Canadian Journal of Forest Research
Revue canadienne de recherche forestière

Mechanical site preparation and nurse-plant facilitation for the restoration of subarctic forest ecosystems

Journal:	<i>Canadian Journal of Forest Research</i>
Manuscript ID	cjfr-2016-0448.R2
Manuscript Type:	Article
Date Submitted by the Author:	17-Mar-2017
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Keyword:	restoration, boreal forest, conifer, nutrition, competition
Please Select from this Special Issues list if applicable:	N/A

1 **Mechanical site preparation and nurse-plant facilitation for the restoration of**
2 **subarctic forest ecosystems**

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15
16 **Abstract**

17 Sustainable forest management implies successful regeneration following disturbances.
18 Tree regeneration in subarctic ecosystems can however be constrained by limitations to
19 seedling establishment related to cold soils, slow decomposition rates, and competition
20 by ericaceous species. We established a field trial at the northern limit of commercial
21 forests in Québec, Canada, to evaluate how mechanical site preparation (MSP) and
22 planting of a nurse N₂-fixing species can promote conifer establishment on a site burned
23 in 2007. The experiment comprised four treatments applied in 2010: standard MSP (disc

trenching); standard MSP + planting of *Alnus crispa*; intensive MSP, with larger furrows than standard MSP; and a control. Main plots were divided and planted in 2011 with *Picea mariana* or *Pinus banksiana*. We monitored seedling survival, growth, nutrition and microsite after three years. Results revealed interactions between treatments and planted species. Mechanical site preparation resulted in higher conifer growth relative to the control conditions, and planting *Alnus* resulted in growth gains similar as those obtained from intensive MSP. We measured competitive interactions between *Alnus* and the conifers that might eventually cancel out the initial benefits derived from facilitation by planting the species. Longer-term monitoring of interspecific interactions are needed to further illuminate the mechanisms responsible for the facilitative effect and identify the best management practices.

Keywords

Reforestation, restoration, boreal forest, conifer, nutrition, competition, regeneration

Résumé

L'aménagement durable des forêts implique que la régénération forestière s'établit avec succès après les perturbations. La régénération forestière dans les écosystèmes subarctiques peut toutefois être problématique en raison des limitations à l'établissement des semis et à la productivité végétale associées aux sols froids, aux faibles taux de décomposition, et à la végétation de compétition dominée par les plantes éricacées. Nous avons installé une expérience à la limite nordique des forêts commerciales du Québec, Canada, pour évaluer comment la préparation mécanique du sol (PM) et la plantation d'une espèce compagne fixatrice d'azote pouvait améliorer l'établissement des conifères

48 sur un site récemment brûlé. L'expérience comprenait quatre traitements appliqués en
49 2010 : PM standard (scarifiage à disques); PM standard + plantation d'*Alnus crispa*; PM
50 intensive avec des sillons plus larges que PM standard; et un témoin. Les parcelles
51 principales ont été divisées et plantées en 2011 avec *Picea mariana* ou *Pinus banksiana*.
52 Nous avons mesuré la survie, la croissance, la nutrition et les caractéristiques des
53 microsites des arbres plantés sur une période de trois ans. Les résultats ont révélé des
54 interactions entre la PM et l'espèce plantée. La PM a stimulé la croissance des conifères
55 par rapport au témoin et la plantation d'*Alnus* a résulté en des gains de croissance
56 similaires à ceux associés à la PM intensive. Nous avons mesuré des interactions
57 compétitives entre *Alnus* et les conifères, lesquelles pourraient éventuellement annuler les
58 effets bénéfiques initiaux de facilitation s'il advenait qu'elle domine la station. Un suivi à
59 plus long terme de même que l'étude des interactions interspécifiques sont nécessaires
60 afin d'identifier les mécanismes responsables de l'effet de facilitation et identifier les
61 meilleures pratiques d'aménagement.

62

63 Mots-clés

64 Reboisement, restauration, forêt boréale, conifère, nutrition, compétition, régénération

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Introduction

Tree density and stocking are critical factors that determine forest productivity (Drew and Flewelling 1979). They both depend directly upon successful tree regeneration following natural and anthropogenic disturbances (Burton et al. 2003; Van Bogaert et al. 2015). Whereas some boreal ecosystems are characterized by an abundant and thriving regeneration layer (e.g., sub-boreal forests of Québec, Canada, which are dominated by balsam fir; *Abies balsamea* [L.] Miller), tree regeneration in subarctic climates can be constrained by cold air temperatures, short growing seasons, cold soils, slow decomposition rates and, consequently, strong overall limitations to seedling establishment and plant productivity (Saucier et al. 2015). In boreal ecosystems, the failure of natural regeneration after major disturbances can be exacerbated by the absence of advance regeneration (Brumelis and Carleton 1988), insufficient post-disturbance seed rain (Boiffin and Munson 2013), the lack of suitable seedbeds (Dufour-Tremblay et al. 2012), or phenol-rich leachates from understory species, particularly ericads such as sheep laurel (*Kalmia angustifolia* L.) and Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd; Castells et al. 2005; Nilsson and Wardle 2005). Catastrophic wildfire, which is a common disturbance in boreal landscapes, greatly affects the availability of suitable seedbeds for conifer regeneration (Mallik et al. 2010; Nguyen-Xuan et al. 2000). Although severe fires can expose the mineral soil and promote conifer regeneration when seed sources are available, the residual thick and charred organic material that remains after low-intensity fires is a poor germination substrate (Greene et al. 2007). Lack of abundant and well-dispersed natural regeneration a few years following disturbance can lead to net losses of forest productivity and other ecosystem

