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Article

Afforestation of Boreal Open Woodlands: Early Performance and Ecophysiology of Planted Black Spruce Seedlings

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Abstract: Open lichen woodlands (LWs) are degraded stands that lack the ability to regenerate naturally due to a succession of natural and/or anthropogenic disturbances. As they represent both interesting forest restoration and carbon sequestration opportunities, we tested disc scarification and planting of two sizes of containerized black spruce (*Picea mariana* Mill. (BSP)) seedlings for their afforestation. We compared treatment of unproductive LWs to reforestation of harvested, closed-crown black spruce-feathermoss (BSFM) stands. After one year, seedling survival and nutritional status were equivalent among stand types but despite higher root elongation index (*REI*), planted seedlings in LWs had lower relative growth rate, smaller total biomass and stem diameter than those in BSFM stands. Soil fertility variables, soil temperature, nor seedling water potential, helped at explaining this early growth response. Disc scarification significantly improved seedling first-year survival, biomass and foliar nutrient concentrations of P, Ca, and Mg. Smaller planting stock showed higher *REI*, higher shoot water potential, and higher foliar nutrient concentration of all but one of the measured nutrients (N, P, K and Mg). Hence, preliminary results suggest that planting of smaller containerized black spruce stock, combined with disc scarification, shows potential for afforestation of unproductive LWs. The impact of the lichen mat and other potential growth limiting factors on afforestation of these sites requires further investigation.

Keywords: afforestation; black spruce; *Picea mariana*; lichen woodland; growth limitation; ecophysiology; carbon sequestration

1. Introduction

The spruce-moss bioclimatic domain accounts for most of the extracted coniferous wood volume (~20 millions m^3 per year) in Québec [1]. In this important (412,400 km^2) ecosystem of Québec's closed-crown boreal forest, consecutive disturbances by spruce budworm outbreaks, wildfires and harvesting can cause black spruce natural regeneration failure, leading to stable state unproductive open stands called lichen woodlands (LW) [2–4]. LWs are one type of open woodland (OW) characterised by their important (>40%) lichen ground cover and since 1950, there has been a notable expansion of LWs, between the 70° and 72° W meridians, consequently decreasing closed-crown pure black spruce-feathermoss (BSFM) stand cover [5], which are endemic to northeastern America [4]. This particular stand dynamic, where LWs are alternative stable-states of former BSFM stands, suggests an inherent support capacity of LWs to higher tree density after afforestation, since these stands presented a higher productivity prior to the opening process [4,6–8]. Management of these open stands may generate new productive forest areas and increased wood products, but it can also create increased carbon sinks and greenhouse gas offset opportunities [6,7,9].

Few studies have been carried out on the afforestation potential of LWs [7,9], but some survival and growth limitations in a similar stand type known as *Kalmia-Ledum* heaths—which share similarities with LWs in terms of low tree density and abundant ericaceous shrubs—have been identified [10–12]. Allelopathic interference, water stress and nutrient pool depletion by competitive species and/or reduced soil fertility are all possible limiting factors [7,11,13]. They can be partly counterbalanced with sufficiently aggressive site preparation, in particular soil scarification and herbicide application, that can decrease the impact of competitive vegetation on planted seedlings [7,13]. Potential nutrient limitations in LWs may be inferred through these studies on *Kalmia*-dominated heaths [12,14–16], although correspondence in site fertility between LW and *Kalmia* heaths has not been demonstrated.

Allelopathic influence of ground lichens on conifer seedling growth is not well understood [17]. Fisher [18] showed that the deposition of *Cladina stellaris* mulch over the growing medium of black spruce (*Picea mariana* Mill. (BSP)) seedlings reduced their growth and nitrogen and phosphorous foliar concentrations. On the other hand, Houle and Filion [19] found that although the lichen mat has a negative impact on growth and survival during the establishment phase of young white spruce seedlings, it has a positive effect on growth once the seedlings are established.

In addition, LWs are reputed to be drought-prone habitats where water stress can be a factor contributing to planted conifer growth check [7,20,21]. Water relations of planted conifers in LWs have been investigated in Hébert *et al.* [7], who showed that with disk scarification the water status of black spruce and jack pine (*Pinus banksiana* Lamb.) seedlings planted in site-prepared LWs was not different from that of seedlings planted in adjoining managed BSFM stands, known as less water limiting environments.

In harvested boreal coniferous stands, competition for light is weak and light availability at the seedling level is sufficient to achieve maximum photosynthesis [22,23]. The use of large seedlings is then not necessary and the use of smaller containerized seedlings may be advantageous in "drought prone" habitats since they are less sensitive to water stress [24]. Furthermore, smaller containerized seedlings, compared to traditional containerized stocks could be economically-sound for the afforestation of these remote boreal LWs, especially in the context of growing carbon markets where low carbon-intensive and cost-effective offset options will be the preferred ones for rapid implementation [9,25,26].

This paper presents the first year results—the short but yet critical establishment window for planted seedlings in terms of survival [7,20]—of an experimental plantation network established in LWs and BSFM stands in 2005. The experiment was designed to test the afforestation potential of LWs with different silvicultural treatments. The objectives were to evaluate if harvesting and site preparation in LWs could lead to seedling survival, growth and physiological functions comparable to those observed in BSFM stands subjected to similar disturbances. Another objective was to evaluate the performance of small containerized seedlings compared to the conventional containerized seedling stock. It is hypothesised that (i) contrary to Hébert *et al.* [7] where LWs and BSFM stands were not equally disturbed, similar level in disturbance intensity on LWs and BSFM stands will generate comparable seedling survival, growth and physiological functions; (ii) scarification will increase seedling survival, growth and physiological functions; and (iii) size of planting stocks will not affect seedlings' survival, growth and physiological functions.

