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forest management

Ground-Layer Composition May Limit the Positive Impact of Precommercial Thinning on Boreal Stand Productivity

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In the boreal forest, ground-layer composition may modulate the effects of precommercial thinning (PCT) on stand productivity by affecting tree growth conditions. Based on data from 15 years of PCT monitoring in black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) stands, the objectives of this study were to investigate the effects of PCT on ground-layer composition and the way ground-layer composition is related to tree growth, stand productivity, and the PCT impact on stand productivity. PCT favored lichen expansion in xeric sites. The positive impact of PCT on stand productivity after 15 years was lower in sites with high year-one lichen cover, suggesting that the aboveground positive effect of PCT on growth may have been mitigated by a belowground negative feedback resulting from lichen expansion in xeric sites. Although *Sphagnum* spp. cover was not affected by PCT, 15-year increase in stand productivity was lower in sites with high year-one *Sphagnum* spp. cover. These results suggest that xeric stands with high lichen cover should not be targeted for PCT because of either null or negative effects on stand productivity. Subhydric stands with high *Sphagnum* spp. cover should also be avoided because of lower potential stand productivity.

Keywords: lichen, *Sphagnum*, feather moss, understory, merchantable tree

Precommercial thinning (PCT) is a common silvicultural treatment in conifer stands (Boulay 2015) that reduces density-dependent competition for light in young, high-density stands by mechanically eliminating some of the regenerating saplings. High competition for light and space alters fiber quality by favoring the formation of curved stems. The objective of PCT is to reduce rotation time and improve fiber quality by preempting the natural process of self-thinning and redistributing the space and growth resources to the remaining trees, which will form the mature stand. Consequently, PCT is supposed to increase stem diameter and accelerate stand operability by rapidly increasing the proportion of merchantable trees (Pothier 2002, Gravel et al. 2016). PCT has also been proposed as a method to increase the proportion of softwood trees in the boreal mixed forest, where logging tends to favor deciduous tree species (Prévost and Gauthier 2012). In addition to its positive effects on light availability for the remaining trees, PCT has been shown to accelerate nitrogen mineralization and enhance balsam fir nutritional status by favoring light transmission through the canopy and increasing temperature of the forest's surface soil (Thibodeau et al. 2000).

In the boreal forest, the ground layer is mainly composed of three important groups of cryptogams, i.e. feather mosses (mostly *Pleurozium schreberi* [Brid.] Mitt.), *Sphagnum* spp. mosses, and terricolous lichens, which influence ecosystem processes through their effects on soil physical, chemical, and biological properties (Sedia and Ehrenfeld 2003, Fenton et al. 2006, Cornelissen et al. 2007). Full light exposure and associated microclimatic conditions tend to favor *Sphagnum* spp. mosses (Bisbee et al. 2001) or lichens (Boudreault et al. 2013) depending on site moisture regime. In contrast, feather mosses tend to be restricted to shady microsites in closed-crown forests when *Sphagnum* spp. mosses or lichens are present (Bisbee et al. 2001, Haughian and Burton 2015), likely because of competitive exclusion (Sulyma and Coxson 2001, Fenton and Bergeron

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Table 1. Stand characteristics by moisture regime (mean ± *SE*).

Moisture regime	Xeric	Mesic	Subhydric
Drainage code[1]	1–2	3–4	5–6
Number of stands	10	25	12
Dominant tree species	*P. banksiana*	*P. mariana*	*P. mariana*
Percentage of dominant species stems	51 ± 6	67 ± 5	92 ± 2
Codominant tree species (average percentage of stems)	*P. mariana* (34 ± 7)	*P. banksiana* (21 ± 5) *A. balsamea* (7 ± 2)	*A. balsamea* (4 ± 1)
Surface deposits	Mineral	Mineral	Mineral or organic
Organic layer thickness[2] (mm)	75 ± 10	150 ± 15	280 ± 25
Thinning intensity[3] (%)	55.7 ± 12.5	43.4 ± 8.3	51.5 ± 6.6
Initial density[4] (stems · ha^{-1})	3,881 ± 1,110	3,681 ± 365	4,379 ± 293
Initial basal area[4] (m^2 · ha^{-1})	5.66 ± 1.10	3.17 ± 0.46	1.74 ± 0.17
Average study tree age at t_1 (years)	12 ± 1	16 ± 1	21 ± 1
Average study tree size at t_1			
dbh (cm)	5.90 ± 0.47	4.53 ± 0.29	4.19 ± 0.38
Height (m)	4.97 ± 0.42	4.02 ± 0.18	3.64 ± 0.23

[1] According to MFFP classification (2011).
[2] Stands had not been scarified before tree establishment.
[3] Thinning intensity was estimated as the relative difference in tree basal area at t_1 between the thinned and control plots of each pair and thus corresponds to the proportion of tree basal area that was removed by PCT.
[4] Initial density and basal area correspond to control plot density and basal area at t_1.

