Title

GROWTH RESPONSE AND WATER RELATIONS OF THREE-YEAR-OLD PLANTED BLACK SPRUCE AND JACK PINE SEEDLINGS IN SITE PREPARED LICHEN WOODLANDS

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Abstract

Black spruce-lichen woodlands are low tree density stands within the closed crown, North American boreal forest that represent a diverging post-fire type of black spruce forest. As natural densification of lichen woodlands has never been observed, plantation remains the only way of shifting these stands to closed canopy stands. The objective of the study was to evaluate site preparation effects on growth and water relations of black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) seedlings in black spruce-lichen woodlands (LW), compared to managed black spruce-feathermoss stands (BSFM). Site preparation treatments in LW were no preparation (LWno), patch scarification (LWps), and disk scarification (LWds). The operationally managed BSFM stands stood for the control. Results from the third growing season indicate that soil water availability in intact or lightly prepared patch scarified LW is a limiting variable for seedling growth for both black spruce and jack pine seedlings. However, once LW are prepared with disk scarification, this planting check factor is significantly reduced, to the point of being equal to BSFM in terms of water availability and seedling water relations. The significant seedling growth difference, in favor of BSFM, might be a consequence of the lower level of pre-plantation disturbance in LW, compared to BSFM. Our results also suggest that jack pine, through higher water stress tolerance, could constitute a wise silvicultural choice over black spruce, especially with LW established on coarse drought-prone material.

Keywords: *Picea mariana; Pinus banksiana;* Lichen woodland; Site preparation; Water relations; Afforestation

1. Introduction

Black spruce-lichen woodlands (hereafter shortened to lichen woodlands) are low tree density stands, scattered within the closed-crown black spruce-feathermoss forest sub-zone of the Québec's boreal forest zone (Payette, 1992; Bergeron, 1996). These open stands are characterized by a sparse tree layer of black spruce (*Picea mariana* (Mill.) B.S.P.), and a lichen mat (*Cladina* spp.) often mixed with ericaceous shrub species (mainly *Kalmia angustifolia* L., *Ledum groenlandicum* Oeder, and *Vaccinium angustifolium* Ait.). Lichen woodlands apparently result from repeated catastrophic disturbances (wildfire and insect defoliation) in formerly closed-crown black spruce-feathermoss (BSFM) stands within the boreal forest, and contribute to the progressive and irreversible loss of BSFM stands (Payette, 1992; Payette et al., 2000; Gagnon and Morin, 2001). Presently, lichen woodlands make up to 10% of total forested lands within the closed-crown black spruce-feathermoss forest sub-zone, based on ecoforestry maps of the Québec's Ministry of Natural resources and wildlife (MRNF) (Anonymous, 2005). There is no evidence of natural redensification of lichen woodlands, i.e. a shifting to a closed-crown black spruce-feathermoss stand (Payette, 1992; Riverin and Gagnon, 1996).

Lichen woodlands have not been studied yet for their afforestation potential probably because of their low timber yield (Riverin and Gagnon, 1996; Gagnon and Morin, 2001). Limitations to afforestation have been identified in

Kalmia-Ledum woodlands of the North American boreal forest, which share some similarities with lichen woodlands because of their low tree density and the presence of ericaceous shrubs (Mallik, 1993; Inderjit and Mallik, 1996; Yamasaki et al., 1998). Reduced soil fertility, allelopathic interference and impacts on mycorrhizal colonization have been identified as potential limitations to young spruce growth and survival in *Kalmia-Ledum* woodlands (Zhu and Mallik, 1994; Inderjit and Mallik, 1996; 2002; Parker et al., 1997; Yamasaki et al., 1998; 2002; Thiffault et al., 2003). By contrast, influence of lichens on conifer seedlings have been rarely studied, and mechanisms of interference have not been yet found, if any exist (Kershaw and Rouse, 1971; Sirois, 1993; Steijlen et al., 1995). Water stress is major factor that can contribute to growth check in young conifer plantations (Burdett et al., 1984; Bernier, 1993). Considering that lichen woodlands are reputed drought prone habitats, early afforestation efforts in these environments should also include some investigation on water relations of planted conifers (Mallik, 1991; 1993; Prévost, 1992; Bergeron, 1996).

Silvicultural approaches, such as site preparation, can potentially overcome water stress induced growth check in planted seedlings. For instance, disk scarification, the most common site preparation treatment in Québec, can improve short term growth conditions by diminishing competing vegetation density, and thus, improving water availability for seedling roots (Bassman, 1989; Fleming et al., 1994; Brais 2001). By exposing the mineral horizon of soil and increasing soil temperature, disk scarification is also known to improve water absorption through increased root growth, root cell permeability and hydraulic conductivity, and decreased soil water viscosity (Grossnickle and Heikurinen, 1989; Bowen, 1991; Boucher et al., 1998 and 2001). Scarification can also have negative impacts, principally through increased soil surface evaporation and, consequently, water deficits in small seedlings (Stathers and Spittlehouse, 1990; Prévost, 1992). Patch scarification represents an alternate site preparation method on those sites where disk preparation is impractical, with likely similar, but little studied impacts on soil conditions or on seedling water relations (Örlander, 1986; Tremblay, 1996; Mäkitalo and Hyvönen, 2004). Use of a more water stress tolerant conifer like jack pine (*Pinus banksiana* Lamb.), instead of less tolerant black spruce, is an additional silvicultural choice that may improve success on drought prone sites (Grossnickle and Blake, 1986).

