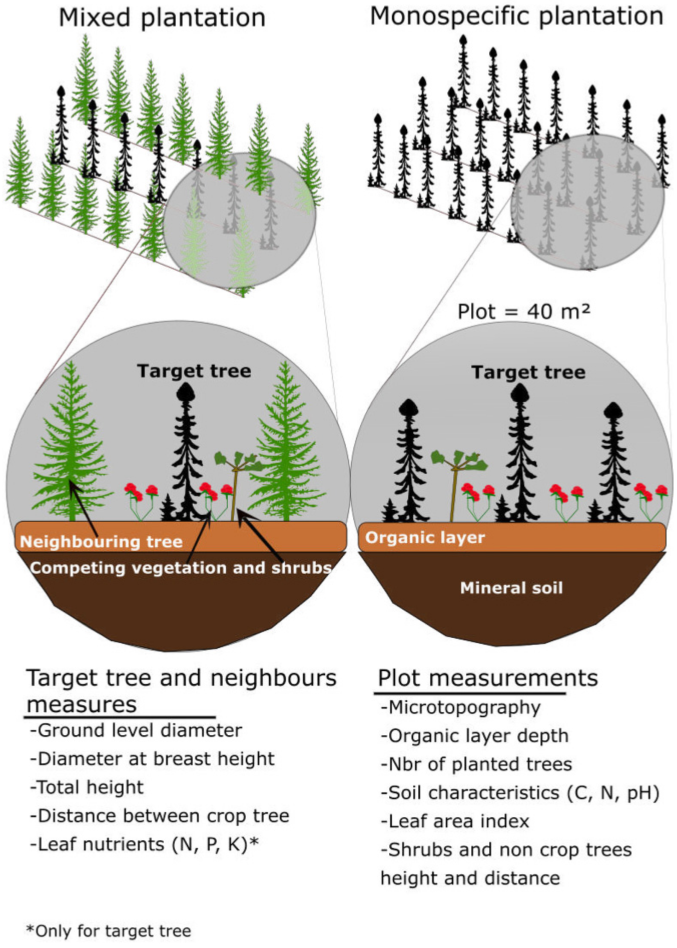
Site description and experimental design

The experimental site was in the Lake Duparquet Research and Teaching Forest (LDRTF) in the northwestern boreal forest of Québec, Canada (48°29’7”N–48°29’5”N; 79°25’5”W–79°26’0”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 and Hardy 1977). The climate is cold and continental with average temperatures of 0 °C and mean annual precipitation of 900 mm (Environment Canada 2021). 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 m^2 (100 m × 50 m). The blocks were divided into two different treatments: black spruce monospecific and 50/50 mixture covering 2500 m^2 (50 m × 50 m) each. All treatments were established with a density of 2500 stems ha^{-1}, 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. 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 brush saws 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.).

Fig. 1. Schematic representation of the plantation design in pure and mixed plots, with the list of variables assessed.



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. 1). The target trees were randomly distributed across all experimental units, irrespective of the treatment applied (Fig. 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 m^2 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. 1). In the mixed planting environment, this allowed us to investigate the effect of neighbouring trees at a ratio of two black spruce trees for six tamarack trees, as the plot is centred on target black spruce (Fig. 1, Table 1).

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 1). All target trees had a height greater than 1.3 m; we therefore calculated stem volume index during the 8th growing year as follows:

$$(1)\quad \mathrm{Vol}_8 = \frac{13\,\pi}{1200} \times \left(\mathrm{GLD}^2 + \mathrm{GLD} \times \mathrm{DBH} + \mathrm{DBH}^2\right) + \frac{\pi\,(\mathrm{DBH})^2\,(H - 130)}{12000}$$

where Vol_8 is the stem volume index (dm^3) based on the volume of a cylinder from 0 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.

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 analysed 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.

Soil and leaf sampling and processing

From 21 June to 25 June 2021, we collected soil samples from both organic and mineral layers using a trowel to analyse 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 and 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 h. 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 20 and 26 June 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 h. The foliar samples were dried using the same method as the soil samples.

Table 1. Plot characteristics as a function of competing neighbours (black spruce or tamarack).

	Black spruce neighbour	Tamarack neighbour
Soil characteristics		
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 ($m^2 \cdot ha^{-1}$)	0.02 ± 0.05	0.80 ± 0.48
Black spruce BA ($m^2 \cdot ha^{-1}$)	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

Notes: 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.

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 using a Perkin-Elmer Optima 7300DV (PerkinElmer, Inc. Waltham, MA, USA).

