

Role of green alder in boreal conifer growth: competitor or facilitator?

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Abstract

Sustainable forest management implies successful regeneration after disturbances. Low N availability and competition can, however, limit tree establishment in boreal ecosystems. To develop silviculture strategies that maintain productivity in such context, we established a field trial in northern Québec, Canada. We evaluated if a companion N₂-fixing species (*Alnus alnobetula*) promotes or hinders *Picea mariana* and *Pinus banksiana* establishment over six growing seasons. We tested if *Alnus* has a facilitation effect through nutritional processes and a competition effect through light interception. Foliar stable nitrogen isotope ratio ($\delta^{15}\text{N} = \frac{^{15}\text{N}}{^{14}\text{N}}$, ‰) results confirmed that *Alnus* obtains a substantial part of its N through biological fixation and represents an N source in this system. Although we did not observe increased foliar N concentrations in either conifer species in the presence of *Alnus*, *Pinus* growth was nonetheless higher in presence of *Alnus*, whereas no difference was observed for *Picea*. In the plots where *Alnus* cohabited with the conifers, the former had a negative impact on seedling growth, suggesting a significant competition for light. Overall, the net effect of *Alnus* was positive for *Pinus* and neutral for *Picea*. Our results have significant implications for silviculture in N-limited systems, especially in the context of climate change that imposes increased levels of stress on regeneration.

Key words: biotic interactions, boreal forests, N fixation, nurse plant, harsh subarctic ecosystem, restoration plantations

Introduction

Competition is the most studied biotic interaction in early community ecology (Bertness and Callaway 1994; Lortie et al. 2004). However, the role of positive interactions such as facilitation in community dynamics has also been demonstrated during the last decades, including in plant communities (Callaway and Walker 1997; Bruno et al. 2003; Lortie et al. 2004; Brooker et al. 2008). Although facilitation and competition are antagonistic interactions, they can simultaneously exist

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within a plant community. They can be the result of indirect interactions through pair-wise competition among multiple species (Callaway and Walker 1997; Bruno et al. 2003; Lortie et al. 2004). Facilitation and competition can also occur simultaneously between two species, but only the net outcome of the dominant interaction is observed on survival, recruitment, or growth (Callaway and Walker 1997; Bruno et al. 2003; Callaway 2007). Space and time play a crucial role in the intensity of the dependences between species within a community. For example, while enemy release leads to an increased success in the establishment of sugar maple (*Acer saccharum* Marsh.) seedlings at its upper elevational range limit, herbivory pressure is high at its lower limit in Mont Mégantic, Québec (Urli et al. 2016). Moreover, the dominant interaction during succession can switch over time between competition and facilitation (Bertness and Callaway 1994; Lortie et al. 2004). This balance between positive and negative interactions is affected by various factors, such as life stages, plant density, physiology, abiotic stress (Callaway and Walker 1997), or stand development (e.g., Cavard et al. 2011). For instance, seedling ontogenetic stages and seasonality influence the interaction outcome of alpine herbaceous vegetation on early seedling establishment of tree species at the treeline of the French Alps (Loranger et al. 2017). Hence, it is a challenge to determine where and when different processes are important within a community over time (Lortie et al. 2004).

Facilitation mechanisms are diverse; for example, they include abiotic stress amelioration, substrate modification, or protection from herbivory (Filazzola and Lortie 2014). The stress gradient hypothesis states that positive interactions such as facilitation increase in communities in abiotically stressful and low productivity environments (Bertness and Callaway 1994; Callaway 2007). Indeed, competition is high when resource acquisition is not limited by abiotic conditions, but its importance decreases compared with facilitation when severe physical conditions limit resource availability. Although this hypothesis is still debated (Brooker et al. 2008), it is supported by many empirical studies (Callaway 2007; Defossez 2012), and facilitative effects such as the “nurse-plant syndrome” are recognized as important and relevant processes in community dynamics (Brooker et al. 2008; Filazzola and Lortie 2014). Therefore, nurse plants can be used as a tool in restoration ecology (Gómez-Aparicio 2009). For example, the facilitative effects of grass or shrubs as nurse plants were observed in the restoration of degraded semiarid steppes or Mediterranean-type mountain ecosystems (Maestre et al. 2001; Castro et al. 2004). In addition to removing competitive species, using nurse shrubs and trees is thus a promising option to restore woody late-successional communities (Gómez-Aparicio 2009).

Facilitation and competition mechanisms have direct implications in the context of the transformation of closed-crown boreal forests into open, unproductive woodlands. Indeed, closed managed forests are progressively opening at their northern limit, mainly due to tree regeneration failure after natural or anthropogenic disturbances (Girard et al. 2009; Oris et al. 2014; Splawinski et al. 2019). In subarctic ecosystems, tree regeneration failure is caused by the absence of advanced regeneration, insufficient post-disturbance seed rain, the lack of suitable seedbeds, and competition by ericaceous species (Thiffault and Hébert 2017; Payette and Delwaide 2018). The boreal forest is a carbon sink and an important source of fibre (Brandt et al. 2013); regeneration failure thus threatens the sustainable provision of these ecosystem services, such as carbon sequestration (Kurz et al. 2013).

Restoration planting is a recognized management option to control community structure and composition, and is thus used to maintain ecosystem services (Stanturf and Madsen 2002; Nunez-Mir et al. 2015). However, many factors, including the nature and abundance of competing vegetation, influence the success of restoration efforts. Pioneer species rapidly establish and compete for light, water, and nutrients with late-successional tree species (Wagner and Robinson 2006). Mechanical site preparation is often used in this context to reduce the competition pressure on regenerating trees (Löf et al. 2012). However, companion vegetation can exert facilitative effects on planted trees by offering protection against stressful environmental conditions (Callaway 2007; Brooker et al. 2008) or by reducing the

competition by other species (Löf et al. 2014). In particular, *Alnus* species can fix and utilize atmospheric N₂ for growth (Bond 1956). As a result, the presence of *Alnus* increases soil N content (Binkley et al. 1992; Titus 2009) and can facilitate the establishment and growth of planted conifers (Haeussler and Coates 1986). However, *Alnus* species can also compete for light and water; therefore, they prevent conifer establishment and growth (Haeussler and Coates 1986; Jobidon 1995). These multiple mechanisms of plant–plant interactions need to be disentangled to better understand the balance between facilitation and competition of the nurse-plant syndrome (Filazzola and Lortie 2014) and identify the best practices for restoration planting in the boreal zone. Moreover, as species' idiosyncratic features play an important role in biotic interactions, it is crucial to understand how facilitation and competition mechanisms converge or diverge between slow-growing versus fast-growing native conifer species.