2. Methods

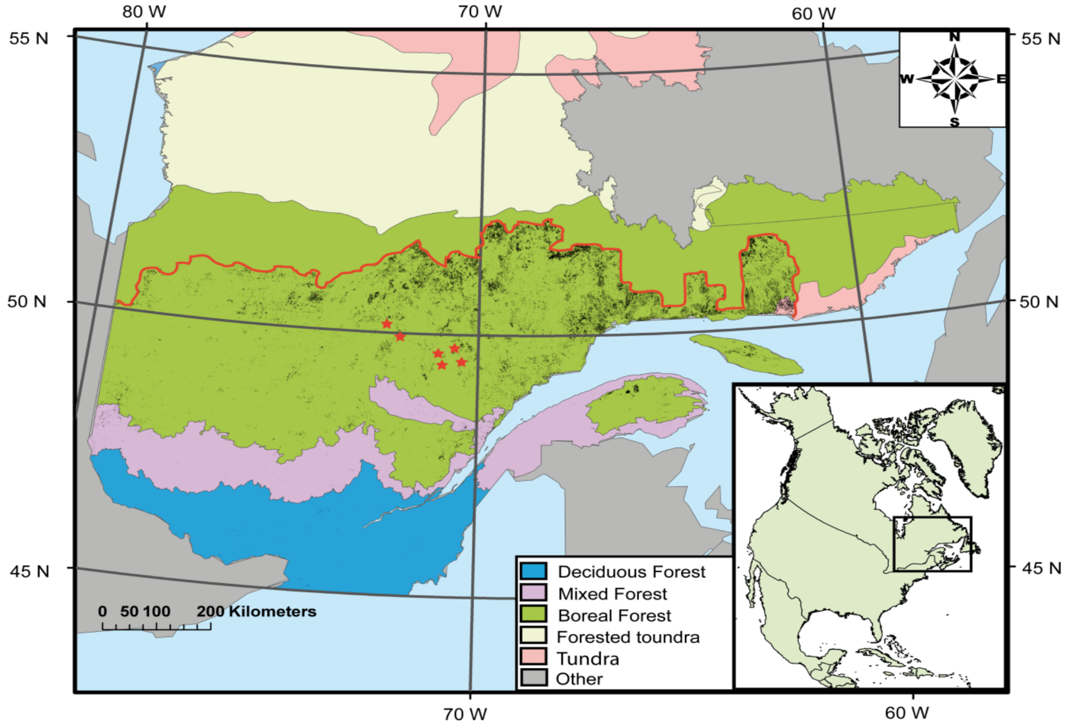
2.1. Site Description

The experiment was carried out on two different forest management units at the junction of the BSFM and the balsam fir-paper birch bioclimatic domains of Québec's boreal forest [27], north of Lac Saint-Jean, Qc, Canada (Figure 1). The climate of this area is cool continental with a mean annual temperature varying from −1.8 °C–1.4 °C with total precipitation varying from 919.8–970.9 mm, with 237.8–309.3 mm as snow. The number of growing degree-days >5 °C ranges from 970.9–1235.4. Frost free days range from 133–151 [28].

Each of the six study blocks were selected on the basis of two criteria: (i) The proximity of a pure BSFM stand of high density to a LW (stands were adjoining in four blocks, and <1 km apart for the two other blocks) presenting the same geomorphologic characteristics (aspect, slope, soil deposit, drainage); (ii) Both stand types had to be over 70 years old with the same age (±10 years), to ensure they originated from the same major disturbance.

The BSFM stands were all dominated by black spruce, representing at least 75% of the basal area of each stand, with jack pine (*Pinus banksiana* Lamb.) and trembling aspen (*Populus tremuloïdes* Michx.) as companion species. The understory included black spruce advance regeneration, ericaceous shrubs and a dense mat of mosses.

Figure 1. Location of the six study blocks (red star) in Québec, Canada. Small black dots represent all open woodlands, including lichen woodlands, under (red line) the northern limit of timber allocation (Québec Ministry of Natural Ressources 3rd decennial forest inventory).



The LWs stands had a tree crown cover <25%, with black spruce representing at least 75% basal area of each stand, with *P. banksiana* and *P. tremuloïdes* as companions species. The lichen ground cover was more than 40%, dominated by *Cladonia* spp. with shrub layers composed of the same species found in the BSFM stands.

Three out of the four blocks of the Péribonka site were located on deep (>100 cm), coarse textured glacial till deposit, overtopped by a 6–32 cm mor humus. The remaining block was located on a deep glaciofluvial outwash deposit overtopped by 6–14 cm mor humus. In the Mistassibi river site, one block was on a moderately deep (<100 cm), medium to coarse textured glacial deposit with an 18–32 cm mor humus, while the LW in the other block was located on a moderately deep (<100 cm), coarse textured glaciofluvial deposit, and the BSFM stand was on a thin (<50 cm), medium to coarse textured deposit. Both stands were overtopped by a 10–18 cm mor humus.

2.2. Experimental Design and Biological Material

The experimental setup is a six block factorial split-split plot design. Each block consists of 2 ha of a harvested BSFM stand adjoining 2 ha of harvested LW. Each stand type was split into two subplots which were randomly submitted to two treatments, with (S1) or without (S0) site preparation (scarification). Each subplot was then split into sub-subplots to which were randomly assigned one of two sizes of containerized black spruce seedling stock. As a result, there were eight experimental units (eu) per block, for a total of 48.

Logging operations took place in summer 2005 following careful logging around advance growth (CLAAG) stem-only method. Scarification of the S1 plots followed with either a mechanical TTS disc trencher (Péribonka site) or a hydraulic TTS disc trencher (Mistassibi site), superimposed on one half of the previously logged area.

Larger 67-50 seedling (67 cavities of 50 cm^3, height = 204 mm, root collar diameter = 2.20 mm) and recently introduced smaller 126-25 (126 cavities of 25 cm^3, height = 122 mm, root collar diameter = 1.39 mm) containerized black spruce seedlings produced from local seed sources grown in a mix of peat moss and vermiculite (3:1 v/v) were used. Thirty seedlings of each stock size were randomly selected in containers before plantation, in order to establish their morphological attributes (height, diameter and biomass) and nutritional status. Plantation took place during the last week of August 2005 (Péribonka site) and during the first week of September 2005 (Mistassibi river site). A total of 49,000 seedlings were planted with a two meters spacing, both in the skid trails (S0) and at the hinge of the scarification furrows (S1). On average, scarification furrows were 16.2 cm deep, 57 cm wide, corresponding to 20.2% of the total area in scarified plots of LWs, and 15.2 cm deep, 67 cm wide, representing 21.4% of the total area in scarified plots of BSFM stands.

2.3. Physiological Measurements

During summer 2006, shoot gas exchange was measured on two randomly chosen seedlings per eu (16 seedlings/block) at two sampling dates, (i) 1–7 June (4 blocks; using one-year old foliage developed in the nursery) and (ii) 8–23 August (5 blocks; using current year foliage). It was not possible to sample from all blocks due to travel time between blocks and weather. Measurements were made at full sunlight (between 10:00 and 14:00 h) to ensure photosynthetically active photon flux density above 1200 µmol photons m^{-2}·s^{-1}. A Li-6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE, USA) with a conifer chamber maintained at 25 °C, 400 ppm of CO_2 and air flow of 500 µmol·s^{-1} was used.

In mid-August 2006, pre-dawn (between 02:00 and 04:00 h) xylem water potential (Ψx), was measured on two randomly chosen seedlings per eu following a minimum 24 h rain free period. Each excised apical shoot was rapidly put in a plastic bag and placed in a cooler with ice until measurement. All shoots in a block were collected within 40 min and measured within 2 h following sampling. Ψx was determined using a pressure chamber (PMS Instruments, Corvalis, OR, USA, Model 610) [29].

