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Intraspecific and interspecific interactions between three boreal conifer species seedlings: a greenhouse experiment

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Abstract
The growth dynamics of seedlings in mixed conifer plantations or early stages of natural regeneration can be influenced by interactions among seedlings and their capacity to quickly acquire soil resources. We carried out a greenhouse experiment to investigate the growth and N uptake of three widespread conifer species in mono- and multispecific pots at different density levels. Tamarack, black spruce and jack pine seedlings were grown in pots with one to three seedlings per pot, in the absence (N–) or presence of ^{15}N-enriched fertilization (N+). In monospecific pots, tamarack seedlings had higher apical growth and benefited more from N fertilization than the two other species. Unexpectedly, increasing seedling density did not reduce seedling growth and even stimulated jack pine's growth and N uptake. In two-species mixtures, jack pine seedlings (1) produced up to 56% and 26% greater biomass than black spruce and tamarack, respectively; (2) achieved ~ 35% higher biomass than in two-seedling monocultures, indicating a stronger intraspecific than interspecific competition for this species; and (3) caused a ~ 20% decline in the biomass of both black spruce and tamarack seedlings relative to monocultures. The three-species mixture achieved similar yield as the most productive three-seedling monoculture and absorbed up to 15% more fertilizer than the three-seedling monocultures. Seedlings in the three-species mixture of the N+ treatment had their biomass increased by on average 16% relative to the three-seedling monocultures. Although these results cannot be extrapolated to predict the future dynamics and structure of mature stands, they clearly indicate that jack pine seedlings are more competitive than the other species in mixtures, particularly under conditions of high nitrogen availability.

Keywords *Picea mariana*, *Pinus banksiana*, *Larix laricina*, Mixing effect, Interactions, Complementarity

1 Introduction

The Canadian boreal forest has a typical low tree species diversity with a few dominant gymnosperm species such as black spruce (*Picea mariana* [Mill] BSP), white spruce (*Picea glauca* [*Moench*] Voss.), tamarack (*Larix laricina* [Du Roi] K. Koch) and jack

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pine (*Pinus banksiana* [Lamb]) [22, 51]. Recent studies have shown that climate change and forestry practices will likely change its structure and composition through species-specific impacts on growth and natural regeneration dynamics [2, 4, 14, 15, 59, 65]. In response to anticipated changes in forest composition and structure, several forest scientists advocate for a diversification of species and management practices, for instance, through species mixing and increased tree density in plantations [48, 54, 63]. In this context, it becomes essential to understand how different tree species interact, not only in mature stands, but also in the early years following establishment or planting, which can determine community structure dynamics [9].

The success of seedling establishment, whether in plantations or during natural regeneration, is influenced by both abiotic factors—including seedbed quality and availability[17, 30, 32, 43, 46]—and biotic factors[31] such as seedlings' vigor and interactions with other plants, including cryptogamic (bryophytes and terricolous lichens), herbaceous and shrub species [25, 31, 32, 37]. Although competition has been shown to be a crucial driver of forest dynamics in Canada in the past decades [67], interspecific interactions among seedlings and the mechanisms by which they share resources in early stages of afforestation or in natural regeneration has to our knowledge received little attention [57, 63].

The interactions between two plants range from competition, which reduces one plant metric (e.g. biomass production) when growing in mixture compared to when growing alone, to facilitation, when at least one plant metric is higher in the presence of a companion plant [1, 9]. The positive or negative outcome of species-mixing depends on factors such as species ontogeny and stand density [7], and varies according to resource availability and environmental conditions [10, 49, 55]. In the context of forest ecology, a positive mixing effect represents a situation in which we observe a greater biomass production of species in mixed than in monospecific stands [18, 19, 21]. This situation occurs when interspecific competition is lower than intraspecific competition due to complementarity mechanisms, which alleviate competition and leads to an optimization of resources use [11, 41, 42, 61, 62, 64]. For instance, a widespread complementarity for N acquisition has been found between jack pine and black spruce in the eastern Canadian boreal forest [28]. While black spruce absorbs N mostly from the humus layer, jack pine takes it up from the underlying mineral soil horizons.

Nitrogen is one of the most limiting factors for biomass production in the boreal forest [39, 58, 60] and the competition for this resource has a strong influence on conifer growth [52] and on early succession in jack pine stands [57]. It is therefore essential to assess the influence of N availability when investigating the interactions between boreal conifer species. A recent study conducted in monospecific plantations with contrasting soil quality has shown that jack pine and tamarack had higher growth rate than spruce species, and that jack pine benefited more than the other species from improved soil quality within five years following planting [47]. The interactions between boreal coniferous species seedlings growing in close vicinity—as is the case in the early stages of natural regeneration, in dense plantations or after reforestation when planted seedlings interact with seedlings derived from natural regeneration—have rarely been studied, and have been mostly assessed through the lens of shade tolerance [5]. Tamarack seedlings have been shown to outperform slower-growing species such as black spruce and eastern white pine due to rapid overtopping and, consequently, greater light pre-emption.

However, this advantage tends to diminish with decreasing density [5]. While the impact of seedling density on intra- and interspecific interactions was assessed in this study, the impact of N availability on these interactions remains, to our knowledge, unknown, particularly in controlled conditions.

In the present study, we carried out a greenhouse experiment to investigate the growth and N uptake of jack pine, black spruce and tamarack seedlings in different conditions of intraspecific and interspecific competitions. The objective was to assess the interactions among these species in the early stages of growth in mixed conifer stands and to look for potential mixing effect on biomass production and N uptake at the level of individual seedlings and mixtures (total yield). Seedlings were grown in pots with one to three seedlings per pot, either in monocultures, or in mixtures involving one or two companion species (2 to 3 species per pot). All monocultures and mixtures were grown in the presence or absence of ^{15}N-enriched fertilizer to assess the N uptake capacity of species and the impact of N availability on their interactions. We hypothesized that (1) increased seedling density would decrease individual biomass production due to increased competition; (2) N fertilization would increase the biomass of all species, with the most pronounced effect in jack pine; and (3) that jack pine would be more competitive than black spruce and tamarack in mixture due to its high N uptake capacity, increasing its biomass relative to monocultures at the expense of both companion species.