This text presents the first results obtained from an experimental plantation network established in 1999 throughout the BSFM sub-zone and designed to test the efficiency of various site preparation methods in the promotion of survival and growth of planted seedlings in lichen woodlands. The objectives of the study were 1) to determine if site preparation of lichen woodlands could generate levels of survival and growth of planted seedlings at least comparable to those found in seedlings planted in harvested black spruce-feathermoss stands, 2) to determine if there was a gain to be made by using the more drought-tolerant jack pine seedlings instead of the black spruce seedlings in the regeneration of lichen woodlands, and 3) to determine if differences in survival and growth found between treatments could be related to water stress.

2. Materials and methods

2.1. Study site description

The experiment was carried out in five experimental blocks split over two sites within black spruce-feathermoss forest of the Quebec's boreal forest (Bergeron, 1996). Both sites were located in the central part of the black spruce-feathermoss forest, one site near the west shore of the Mistassibi River (centered at 50˚04'49'' N, 71˚59'44'' W), and the other site near the east shore of the Péribonka Lake (centered at 50˚10'32'' N, 71˚09'49''W). Site selection was based on two main criteria: i) proximity of black spruce-feathermoss and lichen woodland stands of comparable slope, aspect and topography, and ii) nearby planned harvesting and site preparation operations.

Each of the five blocks included BSFM and LW stands. In all blocks, BSFM stands were originally of about 120 years of age, and were dominated by mature black spruce (*Picea mariana* (Mill.) B.S.P.), with a small component of jack pine (*Pinus banksiana* Lamb.). Pre-harvesting crown cover – expressed as the ground area covered by the crowns of trees as delimited by the vertical projection of crown perimeters – of BSFM stands was between 60 and 80% in blocks 1 and 2, between 40 and 60% in blocks 3 and 4, and between 25 to 40% in block 5. The understory included black spruce advance regeneration, a sparse shrub layer of *Kalmia angustifolia* L., *Ledum groenlandicum* Oeder, *Vaccinium* *myrtilloides* Michx., *Vaccinium angustifolium* Ait., and *Gaultheria hispidula* (L.) Mühl. ex Bigel., and a dense mat of mosses, mostly *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G., *Ptilium crista-castrensis* (Hedw.) De Not., *Rhythidiadelphus triquetrus* (Hedw.) Warnst., *Polytrichum* spp., with some *Sphagnum* spp.

By contrast, the adjoining lichen woodlands were characterized in all blocks by a tree cover of black spruce of less than 25% and a ground cover of lichen greater than 40% and dominated by *Cladina mitis* (Sandst.) Hustich, *Cladina stellaris* (Opiz) Brodo, and *Cladina rangiferina* (L.) Nyl. The lichen woodlands also had a dense shrub layer composed of the same species found in the BSFM stands.

All experimental stands were on moderately deep (50-100 cm) to deep (> 100 cm) coarse glacial till deposits, overtopped by a mor humus with humo-ferric podzolic profiles, except for two lichen woodlands in one block of the Mistassibi site which were on deep glaciofluvial outwashes. Results presented were most likely not influenced by this difference in deposit types between plots of this block, since soil texture and drainage were similar (results not shown). Drainage on both sites was good to moderate. See also Saucier et al. (1994) and Bergeron (1996) for a general description of the black spruce-feathermoss forest in Quebec’s boreal forest zone).

Climate in this central part of the spruce-feathermoss forest is cool continental, with a mean annual temperature of 0.0 °C (±1.3 °C) and a total precipitation of 961 mm, with 302 mm (31 %) as snow (1971-2000 data from the Chapais weather station, 49° 47' N – 74° 51' O) (Environment Canada, 2004). Data loggers set up 40 km West of the Mistassibi River site show that climate was generally close to normal during the course of the experimental period (1999-2002), with average temperature of 0.6 °C (± 0.9 °C) and total rainfall of 603 mm.

2.2. Experimental design and treatments

The experimental design was a five-block, 4 X 2 split-plot design, with four different site preparation/stand combinations (hereafter ''treatment(s)'') and two planted species within each treatment. The four treatments included three types of site preparation in lichen woodlands (LW) and one operationally managed BSFM stand, which included clearcut harvesting, followed by disk scarification (hydraulic TTS) both in and between the skid trails. Because of the combination of disk scarification and harvesting operations, approximately 30 % of the BSFM stand area was disturbed twice (Harvey and Brais, 2002). Harvesting/scarification operations were scheduled as follows: block 1 in 1997/1997, blocks 2 and 3 in 1994/1998, and blocks 4 and 5 in 1999/1999. Notice that only BSFM stands were harvested before performing treatments, so that these experimental plots in BSFM stands should be interpreted as the point of reference in silvicultural terms.