2.4. Survival and Morphological Measurements

Survival of 100 pre-identified seedlings/eu, was recorded in the fall of 2005 (plantation year) and the fall of 2006. For the Husky 2 block, number of seedlings was reduced to 50 in order to avoid side effects as these stands were long and narrow. Seedlings were considered alive when they showed at least 10% of their foliage turgescent and green. Morphological measurements were performed in the laboratory on three randomly selected seedlings per eu. Samples were carefully dug out during the last week of October 2005 and 2006 to extract roots down to a minimal diameter of 1 mm. After washing, the two longest roots of each seedling (R_l; nearest mm), total seedling height (H_t: nearest mm), stem diameter (1 cm above the first root) (D_s; nearest 0.1 mm) and dry mass of the stem, root and foliage (65 °C for 48 h) were recorded. To determine root elongation index (*REI*) (2006 seedlings only), sum of the lengths (mm) of the two longest roots of each seedling was divided by the root total biomass (g). Composite foliage samples of the current year leader of three seedlings from each eu were collected and analysed for their nutrient concentration (N kjeldahl, P, K, Ca, Mg). Analyses were made with an inductively coupled plasma spectrometer (model ICAP 61E and ICAP 9000) following a one hour digestion in concentrated sulphuric acid with selenium and hydrogen peroxide at 370 °C.

Average seedling relative growth rates (RGR) were calculated using the following equation; $RGR = \frac{\overline{\ln(W_2)} - \overline{\ln(W_1)}}{t_2 - t_1}$ where W_2 is total biomass of seedling at t_2 (fall 2006) and W_1 is total seedling biomass at t_1 (fall 2005). This equation takes into account initial seedling size and yields an unbiased estimate of RGR under all conditions [30]. The same calculations were applied on H_t and D_s, but these results are not presented as they were similar to those with biomass.

2.5. Abiotic Variable Measurements

On one block per forest management unit (2), two data loggers (CR10X, CAMPBELL Scientific, Canada Corp, Edmonton, AB, Canada), one per stand (four data loggers total), were installed to monitor mineral soil temperatures at 10 cm deep in the skid trails (2 probes/stand) and in the scarification furrows (2 probes/stand). Measurement were taken each 5 min using temperature probe (107B, CAMPBELL Scientific, Canada Corp) and averaged by hours.

Nutrient concentrations in the mineral soil ("B" horizon, seedlings' root zone) have also been investigated. Samples were collected with an AUGER soil sampler (Soil moisture equipment, Santa Barbara, CA, USA) on 2 perpendicular transects of ten sampling spots in each eu (10 m spacing between the sampling spots). Soil samples have been pooled at the eu level and analysed for nutrient concentrations (N, K, Ca, Mg, Mn, Al, Fe, Na, S). Analyses were made with an inductively coupled plasma spectrometer (model ICAP 61E and ICAP 9000) following a one hour digestion in concentrated sulphuric acid with selenium and hydrogen peroxide at 370 °C.

2.6. Statistical Analysis

Analyses of variance (ANOVA) were performed using a six block complete split-split-plot design for each seedling morphological variable, with stand type as the main plot, site preparation as the subplot and planting stock size at the sub-subplot level. For physiological variables, the sampling dates were considered as another split level (two dates).

For seedling foliage nutrient content, plot levels were the same as for physiological variables but with three dates instead of two. In case of interaction with date, polynomial contrasts were performed to determine if it was linear or quadratic and the most significant was taken into account [31]. Additionally, another contrast was performed on the last sampling date to determine if there was a difference between stand types, site preparation treatment and planting stock in seedling foliar nutrient concentration. A Bonferroni correction was applied in order to diminish type I error rate, so $p \leq 0.025$ was deemed significant [32]. For soil nutrient concentrations, ANOVAs on a six block complete split-plot design were performed with the stand type at the main plot and the treatment (S0 or S1) at the sub-plot level, significance was set to $p < 0.05$.

ANOVAs were performed using the REML procedure of JMPin 7.0 software (SAS Institute, Cary, NC, USA) and polynomial contrasts with the GLM procedure of SAS 9.1 software (SAS Institute, Cary, NC, USA). For each variable, homogeneity of variance was verified by visual analysis of the residuals [33] and data transformations performed when necessary [32].

3. Results

3.1. Seedling Survival and Growth

Seedling survival was high (>85%) and similar between stand types, but scarified plots (S1) showed a 6% (92% *vs.* 86%) higher survival rate compared to seedlings in unscarified conditions (S0). Planting stock size also significantly affected seedling survival rate with 93% *vs.* 87% for the larger and smaller stock, respectively (Table 1).

Seedlings total biomass (B_T) and stem diameter (D_S) had respectively 27 and 12% higher values in BSFM stands compared to LWs (Table 1, Figure 2A,G) and their *RGR* was also higher in BSFM stands compared to LWs (Figure 2D).

Scarification significantly increased S1 seedling biomass (33%) compared to seedlings in S0 plots (Table 1, Figure 2B). As expected for containerized seedlings with initial difference in size, B_T, H_T and D_S were significantly (Table 1) higher in the larger stock size compared to the smaller one, but relative growth rate (*RGR*) of the smaller stock size was significantly higher, nearly twice that of the larger stock size (Table 1, Figure 2C).

Seedlings in LWs had higher *REI* values than those in BSFM stands (Table 1, Figure 2F). In fact, site preparation and planting stock size interacted to affect seedling *REI* resulting in smaller black spruce stock being negatively affected by scarification whereas larger seedling stock were not (Table 1, Figure 2E).

A Stand types * Site preparation * Planting stock interaction significantly influenced the seedling root/shoot dry mass ratio (*R*/*S*), the *R*/*S* of smaller seedlings being lower in scarified BSFM stands, while that of larger seedlings was significantly lower in scarified LWs (Table 1, Figure 3A). A Stand types * Site preparation * Planting stock interaction also significantly influenced seedling total height, revealing that seedlings in the BSFM were always taller than in the LWs, except for the larger seedlings in the LWs scarified plots where LWs seedling were taller than in BSFM (Table 1, Figure 3B).

Table 1. Summary of analysis of variance (ANOVA) results for total dry biomass (B_T), total height (H_T), stem diameter (D_S) and biomass relative growth rate (*RGR*), survival, root to shoot ratio (R/S_{Ratio}) and root elongation index (*REI*) of black spruce seedlings, one year after plantation in lichen woodlands and black spruce feather-moss stands, in scarified or unscarified plots and with smaller (126-25) or larger (67-50) containerized stock size.