2 Materials and methods

2.1 Plant material

Seedlings of black spruce (BS), jack pine (JP) and tamarack (TK) were provided by two private tree nurseries (Pépinière Boucher, Saint-Ambroise, QC, Canada and Groupe Forestra, Laterrière, QC, Canada), which are submitted to the same standards (from the Ministère des Ressources Naturelles et des Forêts du Québec) and use the same seedling growth conditions. At the beginning of the experiment (June 2020), the seedlings had spent a year in the greenhouse and a year outdoor at the tree nursery (2 years old) in containers of 45 cylindric slots of 110 cm^3. Black spruce seedlings were on average ~ 7–8 cm shorter than jack pine and tamarack seedlings at the beginning of the experiment (Table S1). All seedlings were planted in labelled plastic pots (Ø = 27 cm; H = 24 cm) filled with gardening peat (OM = 10.8%; pH = 7.75; see Table S2 for elemental composition) between the 15th and the 17th of June 2020. A total of 324 seedlings were planted in 156 pots.

2.2 Experimental design

The experimental design included six blocks and two factors: N fertilization (2 levels: no fertilization [N−] and fertilization [N+]) and a factor combining tree diversity and density (Fig. 1). Each of the six blocks contained two main plots: one with no fertilization treatment (N−) and one with a N fertilization treatment (N+). Each main plot included 13 pots: (1) nine monospecific pots at one, two or three seedlings per pot; (2) three two-species pots at two seedlings per pot (BS + JP; BS + TK; and JP + TK); and (3) one three-species pot with three seedlings per pot (BS + JP + TK). Pots were repositioned within each main plot weekly throughout the experiment to prevent any potential location effect related to undesired heterogeneity in temperature or irradiance. Each seedling received an individual label. The different density levels (the number of seedlings per

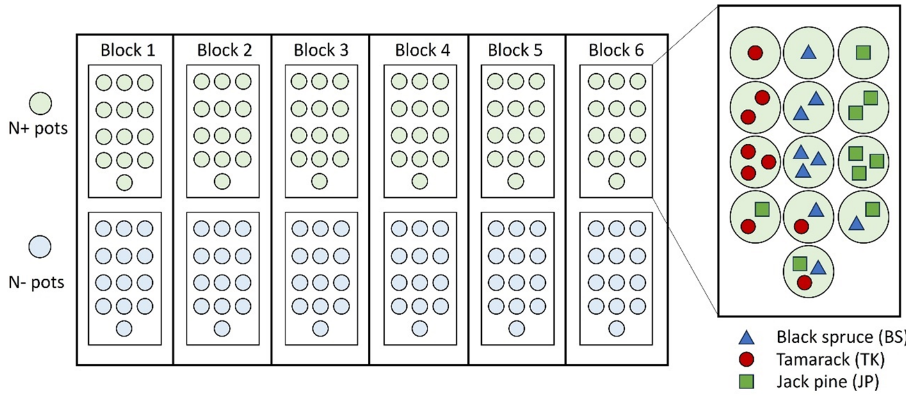

Fig. 1 Schematic representation of the experimental design comprising six blocks (*n* = 6 for each treatment) distributed through the greenhouse. Each block contained two main plots, each with one of the two N fertilization levels (N− and N+). Within each main plot, 13 pots were assigned to 13 diversity × density levels (9 monospecific and 4 multispecific pots)

pot) aimed to assess the effect of intraspecific competition on seedling growth, whereas the different mixture types aimed to assess the interactions between species (e.g., interspecific competition, complementarity). The N fertilization treatment was intended to assess the N uptake capacity of the three species and how N availability impacts the interactions between them.

2.3 Growth conditions

The experiment was conducted at the greenhouse of the University du Québec à Chicoutimi (UQAC) in the province of Québec, Canada. The seedlings were grown under natural photoperiod at a temperature comprised between 7 °C and 25 °C through the two growing seasons (May to October). Each pot received the same amount of deionized water regardless of the number of seedlings per pot. This amount varied between 2 and 3 applications of 0.5 L/week. No symptoms of water stress have been observed during the experiment, and no seedling mortality occurred. The seedlings were moved outside for the winter period (November to early May). All seedlings from blocks 1 to 3 were uprooted in September 2021, i.e. 15 months after the beginning of the experiment, for biomass and N analyses.

2.4 Nitrogen treatments and ^{15}N labelling

Pots of the N+ treatment were fertilized with an ammonium sulfate solution ($[NH_4]_2SO_4$; 1.18 g L^{-1}) once a week (0.5 L/week) for the first four weeks of the experiment (2020 growing season), which corresponded to an annual application of 0.5 g N/pot (~ 87 kg N ha^{-1}). This high N dose was applied to create two distinct fertility levels and elicit rapid responses from the seedlings. At the beginning of the 2021 growing season, the N+ pots were fertilized twice (on May 19 and 25, 2021) with 0.5 L of an ammonium sulfate solution enriched in ^{15}N ($[^{15}NH_4]_2SO_4$; 2.36 g L^{-1}; 10% atom). This fertilization corresponded to a N input of 0.5 g N/pot per year. The ^{15}N-enriched fertilizer was applied in two fractions to reduce fertilizer loss through leaching as much as possible.

2.5 Biometric measurements

Height (cm), i.e. the length between the root collar and main stem's apical bud, was measured on all seedlings of the six blocks ($n=6$) at the beginning and the end of the experiment, using a measuring tape. Apical growth (cm) was calculated as the difference between height at the end of the experiment (September 9, 2021) and height at the beginning of the experiment (June 17, 2020).

Destructive measurements were made only on three out of the six blocks ($n=3$). In September 2021, all the seedlings from blocks 1 to 3 were cutoff at the root collar. The needles were separated from the stems for each seedling and both compartments were put in separated paper bags and then oven-dried at 65 °C for 48 h. Roots were gently separated from the soil using a 2 mm sieve, brushed to remove soil particles, and then put in paper bags and air-dried for 48 h in a drying room. The soil was put in aluminum plates and air-dried for a week in a drying room. Remaining soil at the surface of the roots was gently removed and added to the soil compartment. Roots were then oven-dried at 65 °C for 48 h. In the case of pots with more than one seedling, roots that were not connected to the rooting system (unidentified roots) were allocated to each seedling in proportion of the number of seedlings per pot (i.e. 50% and 33% to each seedling in pots with two and three seedlings, respectively). In all cases, the mass of unidentified roots was unsignificant (< 5% of the total root biomass).