Competition indices

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

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

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 m 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 follows:

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

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

Statistical analyses

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:

$$(4) \qquad \text{Vol}^{8\text{th}}{}_{k} = \beta_0 + \beta_1\,(\text{x1}) + \cdots + \beta\text{k}\,(\text{xk})$$

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 and 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 and 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).

Neighbouring species impact on black spruce

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). 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.

Results

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). The second-ranked model was composed of competing vegetation angles, and the Hegyi competition index (Table 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). None of the other candidate models had a ΔAIC_c within 2; they were not kept for further analysis.

The largest effect on black spruce stem volume was observed from the competition of surrounding shrubs and nocrop trees (sum of competing vegetation angles) (Fig. 2A, Table 2). Competing vegetation detrimentally impacted black spruce at maximum observed competition (angles > 600°) reducing predicted stem volume of black spruce of 86% (−26.9 dm^3) relative to conditions where competing vegetation was absent (Fig. 2A). The predicted size decline associate with intermediate competition values (200° to 400°) ranged between −8 and −16 dm^3, respectively (Fig. 2A). The explained variance of the competing vegetation was the highest among tested parameters at 13.8% (Table 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. 2B). This corresponded to a 43.2% decrease in 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. 2B).

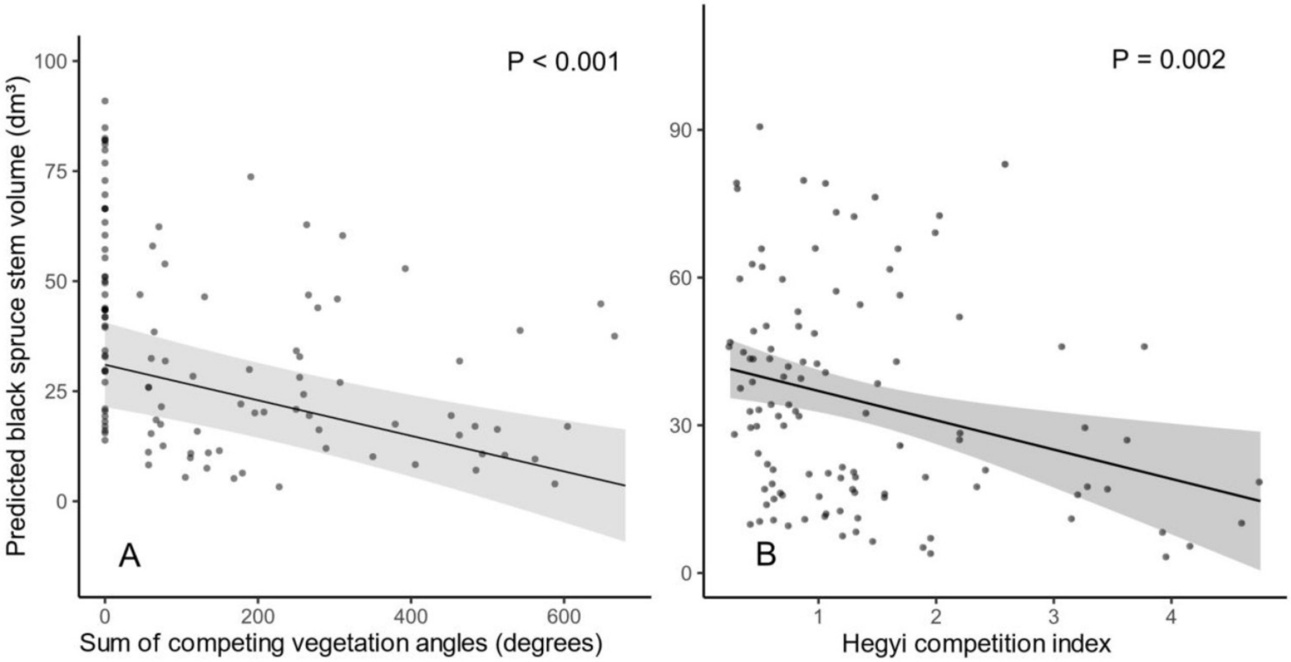
The flat microtopography exhibited a positive effect of black spruce stem volume compared to mounds (Table 2; Appendix A, Fig. A1). In contrast, the presence of a pit at the base of crop trees had a similar effect as mound and flat mi-

Table 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$_c$Wt), and model predictive power (Adjusted R^2).