Sources of variation		B_T		H_T		D_S		*RGR*		*Survival*		R/S_{Ratio}		*REI* *	
	ndf	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*
Block	5	5	0.2577	5.1	0.2252	5.09	0.1816	5	0.1337	3.996	0.8460	4.999	0.7512	5.08	**0.0451**
Stand Types (ST)	1	5	**0.0116**	5.108	0.0683	5.096	**0.0097**	5	**0.0018**	4.056	0.0811	5.045	0.2240	5.16	**0.0447**
Site preparation (S)	1	10	**0.0363**	10.05	0.0538	10.05	0.1516	10	0.0543	10.19	**0.0012**	9.688	0.6031	10.05	**0.0029**
ST * S	1	10	0.8284	10.05	0.4126	10.05	0.6826	10	0.6524	10.19	0.2238	9.696	0.5308	10.05	0.2298
Planting Stock Sizes (PS)	1	20	**<0.0001**	19.99	**<0.0001**	20.15	**<0.0001**	20	**0.0011**	19.6	**0.0006**	20.9	**0.0246**	20.39	**<0.0001**
ST * PS	1	20	0.5809	19.99	0.7759	20.15	0.6494	20	0.4026	19.6	0.8607	20.92	0.4756	20.39	0.5422
S * PS	1	20	0.4358	19.99	0.6217	20.15	0.9345	20	0.2368	19.6	0.9917	20.9	0.2778	20.39	**0.0221**
ST * S * PS	1	20	0.8871	19.99	**0.0462**	20.15	0.7170	20	0.5570	19.6	0.7443	20.92	**0.0190**	20.39	0.6858

Bold indicates significance ($p \leq 0.05$); *ndf* = numerator degrees of freedom; *ddf* = denominator degrees of freedom; * = ln transformed data.

Figure 2. Stand types, site preparation (S) and planting stock (PS) size effects on the (**A**,**B**) total dry mass, (**C**,**D**) relative growth rate, (**E**,**F**) Root Elongation Index and (**G**) stem diameter of containerized black spruce seedlings planted in lichen woodlands and black spruce feather-moss stands, one year after plantation (*n* = 72 (**A**–**D**,**F**,**G**), *n* = 18 (**E**)).

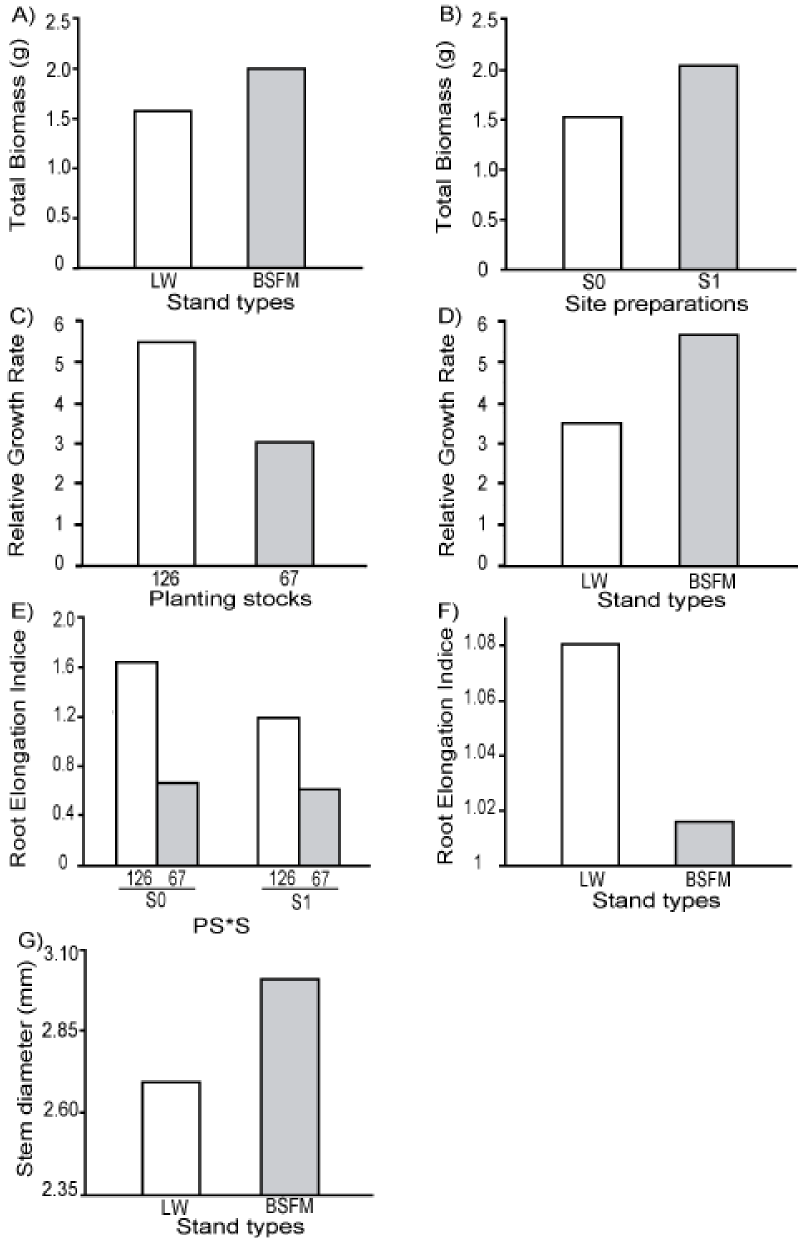
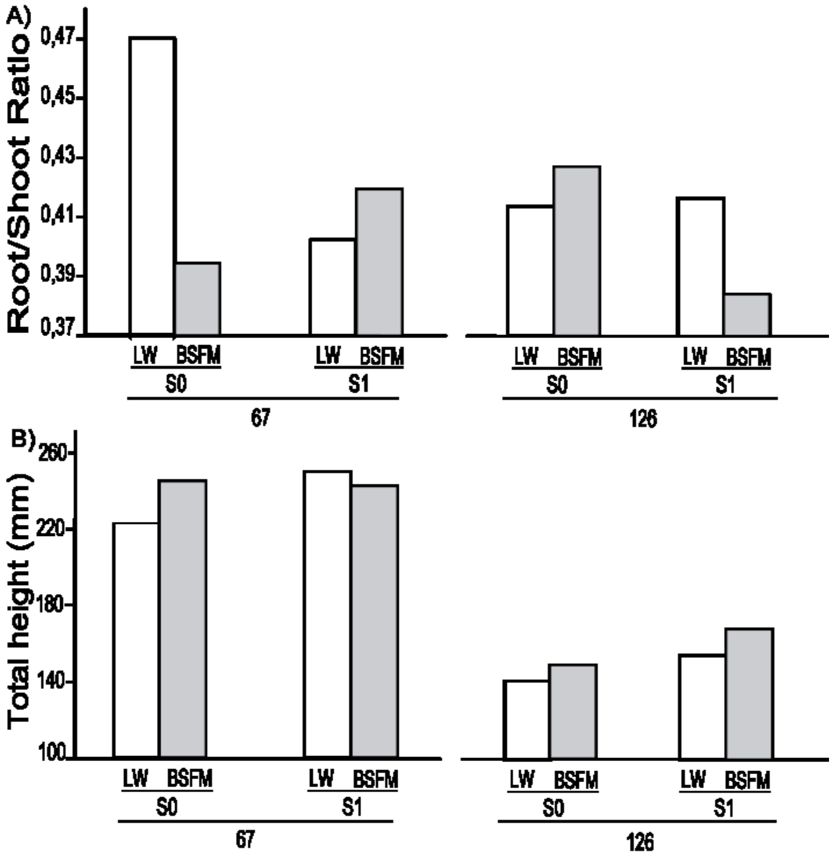