The dry mass of the different biomass components (needles, stems and roots) was then measured with an electronic scale (Sartorius®).

2.6 Chemical analyses

Subsamples of dried needles and dried roots of each seedling from the fertilized main plots (total of 27 seedlings × 3 blocks = 81 seedlings) were collected to measure the ^{15}N in excess (see section below) relative to non-fertilized pots. The ^{15}N natural abundance of non-fertilized seedlings was measured on composite subsamples of needles and roots of seedlings in the monocultures of the N− treatment across density levels (3 species × 3 blocks = 9 subsamples). Needles and roots subsamples were put in individual 50 mL polyethylene tubes with two stainless steel balls. The 180 tubes (81 ^{15}N-enriched needle samples + 81 ^{15}N-enriched root samples + 9 needle control samples + 9 root control samples) were then put in a rotating tumbler for 72 h to grind the samples to a < 300 µm powder.

Total N concentrations and isotopic ratios were analyzed at the Centre de recherche sur la dynamique du système Terre (GEOTOP) in Montréal, QC, Canada. Total N concentration and ^{15}N abundance were measured using an automatic elemental analyzer in continuous flow mode (Vario Micro Cube, Elementar, Germany) coupled to an isotope-ratio mass spectrometer (IRMS) [27]. The ^{15}N values are expressed as δ (‰) and were calculated as follows (Eq. 1):

$$\delta^{15}\mathrm{N} = (\mathrm{R}_{\mathrm{sample}}/\mathrm{R}_{\mathrm{std}} - 1) \times 1000 \quad (1)$$

where R_{sample} and R_{std} are the absolute isotope ratios ($^{15}N/^{14}N$) of the, respectively, sample and standard, which for N is air-N_2.

2.7 Calculations

Total biomass was the sum of the dry mass of needles, stems and roots harvested for each seedling separately at the end of the experiment.

A slightly modified version of the Relative Yield Total (RYT) index [26, 41] was calculated for each species mixture type to quantify a relative gain or loss in total biomass (above- and belowground) relative to monospecific pots:

$$RYT = \frac{\Sigma Yi_{(mix)}}{\Sigma \frac{1}{n} Yi_{(mono)}} \quad (2)$$

where ΣY_i(mix) and ΣY_i(mono) are the seedlings' productivity of the species *i* in multi-species pots (mix) and in monospecific pots (mono), respectively, and n the number of seedlings involved in the mixture.

We calculated the RYT based on the number of seedlings of each species rather than on the basis of coverage as it is the case for herbaceous species. A RYT > 1 indicates a relative gain in productivity due to species mixing.

The fraction of N derived from the fertilizer (Ndff; %) was calculated for samples as follows [12]:

$$\text{Ndff } (\%) = 100 \times \mathrm{e_{sample}}/\mathrm{e_{fert}} \quad (3)$$

where e_{sample} and e_{fert} are the isotopic excess in the sample and in the fertilizer, respectively. e_{sample} was calculated relative to the ^{15}N abundance in the control seedlings ($n = 9$), and e_{fert} was calculated as the difference between the ^{15}N abundance in the fertilizer (A_{fert} = 10%) and 0.3663% (natural abundance of ^{15}N in atmospheric N_2).

The fraction of the added ^{15}N recovered in the seedlings' biomass at the end of the experiment (^{15}N recovery; %) was calculated as follows:

$$^{15}\text{N recovery}(\%) = 100 \times \left(\mathrm{e_{sample}} \times [\mathrm{N}]_{\mathrm{sample}} \times \mathrm{m_{sample}}\right) / \left(\mathrm{A_{fert}} \times [\mathrm{N}]_{\mathrm{fert}} \times \mathrm{m_{fert}}\right) \quad (4)$$

where $[N]_{sample}$ and m_{sample} are the N concentration in the seedlings' biomass (g N g^{-1}) and the biomass (g) of the seedlings, respectively; and A_{fert}, $[N]_{fert}$ and m_{fert} are the ^{15}N abundance in the fertilizer (10%), the N concentration of the fertilizer and the applied mass of fertilizer per pot, respectively.

2.8 Statistical analyses

Mixed effects models were used to assess the impact of the N treatment (2 levels: N− and N+), species (3 levels: black spruce, jack pine and tamarack), density (3 levels: 1, 2 or 3 seedlings per pot) and diversity (3 levels: 1, 2 or 3 species per pot) on growth (apical growth and biomass) and N uptake variables (Ndff and ^{15}N recovery). Blocks and pots (nested in blocks) were set as random effects. Analyses were done in R [56] using the *lmer* function from the *lme4* package [3].

For monospecific pots, we assessed the effect of species, density and N fertilization on both growth and N uptake variables (Y) as follows (the corresponding script for this model in R is shown in Table S1):

$$
\begin{aligned}
\mathrm{Y_{ijklm}} = {} & \alpha + \beta_1 \cdot \mathrm{Species}_i + \beta_2 \cdot \mathrm{Nitrogen\ treatment}_j + \beta_3 \cdot \mathrm{Density}_k \\
& + \beta_4 \cdot (\mathrm{Species} \times \mathrm{Nitrogen})_{ij} + \beta_5 \cdot (\mathrm{Species} \times \mathrm{Density})_{ik} \\
& + \mathrm{Block}_l + \mathrm{Pot}_{l(m)} + \varepsilon_{ijklm}
\end{aligned}
$$

where $\mathrm{Y_{ijklm}}$ is the growth or N uptake variable in Species *i*, Nitrogen treatment *j*, Density *k*, block *l* and pot *m*; α is the intercept, ε is the error parameter, and β_1, β_2, β_3, β_4 and β_5 are the fixed effects of the Species, Nitrogen treatment, Density, Species×Nitrogen and Species×Density variables, respectively.