We addressed these questions using a field trial established in northern Québec, Canada, on a site burned in 2007 (Thiffault and Hébert 2017). The experiment aimed at testing the effects of mechanical site preparation (MSP) and planting of a nurse N₂-fixing species, American green alder (*Alnus alnobetula* subsp. *crispa*), on conifer growth. The site was planted in 2011 with black spruce (*Picea mariana* (Mill.)), considered a slow-growing, shade-tolerant, conservative-type species) and jack pine (*Pinus banksiana* Lamb.; considered a fast-growing, light-demanding, acquisitive-type species) under three silviculture scenarios: MSP, MSP with plantation of green alder, and a control treatment without MSP. Early results have evidenced a higher growth rate for conifers planted in plots treated with MSP, as well as with alder as a companion species, than in control plots (Thiffault and Hébert 2017). However, alder exerted significant competition for light, which could eventually decrease the initial benefits of this nurse species on planted conifers. A better characterization of N pathways was deemed necessary to understand the mechanisms responsible of the facilitative effects, especially on two conifers with different N acquisition strategies. Indeed, jack pine takes up N from the mineral soil (Visser 1995; Houle et al. 2014), whereas black spruce N nutrition mainly comes from the soil organic layer (Houle et al. 2014).

Therefore, we aimed at assessing the balance between the facilitative and the competitive effects of American green alder, a N₂-fixing species, on black spruce and jack pine growth on a northern boreal site characterized by harsh growing conditions. To achieve our objective, we used data describing soil and foliar stable nitrogen isotope ratio $\delta^{15}\text{N}$ and total N concentration, competition level, and seedling growth over six growing seasons and tested the following hypotheses: (i) foliar $\delta^{15}\text{N}$ is different between green alder and the planted conifer species, as alder can fix and utilize atmospheric N₂ for growth; (ii) green alder has a facilitative effect on conifer growth through nutritional processes; and (iii) there is a competitive effect of alder on the planted conifers through light interception. We tested which interaction (facilitation or competition) has the strongest effect on planted conifer growth (i.e., is the net outcome on growth positive or negative in presence of alder?) and if the interaction outcome is similar for both conifers.

Materials and methods

Study area

We studied the role of alder in an experimental plantation containing black spruce and jack pine seedlings, located in northern Québec, Canada (51°50'40.7" N, 68°15'46.9" W) at the actual northern limit of commercial forestry in Québec. This limit is based on the physical environment, timber production capacity, forest vulnerability to fire, and conservation of biodiversity (Jobidon et al. 2015). Vegetation in this region is typical of the black spruce–feather moss bioclimatic domain (Saucier et al. 2009). The region presents a continental sub-polar sub-humid climate with a mean annual temperature of -2.5°C and a mean annual precipitation of 900–1000 mm, of which 40%–45% falls as snow. Growing seasons are short, about 120 d. The soil is a Podzol with occasional induration derived from glacial tills with a loamy-sand texture (71% sand, 19% silt, and 10% clay in the upper-B horizon,

Soil Classification Working Group (1998)). A 12–15 cm thick mor humus covers the mineral soil. In 2007, a wildfire burned the previous stand, which was 61–80 years old and composed of 12–17 m tall black spruce trees with a canopy cover of 41%–60%. Visual assessment conducted in July 2010 showed the abundance of charred organic material (Thiffault and Hébert 2017).

Experimental design

Our experiment builds from a subset of the experimental setup described by Thiffault and Hébert (2017). The establishment of three silviculture scenarios were completed in 2011; they were randomly applied within five blocks on 15 main plots:

- i. standard mechanical site preparation applied in August 2010 with a T26.a disc trencher (Bracke Forest AB, Bräcke, Sweden) (MSP);
- ii. similar to MSP treatment, but followed by systematic planting in June 2011 of 2000 *Alnus alnobetula* subsp. *crispa* (AC) seedlings ha^{-1} that were produced in 110 cm^3 containers from local seed sources (MSP + AC); and
- iii. a control treatment (without mechanical site preparation) (C).

Block size ranged from 4.6 to 7.1 ha. Main plots were 1.1 ha each and separated by 10–15 m buffers. Main plots were divided into two subplots, in which black spruce and jack pine seedlings were randomly assigned to be planted. This experimental design was, therefore, a complete block split-plot assignment with five blocks, three main plots per blocks (MSP; MSP + AC; C), and two subplots per main plot (black spruce; jack pine) (cf. fig. 1 of Thiffault and Hébert 2017).

Conifer seedlings originated from local seed sources and were produced in 110 cm^3 containers. Initial seedling height and root collar diameter at the time of planting were, respectively, 32.4 ± 4.1 cm and 3.8 ± 0.6 mm for black spruce and 29.9 ± 3.6 cm and 3.4 ± 0.4 mm for jack pine. Seedlings were planted in July 2011 at a density of 2000 conifers ha^{-1} . In MSP + AC plots, conifer seedlings were planted independently of alder seedlings; conifer–alder distances, therefore, varied within plots.

Seedling measurements

We established 200 m^2 circular sampling plots in the approximate centre of each subplot. All planted conifer seedlings ($n = 45 \pm 1$) within these sampling plots were tagged to assess their dimensions over time. We measured seedling height (cm), leader's annual shoot length (cm), and root collar diameter (mm) of the tagged seedlings at the end of the first (2011), third (2013), and sixth (2016) growing seasons after planting. We calculated the height at the end of the second (2012) and the fifth (2015) growing seasons after planting by subtracting the leader's annual shoot length from total seedling height at the end of the third and sixth growing seasons, respectively. In 2016, we also measured the distance between conifer seedlings and the nearest alder (cm) and the nearest alder height (cm) in the MSP + AC treatment, to calculate a competition index.

In October 2016, the instantaneous photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) received at mid-height of the seedling and the instantaneous PPFD received above the seedling (i.e., full sunlight) were measured on two or three individuals per conifer species in three blocks in the MSP and MSP + AC treatments between 11:00 and 14:00 h on two consecutive sunny days using a PAR/LAI ceptometer (AccuPAR model LP-80, Decagon Devices, Inc., Pullman, Washington, USA). The ratio of full sunlight received by the seedlings was calculated as the ratio of PPFD measured at mid-height of the seedling over PPFD measured above the vegetation cover.

In 2016, we collected shoots from growing seasons 2014, 2015, and 2016 for two target seedlings of each conifer species and current-year leaves of the corresponding nearest alders in three blocks for

each treatment. For each of these target conifer seedlings, the mineral soil between 5 and 20 cm depth was collected within a 25 cm radius from the base of the stem.

Determination of chemical and isotope composition

We determined the contribution of atmospheric N₂ fixation by alder to conifer N uptake using soil and foliar total N and stable nitrogen isotope ratio ($\delta^{15}\text{N} = {}^{15}\text{N}/{}^{14}\text{N}$, ‰). We first tested if $\delta^{15}\text{N}$ was different between green alder and the planted conifer species. Indeed, foliar $\delta^{15}\text{N}$ of alder close to ambient air $\delta^{15}\text{N}$ (0‰, the standard reference used for the determination of stable nitrogen isotope ratio) implies that alder likely fixes and utilizes atmospheric N₂ for growth. We then tested if green alder had a facilitative effect on conifer growth through nutritional processes by comparing soil and foliar total N and $\delta^{15}\text{N}$ of conifer species in presence and absence of alder.