Figure 3. Stand types * Site preparation * Planting stock interaction effects on (**A**) root/shoot dry mass ratio (*R*/*S*) and (**B**) total height of containerized black spruce seedlings planted in lichen woodlands and black spruce feather-moss stands, one year after plantation (n = 18 for each bar).



3.2. Physiological Response

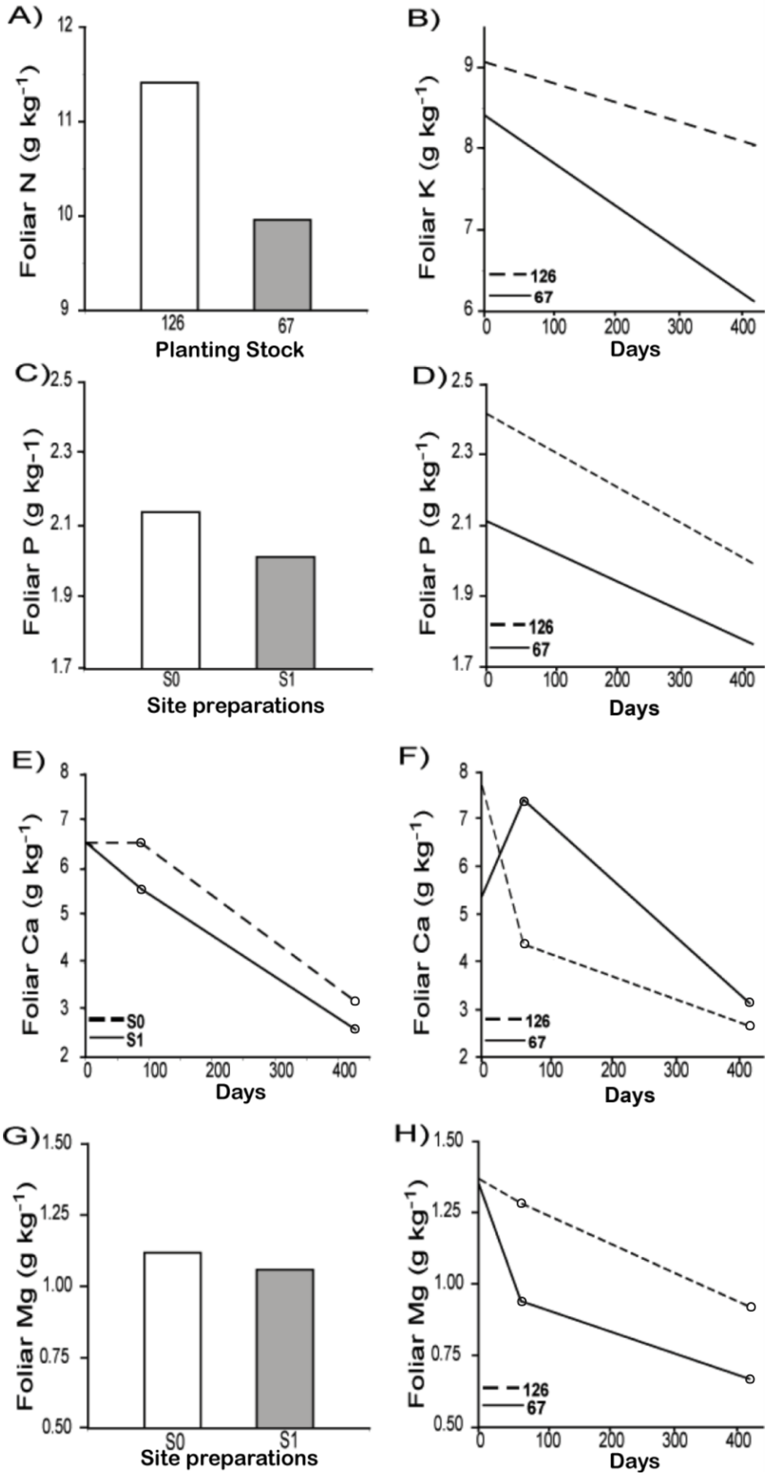
Seedling nutrient foliar concentrations were similar in both stand types, with or without interactions with other factors (Table 2). For its part, scarification negatively affected some nutrient foliar concentration (P, Ca, and Mg) (Table 2, Figure 4C,E,G). Overall, smaller seedlings had significantly higher concentrations of foliar nutrients (except for Ca, Table 2, Figure 4F) throughout the experiment (Table 2, Figure 4A,B,D,F,H) but with some variation among sampling dates as expressed by the quadratic interaction with seedlings type.

Table 2. Summary of ANOVA results for the nutrient concentration (N, P, K, Ca, Mg) in current year foliage of black spruce seedlings one year after plantation in lichen woodlands and black spruce feather-moss stands, in scarified or unscarified plots and with smaller (126-25) or larger (67-50) containerized stock size.