The impact of diversity on individual growth and N uptake variables was assessed by comparing the average seedling values of each species in multispecific vs. monospecific pots at similar density levels (2 or 3 seedlings per pot). For instance, the growth of black spruce in mixture with jack pine (BS + JP) was compared to its growth in two-seedling monoculture at a density of 2 seedlings per pot. For two-species mixtures, we assessed the effect of the companion species ($\mathrm{Species_{comp}}$) and N fertilization (N treatment) on both growth and N uptake variables (Y) for each species using a similar mixed-effect model (Table S1). For three-species mixtures, we assessed the effect of species and N fertilization on both growth and N uptake variables. The corresponding R scripts for these models are shown in the supplementary materials (Table S3).

Least-square means were obtained using the function *lsmeans* function from the *lmerTest* package [36]. Post-hoc pairwise comparisons of least-square means were then assessed using the *lsmeans* function from the *emmeans* package [40], which uses a Tukey adjustment method for multiple comparisons. The normality and the homogeneity of variance of the residuals of the model were assessed using visual plots (e.g., q–q plots) and were satisfactory. A one sample Student's *t*-test was performed to test whether RYT values were significantly higher than 1 using the function *t.test* in R. The significance level was set at $P < 0.05$ for all analyses.

3 Results

3.1 Growing patterns of species in monocultures

There was a significant species and N fertilization effect, as well as a significant species × fertilization interaction on seedlings' apical growth, whereas the effect of density was not significant (Table S4). Apical growth was significantly higher in tamarack (32.3 cm) than in black spruce (13.9 cm) and jack pine (10.6 cm) in the N+ treatment across density levels (Table 2). On average, the fertilization treatment increased apical growth by + 140% in tamarack (+ 18.9 cm) and + 24% in black spruce (+ 2.7 cm) but had no effect in jack pine.

In contrast, no significant difference was found between species for total biomass within each N fertilization treatment (Table 1). Overall, fertilization significantly increased the total biomass of seedlings (Table S5), with a greater effect observed in tamarack and black spruce (+ 81%) compared to jack pine (+ 38%) (Table 2).

3.2 Growing patterns in two-species pots

In two-species pots, apical growth was consistently higher in tamarack than in black spruce and jack pine, but the difference was particularly marked in the N+ treatment, which increased tamarack's apical growth by on average 90% (Table 2). The companion species did not significantly affect the apical growth of any of the species in the

Table 1 Apical growth (cm) and total biomass (g seedling^{-1}) after two growing seasons in the greenhouse for black spruce, jack pine and tamarack seedlings grown in monospecific pots with no N fertilization (N–) or with N fertilization (N+)

		Monocultures	
		N–	**N+**
Apical growth (cm)	Black spruce	11.2 ± 1.6 a	13.9 ± 2.6 a
	Tamarack	13.4 ± 2.1 a	32.3 ± 5.0 b
	Jack pine	10.5 ± 1.7 a	10.6 ± 1.7 a
Total biomass (g seedling^{-1})	Black spruce	10.9 ± 1.8 a	19.8 ± 3.6 bc
	Tamarack	12.8 ± 2.4 a	23.2 ± 3.6 c
	Jack pine	14.5 ± 2.6 ab	20.1 ± 4.6 bc

Values are least square means ± se ($n = 6$ and $n = 3$ for apical growth and biomass, respectively) across density levels (1 to 3 seedlings per pot). Different letters indicate significant differences across species and N fertilization treatments ($P < 0.05$)

Table 2 Apical growth (cm) and total biomass (g seedling^{-1}) of black Spruce (BS), tamarack (TK) and jack pine (JP) grown with a single companion species in two-seedling pots, in the absence or in the presence of N fertilizer (N– and N+ treatments, respectively)

		Companion species		
		Black spruce	**Tamarack**	**Jack pine**
Fertilizer treatment	Species	Apical growth (cm)		
N–	Black spruce	**12.5 ± 3.7 a**	12.2 ± 4.4 a	10.1 ± 2.2 a
	Tamarack	17.2 ± 4.0 a	**16.1 ± 3.6 a**	18.7 ± 2.2 a
	Jack pine	8.5 ± 4.0 a	9.6 ± 4.4 a	**9.9 ± 2.1 a**
N+	Black spruce	**15.0 ± 3.7 a**	23.8 ± 4.4 b	13.8 ± 2.2 a
	Tamarack	33.3 ± 4.0 a	**35.5 ± 3.6 a**	24.5 ± 2.2 b
	Jack pine	8.4 ± 4.0 a	14.5 ± 4.4 b	**10.4 ± 2.1 ab**
		Total biomass (g seedling^{-1})		
N–	Black spruce	**12.2 ± 3.1 a**	11.6 ± 4.0 a	11.2 ± 1.9 a
	Tamarack	12.8 ± 1.1 a	**14.5 ± 2.9 a**	14.6 ± 2.8 a
	Jack pine	16.4 ± 3.3 a	18.3 ± 4.6 a	**14.0 ± 5.8 a**
N+	Black spruce	**20.3 ± 3.1 a**	21.5 ± 3.8 a	15.6 ± 3.6 a
	Tamarack	25.7 ± 1.5 a	**27.9 ± 2.9 a**	21.4 ± 3.6 a
	Jack pine	24.5 ± 7.9 a	24.3 ± 6.5 a	**17.7 ± 4.8 a**

Values are least square means ± se ($n = 6$ and $n = 3$ for apical growth and biomass, respectively). For each species, different letters indicate a significant effect of the companion species ($P < 0.05$). Values in bold indicate monocultures

N– treatment (Table 2). However, in the N+ treatment, apical growth of the three species significantly varied depending on the companion species: the apical growth of black spruce was higher in mixture with tamarack, the apical growth of tamarack was significantly lower in mixture with jack pine, whereas the apical growth of jack pine was higher in mixture with tamarack than with black spruce.

The three species produced similar biomass regardless of the companion species (i.e., no companion species effect) in both fertilization treatments, although in the N+ treatment, all species tended to have lower biomass when grown with jack pine as a companion species (Table 2).