Soil samples were dried at ambient temperature at least 72 h and ground to pass a <0.5 mm screen, whereas foliar samples were oven-dried at 60 °C for at least 72 h to determine total N (N_{tot} , g kg⁻¹) and stable nitrogen isotope ratio ($\delta^{15}\text{N} = {}^{15}\text{N}/{}^{14}\text{N}$, ‰). Total N was determined by high-temperature dry combustion (1350 °C) followed by thermal conductivity detection (TruMac CN elemental analyzer; LECO Corporation, St. Joseph, Michigan, USA). We encapsulated 3.59 ± 0.12 mg of leaf and 60.04 ± 0.81 mg of soil from each sample in tin capsules that were sent to the Davis Stable Isotope Facility (University of California, Davis, California, USA) to determine their $\delta^{15}\text{N}$ signatures using an Isotope Ratio Mass Spectrometer (Europa Scientific Integra, PDZ Europa, Cheshire, UK).

Statistical analyses

We conducted the statistical analyses using the pooled data from shoots from the three years (2014, 2015, and 2016) for the planted conifers. We first used Student *t*-tests to assess the difference of foliar N_{tot} and $\delta^{15}\text{N}$ between alder and black spruce or jack pine. We then performed analyses of variance (ANOVA) to test for significant effects of silviculture scenarios and conifer species on the same variables. Analyses were conducted with (i) linear mixed-effects models (LMMs) to analyze the responses of N_{tot} and $\delta^{15}\text{N}$ for conifer leaves and soils, and ratio of full sunlight received by seedling to silviculture scenario, species, and the interaction silviculture scenario × species, using block, block × silviculture scenario, and block × silviculture scenario × species as random effects and (ii) LMMs with repeated measures to analyze the response of root collar diameter (three growing seasons) and height (five growing seasons) to silviculture scenario, species, number of growing seasons after planting, the three two-way interactions, and the three-way interaction silviculture scenario × species × number of growing seasons, using block, block × silviculture scenario and block × silviculture scenario × species as random effects. A compound symmetry matrix was used as the variance-covariance matrix of the error terms for these LMMs with repeated measures.

Post-hoc tests were performed to test for differences between silviculture scenarios for the LMMs and between silviculture scenarios within species × number of growing seasons for the LMM with repeated measures, when the *F*-values of the ANOVA were significant at $\alpha = 0.05$.

Finally, using conifer and alder height and the distance data from MPS + AC treatment, we calculated angular height as a competition index (Biging and Dobbertin 1992) as follows:

$$A = \arctan\left(\frac{\text{height}_j - \text{height}_i}{\text{distance}_{ij}}\right)$$

where *j* represents the target conifer seedling and *i* the nearest natural or planted alder seedling. We then used LMMs to analyse the response of root collar diameter and height to angular height, conifer species, and their interaction, using block and block × species as random effects.

In all analyses, we conducted standard procedures for model diagnostics. Degrees of freedom associated to the denominators for the tests of fixed-effects were calculated with the Satterthwaite method, as the factors associated to the random effects had few levels and the distribution of their estimators was better approximated by a χ^2 distribution than a normal distribution (Littell et al. 2006). All analyses were conducted using R version 3.6.0 (R Core Team 2019) using the *lmerTest* package (Kuznetsova et al. 2016) for LMMs and *lsmeans* package (Lenth and Love 2018) for post-hoc tests.

Results

Facilitation for nitrogen: differences in $\delta^{15}\text{N}$ and N_{tot} in leaves and soils between species and silviculture scenarios

Both foliar $\delta^{15}\text{N}$ and N_{tot} of alder ($-1.01 \pm 0.03\text{‰}$ and $24.56 \pm 2.29 \text{ g kg}^{-1}$, respectively) were significantly higher than those of black spruce ($-1.49 \pm 0.66\text{‰}$, $t = 6.04$, $p < 0.001$ and $9.58 \pm 0.46 \text{ g kg}^{-1}$, $t = -16.84$, $p < 0.001$, respectively) and jack pine ($-2.05 \pm 0.67\text{‰}$, $t = 7.76$, $p < 0.001$ and $14.97 \pm 0.48 \text{ g kg}^{-1}$, $t = -10.83$, $p < 0.001$, respectively). Foliar $\delta^{15}\text{N}$ of alder was significantly closer to ambient air $\delta^{15}\text{N}$ and showed very small variability compared with black spruce and jack pine. We detected no significant difference in foliar and soil $\delta^{15}\text{N}$ and N_{tot} between silviculture scenarios. Conifer species effect on foliar and soil $\delta^{15}\text{N}$ was not significant, but it was on foliar and soil N_{tot} (Figs. 1 and 2, Table 1).

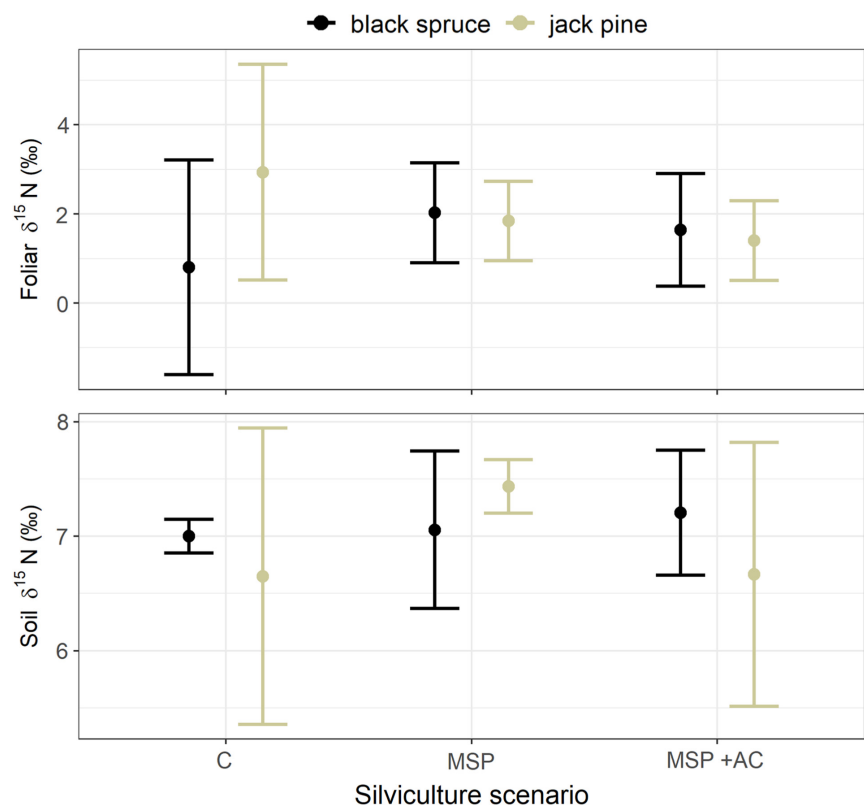


Figure 1. Foliar and soil $\delta^{15}\text{N}$ for black spruce and jack pine in the control treatment (C), i.e., without a mechanical site preparation, with standard mechanical site preparation (MSP) and with a standard MSP followed by systematic planting of alder (MSP + AC). Data are presented as mean \pm standard deviation.