The site preparations in LW were disk scarification (LWds), patch scarification (LWps) and no preparation (LWno). Disk scarification was carried out by a hydraulic TTS disk trencher on the Mistassibi River site, and by a non-hydraulic TTS disk trencher on the Péribonka Lake site. The furrows were 2 m apart and had a mean width of 67 cm and a mean depth of 18 cm (n=24). As a result of disk scarification, approximately 34% of total stand area was disturbed. Patch scarification was carried out in 1999 using a cutter-type portable scarifier that removed the aboveground portion of the brush and reduced the humus layer thickness. The 15 cm-radius patches were done on a 2x2 m spacing, so that approximately 2 % of total stand area was disturbed.

Containerized black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) seedlings were produced from local seeds using 67-cavity-containers with 50 cm^3 root plug volume per cavity (IPL inc., Saint-Damien, Qc, Canada). Mean total height and stem diameter at planting time were of 174 mm and 2.4 mm, and of 168 mm and 2.0 mm for jack pine and black spruce respectively (MRNF, unpublished data). Approximately 200 seedlings of each species were planted at a 2x2 m spacing into two randomized subplots within each one of the main treatment plot. Planting took place in late summer-early fall of 1999. Seedlings were planted at the sides of the disk scarification trails, in the middle patches of the scarification patches, and directly into the forest floor/humus interface of the no preparation plots.

2.3. Soil and seedling measurements

Physiological measurements were taken on one randomly chosen seedling per subplot for each of the following four sampling periods of the 2002 active growth season: June 10-13, July 24-26, August 8-13 and September 17-18. Measurements were done on clear days preceded by at least one day without rain. On each sampling date, predawn water potential (Ψ_{pd}) and shoot conductance to water vapor (g_{wv}) were measured on the top 10 cm of the main shoot excised from each selected seedling. No measurement of Ψ_{pd} could be taken during the August sampling period at the Péribonka site, and during the September sampling period on both sites. Sites were visited on consecutive days, the distance between them preventing same-day measurements.

For Ψ_{pd} measurements, each excised shoot was rapidly put in a plastic bag and placed in a cooler with ice. Measurements were made using a pressure chamber (PMS Instruments, Corvallis, OR) (Scholander et al., 1965). All shoots in a block were collected within 45 minutes and one complete site was collected and measured approximately two to three hours before dawn.

For measurements of g_{wv}, each excised shoot was placed in a sealed plastic bag containing a wet sponge, and was left exposed to natural light before measurement. Measurements were taken using a LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE) with a 0.25 l cuvette, and an halogen lamp approx. 15 cm over the cuvette when the sunlight was not providing saturation (≥ 1200 μmol photons m^{-2} s^{-1}) due to passing clouds. Shoots were measured in a central location less than 30 minutes after excision and all shoots within a block were collected within 45 minutes. Preliminary tests showed that excised shoots from black spruce and jack pine seedlings can be stored in this manner up to 45 minutes without any change in g_{wv} (data not shown). All measurements within a site were taken between 10h00 and 12h00 E.T.

For each seedling used for g_{wv} measurements, a sub-sample of needles placed in the cuvette was used to determine total foliar surface area. Needle surface area estimation method was similar to that in Bernier et al. (2001) with balsam fir (*Abies balsamea* (L.) Mill.). The ratio of estimated area (ratio of estimated area from the needle central section / estimated area from several needle sections) obtained for black spruce was 0.892 and 0.915 for jack pine and was used to estimate total surface area of the sub-samples. The needle sub-samples used for surface area estimation were then dried at 65 °C for 48 hours to obtain leaf dry mass per unit leaf area (LMA). The LMA calculated was then used to find total foliar area in the cuvette; each g_{wv} measurement was then recalculated with actual total needle surface area.

The remaining part of each seedling used for both g_{wv} and Ψ_{pd} measurements was dug out for morphological measurements in the lab. After having carefully washed the root system of each seedling, total seedling height

(H_t; nearest mm), stem hypocotyl diameter (D_s; nearest one-tenth mm), root, stem and foliar dry mass (65° C for 48 hours) were measured. Total seedling dry mass (DM_t), foliar to shoot dry mass ratio (FS_{dm}), and root to shoot dry mass ratio (RS_{dm}) were calculated from these dry mass measurements. Survival of seedlings within each subplot was determined at the end of the growing season from one hundred of the initial seedlings within each subplot.

For each selected seedling within each subplot at each of the four sampling date throughout the 2002 growing season (June 10-13, July 24-26, August 8-13 and September 17-18), three 50 ml samples were collected, using a soil sampler (Soil Moisture Inc., Santa Barbara, CA), within a radius of 15 cm of each seedling at root plug depth. The samples were either from organic and/or mineral horizons, depending on seedlings' respective root plug environment, and were bulked for each seedling (at each sampling date) and used to obtain soil water content (SWC) by the gravimetric method (Rundel and Jarrell, 1991) and organic matter percentage (%OM) by the loss-on-ignition method (Nelson and Sommers, 1983) needed to characterize the microsite of each planted seedling.

2.4. Statistical analyses

Analysis of variance (ANOVA) on incomplete split-split-plot design was used for physiological and soil variables, with site treatments at the main plot level, planted tree species at the subplot level and sampling dates at the sub-

subplot level. An incomplete split-plot design was used for morphological variables, ratios, and survival, using the September data set (no sampling date factor). The incomplete block structure was due to missing black spruce seedlings in LWno plot of two blocks, and to a removed BSFM plot of one block, owing to its particular stand history (wildfire in 1996 before harvesting).