Candidate models	*K*	ΔAIC$_c$	AIC$_c$Wt	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-year 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

Note: The second half of the table shows parameters influencing black spruce 8th-year stem volume and 95% confidence intervals excluding 0. For microtopography, mound was used as the reference level. Model in bold indicate retained model (ΔAIC$_c$ < 2). We included the null model as a reference level for AICc score.

Fig. 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 show the level of significance and grey circles correspond to the original observations.



crotopography, with no significant increase or reduction in the predicted stem volume (Fig. A1).

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$_c$Wt compared to the model without the neighbouring species effect with ΔAIC$_c$ greater than 2, which indicate it was less parsimonious than the model with the neighbouring effect (Table 3).

The predicted stem volume of black spruce exhibited a 38.1% increase (31.5 dm^3) when neighboured by tamarack compared to only other black spruce neighboured (predicted stem volume was = 19.5 dm^3; Fig. 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 tama-

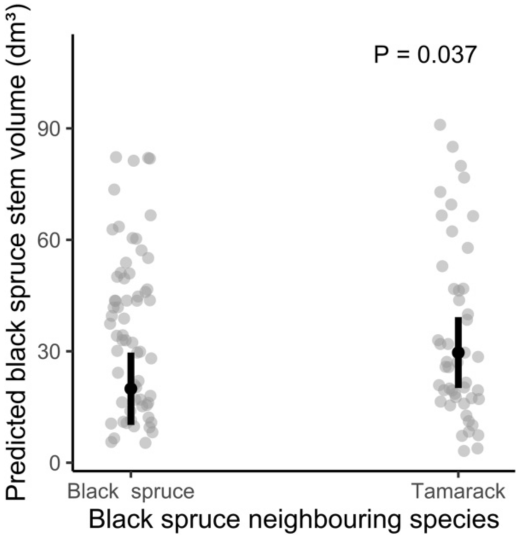
Table 3. Most parsimonious models explaining black spruce 8th-year stem volume with and without the neighbouring species effect, including the number of parameters (*K*), delta AIC_c compared to the highest-ranked model (ΔAIC_c), model weight (AIC_cWt), and model predictive power (adjusted R^2).

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

Notes: Model in bold indicate retained model ($\Delta\text{AIC}_{c} < 2$). The second half of the table shows parameters influencing black spruce 8th years stem volume and 95% confidence intervals excluding 0.

Fig. 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.



rack neighbours nearly overlapped (30.4 dm^3 and 31.5 dm^3, respectively) (Fig. 3).

Effects of neighbouring species on immediate growing environment

The ANOVA revealed significant differences between tamarack and black spruce neighbouring for both measured leaf area indices, total foliar N concentration, and pH of mineral and organic layers (Appendix A; Table A1), with *p*-values ≤ 0.02 (Table A1). However, neighbouring tree species did not have an impact on the other tested variables, i.e., P and K total foliar concentration and C/N ratio of organic and mineral layers (Appendix A; Table A1).

Having tamarack as a neighbour resulted in a 25.6% increase in LAI between closest neighbouring tree (Fig. 4A). The LAI above target trees increased by 55% (Fig. 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. 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 1).

Tamarack neighbours slightly increased pH of both soil layers, thereby reducing soil acidity (Fig. 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 (Table A1; Fig. 5).

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 A1). The variation in total foliar N concentration in black spruce was 0.91% with tamarack neighbouring, compared to 0.87% with black spruce neighbouring.

Discussion

We found an early, positive effect of neighbouring tamarack on the 8th-year stem volume of black spruce. It is unusual to detect such an effect at this stage of stand development since positive effects of neighbouring species usually occur at later stages, under closed canopy (Forrester 2014; Feng et al. 2022). The positive 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 added 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 3). Despite the modest strength of tamarack effect, the 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 the 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 vol-

Fig. 4. Effect of black spruce 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.