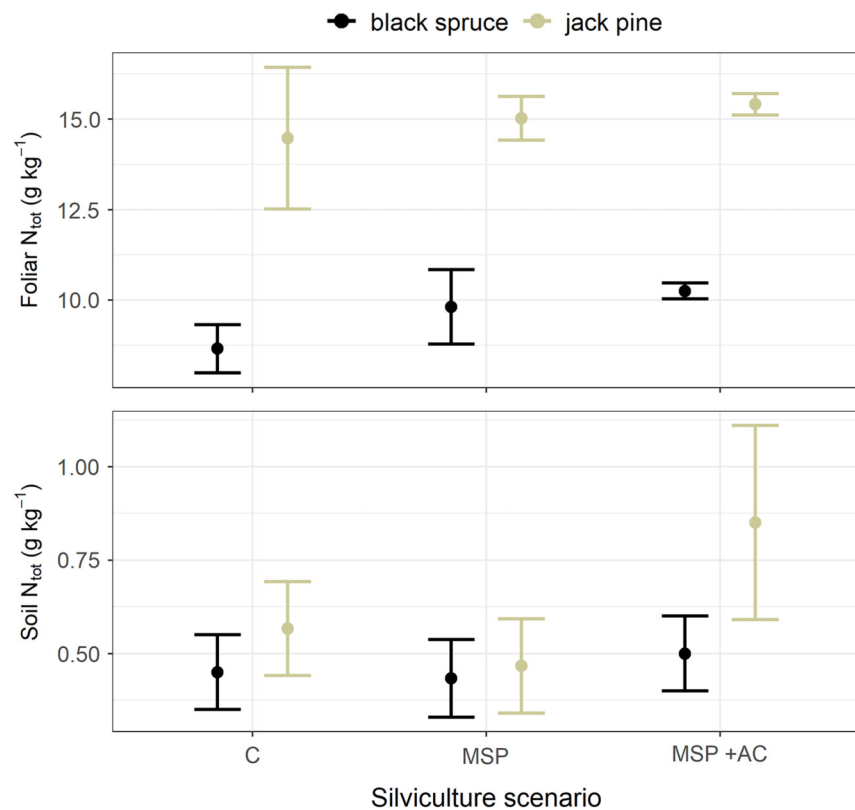


Figure 2. Foliar and soil N_{tot} of black spruce and jack pine in the control treatment (C), i.e., without a mechanical site preparation, with standard mechanical site preparation (MSP) and with a standard MSP followed by systematic planting of alder (MSP + AC). Data are presented as mean \pm standard deviation.

Light interception and competition for light

The ratio of full sunlight received by seedlings was significantly lower in the presence ($76\% \pm 11\%$) than in the absence of alder ($96\% \pm 1.3\%$) for both conifer species (Table 2). The conifer species had no effect on the ratio of full sunlight received by the seedlings (Table 2).

In the MSP + AC treatment, the root collar diameter, and the height of both conifer species significantly decreased with the increase of angular height ($F_{1;374.86} = 107.05$, $p < 0.001$ and $F_{1;416.41} = 152.29$, $p < 0.001$ for diameter and height, respectively, Fig. 3). After six growing seasons, root collar diameter and height were higher for jack pine than for black spruce ($F_{1;4.93} = 223.82$, $p < 0.001$ and $F_{1;4.25} = 57.54$, $p = 0.001$ for diameter and height, respectively, Fig. 3). Competition from alder, as inferred from angular height, was marginally higher on jack pine than on black spruce (significant interaction angular height \times species, $F_{1;240.30} = 4.14$, $p = 0.043$ and $F_{1;399.54} = 4.68$, $p = 0.031$ for diameter and height, respectively, Fig. 3).

Net outcome of facilitation and competition on growth

Jack pine showed greater growth in root collar diameter and height than black spruce over the first six growing seasons after planting (Fig. 4, Tables 3 and 4). The effect of silviculture scenario on growth was significant and differed between species (significant silviculture scenario \times species interaction, Tables 3 and 4). Moreover, this interaction between silviculture scenario and species differed between

Table 1. ANOVA results for $\delta^{15}\text{N}$ (‰) and N_{tot} (g kg^{-1}) of needles and soil between silviculture scenarios and conifer species.

Effect (fixed)	Needles			Soil		
	Degrees of freedom ^a	F	p	Degrees of freedom ^a	F	p
$\delta^{15}\text{N}$						
Silviculture scenario	2, 6	0.084	0.921	2, 11.9	0.525	0.604
Species	1, 6	0.812	0.402	1, 11.9	0.264	0.617
Silviculture scenario \times species	2, 6	1.536	0.289	2, 11.9	0.460	0.642
N_{tot}						
Silviculture scenario	2, 12	2.580	0.117	2, 6	3.201	0.113
Species	1, 12	135.182	<0.001	1, 6	7.031	0.038
Silviculture scenario \times species	2, 12	0.209	0.815	2, 6	2.273	0.184

Note: Values in bold indicate a significant effect at $\alpha < 0.05$.

^aDegrees of freedom presented as numerator, denominator. Denominator degrees of freedom were calculated with the Satterthwaite method (Littell et al. 2006).

Table 2. ANOVA results for ratio of full sunlight received by the seedlings between two silviculture scenarios (mechanical site preparation and mechanical site preparation + *Alnus alnobetula* subsp. *crispa*) and conifer species.

Effect (fixed)	Degrees of freedom ^a	F	p
Silviculture scenario	1, 3.8	11.767	0.027
Species	1, 4.0	0.689	0.456
Silviculture scenario \times species	1, 3.8	1.037	0.370

Note: Values in bold indicate a significant effect at $\alpha < 0.05$.

^aDegrees of freedom presented as numerator, denominator. Denominator degrees of freedom were calculated with the Satterthwaite method (Littell et al. 2006).

growing seasons (significant three-way interaction silviculture scenario \times species \times number of growing seasons). Black spruce root collar diameter and height were significantly higher in the MSP and MSP + AC treatments than in C plots from the third and fifth seasons onward, respectively (Fig. 4) but was similar between the MSP and MSPS + AC scenarios during the six years of our study (Fig. 4). For jack pine, we observed a significant difference in seedling height and diameter between the C treatment and the other scenarios from the third growing season after planting onward. From the third and the fifth growing seasons after planting onward, jack pine diameter and height were higher with than without alder in scenarios with standard mechanical site preparation (significant difference between MSP and MSP + AC, Fig. 4).