Although tamarack tended to have a higher biomass than black spruce and jack pine in the N+ treatment, jack pine was slightly more productive than the companion species in both N treatments. It achieved a 46% and 26% greater biomass than black spruce (16.4 g vs. 11.2 g) and tamarack (18.3 g vs. 14.6 g) in the N– treatment, and a 56% and 13% greater biomass than black spruce (24.5 g vs. 15.6 g) and tamarack (24.3 g vs. 21.4 g), in the N+ treatment (Table 2; Fig S1).

3.3 Growing patterns in three-species pots

In three-species pots, all species had similar apical growth and total biomass in the N− treatment, whereas in the N+ treatment (1) tamarack had a ~ 80% higher apical growth than both black spruce and jack pine (Fig. 2a); and (2) jack pine had a significantly higher total biomass than black spruce and tamarack, accounting for 42% of the pot total biomass vs. 27% and 31% for black spruce and tamarack, respectively (Fig. 2b). The N fertilization increased apical growth for all species but only significantly for tamarack (Fig. 2a). The N fertilization significantly increased the biomass of tamarack and jack pine by about a factor of 2 (Fig. 2b). Both black spruce and jack pine had higher total biomass in the three-species mixture than in three-seedling monocultures (open symbols on Fig. 2b). In particular, jack pine produced 30% more biomass in the three-species mixture (29.4 ± 1.9 g) than in the 3-seedlings monoculture (22.7 ± 2.7 g) in the N+ treatment (Fig. 2b). In contrast, no differences were observed for tamarack between monocultures and the three-species mixture.

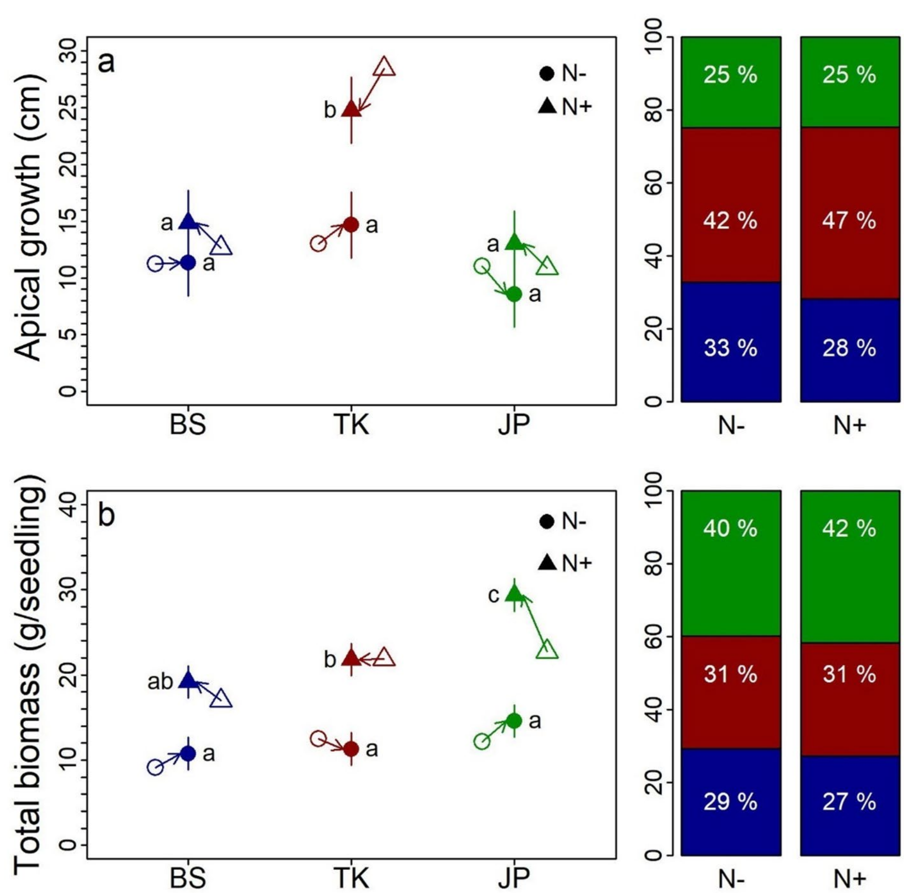

Fig. 2 **a** Apical growth and **b** total dry biomass over a period of 15 months for black spruce (BS; blue), tamarack (TK; red) and jack pine (JP; green) seedlings grown together in three-species pots (filled symbols) and in three-seedling monocultures (open symbols) in the N− and N+ treatments (circles and triangles, respectively). Values are least square means ± SE ($n = 6$ and $n = 3$ for apical growth and biomass, respectively). Values not sharing the same letters are significantly different ($P < 0.05$). Arrows show changes from monocultures to three-species mixtures. Barplots show the contributions of the three species to the mixtures' apical growth and biomass in the N− and N+ treatments

3.4 Effect of species mixing on total yields

In pots comprising two seedlings, the total yield (i.e. the total biomass per pot) was similar among all monocultures and the three mixtures in the N− treatment (Fig. 3a). However, in the N+ treatment, the total yield was 55% higher in the tamarack monoculture (55.7 g pot^{-1}) than in the jack pine monoculture (35.4 g pot^{-1}). In three-seedling pots, total yield was ~25% lower for the black spruce monoculture (27.3 and 51.0 g pot^{-1} in the N− and N+ treatments, respectively) than for jack pine and tamarack monocultures. Total yield was also significantly lower in the black spruce monoculture than in the three-species mixture (37 and 65–70 g pot^{-1} in the N− and N+ treatments, respectively).