Sources of variation		**Foliar N**		**Foliar P**		**Foliar K**		**Foliar Ca**		**Foliar Mg**	
	ndf	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*
Block (B)	5	8.867	0.8042	9.056	0.3573	9.03	0.6334	8.54	0.4567	9.12	0.4805
Date (D)	2	8.886	0.4977	9.059	0.3156	9.03	0.1790	8.593	**<0.0001**	9.13	**<0.0001**
Stand types (ST)	1	13.87	0.1201	14.16	0.6597	13.77	0.8819	14.03	0.0652	13.56	0.5662
D * ST	2	13.87	0.2141	14.16	0.9292	13.77	0.5256	14.02	0.2887	13.56	0.8379
Site preparation (S)	1	27.84	0.2584	27.45	**0.0095**	27.28	0.9884	26.84	**<0.0001**	27.35	**0.0415**
D * S	2	27.85	0.7031	27.45	0.0684	27.28	0.2891	26.84	**0.0034**	27.35	0.1759
Contrasts											
D (Linear) * S		-	-	-	-	-	-	26.80	**0.0002**	-	-
D (Quad) * S		-	-	-	-	-	-	26.88	**0.0001**	-	-
S0 *vs*. S1 (D 427)		-	-	-	-	-	-	26.78	**0.0024**	-	-
ST * S	1	27.84	0.5920	27.45	0.6095	27.28	0.6999	26.84	0.3278	27.35	0.9673
D * ST * S	2	27.85	0.9234	27.45	0.6169	27.28	0.6759	26.84	0.7372	27.35	0.6749
Planting Stock size (PS)	1	54.90	**0.0002**	55.03	**0.0034**	54.99	**<0.0001**	54.33	0.3094	55.08	**<0.0001**
D * PS	2	54.90	0.2282	55.03	**0.0338**	55.00	**<0.0001**	54.33	**<0.0001**	55.09	**0.0088**
Contrasts											
D (Linear) * PS	1	-	-	54.73	**0.0011**	54.69	**<0.0001**	54.21	0.8724	54.81	**0.00014**
D (Quad) * PS	1	-	-	55.35	**0.0373**	55.33	0.1309	54.45	0.1916	55.38	**0.00013**
126 *vs*. 67 (D 427)	1	-	-	54.63	**0.0242**	54.58	**<0.0001**	54.17	0.4629	54.17	0.4629
ST * PS	1	54.90	0.9805	55.03	0.6403	54.99	0.7788	54.33	0.9998	55.08	0.9890
S * PS	1	54.90	0.3652	55.03	0.8205	54.99	0.5825	54.33	0.6941	55.08	0.6729
D * ST * PS	2	54.90	0.8622	55.03	0.7129	55.00	0.7515	54.33	0.9413	55.09	0.6763
D * S * PS	2	54.90	0.6127	55.03	0.8093	55.00	0.6828	54.33	0.9556	55.09	0.9260
ST * S * PS	1	54.90	0.1929	55.03	0.6372	54.99	0.9855	54.33	0.8922	55.08	0.7861
D * ST * S * PS	2	54.90	0.5862	55.03	0.9430	55.00	0.7234	54.33	0.9672	55.09	0.9696

Bold indicates significance ($p \leq 0.05$) or ($p \leq 0.025$) for the contrast; *ndf* = numerator degrees of freedom; *ddf* = denominator degrees of freedom.

Figure 4. Stand type (ST), date (D), site preparation (S) and planting stock size (PS) effects on (**A**) foliar N, (**B**) foliar K (linear D * PS interaction), (**C** and **D** (linear D * PS interaction)) Foliar P, (**E** (quadratic D * S interaction)) and (**F** (quadratic D * PS interaction)) foliar Ca and (**G** and **H** (quadratic D * PS interaction)) foliar Mg in containerized black spruce seedlings planted in lichen woodlands and black spruce feather-moss stands, one year after plantation (n = 72 (**A**,**C**,**G**), n = 36 (**B**,**D**), n = 24 (**E**,**F**,**H**)). In Figure 4B,D–F,H, the x axis represent days since plantation. The three dates shown in Figure 4B,D,H are day 1 (plantation time), day 67 and day 427.



Stand types, and seedling sizes did not affect any seedling gas exchange variable (Table 3).

Table 3. Summary of ANOVA (degrees of freedom and *p*-values) for gas exchange (light-saturated CO_2 assimilation rate or *A*, stomatal conductance for water vapour or g_s, and water-use efficiency or *WUE*) measured during the first growing season after plantation, of black spruce seedlings planted in lichen woodlands and black spruce feather-moss stands, in scarified or unscarified plots and with smaller (126-25) or larger (67-50) containerized stock size.

Sources of variation		***A***		**g_s ***		***WUE***	
	ndf	*ddf*	*p*	*ddf*	*p*	*ddf*	*p*
Block	3	3.079	0.2727	2.991	0.7195	2.893	0.1593
Date (D)	1	3.08	0.0516	2.991	0.4087	2.893	**0.0455**
Stand type (ST)	1	6.172	0.6319	5.342	0.4799	3.986	0.8498
D * ST	1	6.172	0.1506	5.342	0.5902	3.986	0.2679
Site preparation (S)	1	11.73	0.3687	8.797	0.8045	9.998	0.8657
D * S	1	11.73	0.9808	8.797	0.7468	9.998	0.6900
ST * S	1	11.73	0.7314	8.797	0.5180	9.998	0.9575
D * ST * S	1	11.73	0.4305	8.797	0.2651	9.998	0.5686
Planting stock sizes (PS)	1	24.4	0.0669	18.58	0.1875	23.48	0.1136
D * PS	1	24.4	0.1872	18.58	0.2814	23.48	0.1211
ST * PS	1	24.37	0.4089	18.58	0.9452	23.46	0.4749
S * PS	1	24.39	0.7785	18.59	0.0788	23.48	0.6637
ST * S * PS	1	24.37	0.4348	18.58	0.2722	23.46	0.3353
D * ST * PS	1	24.39	0.5721	18.59	0.7157	23.48	0.5757
D * S * PS	1	24.39	0.4501	18.59	0.5247	23.48	0.0792
D * ST * S * PS	1	24.39	0.4122	18.59	0.6049	23.48	0.1543

Bold indicates significance ($p \leq 0.05$); *ndf* = numerator degrees of freedom; *ddf* = denominator degrees of freedom; * Data transformed; log (Stom cond * 10,000).

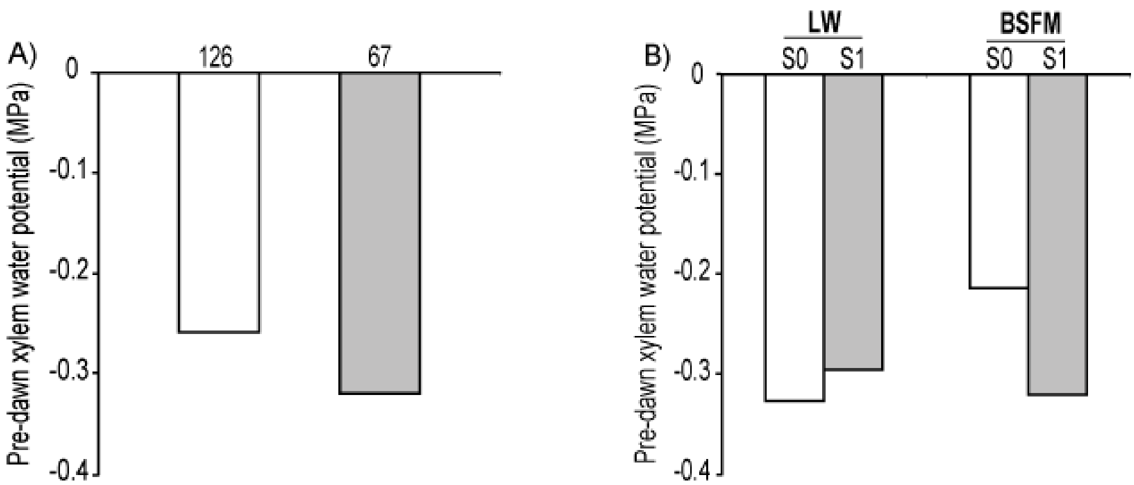
Seedling water potential was significantly different between planting stock sizes, with higher values for the smaller (126-25) than the conventional (67-50) seedling stock size (Table 4, Figure 5A). A significant stand types * site preparation interaction revealed that the seedling predawn water potential was lower in LWs compared to that in BSFM stands in S0 plots, but was equal between stand types in S1 plots (Table 4, Figure 5B).