89 services, such as carbon sequestration (Kurz et al. 2013). In such cases, rehabilitation
90 efforts are needed to restore desired structure, species compositions, and ecosystem
91 processes (Stanturf and Madsen 2002; Stanturf et al. 2014; Nunez-Mir et al. 2015).
92
93 Restoration planting can be used to accelerate the reconstruction of forest ecosystems on
94 sites where succession would be otherwise delayed for many decades or susceptible to
95 the creation of alternative stable states (Beisner et al. 2003; Hébert et al. 2014). Planted
96 seedlings are exposed to various environmental stresses, which affect their survival and
97 growth (Burdett 1990; Margolis and Brand 1990; Grossnickle 2012). In northern
98 ecosystems, mechanical site preparation offers the potential for improved seedling
99 establishment by reducing competing vegetation cover, increasing soil temperature,
100 mitigating air temperature extremes, and stimulating organic matter decomposition
101 (Prévost 1992; Löf et al. 2012). Successful seedling establishment is often reported as
102 being dependent upon the intensity of mechanical site preparation (e.g., Thiffault et al.
103 2004). For example, the use of double-pass treatments (Thiffault et al. 2005) or
104 increasing disc angle to create larger furrows (Buitrago et al. 2015) is expected to
105 increase planted seedling growth, given that the treatments create larger areas free of the
106 direct and indirect interferences of competing species, especially ericaceous species. Site
107 preparation intensity, however, interacts with site characteristics; more severe treatments
108 are not always followed by increased seedling growth (e.g., Fleming et al. 2014). Also,
109 responses to mechanical site preparation are routinely species-specific. For example, we
110 observed that 15th-year leader growth of black spruce (*Picea mariana* [Miller] BSP)

increased with scarification on a boreal site in Newfoundland (Canada), whereas jack pine (*Pinus banksiana* Lambert) did not benefit from the treatment (Thiffault et al. 2010).

Competing vegetation generally hinders the growth and survival of planted conifers. Indeed, studies worldwide have demonstrated that in most cases, the control of competing vegetation results in increased growth of planted seedlings (Walstad and Kuch 1987; Wagner et al. 2005; McCarthy et al. 2011). Yet surrounding vegetation can improve soil moisture, nutrient availability and structure, as well as regulate microclimatic variation (Brooker et al. 2008). These vegetation effects on seedling microclimate can sometimes favour increased nutrient status, which is a positive influence on early seedling growth (Buitrago et al. 2015). In particular, the colonization of bare soils by N₂-fixing species potentially ameliorates the growing substrate for later successional species (Walker et al. 2003). For example, species within the genus *Alnus* can fix and utilize atmospheric N₂ for growth (Bond 1956), thereby facilitating successional processes (Chapin et al. 1994; Callaway and Walker 1997; Bellingham et al. 2001). Over the long-term, facilitation can increase productivity in planted, mixed-species forests (Piotto 2008; Benomar et al. 2013; Mason and Connolly 2014). Yet gains in productivity are not always measured and they may be highly dependent upon the species that are used (e.g., Nguyen et al. 2012). Thus, there is a trade-off that needs to be addressed between competition and facilitation (Simard et al. 2006). Although companion species can offer protection from harsh conditions (e.g., desiccation, sunscald, or soil N depletion) and promote conifer survival, they can significantly reduce planted species growth through competition for light, water or nutrients (e.g., Nelson et al. 2012).

134

135 Our general objective was to assess the potential for mechanical site preparation and
136 planting of a companion N₂-fixing species, mountain alder (*Alnus viridis* (Chaix) DC ssp.
137 *crispa* (Aiton) Turrill (Syn = *A. crispa* [Aiton] Pursh)), to promote planted black spruce
138 and jack pine seedling establishment on a subarctic forest site in northern Québec lacking
139 natural regeneration. We studied black spruce and jack pine because both species
140 naturally regenerate in the study region and constitute the dominant canopy species in
141 these ecosystems. Three growing seasons after planting, we aimed: *i*) to evaluate the
142 effects of mechanical site preparation and its intensity, planting of mountain alder, and
143 planted species on ericaceous species cover in planting microsites; *ii*) to assess the effects
144 of mechanical site preparation intensity, planting of mountain alder as a companion
145 species, and planted conifer species on seedling survival, third year dimensions, leader
146 growth, foliar nutrition, and microsite nutrient availability; and *iii*) to evaluate whether
147 the effects of alder on black spruce and jack pine are species and distance-dependent.