The RYT index averaged 1.07 ± 0.08 across all mixture types and N fertilization treatments (Fig. 3b). It was on average 13–18% higher in the three-species mixture (BS/TK/JP) than in the two-species mixtures in the N+ treatment (1.16 ± 0.13 vs. 0.98–1.03). The

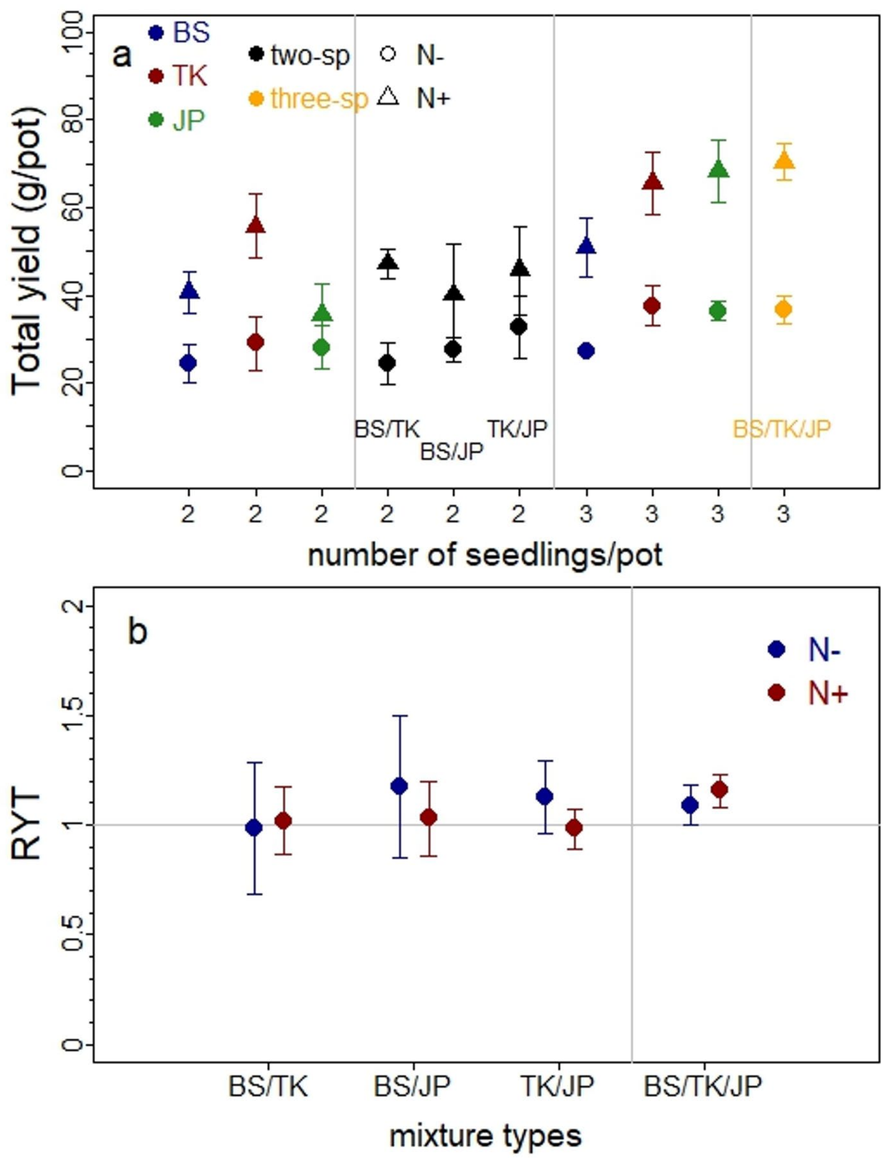

Fig. 3 **a** Total yield (g pot^{-1}) in monospecific and multispecific pots (two or three species) and **b** relative yield total (RYT) in two-species and three-species pots in the absence (N–) or presence (N+) of N fertilizer. Values are means ± SE (n = 3)