2006). Several studies have suggested that lichens and *Sphagnum* spp. mosses offer less favorable tree growth conditions than feather mosses. Compared with a cover of feather mosses, lichens have been shown to reduce the growth of black spruce (*Picea mariana*; Wheeler et al. 2011) and jack pine (*Pinus banksiana*; Pacé et al. in preparation) through their effects on soil microorganisms and nutrient availability (Ohtonen and Väre 1998, Sedia and Ehrenfeld 2005, 2006). Similarly, *Sphagnum* spp. mosses reduce spruce growth through their effects on soil oxygenation, temperature, and nutrient availability (Fenton et al. 2006, Simard et al. 2007, Lafleur et al. 2011). Thus, by affecting tree growth conditions, ground-layer composition may constitute an important factor of variability in PCT effects on stand productivity.

Fire usually leads to high regeneration density that favors the rapid establishment of a closed canopy, which in turn favors the colonization of the understory by feather mosses (Foster 1985). In contrast, clearcut followed by PCT leads to lower regeneration density (Pothier 2002) and a more open canopy that may favor lichen or *Sphagnum* spp. dominance (Bisbee et al. 2001, Boudreault et al. 2013), especially in sites with extreme moisture regimes (i.e., excessively [xeric] and poorly [subhydric to hydric] drained sites). This change in understory composition may have a negative feedback effect on tree growth and thus limit the positive impact of PCT under extreme moisture regimes. Maintaining closed-canopy stands and avoiding a transition in productive stands to either open lichen woodlands (Jasinski and Payette 2005) or open paludified forest (Simard et al. 2007) remains a cause of concern in the management of boreal stands, especially at the northern limit of the managed forest, where a recent expansion of open-canopy stands has been documented (Girard et al. 2008). Based on data from 15 years of PCT monitoring in black spruce and jack pine stands, the main objectives of this study were to investigate the effects of PCT on ground-layer composition and the way ground-layer composition is related to tree growth, stand productivity, and the PCT impact on stand productivity 15 years after treatment. We hypothesized that PCT was likely to favor lichen and/or *Sphagnum* spp. expansion at the expense of feather mosses under extreme moisture regimes and that this change in ground-layer composition would have a negative feedback effect on tree growth, thus mitigating the direct positive effect of PCT.

Materials and Methods

Study Area and Design

This study is part of a larger study established between 1995 and 1999 by the Ministère des Forêts, de la Faune et des Parcs du Québec, which included the whole province of Québec (Laflèche and Tremblay 2008). For this study, we retained data from the regions of Abitibi-Témiscamingue and Nord-du-Québec, which roughly corresponds to the western spruce-moss and the balsam fir-white birch bioclimatic regions (Laflèche and Tremblay 2008, Saucier et al. 2011). Average annual temperatures follow a north–south gradient, from 0.0 °C (Joutel, QC) to 3.1 °C (Ville-Marie, QC; Environment Canada 2017). Average annual precipitation varies from 885.9 (Lac Berry, QC) to 995.8 mm (Chapais, QC). Within these regions, data were collected from 50 young postfire or postharvest stands (Table 1) composed primarily of black spruce (*P. mariana* [Mill.] B.S.P.) and jack pine (P. banksiana Lamb.). Balsam

Management and Policy Implications

High lichen cover at the time of thinning may indicate that the stand is less susceptible to respond efficiently to a precommercial thinning (PCT) treatment, especially in black spruce-dominated stands. Therefore, it may be more appropriate to plan PCT in mesic stands with a low cover of lichens. Precaution should be taken, especially in xeric sites where PCT is more likely to favor ground-layer colonization by lichens. Because feather mosses outcompete lichens only in closed-canopy conditions, scarification before tree establishment is not likely to control lichen expansion in these sites. Although the increase in *Sphagnum* spp. cover did not seem to affect deeply rooted trees, it was associated with a reduction in the basal area and density of merchantable trees at the stand scale, suggesting that it offers less appropriate growth conditions for saplings. Therefore, precaution should also be taken in the subhydric sites that are already advanced in the paludification process to avoid tree growth problems that would result in long-term forest productivity loss. Furthermore, although the PCT impact might be positive even in sites with high *Sphagnum* spp. cover, it is probably more profitable, considering the cost for this forest treatment, to target more promising sites for PCT.

fir (*Abies balsamea* (L.) Mill.) was also abundant in some stands. *P. schreberi* (Brid.) Mitt., *Dicranum* spp., *Hylocomium splendens* (Hedw.) Schimp., *Polytrichum* spp., and *Sphagnum* spp. were the most frequent bryophyte species. Terricolous lichens were mainly represented by *Cladonia stellaris* (Opiz) Pouzar & Vêzda, and *Cladonia rangiferina* (L.) F.H. Wigg.