Discussion

Facilitation for N nutrition

As expected, alder fixed atmospheric N_2 for growth in these plantations. Indeed, the foliar $\delta^{15}\text{N}$ of alder was significantly closer to ambient air $\delta^{15}\text{N}$ and showed very small variability compared with black spruce and jack pine, as should be expected when N is taken from a homogenous source. Conversely, the foliar $\delta^{15}\text{N}$ of conifers presented higher variability reflecting the spatial variability of

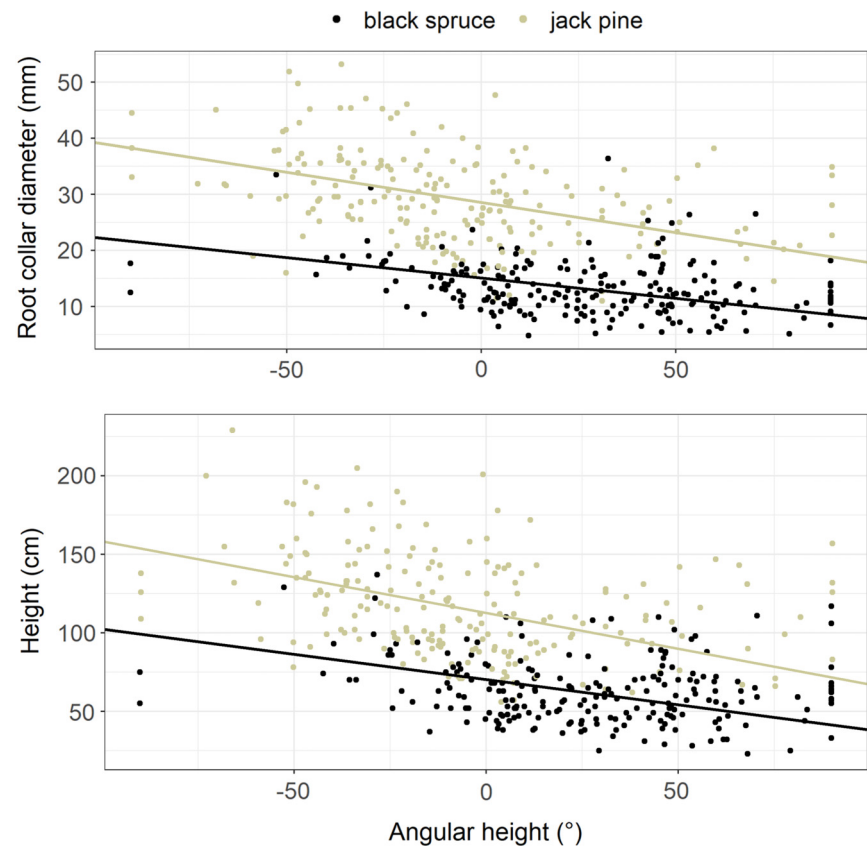


Figure 3. Root collar diameter (RCD, mm) and height (H , cm) of black spruce and jack pine after six growing seasons, as a function of angular height (A , °) in the mechanical site preparation followed by systematic planting of alder treatment during this same season. When $A < 0$, conifer seedlings are taller than the nearest alder seedlings. Lines represent the linear regression of root collar diameter or height as a function of the angular height with the following equations: $RCD = -0.07290A + 15.08393$ and $H = -0.32140A + 70.30002$ for black spruce, and $RCD = -0.10756A + 28.57438$ and $H = -0.45695A + 112.66465$ for jack pine.

soil $\delta^{15}\text{N}$. However, we detected no facilitative effect of alder through nutrition on the planted conifers during their sixth growing season (no significant difference in foliar and soil $\delta^{15}\text{N}$ and N_{tot} between silviculture scenarios), although soil N concentration under jack pine tended to be higher in the presence of alder (but not significantly). Fixation of atmospheric N by alder under field conditions has been known for several decades (Bond 1956). The presence of alder in conifer stands thus increases soil fertility, levels of N, and exchangeable base cations (Binkley et al. 1992). For instance, lodgepole pine (*Pinus contorta*) foliar N concentration decreased by 20% with Sitka alder (*Alnus viridis*) density reduction (from 2000 to 0 clumps ha^{-1}) (Brockley and Sanborn 2003). It is thus surprising that we did not detect these effects in our experiment. One reason might be related to the low input to soil N by alder relative to the total soil N pool on the site. Also, the additional N uptake by conifers in alder-planted plots might have occurred but remained undetected with isotopic analyses because of the dilution of $\delta^{15}\text{N}$ in plant tissues.

Competition

The presence of alder decreased available light to the planted conifers by 21%, on average. Jack pine was slightly more affected by light competition than black spruce, as shown by the more negative

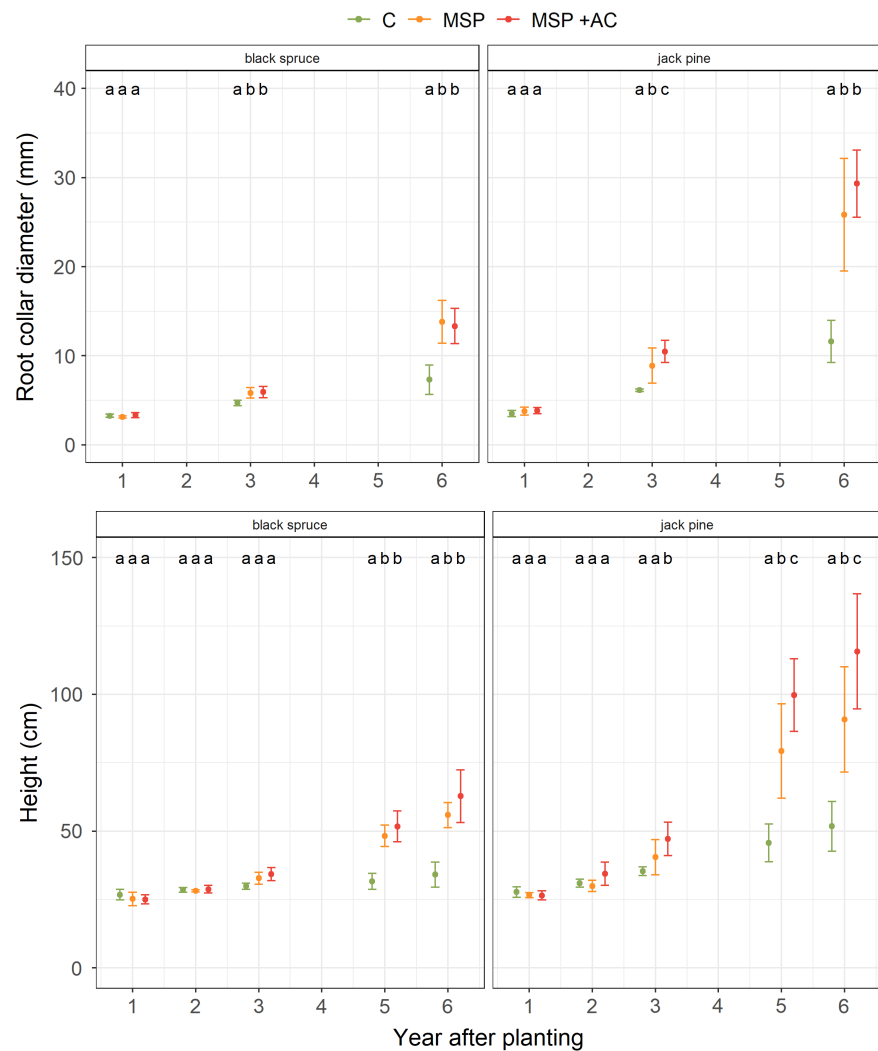


Figure 4. Evolution of root collar diameter (mm) and height (cm) of black spruce and jack pine for each silviculture scenario (C: control treatment; MSP: standard mechanical site preparation; MSP + AC: standard mechanical site preparation followed by systematic planting of alder) from the first to the sixth growing seasons after planting. Data are presented as mean \pm standard deviation. Different letters show a significant difference at $\alpha < 0.05$ between treatments for each species \times number of growing seasons combination.