Relative growth rate (RGR_{dm}) was used to analyze treatment or species effects on seedling growth, using the Poorter and Lewis method (1986), based on analysis of variance, with ln-transformed total dry mass as the dependent variable. A significant Treatment *Time interaction indicates a difference in relative growth rates between treatments. Calculated ratios (FS_{dm}, RS_{dm}, and LMA) were adjusted by the Bauce et al. method (1994) in order to respect fundamental statements of ANOVA (Zar 1999). This method standardizes the ratios by adjusting the numerators of each ratio to a common denominator before conducting the ANOVA's. Homogeneity of variance was verified for all data by visual analysis of residues (Devore and Peck, 1994), and logarithmic transformations were performed when necessary to homogenize the variance. Seedling survival was transformed using $Sin^{-1}(\sqrt{(survival*.01)}*(180*\pi^{-1})$.

ANOVA's were performed using the MIXED procedure of SAS 8.1 software (SAS Institute, Cary, NC). The SLICE command in the MIXED procedure was made after the ANOVA when the Treatment*Species interaction was significant, in order to determine if each of both species was influenced significantly by the treatments. This procedure allows one to make a separate ANOVA for each species to determine if there were differences among treatments. Differences among treatments were determined by three a-priori contrasts (Steel and Torrie, 1980) aimed at, first, evaluating the respective impact of both site preparations tested within LW and, secondly, verifying how disk scarified LW compares with the point of reference, BSFM stands, since LWdisk corresponds to the nearest silvicultural approach compared to operationally managed BSFM: i) LWps vs LWno; ii) LWds vs LWno; iii) LWds vs BSFM. Differences were considered significant at $P < 0.05$.

3. Results

3.1. Morphological variables and survival

In lichen woodlands (LW), patch scarification did not influence seedling growth, but disk scarification significantly increased growth of both species compared to the no site preparation (LWno) plots (Table 1 and Fig. 1). Values of total height (H_t), stem hypocotyl diameter (D_s), and total dry mass (DM_t) were, respectively, 27%, 63% and 200% greater in the LWds plot than in the LWno plots. However, seedling growth variables in LWds were not as high as those found for the seedlings in the black spruce-feathermoss stands (BSFM). Values of total height (H_t), stem hypocotyl diameter (D_s), and total dry mass (DM_t) were, respectively, 18%, 29%, and 52% higher in BSFM than in LWds (Table 1 and Fig. 1 a,c,e). Growth of both species followed a similar pattern (no significant treatment*species interaction), but jack pine seedlings showed overall higher growth values than black spruce seedlings, with H_t, D_s, and DM_t respectively 37%, 47%, and 35% higher in jack pine than in black spruce (Table 1, Fig. 1 b, d, f). Biomass allocation in seedlings was not influenced by the different site preparations in LW (Table 1), but allocation to root (root-to-shoot dry mass ratio or RS_{dm}) of seedlings was significantly higher in LWds plots than in BSFM plots (Table 2, Fig. 1g). Neither the above-ground allocation to foliage (FS_{dm}) nor the leaf mass per unit area (LMA) were influenced by treatments (Table 2). No interaction between time and treatment or species was found for the ln transformed dry masses indicating that relative growth rate (RGR_{dm}) was not influenced by either treatment or species (Table 3).

Both patch and disk site preparations in LW significantly increased the survival of seedlings after three years of growth in the field, regardless of the tree species (Table 1, Fig. 1h). Seedling survival in LWds was equal to that of seedlings in BSFM (Table 1, Fig. 1h).

Table 1: Summary of ANOVA (*F and P*-values) for total height (H_t), shoot diameter (D_s), total dry mass (DM_t) and survival in black spruce and jack pine seedlings after three growing seasons. Bold indicates significance ($P < 0.05$). ndf = numerator degrees of freedom, LW= lichen woodlands (subscripts ps for patch scarification, ds for disk scarification and no for no preparation), and BSFM = black spruce-feathermoss stands.

Source of variation		H_t		D_s		DM_t*		Survival†	
	ndf	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Treatment (T)	3	33.59	< **0.0001**	38.20	< **0.0001**	36.91	< **0.0001**	12.71	**0.0004**
Species (S)	1	36.44	**0.0006**	43.93	< **0.0001**	12.47	**0.0008**	1.31	0.2972
T*S	3	0.53	0.6658	2.64	0.0573	0.56	0.6431	1.88	0.1907
Contrasts									
LWps vs LWno	1	3.82	0.0555	0.08	0.7841	0.48	0.4901	11.38	**0.0050**
LWds vs LWno	1	35.07	< **0.0001**	28.73	< **0.0001**	45.33	< **0.0001**	35.36	< **0.0001**
LWds vs BSFM	1	13.44	**0.0005**	15.44	**0.0002**	0.48	0.0514	1.75	0.2081

*Ln transformed data
†Transformed data $((\sin^{-1}(\sqrt{(survival/100)})*180/\pi)$

Table 2: Summary of ANOVA (*F and P*-values) for root to shoot ratio (RS_{dm}), foliar dry mass to shoot dry mass ratio (FS_{dm}) and leaf mass per unit leaf area (LMA) in black spruce and jack pine seedlings during the September sampling period. Bold indicates significance ($P < 0.05$). Abbreviations are as in Table 1.