The area treated by PCT was randomly chosen in each stand; that is, there was no difference between control and treated areas before treatment. Pairs of control (unthinned) and thinned plots were established in each stand the year after PCT intervention by forest companies. The two plots of a unique pair presented similar site physical characteristics as well as similar prethinning stand structure, age, and composition. Control plots were established in unthinned areas that were at least 50 × 50 m in size to avoid border effects. A thinned plot was localized as close as possible, but with a minimum of 20 m from the edge of the unthinned area. PCT was completed following current inventory standards, including a target spacing of 2 m between trees and an average density of 2,500 trees · ha^{-1} (Ministère des Ressources Naturelles, de la Faune et des Parcs du Québec 2003). Nested circular plots 400 m^2 and 100 m^2 in area were established. Nonmerchantable trees (dbh ≤ 9 cm) that were at least 60 cm tall were counted by species and 2-cm dbh class (0, 2, 4, 6, and 8 cm) inside of the 100-m^2 subplot, whereas merchantable trees (dbh > 9 cm) were counted by species and dbh class (2-cm dbh class from 10 to 24 cm) in the main 400-m^2 plot. Basal area ($m^2 \cdot ha^{-1}$) and density ($trees \cdot ha^{-1}$) were estimated for each plot including both merchantable and nonmerchantable trees. Twenty study trees that were representative of the dominant and codominant trees of the stand and that were evenly distributed were selected in the 400-m^2 plots. Their dbh (cm) and height (m) were measured, and their age was established by counting the whorls, evaluating the time since the last major disturbance (fire or logging), or counting tree rings based on nondestructive cores. The composition and percentage cover of the moss and lichen layer were visually assessed inside of each 400-m^2 plot. In the field, species cover was assessed by using eight cover classes. The average value of each cover class was used as a numerical estimation of species cover. Cover per species group (lichens, feather, and *Sphagnum* spp. mosses) was then calculated by adding the covers of each component species. Moisture regime was evaluated for each 400-m^2 plot following an intensity scale (from 1 [*rapid*] to 6 [*very poor*]; Berger et al. 2008). All tree and understory measurements were repeated four times (i.e., every 5 years from the 1st year after PCT [t_1] to the 15th year [t_{15}]).

Statistical Analyses

Plots for which we lacked information on ground-cover composition at t_1 were not considered and uncomplete pairs were removed. Therefore, of the 50 pairs of plots that were available for the study area, only 47 were retained for the statistical analyses. Because feather moss cover is likely to be inversely correlated to lichen and *Sphagnum* spp. cover, this ground-cover type was not considered in the following analyses.

To address objective 1, PCT effects on lichen and *Sphagnum* spp. cover were tested using repeated-measure models based on the four measurement periods (1, 5, 10, and 15 years after treatment). Because lichen and *Sphagnum* spp. abundance depends on site moisture regime (Carleton et al. 1990, Bisbee et al. 2001), this parameter was also included in the models. Plot pairing was considered in the model by introducing stand as a random factor. Because the data did not accurately fit a specific distribution, we applied a bootstrap procedure in which treatment effect significance was deduced from the probability that the associated individual coefficient of the linear model was equal to zero considering the bootstrap confidence intervals (Sánchez-Espigares and Ocaña 2009, Fox and Weisberg 2012).

To address objective 2, we assumed that the rate of tree growth and sensitivity to surface soil conditions decreased with age. Therefore, the effects of ground-layer composition on tree growth are likely to be crucial soon after treatment (t_1), with the accumulation of consequences of these effects becoming visible 15 years after treatment (t_{15}). This is why we considered lichen and *Sphagnum* spp. cover 1 year after treatment (t_1) to investigate the way ground-layer composition was related to tree growth, stand productivity, and the PCT impact on stand productivity 15 years after treatment.

Tree growth over 15 years was estimated as tree relative growth in dbh between the 1st and the 15th year after PCT (expressed in % of increase). Because jack pine and black spruce do not have the same growth rate, the relationship between ground-cover composition at t_1 and 15-year growth of the study trees was analyzed separately for the two species. All of the study trees were considered in the analysis ($N = 308$ pines and $N = 1{,}135$ spruce). Data distribution was not normal, and relationships among study tree growth in dbh, initial study tree dbh, and ground-layer composition at t_1 for the whole 400-m^2 plot were analyzed using a bootstrap procedure applied to a mixed regression model (Sánchez-Espigares and Ocaña 2009, Fox and Weisberg 2012), in which stand and plot (nested in stand) were introduced as random factors.

In addition to the tree-level analyses previously mentioned, stand-level relationships between lichen and *Sphagnum* spp. cover at t_1 and stand characteristics 15 years after treatment were investigated using model selection because the error distribution was normal. Analyses were conducted on four stand properties: basal area of the merchantable trees (dbh > 9 cm, BA_{MT}), total stand basal area (BA_{tot}), density of the merchantable trees ($Dens_{MT}$), and total stand density ($Dens_{tot}$). Model selection was based on the comparison of corrected Akaike information criteria (*AICc*), which are well adapted for small sample sizes ($N = 47$ for a maximum of seven parameters) using the package AICcmodavg (Mazerolle 2016). Because jack pine, which was the second most abundant tree species in the sampled stands, is a faster-growing species than black spruce, its abundance in the stand was likely to have a large influence on stand characteristics after 15 years. Jack pine stand density was also a good indicator of site moisture regime and fertility in our study (Table 1). Therefore, jack pine density per hectare was introduced as a covariate in the models (*JP*).

To estimate the PCT impact on stand productivity 15 years after treatment, we calculated a thinning efficiency index (TEI) based on the comparison of basal area of the merchantable trees (BA_{MT}) 15 years after treatment in the thinned plots versus the control plots:

$$TEI = \log\left[\frac{(BA_{MT})_{\text{thinned}}}{(BA_{MT})_{\text{control}}}\right]$$

If TEI < 0, then PCT had a negative effect on BA_{MT}; if TEI = 0, then PCT had no effect on BA_{MT}; and if TEI > 0, then PCT had a positive effect on BA_{MT}, and the higher the TEI, the higher the positive effect of PCT on BA_{MT}. The relationships between this index and the initial ground-layer composition of the thinned plot were analyzed using model selection based on *AICc* (Table 2). Because the two tree species were likely to respond differently to PCT, especially because of the difference in growth rate and light dependence, jack pine density per hectare was introduced as a covariate in

Table 2. Explanatory variables and models used to explain stand characteristics 15 years after treatment.