slope between root collar diameter and angular height for jack pine than black spruce, an effect compatible with the fact that black spruce is more shade tolerant than jack pine (Bérubé-Deschênes et al. 2017). These results reinforce those of Thiffault and Hébert (2017) determined over the three first growing seasons.

The fast growth of alder and its negative effects on seedling and tree growth via competition for light, has been shown for conifer species (Haeussler and Coates 1986; Jobidon 1995; Fang et al. 2019).

Alder could also have negatively influenced the water availability of conifer species. The level of plant water stress can be assess using foliar or wood isotopic discrimination for ^{13}C ($\Delta^{13}\text{C}$) as in non-stressful conditions, plants favor the absorption and the assimilation of ^{12}C and thus are depleted in

Table 3. ANOVA results for plant root collar diameter among silviculture scenarios, conifer species, and number of growing seasons after planting.

Effect (fixed)	Degrees of freedom ^a	F	p
Silviculture scenario	2, 8.0	31.8	<0.001
Species	1, 11.8	334.4	<0.001
Number of growing seasons	4, 2727.1	12713.4	<0.001
Silviculture scenario × species	2, 11.8	9.7	0.003
Silviculture scenario × number of growing seasons	8, 2727.2	423.9	<0.001
Species × number of growing seasons	4, 2727.1	453.9	<0.001
Silviculture scenario × species × number of growing seasons	8, 2727.1	10.5	<0.001

Note: Values in bold indicate a significant difference at $\alpha < 0.05$.

^aDegrees of freedom presented as numerator, denominator. Denominator degrees of freedom were calculated with the Satterthwaite method (Littell et al. 2006).

Table 4. ANOVA results for plant height among silviculture scenarios, conifer species, and number of growing seasons after planting.

Effect (fixed)	Degrees of freedom ^a	F	p
Silviculture scenario	2, 20.2	38.0	<0.001
Species	1, 20.4	88.7	<0.001
Number of growing seasons	4, 5417.6	60230.3	<0.001
Silviculture scenario × species	2, 20.4	4.6	0.022
Silviculture scenario × number of growing seasons	8, 5417.7	616.0	<0.001
Species × number of growing seasons	4, 5417.6	798.2	<0.001
Silviculture scenario × species × number of growing seasons	8, 5417.7	42.3	<0.001

Note: Values in bold indicate a significant difference at $\alpha < 0.05$.

^aDegrees of freedom presented as numerator, denominator. Denominator degrees of freedom were calculated with the Satterthwaite method (Littell et al. 2006).

¹³C relative to the air (Farquhar et al. 1989). However, the absence of difference in foliar $\Delta^{13}\text{C}$ between silviculture scenarios for both conifer species led us to reject this hypothesis (data not shown).

Net outcome of facilitation and competition on growth

Although in the plots where alder cohabits with the conifers (MSP + AC), alder exerted a significant negative effect on both species diameter and height, jack pine net growth increased in the presence of alder, and the net growth of black spruce was not influenced by the latter (difference between MSP and MSP + AC) (Table 5). These results are in line with the early results of Thiffault and Hébert (2017) who found a facilitative effect of alder on conifer regeneration in this subarctic ecosystem but did not clearly identify the mechanisms at play. The aim of our study was to identify the specific mechanism underlying the facilitative effect of alder on conifer species. Overall, our results do not support our hypothesis of a facilitative effect via nutrition of alder on growth of black spruce and jack pine during this early successional stage at this subarctic site (Table 5). The positive effect

Table 5. Synthesis of the facilitative and the competitive effects of American green alder on root collar diameter (RCD) and seedling height (*H*) of planted black spruce and jack pine.

Planted species	Facilitation via nutrition	Competition for light		Net outcome on growth	
		RCD	<i>H</i>	RCD	<i>H</i>
Black spruce	—	↓	↓	—	—
Jack pine	—	↓↓	↓↓	↑	↑

Note: ↑, positive effect; ↓, negative effect; —, no effect.

of alder on jack pine growth and the absence of negative effect on black spruce growth, however, suggest that facilitative interactions have indeed occurred, but we did not capture them with the variables we have monitored or the precision of our measurements. For example, alder might have increased soil inorganic N availability enough so that less photosynthates had to be invested in mycorrhizal symbioses to maintain the same nutritional status. Other potential facilitation mechanisms also include protection from harsh environmental conditions (e.g., freeze–thaw cycle, soil temperature) (Haeussler and Coates 1986).

In northern Alberta, Canada, no relationships were found between soil N and alder (*Alnus crispa*) abundance and between foliar N of lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*) and alder abundance, suggesting no nutritional benefit from alder, whereas it competed for light (Cortini and Comeau 2008). On an Alaska floodplain, competition for light by alder (*Alnus tenuifolia*) on willow (*Salix alaxensis*), poplar (*Populus balsamifera*), and white spruce (*Picea glauca*) seedling growth was higher than facilitative interactions through soil nitrogen addition (Walker and Chapin 1986). The results of a long-term experiment on the same region showed that the presence of alder (*Alnus incana*) initially increased the survival and the growth of white spruce and then, within six years after canopy closure, decreased them (Chapin et al. 2016). However, in our study, facilitation might prevail over time as alder litter accumulates. Such a pattern was observed in a 15-year study in southern interior British Columbia, Canada, in which stand composition was manipulated from pure lodgepole pine to mixtures with native Sitka alder or herbs (Simard et al. 2006). Controlling the density of the planted alder could be efficient to balance the facilitative and competitive effects on conifer growth (Jobidon 1995). For example, Fang et al. (2019) suggested that 100–400 red alder (*Alnus rubra*) trees per hectare could improve soil N level on nutrient-poor sites without substantially decreasing stand volume of western redcedar (*Thuja plicata*) and Douglas fir (*Pseudotsuga menziesii*). Légaré et al. (2004) evidenced higher diameter and height of black spruce in mixed-stand with proportion of aspen (*Populus tremuloides*) less than 41% of the total stand basal area.