148

149 To achieve these objectives, we established a field experiment to test the following
150 hypotheses. First, we predicted that mechanical site preparation results in a lower
151 ericaceous shrub cover than a control treatment (prediction P1), the effect being more
152 important in intensively prepared plots than in plots submitted to a standard treatment
153 (prediction P2). We postulated that planting mountain alder in mechanically prepared
154 plots results in a lower ericaceous cover than following standard mechanical site
155 preparation alone (prediction P3), and that this effect is similar to that of performing an
156 intensive treatment (prediction P4). We did not expect the planted conifer species to

influence the ericaceous shrub cover (prediction P5). We posited that mechanical site preparation positively influences foliar nutrition of the planted conifers, as well as soil nutrient concentrations in their rooting zone (prediction P6). We expected that planting mountain alder results in similar foliar nutrient and soil nutrient concentrations as performing an intensive mechanical site preparation treatment (prediction P7). The magnitude of the treatment effects on foliar and soil characteristics is expected to vary between the planted conifer species (significant interactions) (prediction P8). We hypothesized that seedling survival, dimensions and leader growth are positively related to mechanical site preparation intensity (prediction P9), and that planting mountain alder after standard mechanical site preparation results in similar seedling survival, dimensions and leader growth as performing an intensive site preparation treatment (P10). The planted conifer species is expected to interact with treatments to influence seedling survival, dimensions and growth (significant interactions); we predicted that jack pine is more responsive than black spruce (prediction P11). Finally, we hypothesized that the magnitude of the conifer seedling responses is a function of mountain alder competition expressed as a function of distance and relative height, conifer species, and the interaction between the two (prediction P12).

Materials and methods

Study area and site description

We established an experimental plantation in northern Québec, Canada (51°50'40.7" N, 68°15'46.9" W). The site is about 290 km north of Baie-Comeau, within the black spruce-feather moss bioclimatic domain, which has been described by Saucier et al. (2009). The

plantation is located at the actual northern limit of commercial forestry in Québec, a limit that is based upon a broad set of criteria (physical environment, timber production capacity, forest vulnerability to fire, and conservation of biodiversity; Jobidon et al. 2015). Climate is continental sub-polar sub-humid, with a short growing season (120 days). Mean annual temperature is -2.5°C and annual precipitation is 900–1000 mm, of which 40–45 % falls as snow, forming a snow cover of 400–450 cm deep. The study site is about 32 ha in area and characterized as glacial till with a loamy-sand texture (71 % sand, 19 % silt, and 10 % clay in the upper-B horizon). The soil that has developed from this parent material is a Podzol (Soil Classification Working Group 1998) with occasional induration. The mineral soil is covered by a 12–15 cm-thick mor humus. The previous stand, which was 61- to 80-years-old and composed of 12–17 m-tall black spruce with a canopy cover of 41–60 %, had been burned by a wildfire in 2007. The area was not subjected to salvage logging. We conducted visual observations in July 2010 that indicated the abundance of charred organic material and reindeer lichen (*Cladina*), a lack of natural conifer regeneration, and gradual site encroachment by ericads (mainly Labrador tea).

Experimental design and treatments

We delimited five blocks varying from 4.6 ha to 7.1 ha (mean of 5.5 ha; standard deviation of 0.9 ha), which we further divided into four main plots of 1.1 ha each separated by 10–15 m buffers. Blocks were irregular in shape and size and delimited to reduce soil variability within each replicate. Within each block, the main plots were randomly assigned to receive one of the following treatments (Fig. 1):

- i) standard mechanical site preparation was applied in August 2010 with a T26.a disc trencher (Bracke Forest AB, Bräcke, Sweden) (MSP_S);
- ii) similar to MSP_S treatment, but followed by systematic planting in June 2011 of alder seedlings that were produced in 110 cm^3 containers from local seed sources, at an approximate density of $2000\text{ seedlings}\cdot\text{ha}^{-1}$ (MSP_S+AC);
- iii) intensive mechanical site preparation that was applied in August 2010 with a T26.a disc trencher, involving a first pass (as in the MSP_S treatment), followed by a second pass within the same furrows but with an amplified disc angle (relative to the trencher), to create larger furrows (MSP_L); and
- iv) a control treatment (without mechanical site preparation; C).

Furrows in the MSP_S and MSP_S+AC treatments (measured in July 2011) were 60 cm wide (standard deviation = 16 cm). Furrows in the MSP_L treatment were 64 cm wide (standard deviation = 18 cm). Although the increase in width was small, the MSP_L treatment was effective in creating significantly larger furrows than the MSP_S and MSP_S+AC treatments ($F_{1,3.68} = 16.43$, $P = 0.018$). Furrow depth was similar in all treatments involving MSP (mean = 31 cm; standard deviation = 10 cm; $F_{1,1307} = 3.80$, $P = 0.052$).

We divided each main plot into two subplots, which were assigned to be planted randomly either with black spruce or with jack pine seedlings. The resulting experimental design (Fig. 1) was a complete block split-plot assignment with five blocks, four main plots per block, and two subplots per main plot, for a total of 40 experimental units.