Source of variation		RS_{dm}		FS_{dm}		LMA	
	ndf	*F*	*P*	*F*	*P*	*F*	*P*
Treatment (T)	3	2.99	**0.0477**	0.51	0.6746	1.68	0.1933
Species (S)	1	0.95	0.3386	0.74	0.3934	1.75	0.1970
T*S	3	2.15	0.1168	0.57	0.6343	0.16	0.9226
Contrasts							
LWps vs LWno	1	0.00	0.9515				
LWds vs LWno	1	1.70	0.2031				
LWds vs BSFM	1	8.97	**0.0057**				

Table 3: Summary of ANOVA (*F* and *P* values) for total dry mass relative growth rate (RGR_{dm}) in black spruce and jack pine seedlings throughout the third growing season. Bold indicates significance ($P < 0.05$). Abbreviations are as in Table 1.

Source of variation		RGR_{dm}	
	ndf	*F*	*P*
Treatment (T)	3	27.85	< **0.0001**
Species (S)	1	5.21	0.0725
T*S	3	1.90	0.1299
Date (D)	3	9.00	< **0.0001**
D*T	9	1.34	0.2189
D*S	3	2.02	0.1117
T*S*D	9	0.58	0.8120

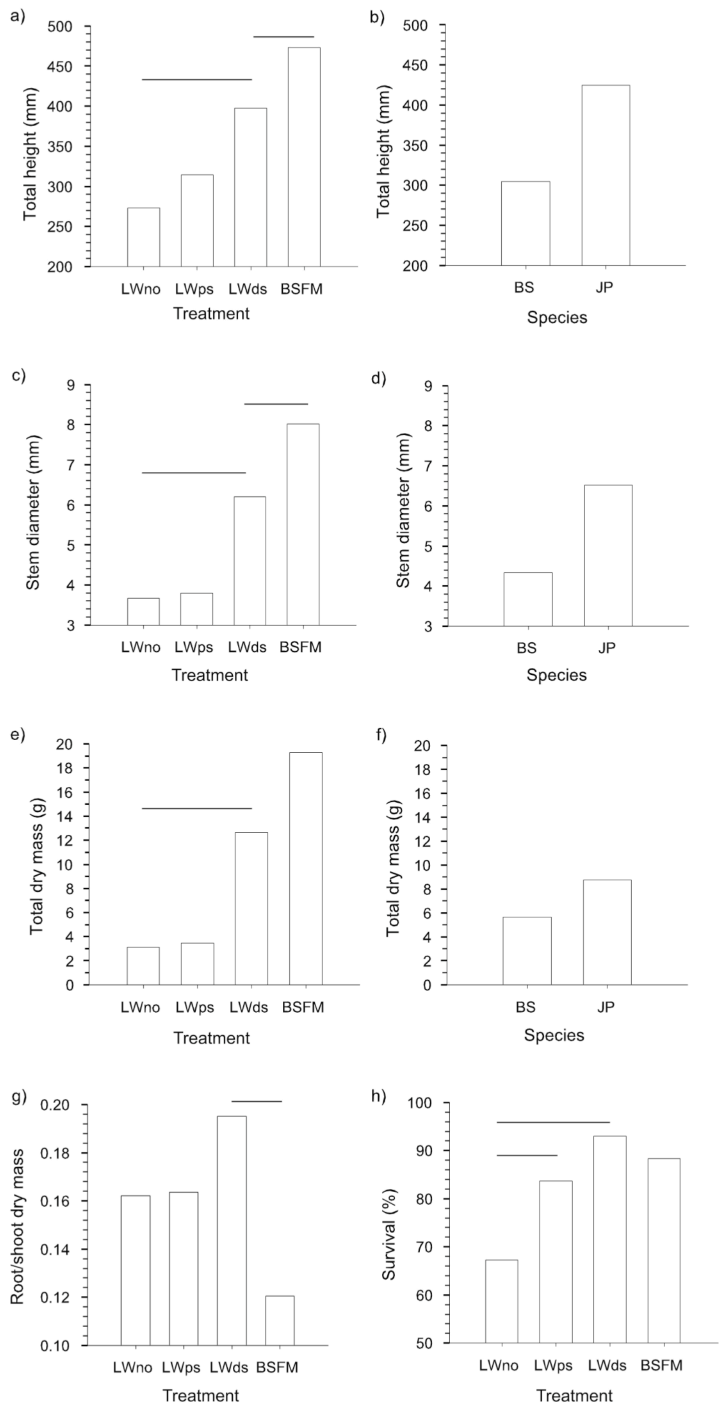

Fig. 1. Significant treatment and species effects on total height (a and b), stem diameter (c and d), total dry mass (e and f), root to shoot ratio (g), and survival (h) from the September sampling period. Each bar in (a), (c), (e), (g), and (h) represents the mean from 5 blocks, 2 species, and 2 samples per plot (n=20 for LWds and LWps, and n=16 for LWno and BSFM), and from 5 blocks, 4 treatments, and 2 samples per plot in (b), (d), and (f), (n=34 for BS, and n=38 for JP). Horizontal lines above the bars show significant treatment differences revealed by the contrasts (see Tables 1 and 2). Abbreviations are as in Table 1, plus BS = black spruce, JP = jack pine.