Longer-term studies are needed to evaluate the net outcome of the facilitative and competitive interactions between alder and the planted conifers in this harsh subarctic ecosystem. Indeed, this net outcome would be dependent on individualistic site and community features that can lead to divergent successions detectable only decades later (Simard et al. 2006; Chapin et al. 2016).

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Author contributions

NT conceived and designed the study. MU performed the experiments/collected the data. MU, NT, and DH analyzed and interpreted the data. NT, DH, and YB contributed resources. MU, NT, DH, SG, and YB drafted or revised the manuscript.

Competing interests

The authors have declared that no competing interests exist.

Data availability statement

All relevant data are within the paper.

References

- Bertness MD, and Callaway R. 1994. Positive interactions in communities. *Trends in Ecology & Evolution*, 9(5): 191–193. PMID: [21236818](#) DOI: [10.1016/0169-5347\(94\)90088-4](#)
- Bérubé-Deschênes A, Franceschini T, and Schneider R. 2017. Quantifying competition in white spruce (*Picea glauca*) plantations. *Annals of Forest Science*, 74: 26. DOI: [10.1007/s13595-017-0624-3](#)
- Biging GS, and Dobbertin M. 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. *Forest Science*, 38(3): 695–720. DOI: [10.1093/forestscience/38.3.695](#)
- Binkley D, Sollins P, Bell R, Sachs D, and Myrold D. 1992. Biogeochemistry of adjacent conifer and alder-conifer stands. *Ecology*, 73(6): 2022–2033. DOI: [10.2307/1941452](#)
- Bond G. 1956. Evidence for fixation of nitrogen by root nodules of alder (*Alnus*) under field conditions. *New Phytologist*, 55(2): 147–153. DOI: [10.1111/j.1469-8137.1956.tb05276.x](#)
- Brandt JP, Flannigan MD, Maynard DG, Thompson ID, and Volney WJA. 2013. An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. *Environmental Reviews*, 21(4): 207–226. DOI: [10.1139/er-2013-0040](#)
- Brockley RP, and Sanborn P. 2003. Effects of Sitka alder on the growth and foliar nutrition of young lodgepole pine in the central interior of British Columbia. *Canadian Journal of Forest Research*, 33(9): 1761–1771. DOI: [10.1139/x03-098](#)
- Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, et al. 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, 96: 18–34. DOI: [10.1111/j.1365-2745.2007.01295.x](#)
- Bruno JF, Stachowicz JJ, and Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, 18(3): 119–125. DOI: [10.1016/S0169-5347\(02\)00045-9](#)
- Callaway RM. 2007. Interaction between competition and facilitation. *In* Positive interactions and interdependence in plant communities. Springer, Dordrecht, Netherlands. pp. 179–254. DOI: [10.1007/978-1-4020-6224-7_4](#)

- Callaway RM, and Walker LR. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, 78(7): 1958–1965. DOI: [10.2307/2265936](https://doi.org/10.2307/2265936)
- Castro J, Zamora R, Hódar JA, Gómez JM, and Gómez-Aparicio L. 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. *Restoration Ecology*, 2(3): 352–358. DOI: [10.1111/j.1061-2971.2004.0316.x](https://doi.org/10.1111/j.1061-2971.2004.0316.x)
- Cavard X, Bergeron Y, Chen HYH, Paré D, Laganière J, and Brassard B. 2011. Competition and facilitation between tree species change with stand development. *Oikos*, 120(11): 1683–1695. DOI: [10.1111/j.1600-0706.2011.19294.x](https://doi.org/10.1111/j.1600-0706.2011.19294.x)
- Chapin FS, Conway AJ, Johnstone JF, Hollingsworth TN, and Hollingsworth J. 2016. Absence of net long-term successional facilitation by alder in a boreal Alaska floodplain. *Ecology*, 97(11): 2986–2997. PMID: [27870053](https://pubmed.ncbi.nlm.nih.gov/27870053/) DOI: [10.1002/ecy.1529](https://doi.org/10.1002/ecy.1529)
- Cortini F, and Comeau PG. 2008. Evaluation of competitive effects of green alder, willow and other tall shrubs on white spruce and lodgepole pine in Northern Alberta. *Forest Ecology and Management*, 255(1): 82–91. DOI: [10.1016/j.foreco.2007.08.027](https://doi.org/10.1016/j.foreco.2007.08.027)
- Defossez E. 2012. Effects of biotic interactions on forest regeneration along climatic gradients. PhD thesis, Université de Grenoble, Grenoble, France. 263 p.
- Fang C, Comeau PG, and Harper GJ. 2019. Effects of red alder on growth of Douglas-fir and western redcedar in southwestern British Columbia. *Forest Ecology and Management*, 434: 244–254. DOI: [10.1016/j.foreco.2018.12.023](https://doi.org/10.1016/j.foreco.2018.12.023)
- Farquhar GD, Ehleringer JR, and Hubick KT. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Biology*, 40: 503–537. DOI: [10.1146/annurev.pp.40.060189.002443](https://doi.org/10.1146/annurev.pp.40.060189.002443)
- Filazzola A, and Lortie CJ. 2014. A systematic review and conceptual framework for the mechanistic pathways of nurse plants. *Global Ecology and Biogeography*, 23(12): 1335–1345. DOI: [10.1111/geb.12202](https://doi.org/10.1111/geb.12202)
- Girard F, Payette S, and Gagnon R. 2009. Origin of the lichen–spruce woodland in the closed-crown forest zone of eastern Canada. *Global Ecology and Biogeography*, 18(3): 291–303. DOI: [10.1111/j.1466-8238.2009.00449.x](https://doi.org/10.1111/j.1466-8238.2009.00449.x)
- Gómez-Aparicio L. 2009. The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology*, 97(6): 1202–1214. DOI: [10.1111/j.1365-2745.2009.01573.x](https://doi.org/10.1111/j.1365-2745.2009.01573.x)
- Haeussler S, and Coates KD. 1986. Autecological characteristics of selected species that compete with conifers in British Columbia: a literature review. Land Management Report 33. British Columbia Ministry of Forests, Victoria, BC. 180 p.
- Houle D, Moore J-D, Ouimet R, and Marty C. 2014. Tree species partition N uptake by soil depth in boreal forests. *Ecology*, 95(5): 1127–1133. PMID: [25000744](https://pubmed.ncbi.nlm.nih.gov/25000744/) DOI: [10.1890/14-0191.1](https://doi.org/10.1890/14-0191.1)
- Jobidon R. 1995. Autoécologie de quelques espèces de compétition d'importance pour la régénération forestière au Québec. *Revue de littérature. Mémoire de recherche forestière n°117*. Direction de la recherche forestière, Ministère des Forêts, de la Faune et des Parcs, Sainte-Foy, QC. 196 p.