226 *Planting material*

227 Conifer seedlings were produced in 110 cm³ containers from local seed sources. Initial
228 stock type dimensions at the time of planting (mean $\pm$ standard deviation) were estimated
229 from a sub-sample of 60 seedlings of each species randomly collected on site. Seedling
230 height (cm) and root-collar diameter (mm) were respectively 32.4 ± 4.1 cm and 3.8 ± 0.6
231 mm for black spruce, and 29.9 ± 3.6 cm and 3.4 ± 0.4 mm for jack pine.

232

233 Foliar samples were collected from the same seedlings, oven-dried at 65 °C for 48 h, and
234 ground to pass a 40-mesh screen (particles size < 420 micron). Ground samples were
235 digested in boiling H₂SO₄ and H₂O₂ (Parkinson and Allen 1975). Nutrient concentrations
236 were determined by flow-injection colorimetry (Quickchem, Lachat, Milwaukee, WI) and
237 inductively coupled plasma spectroscopy (ICAP-9000, Thermo Instruments, Franklin,
238 MA). Initial foliar concentrations did not reveal any major nutrient deficiencies. For
239 black spruce, mean ($\pm$ standard deviation) concentrations of N, P and K were 20 ± 23
240 mg·g⁻¹, 1.9 ± 0.2 mg·g⁻¹, and 5.3 ± 0.6 mg·g⁻¹, respectively. Nitrogen, phosphorus and
241 potassium estimates in jack pine were 15 ± 12 mg·g⁻¹, 1.5 ± 0.2 mg·g⁻¹, and 5.8 ± 0.7
242 mg·g⁻¹, respectively.

243

244 *Planted period and method*

245 Seedlings were planted on 11–15 July 2011 using a container seedling dibble at 2.0×2.5
246 m spacing, resulting in a planting density of 2000 conifers·ha⁻¹. In scarified plots (MSP_S,
247 MSP_S+AC, MSP_L), seedlings were planted in the hinge position (trench–berm interface).

In MSP_S+AC plots, we planted the conifer seedlings independently of the alder seedlings, thereby resulting in various conifer–alder distances over the plots.

Seedling measurements and microsite characteristics

In the approximate centre of each subplot, we established a circular sampling plot of 200 m² (8 m radius) in which we tagged all planted conifer seedlings for long-term growth assessments (Fig. 1). Each circular sampling plot contained 45 ± 1 planted conifers (mean $\pm$ standard deviation). In each sampling plot, the three seedlings that were closest to the centre were used for further soil and foliage sampling in October 2013. For each of these, we collected a sample of current-year shoots and soil within a 10 cm radius from the root plug. Foliar samples were used to determine nutrient concentrations (as described above). Soil samples were dried at ambient temperature and ground to pass a 2 mm-mesh screen. Total N and total C were determined by high temperature dry combustion (1350 °C), followed by infrared detection of total C and thermal conductivity detection of total N (TruMac CN Elemental Analyzer, LECO Corporation, St. Joseph, MI, USA). Extractable P, K, Ca, and Mg were extracted in Mehlich-III solution and measured by inductively coupled argon plasma–optical emission spectrometry (Optima 4300 DV, Perkin-Elmer, Norwalk, CT, USA). We determined soil pH in a 10 g slurry with deionized water (Fisher Scientific accumet 50, Denver Instrument, Bohemia, NY, USA).

Tagged seedlings were measured for height (cm) and ground-level diameter (gld; mm) in October of the first (2011) and third (2013) growing seasons after planting. In 2011 and 2013, we measured the distance between the tagged seedlings and the nearest planted or

naturally established alder seedling in MSP_S+AC plots. In 2013, we measured the height of the nearest alder seedling, and also visually estimated the percent cover of ericaceous species within a 50 cm radius of the planted seedlings (done in the field, using 5 % classes; mean of two observers' estimates) (Vanha-Majamaa et al. 2000).

Statistical analyses

We analyzed the 2013 percent cover of ericaceous shrubs (predictions P1 to P5), foliar and soil nutrient concentrations (predictions P6 to P8), and seedling mensurational data (height, gld, leader growth, the volume index based on the volume of a cone; Wagner and Robinson 2006) (prediction P9 to P11) using mixed-effects analyses of variance (ANOVA), with respect to the experimental design (Littell et al. 2006). Treatments at the whole-plot level (C, MSP_S, MSP_S+AC, MSP_L), at the subplot-level (black spruce, jack pine), and their interactions were considered as fixed effects, while blocks and interactions with blocks were considered as random effects. Survival data were not subjected to statistical analyses, as seedling mortality was marginal (see Results). All data were verified for normality and homoscedasticity assumptions using the Shapiro–Wilk statistics and standard graphical approaches (plots of residuals against fitted values and probability plots). Natural-log, square-root, or inverse sine transformations were applied when necessary (see table footnotes). In such cases, for the sake of clarity we present back-transformed means and confidence intervals after bias correction (Ung and Végiard 1988; Végiard and Ung 1993). All ANOVAs were conducted with the MIXED procedure of SAS (v. 9.3, SAS Institute, Cary, NC, USA). Denominator degrees of freedom for the *F*-tests were computed using the Kenward-Roger approximation (Schaalje et al. 2001). In

case of significant F of the ANOVAs, treatments were compared using least square mean tests. Inferential statistics were based on $\alpha = 0.05$ as the significance threshold.