Stand characteristics	#	Explanatory variables	Model meaning
BA_{MT}	1	$Treat + JP + BA_1 + Lich_1 + Spha_1 + (1\|Site)$	Complete model
$Dens_{MT}$	2	$Treat + JP + BA_1 + (1\|Site)$	Not related to ground-layer composition
BA_{tot}	3	$Treat + JP + BA_1 + Lich_1 + (1\|Site)$	Only related to lichen cover
$Dens_{tot}$	4	$Treat + JP + BA_1 + Spha_1 + (1\|Site)$	Only related to *Sphagnum* spp. cover
TEI	1	$JP * Lich_1 + JP * Spha_1$	Complete model
	2	JP	Not related to ground-layer composition
	3	$JP * Lich_1$	Only related to lichen cover
	4	$JP * Spha_1$	Only related to *Sphagnum* spp. cover

Note: BA, basal area; *Dens*, density; $_{MT}$, merchantable trees; $_{tot}$, total; TEI, thinning efficiency index; *Treat*, treatment; $Lich_1$, lichen cover at t_1; $Spha_1$, *Sphagnum* spp. cover at t_1; BA_1, basal area at t_1; *JP*, jack pine tree density per hectare.

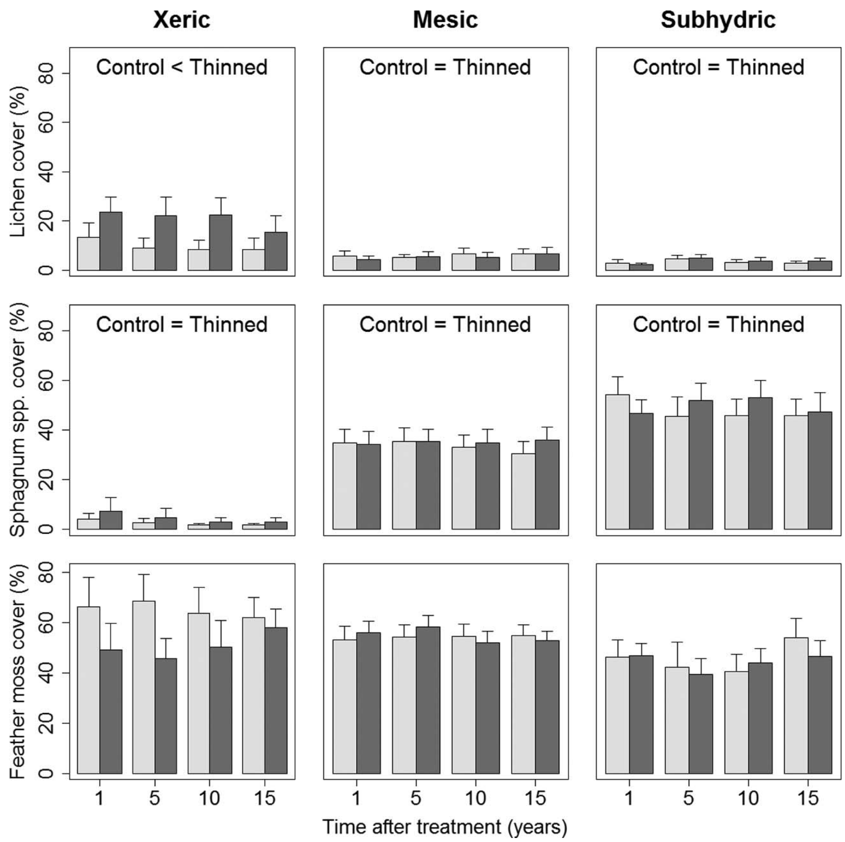

Figure 1. Temporal variations in lichen, *Sphagnum* spp., and feather moss cover by thinning treatment (mean ± SE). Data are presented by moisture regime (i.e., xeric [1–2], mesic [3–4], and subhydric [5–6]). Light and dark gray bars correspond to control and thinned plots, respectively.

the models (*JP*). This covariate also reflected variations in site moisture regime and fertility across stands (Table 1).

When necessary, the dependent variables were transformed to improve homoscedasticity (square root or log transformation). The strength of the correlation between each pair of explanatory variables was verified before conducting analyses ($r < 0.7$). All analyses were performed on R software (R Core Team 2014) using the packages nlme (Pinheiro et al. 2014), lme4 (Bates et al. 2014), car (Fox and Weisberg 2011), and MASS (Venables and Ripley 2002).

Results

Effect of PCT on Ground-Layer Composition

Reduced cover of lichen and *Sphagnum* spp. tended to be associated with greater feather moss cover (Figure 1). Lichen cover was significantly higher in the thinned plots, especially in xeric sites (Figure 1 and Table 3), and this effect was the same for all of the measurement periods. Although lichen cover was poorly related to moisture regime in the control plots, the positive effect of PCT on lichen cover was visible only in xeric sites, as suggested by the highly significant effect of the interaction between treatment and moisture regime (Table 3). In contrast, thinning treatment did not affect *Sphagnum* spp. cover, for which distribution was related only to site moisture regime (Figure 1 and Table 3). In the thinned plots of the xeric sites, the lichen cover remained relatively high for 10 years and tended to decrease slightly 15 years after PCT. *Sphagnum* spp. cover did not change with time in any of the moisture regime classes (Figure 1).