3.2. Physiological variables

Shoot predawn water potential (Ψ_{pd}) in seedlings was significantly increased by disk scarification in LW throughout the season, with values of Ψ_{pd} in LWds plots 47 % higher than that in LWno plots (Table 4, Fig. 2a). Patch scarification in LW did not result in higher values of Ψ_{pd}, compared to that in LWno, and values measured in seedlings in LWds plots were equal to that in BSFM stands (Table 4, Fig. 2a). Values of Ψ_{pd} in jack pine were 21 % higher than those in black spruce seedlings (Table 4, Fig 2b). Treatments had no effect on stomatal conductance for water vapor (g_{wv}) in black spruce seedlings (0.0395 ± 0.0029 mol m^{-2} s^{-1}). However, g_{wv} of jack pine seedlings was significantly greater in LWds than in LWno (Table 4, Fig. 3).

Table 4: Summary of ANOVA (*F* and *P*-values) for predawn water potential (Ψ_{pd}) and stomatal conductance for water vapor (g_{wv}) measured in black spruce and jack pine seedlings during four sampling periods of the third growing season. Bold indicates significance ($P < 0.05$). Abbreviations are as in Table 1.

Source of variation	Ψ_{pd}			g_{wv}		
	ndf	*F*	*P*	ndf	*F*	*P*
Treatment (T)	3	5.58	**0.0030**	3	0.75	0.5288
Species (S)	1	6.16	**0.0182**	1	1.83	0.1818
T*S	3	1.59	0.2101	3	2.84	**0.0462**
Date (D)	2	9.18	**0.0006**	3	5.95	**0.0014**
D*T	6	0.32	0.9234	9	0.63	0.7638
D*S	2	2.72	0.0803	3	1.45	0.2381
T*S*D	6	0.53	0.7852	9	0.90	0.5350
Contrasts[*]						
LWps vs LWno	1	0.07	0.8000	1	0.89	0.3501
LWds vs LWno	1	8.82	**0.0052**	1	10.00	**0.0029**
LWds vs BSFM	1	0.05	0.8236	1	0.13	0.7191

*Contrasts on g_{wv} were after a separate ANOVA made only for jack pine.

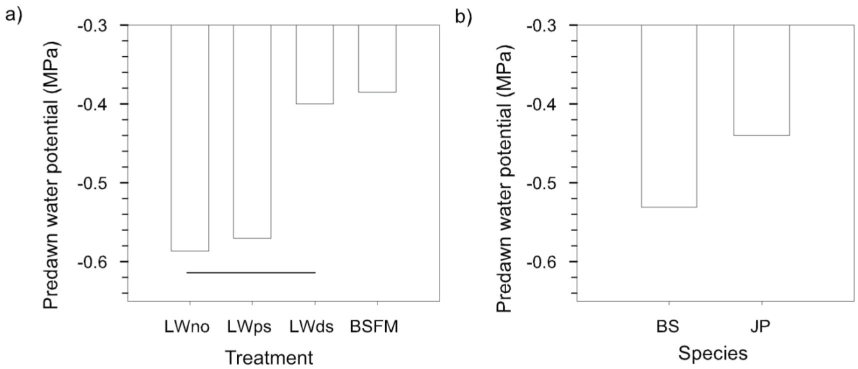

Fig. 2. Significant treatment (a) and species (b) effects on seedling predawn water potential measured throughout the 2002 growing season. Each bar represents the mean from 5 blocks, 2 species, and 3 dates in (a) (n=26 for LWds and LWps, n=22 for LWno, and n=20 for BSFM), and from 5 blocks, 4 treatments, and 3 dates in (b) (n=45 for BS, and n=49 for JP). Horizontal lines above the bars show significant treatment differences revealed by the contrasts (see Table 4). Abbreviations are as in Table 1, plus BS = black spruce, JP = jack pine.

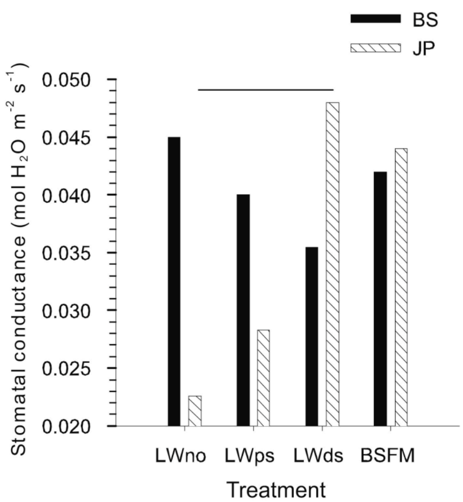

Fig. 3. Significant interaction between treatments and species on seedling stomatal conductance for water vapor measured throughout the 2002 growing season. Each bar represents the mean from 5 blocks and 4 dates (for BS n=20 for LWds and LWps, n=16 for BSFM, and n=12 for LWno; for JP n=20 for LWds, LWps, and LWno, and n=16 for BSFM). Horizontal lines above the bars show significant treatment differences revealed by the contrasts (see Table 4). Abbreviations are as in Table 1, plus BS = black spruce, JP = jack pine.