To test prediction P12, we used data from only the MSP_S+AC plots and investigated how distance between planted conifers and the nearest alder seedling influenced tree diameter. To do so, the distance and relative height of alder in relation to the target conifers were used to calculate angular height (Fig. 2), a distance-dependent competition index (Biging and Dobbertin 1992). Angular height, in turn, was considered, together with species and their interaction, in a linear regression as a predictor of tree diameter using the MIXED procedure of SAS, with Block and Block $\times$ Species as random effects. We used diameter as a response variable because of its known sensitivity to competition for light compared to height (e.g., Wagner and Robinson 2006). Given that the Angular height $\times$ Species interaction was not significant ($F_{1,305} = 2.88$, $P = 0.091$), we re-ran the model without the interaction term, thereby accounting for a common slope but distinct intercepts between species. We took into account the heterogeneous variance among species using the GROUP option of the REPEATED statement in the MIXED procedure of SAS (Littell et al. 2006). We then calculated the likelihood-ratio-based R^2 (R^2_{LR}) for the relationship (Magee 1990).

Results

Percent cover of ericaceous shrubs (predictions P1 to P5)

There was a significant effect of mechanical site preparation on percent cover of ericaceous species after three growing seasons ($F_{3,32.3} = 32.91$, $P < 0.001$); percent cover

was significantly higher ($t_{32.3} \geq 7.97$, $P < 0.001$) in the controls (33 %) compared to the other treatments including the *Alnus* planted plots (8 %). The MSP_S , MSP_{S+AC} and MSP_L treatments did not differ from one another ($t_{32.6} \leq 0.24$, $P \geq 0.816$). The planted species did not significantly influence the percent cover of ericaceous shrubs ($F_{1,32.3} = 0.94$, $P = 0.340$; data not shown).

Foliar nutrient concentrations and soil characteristics (predictions P6 to P8)

Treatment effects on seedling foliar nutrient concentrations were similar across species (no significant interaction; Table 1). All treatments increased foliar N (16 mg g^{-1}) and P (1.9 mg g^{-1}) concentrations relative to the controls ($N = 11 \text{ mg g}^{-1}$; $P = 1.7 \text{ mg g}^{-1}$; $t_{31.8} \geq |-2.18|$, $P < 0.001$), but did not differ from one another ($t_{32.3} \leq 1.82$, $P \geq 0.077$). Foliar K, Ca and Mg were not influenced by the treatments (Table 1). Regardless of the treatments, the species effect was highly significant for foliar N, P, K and Ca (Table 1), but its direction varied depending upon nutrient. We measured higher foliar P, K and Ca concentrations in black spruce ($P = 2.05 \text{ mg g}^{-1}$; $K = 6.7 \text{ mg g}^{-1}$; $Ca = 3.02 \text{ mg g}^{-1}$) than in jack pine ($P = 1.65 \text{ mg g}^{-1}$; $K = 5.2 \text{ mg g}^{-1}$; $Ca = 1.97 \text{ mg g}^{-1}$), but foliar N was higher in jack pine (16 mg g^{-1}) than in black spruce (13 mg g^{-1}). Foliar magnesium concentrations were similar across species (Table 1).

Species and the treatments interacted to influence concentrations of soil nutrients, pH and cation exchange capacity (Table 1). Detailed analysis of the interaction showed that for both species, soil N and P concentrations were similar in control, MSP_S , MSP_{S+AC} and MSP_L plots ($P \geq 0.088$), but species had significant effects on these variables in some

treatments. For example, soil N was similar under jack pine seedlings and black spruce seedlings in control plots, but higher under jack pine than black spruce in MSP_S and MSP_S+AC plots. The species effect was reversed in MSP_L plots. Soil P concentrations were higher under black spruce than jack pine in MSP_S plots ($F_{1,95} = 69.07$, $P < 0.001$), but similar among species in the other treatments ($F_{1,95} \leq 1.05$, $P \geq 0.308$). Soil K was lower in all treated plots compared to control plots, but only when black spruce was planted ($F_{3,21.4} = 5.26$, $P = 0.007$). We measured no such effect in jack pine-planted plots ($F_{3,21.2} \leq 2.66$, $P = 0.074$). Soil K concentrations were higher under jack pine than black spruce in the MSP_S and MSP_S+AC plots ($F_{1,95} \geq 12.07$, $P < 0.001$). Soil pH was similar across treatments in the jack pine-planted plots ($F_{3,14.3} = 0.72$, $P = 0.554$), but not in black spruce-planted plots ($F_{3,14.4} = 4.21$, $P = 0.025$). We measured no treatment effect on CEC ($F_{3,17.6} \leq 0.77$, $P = 0.525$), but species affected this variable in the MSP_S and MSP_S+AC plots ($F_{1,95} \geq 6.65$, $P \leq 0.012$).