Table 4. Summary of ANOVA (degrees of freedom and *p*-values) for August predawn shoot water potential (Ψ*x*) during the first growing season after plantation, of black spruce seedlings planted in lichen woodlands and black spruce feather-moss stands, in scarified or unscarified plots and with smaller (126-25) or larger (67-50) containerized stock size.

Sources of variation	Ψx_{pd}		
	ndf	*ddf*	*P*
Block	3	3.03	0.1302
Stand type (ST)	1	3.05	0.3873
Site preparation (S)	1	6.21	0.1511
ST * S	1	6.21	**0.0232**
Planting stock sizes (PS)	1	12.30	**0.0474**
ST * PS	1	12.30	0.1860
S * PS	1	12.30	0.7778
ST * S * PS	1	12.30	0.9613

Bold indicates significance ($p \leq 0.05$); *ndf* = numerator degrees of freedom; *ddf* = denominator degrees of freedom.

Figure 5. Planting stock size (**A**) and Stand types * Site preparation interaction (**B**) effects on the predawn shoot water potential measured during the first growing season after plantation in black spruce seedlings planted in lichen woodlands and black spruce feather-moss (n = 32 (**A**), n =16 (**B**)).



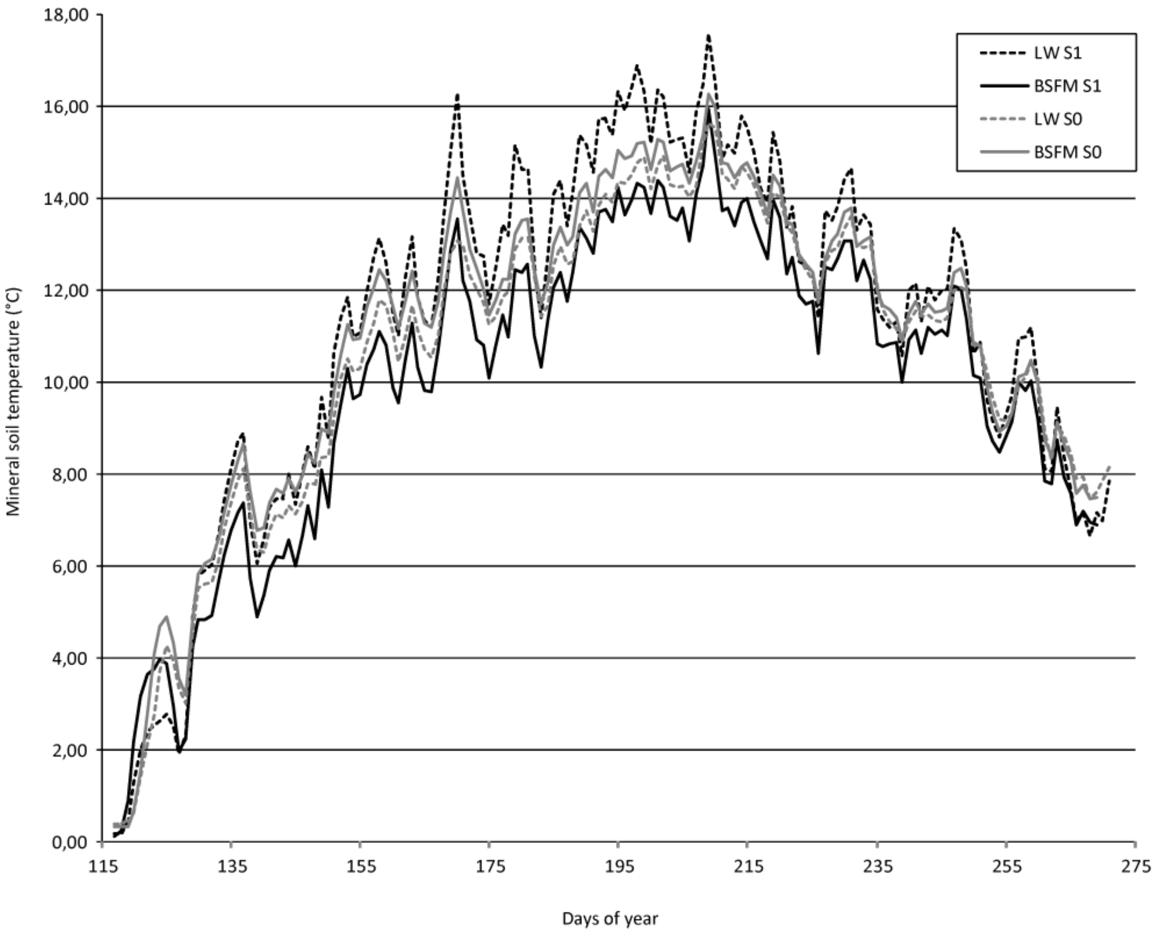
Soil analysis results revealed there was no significant difference in the concentrations of any soil mineral nutrient (see Table 5 for stand type averages).

Table 5. Mineral soil nutrient concentrations (N = g·kg^{-1}, and K, Ca, Mg, Mn, Al, Fe, Na, S = mg·kg^{-1}) in scarification furrows and skid trails of harvested and scarified lichen woodlands (LW) and black spruce feather-mosse (BSFM) stands.

Stand type	N	K	Ca	Mg	Mn	Al	Fe	Na	S
BSFM	1.09	13.01	79.65	9.08	1.95	206.24	72.61	6.92	45.32
LW	1.31	14.64	43.48	5.67	1.43	200.4	82.38	7.63	49.3

Soil temperature probes revealed that the mineral soil of the scarification furrows (S1) was slightly warmer in BSFM stands than in the LWs during early spring. However, during most of the growing season LWs' soil were up to two degrees warmer than in BSFM stands (Figure 6). For the skid trail (S0), soil temperatures of BSFM stands were always just above LWs trough the whole monitored period.