Ground-Layer Composition and 15-Year Growth of the Study Trees

PCT treatment had a positive impact on both jack pine and black spruce growth in dbh (Figure 2 and Table 4). Study tree growth in dbh was inversely proportional to initial tree size. Relationships between tree dbh growth and lichen cover differed between the two tree species (Figure 2, A and C). Although jack pine growth was positively correlated to year-one lichen cover (Figure 2 and Table 4), the inverse tended to be true for the study black spruce trees that were small at the time of the treatment (Table 4). Neither jack pine nor black spruce dbh growth was related to year-one *Sphagnum* spp. cover (Figure 2, C and D). Because the effect of the interaction between treatment and ground-cover composition was not significant in any of the two models, this parameter was not conserved.

Table 3. Thinning effect on the composition of the ground layer by moisture regime and measurement period.

	Lichen[1]		*Sphagnum* spp.[2]	
Explanatory variables	Coefficient	*P*	Coefficient	*P*
Treatment	13.68	**<0.001**	3.66	ns
Moisture regime	−1.48	ns	10.20	**<0.001**
Year 5	0.22	ns	−0.28	ns
Year 10	0.20	ns	−1.21	ns
Year 15	−0.12	ns	−2.35	ns
Treatment × moisture regime	−3.18	**<0.001**	−0.46	ns

Note: P values were estimated following a bootstrap procedure. The coefficients that are significantly different from 0 are indicated by a *P* value in bold. The interaction between treatment and year was not significant (ns) in any of the models.

[1] Repeated-measure models with uncorrelated random intercept and random slope within the stands.

[2] Repeated-measure models with correlated intercept and random slope within the stands.

Ground-Layer Composition and Stand Characteristics 15 Years after Treatment

The two best models explaining BA_{MT} at t_{15} (weight > 0.40) included *Sphagnum* spp. cover at t_1 or did not include any of the ground-layer parameters (Table 5). The best models explaining $Dens_{MT}$ and $Dens_{tot}$ at t_{15} included *Sphagnum* spp., but not lichen

Table 4. Relationships between relative growth and dbh at t_1 of jack pine and black spruce and ground-cover composition at t_1.

Explanatory variables	Coefficient	*P*
Pine relative growth in dbh (sqrt)		
Treatment	1.2	<0.01
dbh at t_1 (cm)	−0.46	<0.001
Lichen at t_1 (%)	9.8×10^{-2}	<0.01
Sphagnum spp. at t_1 (%)	-7.2×10^{-3}	ns
dbh at t_1 * Lichen at t_1	-1.0×10^{-2}	<0.001
dbh at t_1 * *Sphagnum* spp. at t_1	1.2×10^{-3}	ns
Spruce relative growth in dbh (sqrt)		
Treatment	2.4	<0.001
dbh at t_1 (cm)	−1.2	<0.001
Lichen at t_1 (%)	-5.9×10^{-2}	<0.05
Sphagnum spp. at t_1 (%)	3.5×10^{-3}	ns
dbh at t_1 * Lichen at t_1	1.4×10^{-2}	<0.001
dbh at t_1 * *Sphagnum* spp. at t_1	-2.9×10^{-3}	<0.05

Note: ns, nonsignificant; sqrt, square root transformed.