Seedling survival, dimensions and leader growth (predictions P9 to P11)

Seedling survival was > 99 % for both species after three growing seasons, preventing any statistical analysis (the occurrence of dead seedlings was too low for models to converge). The treatments and species had significant effects on seedling third-year height, diameter, volume and leader growth, either alone or in combination (Table 2). While standard mechanical site preparation (MSP_S) did not result in significantly higher third-year height compared to control conditions, both the planting of an N₂-fixing companion species (MSP_S+AC) and the creation of larger furrows (MSP_L) resulted in taller seedlings than the control and MSP_S treatments three years after planting,

regardless of the species (Fig. 3a). After three growing seasons, jack pine seedlings were taller than black spruce seedlings (Fig. 3b). Treatments had a significant, positive effect on seedling third-year diameter, but the effect was not the same for black spruce and jack pine. Large furrows (MSP_L) further increased black spruce diameter compared to MSP_S and MSP_S+AC, but did not differ from MSP_S+AC for jack pine diameter (Fig. 3c). Leader growth also responded to a significant Treatment × Species interaction: black spruce was sensitive to an increase in treatment intensity, whereas jack pine only responded to the presence or absence of mechanical site preparation (Fig. 3d). Seedling volume index positively responded to mechanical site preparation intensity and jack pine seedlings attained a volume index three times greater than that of black spruce seedlings (data not shown).

Competitive effect of the nearest alder (prediction P12)

Alder seedlings were taller, in average, than both black spruce and jack pine seedlings (Fig. 3b). Angular height between alder seedlings and planted conifers (measured in October 2013) was a significant predictor of seedling ground-level diameter ($F_{1,329} = 8.79, P = 0.003$; Fig. 4). Conifer seedling diameter significantly decreased as angular height increased. The linear model explained two thirds of the variation in the response variable (Fig. 4).

Discussion

Effects of mechanical site preparation and its intensity

Conifer seedling growth responded positively to mechanical site preparation when compared to direct planting without humus management. This response to scarification is typical for newly planted conifers on boreal sites (e.g., Johansson et al. 2013). However, this study is one of the few (Hébert et al. 2014) that has tested the treatment at the northern limit of commercial forestry in Québec, demonstrating the potential for silviculture to restore forest cover in this sensitive zone (sensu Van Bogaert et al. 2015). The positive effect of mechanical site preparation on seedling growth was related to improved microsite conditions (Löf et al. 2012), such as an increase in soil temperature (Thiffault and Jobidon 2006; Wallertz and Malmqvist 2013), a decrease in competing vegetation cover (e.g., Nilsson and Örlander 1999), and positive effects of soil mixing on organic matter decomposition (Salonius 1983; Pelletier Bergeron et al. 2013). Indeed, mechanical site preparation reduced ericaceous species cover four-fold around the planted seedlings, which resulted in increased foliar N and P, thereby promoting seedling growth (Yamasaki et al. 2002).

In Europe and parts of Asia, mechanical site preparation is effective in reducing planted seedling mortality that is due to insect attacks, particularly weevils (Björklund et al. 2003; Löf et al. 2012; Wallertz and Malmqvist 2013). The exposed bare soil creates a protective barrier minimizing damage that is incurred by insect pests (Petersson et al. 2005). In the present study, seedling survival was not affected by mechanical site preparation. In fact, less than 1 % of the seedlings had died after three growing seasons and, thus, all treatments were confounded. We attribute the high survival rate to the scarcity of defoliating insects or bark beetles in this region (Beaudoin et al. 2014). Also,

the high precipitation regime and thick snow cover likely reduced risks of water stress during summer (Grossnickle 2012) and desiccation during winter (Frey 1983).

Increasing the intensity of silviculture generally results in accelerated growth of planted conifers (Park and Wilson 2007). In this harsh subarctic ecosystem, black spruce and jack pine seedlings positively responded to the creation of slightly larger furrows in the MSP_L plots, compared to those found in the MSP_S plots. By exposing the mineral soil, mechanical site preparation causes soil warming because of increased solar radiation and thermal diffusivity (Sutherland and Foreman 1995). Removing the humus layer (which acts as a thermal insulator) over a larger surface in the MSP_L plots compared to the MSP_S plots might have enabled higher soil temperatures in this treatment (Spittlehouse and Stathers 1990). We did not measure this variable, but it might have had positive impacts on seedling growth (Thiffault and Jobidon 2006).

Facilitative and competitive effects of alder

The facilitative nature of alder species has been observed in various contexts (e.g., Binkley et al. 1992). For example, mountain alder naturally colonizes boreal sites after major perturbations (Matthews 1992); it then modifies site conditions in ways that favour the survival and growth of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), for example, and other late-successional species (Blundon and Dale 1990). Yet natural alder regeneration might not establish rapidly enough (or not at all) to play a significant role as a nurse species for desirable conifers in a restoration context (Castro et al. 2002).

We evaluated whether planting alder as a N₂-fixing nurse-species after conventional disc-trenching would lead to accelerated growth of conifers planted on a site that was subject to harsh subarctic conditions, compared to direct planting or scarification only. Planting alder in scarified plots resulted in third-year conifer height responses similar to those using intensive mechanical site preparation (large furrows). We measured the same type of response for jack pine seedling diameter, demonstrating a facilitation effect of the N₂-fixing species on conifer regeneration in a harsh subarctic ecosystem.