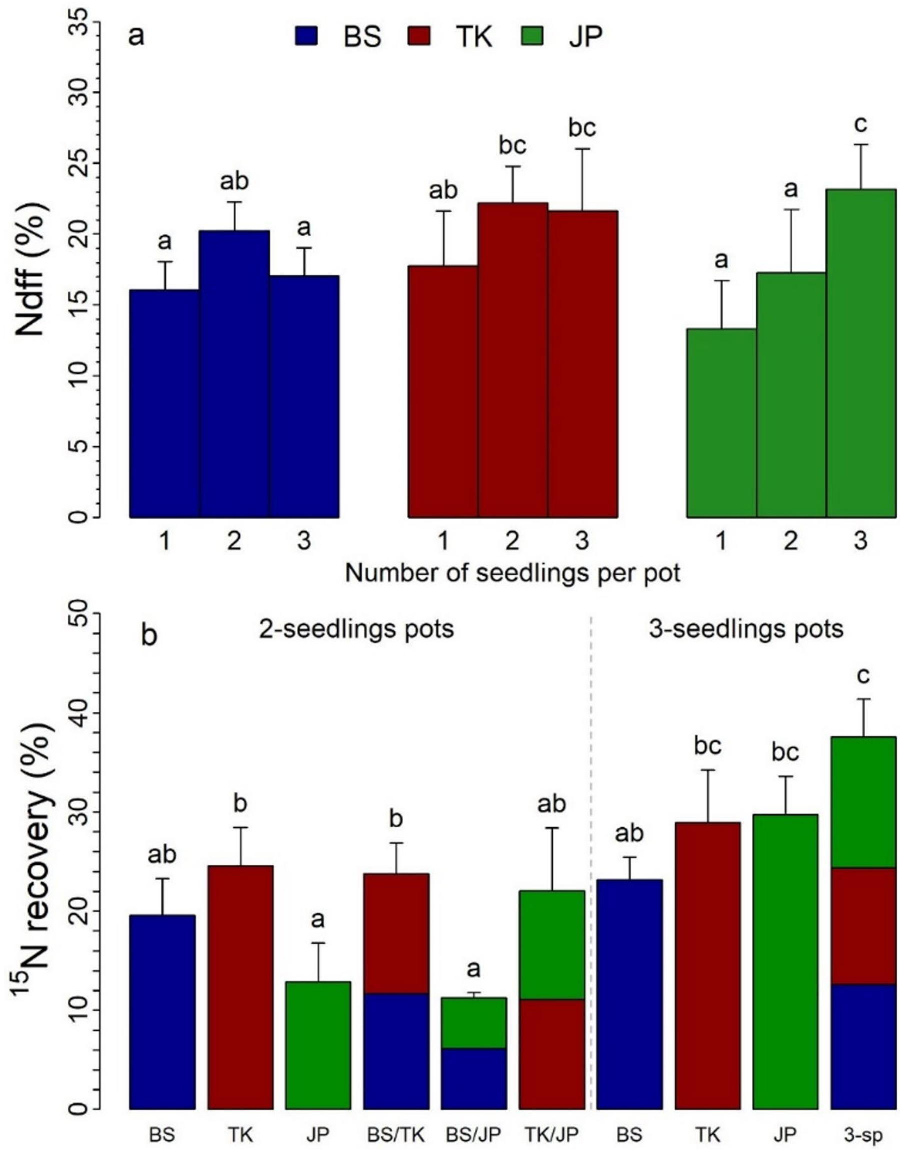

Fig. 4 **a** Nitrogen derived from the fertilizer (Ndff) for black spruce (BS), tamarack (TK) and jack pine (JP) seedlings in monospecific pots with one to three seedlings per pot; and **b** ^{15}N recovery (%) in mono- and multispecific pots with two to three seedlings per pot. Values are means ± SE ($n = 3$). Values not sharing the same letters are significantly different across species and density levels ($P < 0.05$)

RYT in the BS/TK/JP mixture tended to be > 1 (t = 2.26; df = 5; $P = 0.07$). The variability in RYT was also much lower (smaller SE) in the three-species mixture than in the two-species mixture types, regardless of the fertilization treatment.

3.5 Nitrogen fertilizer uptake

In monospecific pots (Fig. 4a), Ndff significantly varied among species and density levels (Table S6). The most noticeable results are (1) the higher average Ndff in tamarack (20.5 ± 1.2%) than in both black spruce (16.4 ± 1.8%) and jack pine (18.0 ± 1.2%), and (2) the significant increase in Ndff with increased density in jack pine, from 13 to 23% in one- and three-seedlings pots, respectively.

In two-seedlings pots, the percentage of ^{15}N derived from the fertilizer recovered in the seedlings' biomass (^{15}N recovery) was significantly lower in jack pine two-seedling monocultures and the BS/JP mixture (~ 11%) than in the tamarack monoculture and the BS/TK mixture (25%) (Fig. 4b). In three-seedlings pots, ^{15}N recovery was the highest in the three-species mixture, averaging 37.6 ± 6.6% versus ~30% for tamarack and jack pine monocultures, and only 25% for the black spruce monoculture. In the three-species mixture, the three species took up about the same amount of N derived from the fertilizer.

4 Discussion

Our experimental design enabled us to compare the growth of each species in monospecific and multispecific pots at a given seedling density, thus evaluating the relative intensity of intraspecific vs. interspecific competition. In addition, we showed a significant effect of N availability on species interactions and N uptake.

4.1 Growth patterns and N fertilization effect in monocultures

The results highlighted intrinsic differences in the growth patterns of the three species. Tamarack achieved significantly higher apical growth than the other species, especially in the N+ treatment, which is consistent with previous research [5] and its shade intolerance, which is associated with traits such as short leaf life span and high specific leaf area, both confering higher photosynthetic rates [16]. However, this did not necessarily translate into significantly higher biomass. For instance, jack pine achieved similar or even higher total biomass than the two other species despite lower apical growth. This mostly reflected differences in canopy architecture among species. Tamarack is characterized by a strong apical dominance and the production of mostly short-type shoots on lateral branches [13, 29], thus limiting the lateral expansion of the canopy. In contrast, jack pine and black spruce invest more biomass in lateral branches, which likely explained why they achieved similar or higher biomass than tamarack despite much lower height. Wood density is also known to be high in mature black spruce and jack pine trees relative to other boreal species [23]. Higher wood density in black spruce and jack pine relative to tamarack may therefore have also contributed to this pattern. Overall, black spruce tended to produce less biomass than tamarack and jack pine across density and fertilization treatments. This result is consistent with its intrinsic low growth rate and its sensitivity to water stress and high temperatures compared to other boreal conifer species [20, 38, 44, 47, 66]. Black spruce is also a shade-tolerant species, and its early growth has been shown to be facilitated by taller species, since shading from canopy vegetation can ameliorate growing conditions for these species [5].

In contrast with our first hypothesis, increasing seedling density in the monospecific pots did not significantly affect apical growth and total biomass, suggesting that resources such as water, N and light did not become significantly more limiting for seedlings' growth as density increased. On the contrary, jack pine's growth tended to be higher in three-seedling pots than in the one- and two-seedling pots in both N fertilization treatments. The uptake of N derived from the fertilizer by individual jack pine seedlings also increased with seedling density, suggesting that the three species may have different sensitivity to density. This contrasts with observations made for eastern white pine seedlings (*Pinus strobus* L.), which tends to be more affected by high densities [5].

As expected, N fertilization significantly improved seedlings' growth but its effect varied among species and growth indices. For instance, in monocultures, N fertilization (1) enhanced apical growth by 135% in tamarack, whereas it had no impact on black spruce and jack pine, and (2) almost doubled the biomass of tamarack and black spruce, whereas the effect was much lower for jack pine (Table 1). These results contrast with the generally high apical growth of jack pine and its high responsiveness to increased N availability reported elsewhere [8, 47, 53]. They also contrast with our second hypothesis that jack pine would produce more biomass and would benefit more from the N fertilization treatment than black spruce and tamarack. The lower N fertilization effect on jack pine's growth was consistent with its lower uptake of N derived from the fertilizer, especially in one- and two-seedlings pots (Fig. 4). The reason for this pattern is not clear but jack pine may be more sensitive to high doses of ammonium compared to black spruce and tamarack. While most conifers, especially in the boreal forest, have a higher affinity for ammonium than for nitrate [34], some early-successional tree species exhibit costly and inefficient uptake of NH_4^+, limiting their ability to benefit from this N source [6, 35, 45]. To our knowledge, it is unknown whether jack pine is more sensitive to ammonium toxicity than tamarack and black spruce, but differences have been shown to exist among boreal tree species, with white spruce having a higher tolerance to high ammonium concentration than Douglas fir and trembling aspen [35]. Interestingly, despite its relatively poor performance in monoculture, jack pine competed very well in multispecies pots with respect to both companion species and monocultures (see below).