3.3. Soil variables

Patch scarification did not influence the gravimetric soil water content (SWC) in LW plots compared to LWno, but disk scarification significantly increased it throughout the season (Table 5, Fig. 4). All three factors significantly interacted to control organic matter percentage (%OM) in seedling soil microsites. Organic matter percentage (%OM) was highly variable and unstable across all treatments, especially in BSFM stands (Table 5, Fig. 5). Overall, patch scarified sites had higher %OM than disk-scarified sites (Fig. 5).

Table 5: Summary of ANOVA (*F* and *P*-values) for gravimetric soil water content (SWC) and percentage of soil organic matter (%OM) measured during four sampling periods of the third growing season. Bold indicates significance ($P < 0.05$). Abbreviations are as in Table 1.

Source of variation		SWC		%OM	
	ndf	*F*	*P*	*F*	*P*
Treatment (T)	3	3.09	**0.0418**	1.17	0.3361
Species (S)	1	1.95	0.1726	1.26	0.2714
T*S	3	0.37	0.7761	0.13	0.9441
Date (D)	3	1.13	0.3724	0.61	0.6102
D*T	9	0.85	0.5703	0.81	0.6134
D*S	3	0.51	0.6779	1.64	0.1830
T*S*D	9	0.54	0.8383	2.56	**0.0092**
Contrasts					
LWps vs LWno	1	0.05	0.8266		
LWds vs LWno	1	5.72	**0.0238**		
LWds vs BSFM	1	2.99	0.1319		

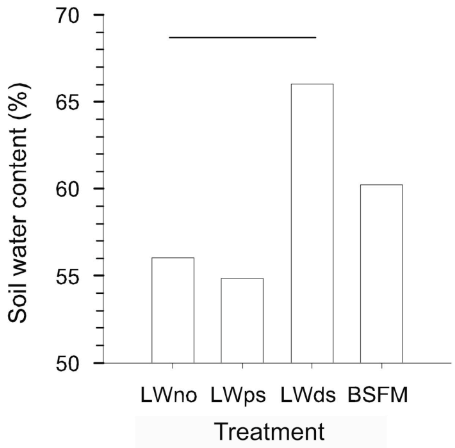

Fig. 4. Significant treatment effects on soil water content measured throughout the 2002 growing season. Each bar represents the mean from 5 blocks, 4 dates, 2 species, and 2 samples per plot (n=80 for LWds and LWps, and n=64 for BSFM and LWno). Horizontal lines above the bars show significant treatment differences revealed by the contrasts (see Table 5). Abbreviations are as in Table 1, plus BS = black spruce, JP = jack pine.

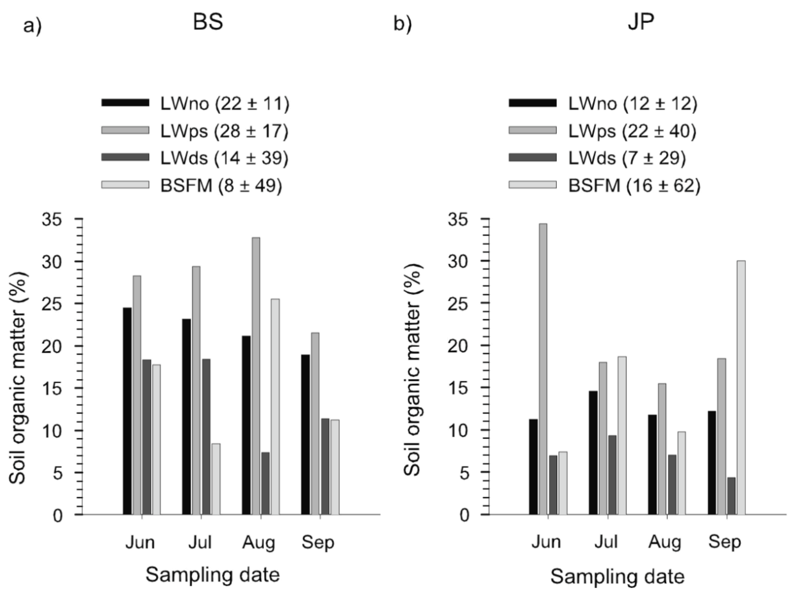

Fig 5. Significant interaction between treatments, species microsite, and dates on soil organic matter content measured throughout the 2002 growing season. Each bar represents the mean from 5 blocks, and 2 samples per plot (for BS in each date, n=10 for LWds and LWps, n=8 for BSFM, and n=6 for LWno; for JP in each date, n=10 for LWds, LWps, and LWno, and n=8 for BSFM). Abbreviations are as in Table 1, plus BS = black spruce, JP = jack pine.

4. Discussion

4.1. Site preparation impacts in lichen woodlands

Disk scarification and patch scarification produce contrasting results with respect to the soil environment, as well as the physiological response of planted conifer seedlings in lichen woodlands (LW). Disk scarification appears to have a greater ability to improve microsite water availability, resulting in higher seedling growth, survival, and water potential, for both black spruce and jack pine. Patch scarification, on the contrary, appears to provide no incremental gains in growth compared to unscarified LW sites, in spite of its ability to improve seedling survival. The beneficial impact of disk scarification on both growth and survival of young planted conifers, especially during the establishment phase, has been shown in a number of studies (Bassman, 1989; Grossnickle and Heikurinen, 1989; Boucher et al., 1998; Örlander et al., 1998; Bedford and Sutton, 2000; Thiffault et al., 2004).