Our study did not allow us to identify the specific mechanism responsible for this positive effect of alder on conifer dimensions. We expected that alder would benefit conifer growth principally by increasing soil available-N through litter decay, but we did not detect this effect when measuring mineral-N concentrations in the vicinity of the seedling root plug. However, conifers are known to produce adventitious roots in the organic layer (Krause and Morin 2005), a horizon in which seedlings might have benefited from the mineralization of N-rich alder litter (Titus 2008). We also posited that increasing alder cover through planting would deter ericaceous shrub encroachment on conifer microsites, thereby reducing competition by problematic species such as Labrador tea or sheep laurel. After three growing seasons, we did not measure a significant effect of alder on ericaceous shrub cover around the planted conifers, possibly because the nearest alder seedlings were still more than 50 cm away from the conifers (on average). This suggests the facilitation effect that alder exerted on spruce and pine was related to other mechanisms, such as seedling protection from harsh environmental conditions (Callaway and Walker 1997; Castro et al. 2002). This response is consistent with conclusions that

were reached by Van Bogaert et al. (2015), who identified climatic factors as the principal constraint on conifer regeneration growth at the northern limit of commercial forestry in Québec.

The presence of alder had an overall positive effect on black spruce and jack pine, but our results demonstrate that competitive interactions occurred between the nurse-species and the planted conifers. We indeed measured a negative relationship between angular height and seedling diameter, indicating that both conifer species were sensitive to overtopping by alder. Cortini and Comeau (2008) similarly reported significant competition by red alder (*Alnus rubra* Bongard) at the expense of planted western redcedar (*Thuja plicata* Donn ex D.Don) in British Columbia. We anticipated this negative effect of light competition by mountain alder on seedling growth. Because of their inherent differences in terms of both shade tolerance (Burns and Honkala 1990) and efficiency in absorbing and using nutrients (Reich et al. 1998; Burgess et al. 2010), jack pine was predicted to be more responsive than black spruce; however, the regression analysis revealed similar responses for both conifer species with respect to increasing competitive pressure exerted by alder. Moreover, survival was almost 100 % for both species. Wang and Kembell (2010) reported a similar competitive effect on jack pine and black spruce seedlings during the third growing season after planting on a recently burned site in Manitoba. Competitive interactions change though time, thereby altering species-specific responses to environmental modifications (Hartmann and Messier 2011). If planted alder seedlings gradually dominate the site over the next few years, we expect that jack pine mortality would increase drastically, but black spruce seedlings could survive long enough to

eventually emerge from the alder canopy. Further monitoring is necessary to test these predictions.

Conclusions

Our study demonstrates that mechanical site preparation can be used to enhance conifer seedling growth over the first few years to accelerate the rehabilitation of subarctic forest ecosystems. Increasing scarification treatment intensity by creating larger furrows provide a significant gain in seedling dimensions compared to a standard treatment, and could thus be used when intensive treatments do not create social, economic or environmental issues. Our results support simultaneous planting of a nurse-plant and the desired species as a promising restoration practice, especially in harsh environments such as subarctic ecosystems. Planting alder after conventional disc trenching resulted in growth gains for conifers that were similar to using an intensive mechanical site preparation treatment, which could be useful in environmentally and socially sensitive conservation areas where intensive preparation is not desirable. On the other hand, there is a risk that planted mountain alder seedlings, together with the natural regeneration of this species, would overgrow the planted conifers due to their rapid growth rate. Growth reductions that are associated with this increased competition pressure might offset the initial benefits that could be derived from planting the species. Longer-term monitoring is necessary to determine whether competitive interactions between alder and planted conifers would become more important than the positive effects that are incurred by the species. Long-term data acquisition is also necessary to compare treatments from an economic perspective, which is an issue of particular importance when conducting

forestry operations in remote areas. Finally, detailed assessments of the interspecific interactions are required to disentangle the mechanisms by which facilitation takes place.

Acknowledgements

We are indebted to Jacques Carignan, Maïté Brémont, Alexandre Fortin-Pelletier, Evelyne Gaillard and summer students from the *Direction de la recherche forestière* (DRF), *Ministère des Forêts, de la Faune et des Parcs du Québec* (MFFP), for their contributions to field work and data management, to Jacques Duval (MFFP), Luc Hovington (MFFP), and Denis Villeneuve (Resolute Forest Products, Montreal, QC) for technical assistance, and to the staff of the *Laboratoire de chimie organique et inorganique* of the DRF-MFFP for conducting the chemical analyses. We thank Josianne DeBlois (DRF-MFFP) for statistical advice, and Maripierre Jalbert (DRF-MFFP) for her help in editing Fig. 1 and Fig. 2, together with Martin-Michel Gauthier, two anonymous reviewers and an Associate Editor of the journal for providing constructive advice on an earlier version of the manuscript. We acknowledge the contribution of W.F.J. Parsons for English revision. This study is part of DRF-MFFP project 142332106 and was partially financed by the *Programme de mise en valeur des ressources du milieu forestier*.