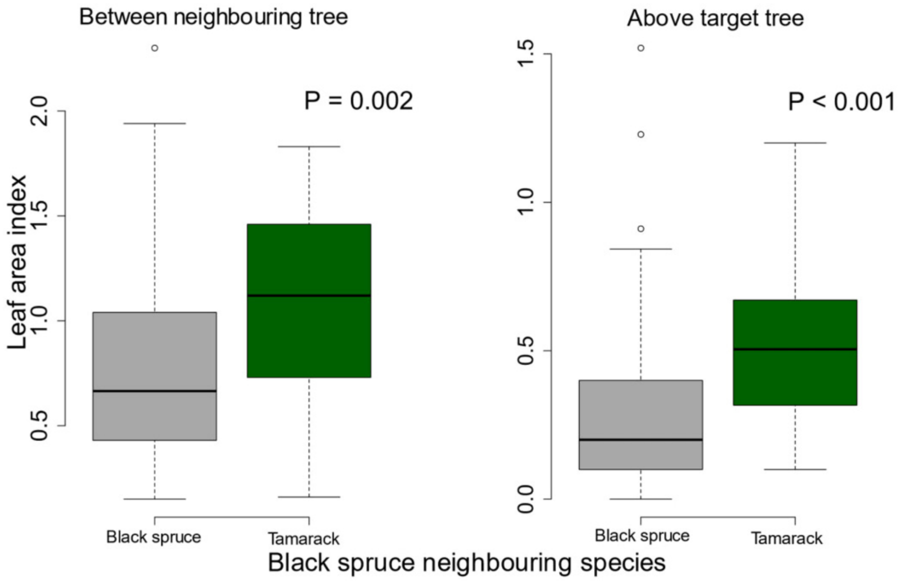
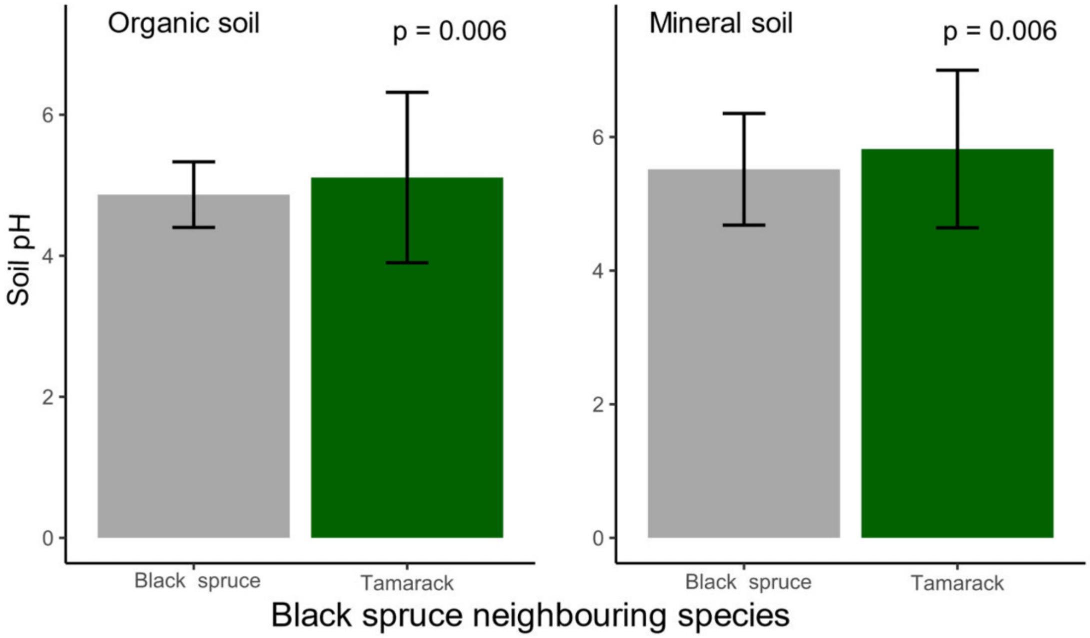


Fig. 5. Effect of black spruce neighbouring species on the pH of organic and mineral soil. The *p*-values show the differences between groups.



ume 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). 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 any 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 overyielding 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 cannot 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 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 and Roi 1983; Jucker et al. 2015; Lu et al. 2018). Slow-growing shade tolerant mixed with shade-intolerant fast-growing trees usually lead to over-yielding (Cordonnier et al. 2018). Furthermore, tamarack growth can also 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 not only enhance stand yield (Pretzsch et al. 2015), but also improve growth stability through stand rotation (Del Rio et al. 2017; Aussenac et al. 2019). 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 and 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 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 soil 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 not only 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 and 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 and 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 that we detected 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 detected a biologically significant effect 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, 10 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 complex that is resistant 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^{-1}, despite the initial density being 2500 ha^{-1}, with a maximum sampled density of 2325 ha^{-1} and a minimum of 1125 ha^{-1} (Table 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^{-1}; 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 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, 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.

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 positive 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 8 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 and 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.

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Data will be made available on request.

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Competing interests

The authors declare that they have no competing interests.

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Appendix A

Table A1. ANOVA results (*p*-values) testing the neighbouring tree species effect between black spruce (*Picea mariana*) and tamarack (*Larix laricina*).

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****

Note: Significant effects are presented in bold.

Fig. A1. Predicted black spruce stem volume at the 8th year (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.