Figure 6. Mineral soil temperature (°C, 10 cm deep) in scarification furrows (S1) and skid trail (S0) of harvested and scarified lichen woodlands (LW) and black spruce feather-mosse (BSFM) stands.



4. Discussion

4.1. Seedling Response to Stand Type

Unlike what was first hypothesised, morphological and growth variables revealed some differences between stand types. Contrarily to that hypothesised in Hébert *et al.* [7], where LWs were less intensively disturbed than BSFM stands (BSFM stands harvested + scarified, LWs scarified only), the present study suggests that disturbance level alone does not explain early growth differences.

These differences between BSFM and LW's seedling early growth and morphology cannot be explained by the existing abiotic factors (slope, aspect, drainage, and soil deposit type, depth, temperature and nutrient concentrations) nor the physiological variables monitored in this study as they were equivalent. Thereby, it can be hypothesised that seedling response may at least be partially controlled by factors not related to these environmental variables. The lichen mat in LWs may have limited seedlings' resource access via its negative effect on mycorrhizae [18,34]. The potential reduced root fungi infection in LW seedlings could have led to less efficient nutrient and water uptake [35] explaining the superior growth of BSFM seedlings and the more extensive root network (root elongation index or *REI*) developed by seedlings in LWs which compensate for the lack of mycorrhizae. Higher *REI* may have enabled seedlings in LWs to explore a larger soil volume, on a root biomass basis, improving their chance of meeting their physiological needs, in these initially less fertile soils in the soil solution [22], to the point of finding no difference in seedling foliar nutrient concentrations and photosynthetic rates between the stands. The possible allelopathic interference from competing species [11,18], and the apparent discrepancy between the nutrient availability in the soil solution in [22] and the nutrient concentrations in the mineral soil in this study, might deserve further investigation.

4.2. Planting Stock Size

As shown for Norway spruce [36], the smaller containerized stock seedlings had higher height and diameter increments (not shown) and biomass growth rates than the conventional and larger ones. Higher *REI* and, possibly, root hydraulic conductivity of the smaller seedlings may partly explain these differences [24,37]. As smaller containerized seedlings produced more root elongation on a biomass basis, they exposed more rapidly unsuberized and water permeable root tips [37–39], which could explain their higher water status (shoot water potential) compared to the conventional containerized stock [20,40,41]. A longer term assessment will be needed to value if this short term mechanism is sufficient to compensate for the initial dimensions of the smaller seedlings.

To stop height growth and improve freezing tolerance at time of planting, [42] smaller seedlings were submitted to a short day treatment at the nursery, which could have lead to the lower survival rates observed in the smaller seedlings. Short day treatment sometimes results in earlier spring dehardening and budbreak the following year, therefore increasing susceptibility to frost and mortality [43,44]. It should be noted, however, that the seedling survival absolute values were relatively high in all experimental units, including that of smaller seedlings with mean survival rate at 87%.

After one growing season, almost all foliar nutrient concentrations were higher in the smaller seedlings explaining a part of their superior growth increments. Differences in seedling's stock *REI* could explain foliar nutrient concentrations, with possible enhanced hydraulic conductivity of smaller seedlings improving passive nutritional processes. On the other hand, initial (at day = 0) higher values for most of foliar nutrients suggests that the different nursery treatments for each of the containerized stock may have engendered seedlings with slightly higher nutrient loading for the smaller seedlings, which is a potential early growth advantage during the establishment window [45]. A possible "dilution effect" of nutrients in larger seedlings may have also contributed to this difference between seedling stock sizes [46].

Observed differences in nutritional and water status between planting stock sizes did not influence gas exchange measurements (results not shown), supporting the idea that black spruce seedlings do not adjust their photosynthetic rate and/or stomatal aperture to their water status [7,47–50]. Black spruce's drought response may in fact be to maximise photosynthesis [51].

4.3. Seedling Response to Site Preparation

Disk scarification positively influenced black spruce seedlings' survival and total biomass, while height and relative growth rate tended to be higher in scarified plots, though not significantly. Site preparation has been shown to positively influence seedlings growth and survival in numerous studies [52–58]. Removal of ericaceous shrub layers in the furrows of scarified plots most likely reduced resources competition for planted seedlings [14,59]. In addition, scarification increases the root zone soil temperature [54,56] which may improve root cell membrane permeability and decreases water viscosity [40,60–62], leading to enhanced water uptakes. In fact, seedling water potential in scarified LWs was similar to that measured in scarified BSFM stands (as observed by Hébert *et al.* [7]) supporting that scarification may help to overcome water limitations in "drought prone" habitats such as LWs.

Phosphorous, calcium and magnesium foliar concentrations were higher in the unscarified plots. As skid trail use during the harvest and skidding operations resulted in the soil surface close to a mechanical mixing site preparation, roots of seedlings in unscarified plots were closer to or even directly into organic soil. The absence of competition, the proximity of the incoming nutrient pool, the slightly warmer soil temperatures (in BSFM), the higher *REI*, and possibly the beneficial compaction effect on the soil macroporosity in coarse-textured soils during the early establishment period [63], were all plausible positive impacts of the of skid trails (S0 treatment) on seedlings' nutritional status. Alternatively, higher growth observed in seedlings in scarified plots may have created a growth dilution of foliar nutrients [64].

5. Conclusions

Based on early growth and physiological response of black spruce seedlings, this study indicates that the afforestation of LWs can generate high survival rates of planted seedlings under the particular conditions found during the short time elapsed, with viable growth rate and physiological acclimation, be it with smaller growth values than planted seedlings in adjacent BSFM productive stands. As water and nutrient limitations do not directly explain the differences in growth between stand types, the impact of the lichen mat and the ericaceous shrubs, with their potential competitive and allelopathic interferences, requires further investigation. Nonetheless, with a sufficient site preparation, such as disk scarification, the afforestation of lichen woodlands looks feasible. The cheaper and smaller containerized planting stock (126–25), compared to the conventional stock size (67–50), showed promising potential for the LW afforestation. The lower production, transport and planting costs associated with the use of a smaller containerized stock (higher container density in nursery and transport crates, and lighter weight), should be taken into account as the afforestation of unproductive open woodlands may represent a more risky investment than that on sites of known productivity, as long term survival and growth yield of this type of stand are still unknown [65]. Altogether, the early growth results in this study are contributing to the first efforts needed to help progressing the idea of LW afforestation from a potential new niche to a productive silvicultural activity [7,9], with particular relevance as a climate change mitigation measure under the growing carbon markets [9,30,66]. Moreover, plantation could be applied as underplanting without harvest prior to site preparation [7,66], thereby, leaving a part of the local genetics in the stand and recreating structural heterogeneity that is naturally occurring in natural old forests.

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Conflict of Interest

The authors declare no conflict of interest.

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