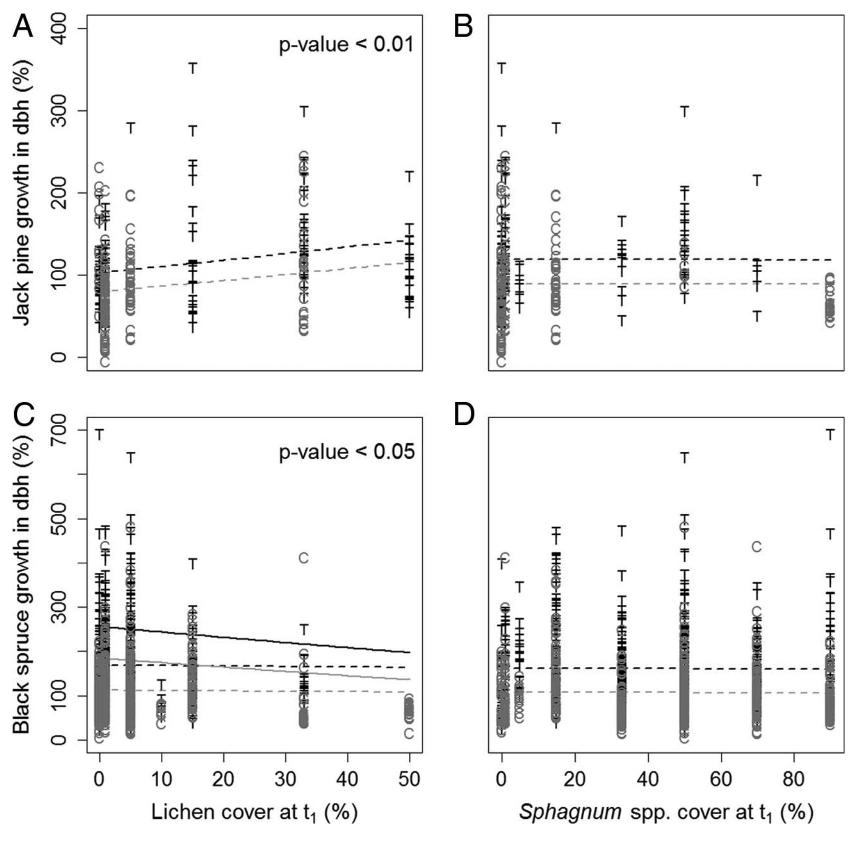

Figure 2. Relative growth in dbh of the study trees as a function of tree species and ground-cover composition at t_1. (A) Jack pine × lichen cover (*N* = 308), (B) jack pine × *Sphagnum* spp. cover (*N* = 308), (C) black spruce × lichen cover (*N* = 1,135), and (D) black spruce × *Sphagnum* spp. cover (*N* = 1,135). Gray "C" and black "T" correspond to control and thinned plots, respectively. Gray and black dashed lines correspond to the predictions of the models given in Table 4 for control and thinned plots, respectively, considering an average dbh at t_1 (i.e., 6-cm dbh for jack pine [A and B] and 4-cm dbh for black spruce [C and D]). Because the relationship between black spruce growth and lichen cover was tree size dependent, model predictions for 1.5-cm dbh at t_1 are also given for each treatment in panel C (gray and black solid lines for control and thinned plots, respectively). Significant relationships are indicated by the corresponding *P* value threshold.

Table 5. Degrees of freedom (*df*), *AICc*, differences in *AICc* compared with the best model (Δ*AICc*), and weights of the models used to explain stand characteristics 15 years after treatment.

#	Explanatory variables	*df*	*AICc*	Δ*AICc*	Weight
Basal area of merchantable trees at t_{15} (sqrt)					
4	$Treat + JP + Spha_1 + BA_1$	87	312.8	0	0.57
2	$Treat + JP + BA_1$	88	313.4	0.7	0.41
3	$Treat + JP + Lich_1 + BA_1$	87	321.1	8.4	0.01
1	$Treat + JP + Lich_1 + Spha_1 + BA_1$	86	321.7	8.9	0.01
Total basal area at t_{15}					
2	$Treat + JP + BA_1$	88	590.6	0	0.84
3	$Treat + JP + Lich_1 + BA_1$	87	594.1	3.5	0.14
4	$Treat + JP + Spha_1 + BA_1$	87	598.7	8.1	0.01
1	$Treat + JP + Lich_1 + Spha_1 + BA_1$	86	602.6	12.0	0.00
Merchantable tree density at t_{15} (sqrt)					
4	$Treat + JP + Spha_1 + BA_1$	87	690.4	0	0.72
2	$Treat + JP + BA_1$	88	693.1	2.7	0.18
1	$Treat + JP + Lich_1 + Spha_1 + BA_1$	86	695.1	4.7	0.07
3	$Treat + JP + Lich_1 + BA_1$	87	696.8	6.4	0.03
Total stand density at t_{15} (sqrt)					
4	$Treat + JP + Spha_1 + BA_1$	87	905.2	0	0.56
2	$Treat + JP + BA_1$	88	906.6	1.4	0.27
1	$Treat + JP + Lich_1 + Spha_1 + BA_1$	86	908.6	3.4	0.10
3	$Treat + JP + Lich_1 + BA_1$	87	909.5	4.2	0.07
TEI					
2	JP	45	149.7	0	0.47
3	$JP * Lich_1$	43	149.8	0.1	0.44
1	$JP * Lich_1 + JP * Spha_1$	41	154.2	4.5	0.05
4	$JP * Spha_1$	43	154.5	4.8	0.04

Note: Abbreviations of the explanatory variables are given in Table 2. Sqrt, square root transformed.