Our results support the assumption that the positive effect of disk scarification might be related, at least in part, to increased soil water availability and uptake by seedlings, that leads to enhanced seedling water relations. The most direct influence of scarification on soil water is through decreased interception and competition, which results in more water available for planted seedlings (Prévost, 1992; Morris et al., 1993; Burgess et al., 1995; Boucher et al., 1998; Brais, 2001). Decreased rainfall interception following scarification can also be the consequence of reduced woody debris and humus thickness (Prévost, 1992). Enhanced soil temperature following disk scarification should also contribute to higher seedling water functions and growth, through increased root growth, and root water and nutrient absorption (Bassman, 1989; Bowen, 1991; Lyr and Garbe, 1995; Boucher et al., 1998, 2001). Soil temperature, although not measured in the present study, may be an important growth-limiting factor in intact LW because of the high albedo of the lichen mat (Kershaw and Rouse, 1971).

Other important changes resulting from disk scarification include the diminished influence of competition on nutrient availability, ectomycorrhizal interference on seedling roots, and allelopathic influence (Lanini and Radosevich, 1986; Mallik, 1993; Zhu and Mallik, 1994; Bradley et al., 1997; Yamasaki et al., 1998, 2002). Decreased light interception by competition due to scarification normally contributes to seedling response, but this influence was probably moderate in the present study, since light availability was relatively high even in intact LW plots, with 78% of full light available at seedling height (Girard, 2004). Absence of a positive effect by patch scarification on seedling growth might be simply because of the mildness of this manual scarification method. The method used in the study removed the aerial part of competing vegetation in a 15-cm radius only, and decreased partially the humus layer, rarely reaching the mineral soil.

Values of stomatal conductance for water vapor in black spruce were essentially unaffected by treatments, contrary to those in jack pine that were strongly reduced in the LWno and the LWps treatments. Black spruce is much more shade tolerant than jack pine, and a lack of physiological plasticity is a general feature of shade tolerant tree species (Givnish, 1988; Canham, 1989; Bazzaz and Wayne, 1994; Walters and Reich, 2000). Black spruce robustness to contrasting soil water conditions has been documented in Zine El Abidine et al. (1995), but Grossnickle and Blake (1986) found that black spruce seedlings are more sensitive than jack pine to atmospheric humidity deficit. However, since atmospheric conditions were comparable among treatments (Girard, 2004), we believe that soil water and possibly soil temperature (Boucher et al., 2001) were the variables controlling the seedling's water relations on our sites. A portion of the higher growth rate observed in jack pine could therefore be attributed to its greater water stress tolerance, expressed as higher values of stomatal conductance and of predawn water potential compared to black spruce (Grossnickle and Blake, 1986; Raison et al., 1992; Bernier, 1993). Furthermore, Tan et al. (1992) and Stewart et al. (1995) suggest that the drought response of black spruce is to maximize the rate of photosynthesis, while that of jack pine may be to optimize photosynthesis in balance with water loss. The former response would be better suited to shorter and less frequent drought events, and the latter more suited to continuous or recurring drought, such as in lichen woodlands (Bergeron 1996).

4.2. Comparison of treated lichen woodlands with managed black spruce-feathermoss stands

Growth and water relations of the planted seedlings (both species) associated with the disk scarified LW plots were generally comparable to those associated with the managed black spruce-feathermoss stands (BSFM), although significant differences in seedling growth suggest higher productivity in BSFM. In spite of the usual positive impact of disk scarification on seedling growth and survival, nutritional constraints may further limit seedling growth on the scarified LW sites. A parallel study on the same sites has found a lower foliar nitrogen of black spruce seedlings in disk scarified LW compared to BSFM sites. Results from the same study also suggest an influence of the residual plant competition on these nutritional differences (Girard, 2004). The higher relative biomass allocation to roots in seedlings in LW compared to that in BSFM may be an additional indication of greater resource limitations in the soils of LW (Grime, 1994; Canham et al., 1996).

4.3. Silvicultural implications

The present study constitutes a first step at the determination of optimal practices for the afforestation of black spruce lichen woodlands. One important issue in this particular challenge is the planting check caused by water stress, because of the putative – but still not documented – xeric conditions that characterize LW (Burdett et al. 1984; Bergeron, 1996). Our results indicate that soil water availability in intact or lightly prepared patch scarified LW is likely a critical variable for early seedling growth. However, in LW prepared with disk scarification, this constraint appears to be significantly reduced, but nutritional constraints generated by the residual plant competition may still limit growth. The level of disturbance before planting necessary to achieve full seedling growth potential in LW should be further investigated, for example by combining harvest with scarification before planting, or by testing more aggressive site preparation methods (Prévost, 1996; Örlander et al., 1998; Brais, 2001). Our results also suggest that jack pine could constitute a wise silvicultural choice over black spruce, especially with LW established on highly drought-prone sites such as sandy deposits or steep south-facing slopes.

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