4.2 Interactions among species and mixing effect

Our results highlighted two main elements regarding species interactions: (1) the strong competitiveness of jack pine, particularly in the N+ treatment; and (2) the effect of N fertilization not only on the growth of individual seedlings, but also on the interactions between the three species.

The strong competitiveness of jack pine was supported by two related observations. First, although the difference was not statistically significant, the total biomass of black spruce and tamarack in the N+ treatment tended to be lower in two-seedling pots when mixed with jack pine than in monocultures and other mixture types (Table 2). Interestingly, this effect was not as marked in the three-species mixture (Fig. 2b; see below). Second, jack pine exhibited higher total biomass in two- or three-species mixtures than in monocultures by up to 25% in the N− treatment and up to 30% in the N+ treatment (Table 2; Fig. 2b), suggesting that (1) the competition was alleviated for jack pine when it was mixed with another species; and/or (2) there was a complementarity between jack pine and the companion species in mixtures. Results from ^{15}N-labelling suggest that the strong growth rate of jack pine in mixtures might not be exclusively related to high N acquisition. In fact, ^{15}N-recovery in jack pine's biomass was not particularly high in multi-specific pots, although in the three-species mixture it represented 42% of the total biomass of the mixture. This result points toward a high N use efficiency and suggests that jack pine might be competitive for other resources, possibly water. Even though the pots were watered throughout the experiment period to avoid water stress, water remains the main limiting factor for plant growth. Jack pine is known for its high water use efficiency, and for maintaining higher stomatal conductance than black spruce even when soil moisture is low [44]. Interestingly, the competition effect of jack pine did not manifest as strongly on the companion species in the three-species mixtures. In fact, both black spruce and tamarack achieved slightly higher or similar biomass in the three-species mixtures relative to three-seedlings monocultures, regardless of the N fertilization treatment (Fig. 2). In addition, jack pine achieved 20–35% higher biomass relative to three-seedlings monocultures, indicating that at such high density, interspecific competition was lower than intraspecific competition. The sum of these specific responses resulted in the observed RYT > 1 in the three-species mixture of the N+ treatment. A RYT > 1 occurs when the productivity of a mixture is higher than the average productivity of the monocultures, reflecting a complementarity between the species present in the mixture. In the N+ treatment, species produced on average 16% more biomass compared to the average of the three-seedlings monocultures (RYT of 1.16). This result seems to indicate higher complementarity between the species at high densities, which is consistent with studies that have shown that the manifestation of complementarity mechanisms depends on several factors, including stand density and water availability [24, 49]. In the present study, this could have resulted from a better interception of light or water in three-species mixtures or a temporal complementarity of resource uptake between species, but this will have to be further investigated. Such a relative increase in biomass production (RYT > 1), however, does not necessarily result in transgressive overyielding, i.e. higher yield in the mixture than in the most productive monoculture. This indeed depends on the productivity discrepancy among companion species and/or on the magnitude of the complementarity effect [18, 19, 21]. In the present study, the yield of the three species-mixture was similar to that of the most productive monoculture (jack pine monoculture), and 35–40% higher than the less productive monoculture, namely the black spruce one (Fig. 3a), indicating that complementarity was strong enough to compensate for the presence of a low productive species (black spruce) in the mixture.

The N fertilization had an effect on seedling growth but also on the interactions between the three species. For instance, in two-species pots, black spruce, and to a lesser extent jack pine, increased their apical growth in mixture with tamarack relative to other mixtures, whereas no difference was found in the N− treatment (Table 2). The increase in apical growth for black spruce and jack pine in contact with tamarack (the tallest species) likely resulted from increased competition for light as it is often observed in trees growing inside closed forests compared to trees growing at the edges [33, 50]. An alternative explanation for the increased apical growth in black spruce may be the facilitation effect of shading by tamarack, as reported by [5]. In addition, the N fertilization impacted the interaction between the three species in the three-species mixture. While they produced similar biomass in the N− treatment, jack pine produced a significantly higher biomass in the N+ treatment (Fig. 2), showing that increased N availability was more beneficial to jack pine in a context of intense crowding. Similarly, while black spruce and tamarack produced similar biomass in two-species pots of the N− treatment, regardless of the companion species, their biomass tended to be lower in mixture with jack pine in the N+ treatment, further supporting the higher competitiveness of jack pine when N availability is high. These results are in contradiction with the apparent low ammonium uptake capacity of jack pine in monoculture but seem to indicate that jack pine's ability to use this N form increases with the level of intraspecific and interspecific competition.

5 Conclusion

In the present study, we compared the growth patterns in mono- and multispecific pots at different density levels, as well as the interactions of three widespread boreal conifer species under two levels of N availability. Our results showed that although tamarack had the largest apical growth and benefited the most from N fertilization in monocultures, jack pine was the most productive species in two-species and three-species pots, especially in the fertilized treatment. In addition, the three-species mixture in the N+ treatment exhibited RYT > 1 and slightly higher uptake of N derived from the fertilizer, pointing towards a complementarity between the species at high density. While acknowledging that these results may change throughout tree species ontogeny and may not directly apply to mature stands, we contend that they offer valuable insights into the interactions among these three dominant species of the Canadian boreal forest in early stages of seedling establishment in mixed conifer plantations and naturally regenerated stands.

Supplementary Information

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Supplementary Material 1

Author contributions

C.M, L.B. and O.F. designed the study. L.B collected the data. L.B., C.M and P.F. analyzed the data. C.M wrote the main manuscript text and prepared the figures. R.R.P., P.F. and O.F. reviewed the manuscript.

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Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

The collection of the plant parts of jack pine (*Pinus Banksiana* [Lamb]), black spruce (*Picea mariana* [Mill]) and tamarack (*Larix laricina* [Du Roi] K. Koch) complied with local and national guidelines. No permissions or licences were necessary.

Consent for publication

All authors have read and approved the final version of the manuscript and consent to its submission for publication.

Competing interests

The authors declare no competing interests.

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