- Jobidon R, Bergeron Y, Robitaille A, Raulier F, Gauthier S, Imbeau L, et al. 2015. A biophysical approach to delineate a northern limit to commercial forestry: the case of Quebec's boreal forest. *Canadian Journal of Forest Research*, 45: 515–528. DOI: [10.1139/cjfr-2014-0260](https://doi.org/10.1139/cjfr-2014-0260)
- Kurz WA, Shaw CH, Boisvenue C, Stinson G, Metsaranta J, Leckie D, et al. 2013. Carbon in Canada's boreal forest — a synthesis. *Environmental Reviews*, 21(4): 260–292. DOI: [10.1139/er-2013-0041](https://doi.org/10.1139/er-2013-0041)
- Kuznetsova A, Brockhoff PB, and Christensen RHB. 2016. lmerTest: tests in linear mixed effects models. 1–20 p. [online]: Available from <https://mran.microsoft.com/snapshot/2017-02-04/web/packages/lmerTest/index.html>.
- Légaré S, Paré D, and Bergeron Y. 2004. The responses of black spruce growth to an increased proportion of aspen in mixed stands. *Canadian Journal of Forest Research*, 34(2): 405–416. DOI: [10.1139/x03-251](https://doi.org/10.1139/x03-251)
- Lenth R. 2018. Least-squares means. 1–5 p. [online]: Available from <https://cran.r-project.org/web/packages/lsmmeans/index.html>.
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD, and Schabenberger O. 2006. SAS system for mixed models. 2nd edition. SAS Institute Inc., Cary, North Carolina.
- Löf M, Bolte A, Jacobs DF, and Jensen AM. 2014. Nurse trees as a forest restoration tool for mixed plantations: effects on competing vegetation and performance in target tree species. *Restoration Ecology*, 22(6): 758–765. DOI: [10.1111/rec.12136](https://doi.org/10.1111/rec.12136)
- Löf M, Dey DC, Navarro RM, and Jacobs DF. 2012. Mechanical site preparation for forest restoration. *New Forests*, 43(5): 825–848. DOI: [10.1007/s11056-012-9332-x](https://doi.org/10.1007/s11056-012-9332-x)
- Loranger H, Zotz G, and Bader MY. 2017. Competitor or facilitator? The ambiguous role of alpine grassland for the early establishment of tree seedlings at treeline. *Oikos*, 126: 1625–1636. DOI: [10.1111/oik.04377](https://doi.org/10.1111/oik.04377)
- Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire FI, et al. 2004. Rethinking plant community theory. *Oikos*, 107: 433–438. DOI: [10.1111/j.0030-1299.2004.13250.x](https://doi.org/10.1111/j.0030-1299.2004.13250.x)
- Maestre FT, Bautista S, Cortina J, and Bellot J. 2001. Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. *Ecological Applications*, 11(6): 1641–1655. DOI: [10.1890/1051-0761\(2001\)011\[1641:PFUFBG\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1641:PFUFBG]2.0.CO;2)
- Nunez-Mir GC, Iannone BV, Curtis K, and Fei S. 2015. Evaluating the evolution of forest restoration research in a changing world: a “big literature” review. *New Forests*, 46(5): 669–682. DOI: [10.1007/s11056-015-9503-7](https://doi.org/10.1007/s11056-015-9503-7)
- Oris F, Asselin H, Finsinger W, Hély C, Blarquez O, Ferland M-E, et al. 2014. Long-term fire history in northern Quebec: implications for the northern limit of commercial forests. *Journal of Applied Ecology*, 51(3): 675–683. DOI: [10.1111/1365-2664.12240](https://doi.org/10.1111/1365-2664.12240)
- Payette S, and Delwaide A. 2018. Tamm review: the North-American lichen woodland. *Forest Ecology and Management*, 417: 167–183. DOI: [10.1016/j.foreco.2018.02.043](https://doi.org/10.1016/j.foreco.2018.02.043)
- R Core Team. 2019. R: a language and environment for statistical computing [online]: Available from [R-project.org/](https://www.R-project.org/).

Saucier J-P, Robitaille A, and Grondin P. 2009. Cadre bioclimatique du Québec. *In* Manuel de Foresterie. 2nd edition. Edited by R Doucet and M Côté. Ordre des ingénieurs forestiers du Québec, Éditions Multimondes, Quebec, Quebec. pp. 186–205.

Simard SW, Radosevich SR, Sachs DL, and Hagerman SM. 2006. Evidence for competition and facilitation trade-offs: effects of Sitka alder density on pine regeneration and soil productivity. *Canadian Journal of Forest Research*, 36(5): 1286–1298. DOI: [10.1139/x06-040](https://doi.org/10.1139/x06-040)

Soil Classification Working Group. 1998. The Canadian system of soil classification. 3rd edition. Agriculture and Agri-Food Canada Publication 1646. NRC Research Press, Ottawa, Ontario. 187 p.

Splawinski TB, Cyr D, Gauthier S, Jetté J-P, and Bergeron Y. 2019. Analyzing risk of regeneration failure in the managed boreal forest of northwestern Quebec. *Canadian Journal of Forest Research*, 49(6): 680–691. DOI: [10.1139/cjfr-2018-0278](https://doi.org/10.1139/cjfr-2018-0278)

Stanturf JA, and Madsen P. 2002. Restoration concepts for temperate and boreal forests of North America and Western Europe. *Plant Biosystems — An International Journal Dealing with all Aspects of Plant Biology*, 136(2): 143–158. DOI: [10.1080/11263500212331351049](https://doi.org/10.1080/11263500212331351049)

Thiffault N, and Hébert F. 2017. Mechanical site preparation and nurse-plant facilitation for the restoration of subarctic forest ecosystems. *Canadian Journal of Forest Research*, 47: 926–934. DOI: [10.1139/cjfr-2016-0448](https://doi.org/10.1139/cjfr-2016-0448)

Titus JH. 2009. Nitrogen-fixers *Alnus* and *Lupinus* influence soil characteristics but not colonization by later successional species in primary succession on Mount St. Helens. *Plant Ecology*, 203(2): 289–301. DOI: [10.1007/s11258-008-9549-0](https://doi.org/10.1007/s11258-008-9549-0)

Urli M, Brown CD, Narváez Perez R, Chagnon P-L, and Vellend M. 2016. Increased seedling establishment via enemy release at the upper elevational range limit of sugar maple. *Ecology*, 97(11): 3058–3069. PMID: [27870043](https://pubmed.ncbi.nlm.nih.gov/27870043/) DOI: [10.1002/ecy.1566](https://doi.org/10.1002/ecy.1566)

Visser S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytologist*, 129(3): 389–401. DOI: [10.1111/j.1469-8137.1995.tb04309.x](https://doi.org/10.1111/j.1469-8137.1995.tb04309.x)

Wagner RG, and Robinson AP. 2006. Critical period of interspecific competition for four northern conifers: 10-year growth response and associated vegetation dynamics. *Canadian Journal of Forest Research*, 36: 2474–2485. DOI: [10.1139/x06-058](https://doi.org/10.1139/x06-058)

Walker LR, and Chapin FS. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. *Ecology*, 67(6): 1508–1523. DOI: [10.2307/1939082](https://doi.org/10.2307/1939082)