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Table list

Table 1. ANOVA summary for planted jack pine and black spruce seedling foliar nutrient concentrations and soil characteristics after three growing seasons

	Treatment variable (fixed effects only)					
	Treatment (T)		Species (S)		T × S	
	<i>F</i> -value	<i>P</i> > <i>F</i>	<i>F</i> -value	<i>P</i> > <i>F</i>	<i>F</i> -value	<i>P</i> > <i>F</i>
<i>Foliar nutrient concentrations</i>						
Total N	12.91	<0.001	11.55	0.002	0.13	0.944
P	3.10	0.042	33.97	<0.001	0.24	0.867
K	3.56	0.051	59.74	<0.001	0.78	0.521
Ca	1.35	0.281	27.73	<0.001	1.13	0.355
Mg	0.84	0.474	0.15	0.702	0.77	0.511
<i>Soil nutrient concentrations and characteristics</i>						
Total N	0.35	0.793	12.81	<0.001	15.88	<0.001
P	0.75	0.544	22.17	<0.001	16.91	<0.001
K	3.07	0.058	17.96	<0.001	9.62	<0.001
Ca	1.29	0.323	1.42	0.237	7.03	<0.001
Mg	2.51	0.108	8.74	0.004	11.17	<0.001
pH	2.28	0.132	0.18	0.671	10.98	0.005
CEC	0.39	0.760	4.21	0.043	8.04	<0.001

Numerator degrees-of-freedom were 3, 1, and 3 for the T, S and T × S effects, respectively. Denominator degrees-of-freedom (calculated using the Kenward-Roger method; Schaalje et al. 2001) for the foliar variables varied from 11.1–92, 16.8–92, and 16.3–92 for the T, S and T × S effects, respectively. Denominator degrees-of-freedom for the soil variables varied from 12–16, 95–95.1, and 95–95.1 for the T, S and T × S effects, respectively. Analyses on foliar P and soil P were performed on square-root and ln-transformed data, respectively. CEC = cation exchange capacity. Values in bold are significant at $\alpha = 0.05$.

Table 2. ANOVA summary for planted jack pine and black spruce seedling dimensions and growth after three growing seasons

Treatment variable (fixed effects only)	Num df	Den df	Height		Leader growth in 2013		Ground-level diameter		Volume index	
			<i>F</i> -value	<i>P</i> > <i>F</i>	<i>F</i> -value	<i>P</i> > <i>F</i>	<i>F</i> -value	<i>P</i> > <i>F</i>	<i>F</i> -value	<i>P</i> > <i>F</i>
Treatment (T)	3	12	8.84	0.002	22.46	<0.001	22.99	<0.001	19.83	<0.001
Species (S)	1	15.9	39.47	<0.001	133.24	<0.001	147.55	<0.001	116.35	<0.001
T × S	3	15.9	1.89	0.172	7.53	0.002	3.96	0.028	3.23	0.051

Num df = numerator degrees-of-freedom, Den df = denominator degrees-of-freedom, calculated using Kenward-Roger approximations (Schaalje et al. 2001).

Analyses on leader growth, ground-level diameter and volume index were performed on ln-transformed data. Values in bold are significant at $\alpha = 0.05$.

Figure captions

Figure 1. Schematic representation (not to scale) of one replicate block. Each block is divided into four main plots, each randomly assigned to receive one of four treatments. Each main plot comprises two subplots planted with either black spruce (*Picea mariana*) or jack pine (*Pinus banksiana*). Circular sampling plots of 200 m² are located in the approximate centre of each subplot; all planted conifer seedlings within the circular sampling plots (~45 per plot) are tagged for long-term growth assessments.

Figure 2. Schematic representation of angular height (A), a distance-dependent competition index that was calculated between target conifer seedlings and the nearest *Alnus viridis* ssp. *crispa* seedling (natural or planted). For a given ratio between the heights of the nearest alder seedling and a target conifer seedling, the value of A increases as the distance between individuals decreases.

Figure 3. Third-year seedling height (A, B), ground-level diameter (C) and leader length (D) as influenced by mechanical site preparation and species. For a given panel (and species in C and D), columns that are identified by the same lower-case letter do not significantly differ at $\alpha = 0.05$ (for ANOVA results, refer to Table 2). For treatments and conifer species, data are presented as means $\pm$ standard errors in panels A and B, and as back-transformed means and confidence intervals after bias correction in panels C and D. In panel B, heights of alders are presented for information purposes only; box-and-whisker plots include 10th, 25th, 50th (horizontal bar within the box), 75th and 90th percentiles. Black closed circles denote the 5th and 95th percentiles.

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812 Figure 4. Relationship between third-year ground-level diameter of planted conifer
813 seedlings and their angular heights (A) relative to the nearest *Alnus viridis* ssp. *crispa*
814 seedling (natural or planted). Refer to Figure 2 for a description of angular height. The
815 estimates of the slope coefficient for black spruce and jack pine were similar (-0.011 mm
816 $^{\circ-1}$); the Y-intercept was 6.2 mm for black spruce and 10.7 mm for jack pine. $R^2_{\text{LR}} =$
817 likelihood-ratio-based R^2 (Magee 1990).

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Example of 1 experimental block (~5.5 ha) out of 5

Figure 1.

Figure 2.

Figure 3.

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832 Figure 4.

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