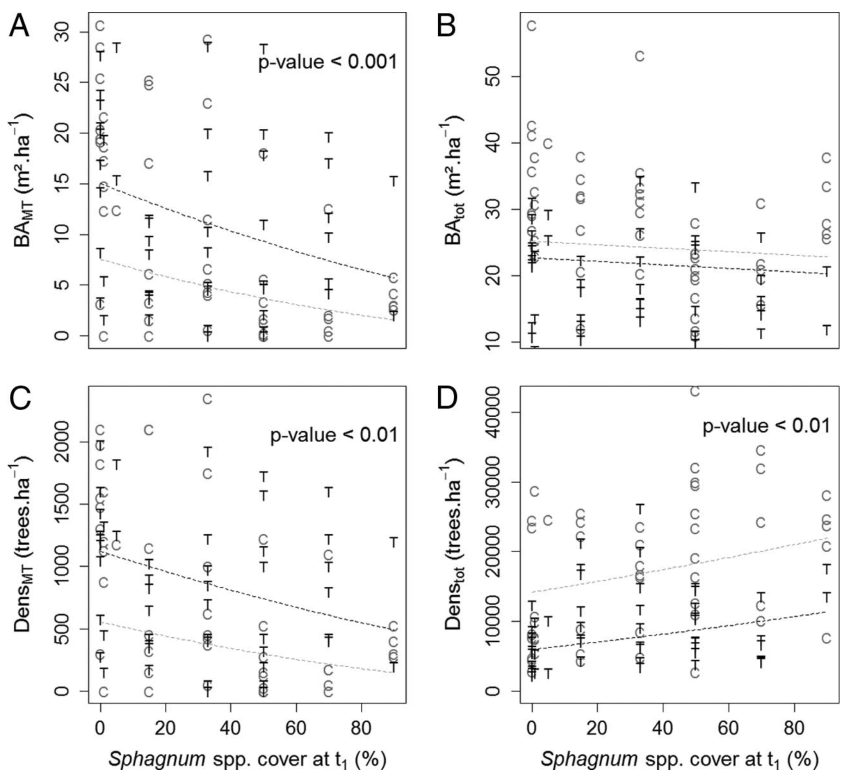

Figure 3. Stand characteristics at t_{15} in relation to *Sphagnum* spp. cover at t_1. (A) Basal area of the merchantable trees, (B) total basal area of the stand, (C) density of the merchantable trees, and (D) total density of the stand. Gray "C" and black "T" correspond to control and thinned plots, respectively. Gray and black dashed lines correspond to the predictions of the models given in Table 6 for control and thinned plots, respectively, considering an average basal area at t_1 (8 $m^2 \cdot ha^{-1}$) and an average pine density (1,900 trees $\cdot$ ha^{-1}). Significant relationships are indicated by the corresponding *P* value threshold.

cover at t_1, whereas the best model explaining BA_{tot} at t_{15} did not include any of the ground-layer parameters (Table 5). Although BA_{tot} and $Dens_{tot}$ of the thinned plots were still lower than BA_{tot} and $Dens_{tot}$ of the control plots 15 years after treatment, PCT had a significant positive effect on BA_{MT} and $Dens_{MT}$ (Figure 3 and Table 6). Except for $Dens_{tot}$, stand characteristics at t_{15} (BA_{MT}, BA_{tot}, and $Dens_{MT}$) were primarily influenced by total stand basal area at t_1 (Table 6). Jack pine density was positively associated with BA_{MT}

Table 6. Analysis of the best models to explain stand characteristics 15 years after treatment.

Explanatory variables	Coefficient Estimate	t	P	Model pseudo R^2
Basal area of merchantable trees at t_{15} (sqrt)				
Treatment	1.13	6.54	**<0.001**	0.86
JP	1.3×10^{-4}	2.71	**0.0095**	
Basal area at t_1	6.7×10^{-2}	3.54	**0.0010**	
Sphagnum spp. at t_1	-1.6×10^{-2}	−3.69	**<0.001**	
Total basal area at t_{15}				
Treatment	−3.16	−3.22	**0.0024**	0.91
JP	-1.8×10^{-4}	−0.72	0.4724	
Basal area at t_1	1.12	10.96	**<0.001**	
Merchantable tree density at t_{15} (sqrt)				
Treatment	9.96	6.66	**<0.001**	0.68
JP	1.2×10^{-3}	2.95	**0.0051**	
Basal area at t_1	0.67	4.13	**<0.001**	
Sphagnum spp. at t_1	−0.13	−3.37	**0.0016**	
Total stand density at t_{15} (sqrt)				
Treatment	−41.5	−1.63	**<0.001**	0.83
JP	-6.2×10^{-3}	−4.63	**<0.001**	
Basal area at t_1	0.45	7.02	0.4343	
Sphagnum spp. at t_1	0.32	2.77	**0.0126**	
TEI				
JP	-4.9×10^{-4}	−2.28	**0.0277**	0.19
Lichen at t_1	-5.0×10^{-2}	−2.07	**0.0447**	
JP * lichen at t_1	2.2×10^{-5}	1.38	0.1762	

Note: Coefficients that are significantly different from 0 are indicated by a *P* value in bold. The stand, which was included as a random factor in the first four models, explained more than half of the total variance of the stand characteristics. This contributed to increase the values of the pseudo R^2 associated with these models.

and $Dens_{MT}$ and negatively associated with $Dens_{tot}$ (Table 6). Finally, *Sphagnum* spp. cover at t_1 was negatively related to BA_{MT} and $Dens_{MT}$ at t_{15} and positively related to $Dens_{tot}$ at t_{15} (Figure 3 and Table 6).

Ground-Layer Composition and the PCT Impact on Stand Productivity 15 Years after Treatment

The two best models explaining TEI 15 years after treatment (weight > 0.40) included lichen cover at t_1 or did not include any of the ground-layer parameters (Table 5). TEI was negatively associated with jack pine density in the stand and negatively related to the proportion of lichen cover in the thinned plots 1 year after treatment (Figure 4 and Table 6).

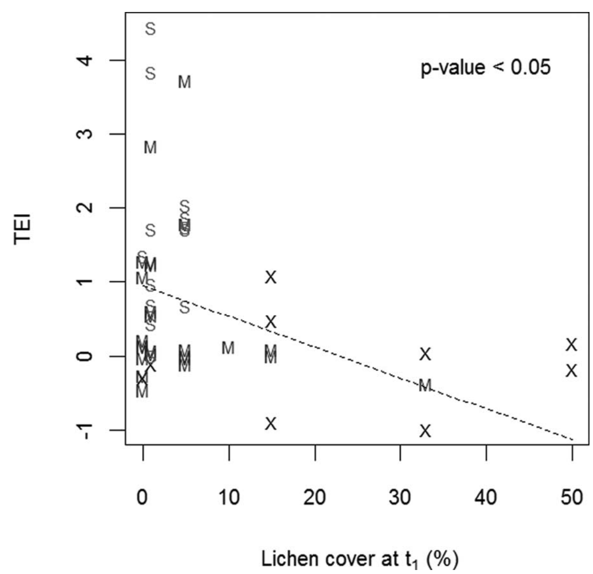

Figure 4. TEI in relation to lichen cover at t_1. X, M and S correspond to xeric, mesic and subhydric stands, respectively. Dashed line corresponds to the prediction of the model presented in Table 6 considering an average pine density (1,900 trees · ha^{-1}).

Discussion

PCT Effect on Ground-Layer Composition Depends on Site Moisture Regime

We expected PCT to favor lichen and *Sphagnum* spp. expansion at the expense of feather moss cover by opening up the canopy and changing the light and microclimatic conditions at the ground layer (Bisbee et al. 2001, Boudreault et al. 2013). In this study, it seems that PCT did favor lichen cover, but only in xeric sites. No more than 1 year after the PCT treatment, lichen cover was already much higher in the thinned than in the unthinned plots. This large difference may not only result from the effect of PCT on the degree of canopy closure but also to some degree from the effect of ground-cover trampling by the workers at the time of the PCT. Because lichens regenerate well from fragmentation (Crittenden 2000) and in open-canopy conditions (Boudreault et al. 2013), understory trampling during PCT and post-PCT advantageous microclimatic conditions may have accelerated lichen expansion at the expense of feather moss cover (Sulyma and Coxson, 2001). However, because lichen cover was visually assessed in the 400-m^2 plot, we can also suppose that lichen fragmentation by trampling may have contributed to an overestimation of year-one lichen cover in the thinned plots. This may explain why the difference observed between treatments was surprisingly high considering the growth potential of lichens (Crittenden 2000, Coxson and Marsh 2001, Boudreault et al. 2013). PCT effect on lichen cover tended to diminish with time since treatment in the thinned plots, presumably because of the gradual reclosing of the stand (Coxson and Marsh 2001). In contrast, lichen cover remained constantly low in the control plots where canopy continuity and ground-layer integrity were not disturbed over the 15 years.

In contrast to lichens, the expansion of *Sphagnum* spp. mosses was not favored by PCT, even in the sites characterized by mesic to subhydric conditions. The absence of effect of PCT on the *Sphagnum* spp. cover may have resulted from the already high proportion of *Sphagnum* spp. mosses in the ground layer before treatment, as suggested by the abundant *Sphagnum* spp. cover in the unthinned plots (≈40% in the mesic sites, 60% in the subhydric sites). The subhydric sites investigated in this study were characterized by high *Sphagnum* spp. cover, high organic layer thickness, and low initial tree basal area, which may indicate that they probably were already paludified at the time of the PCT treatment. Furthermore, initial tree basal area of the sites characterized by subhydric to mesic conditions was lower than that in xeric sites, suggesting that the degree of canopy closure before PCT was also lower in those stands. Therefore, the PCT effect on light availability and microclimatic conditions may have been less significant in those sites, which would explain why PCT had no effect on *Sphagnum* spp. expansion whereas it had a non-negligible effect on lichen cover in the xeric sites.

The Positive Effect of PCT Is Reduced in Sites with High Lichen Cover

At the tree scale, relationships between tree growth and lichen cover differed according to tree species. Because the study area included a large range of environmental conditions, jack pine growth may have been positively associated with lichen cover because of similar environmental preferences between the two species, especially in terms of moisture regime and surface deposits. In contrast, the proportion of lichens in the ground layer soon after PCT tended to be negatively correlated with the growth of the study black spruce trees that were small at the time of treatment. Lichens have been shown to reduce black spruce sapling growth (Brown and Mikola 1974, Wheeler et al. 2011), and it has been suggested that they may affect tree fine root growth through their effects on soil nutrients (Pacé et al. 2017). Therefore, black spruce growth may have been negatively affected by the environmental conditions associated with lichen cover, especially small trees that are likely to be more dependent on surface soil conditions.

Because the relationship between tree growth and lichen cover was tree species dependent and thus varies with stand composition, we were not able to establish any correlation at the stand scale between lichen cover and stand productivity. However, each pair of plots (thinned and control) used to estimate TEI was homogeneous in terms of tree species composition. Therefore, although the relationship between lichen cover and basal area of merchantable trees varied according to tree species in the stand, TEI expresses the way that PCT has improved productivity in a given stand independently of stand composition. The negative relationship we observed between pine density and TEI may partly result from jack pine's association with low-fertility xeric sites, where the effect of PCT was likely to be less beneficial. In addition to this effect, the impact of PCT on the basal area of merchantable trees 15 years after treatment was weaker and even tended to be negative in stands with a high proportion of lichen cover 1 year after treatment. This result suggests that the aboveground effect of PCT on tree growth may have been mitigated by belowground negative feedback resulting from lichen expansion on xeric sites.

Stand Productivity Depends on *Sphagnum* spp. Cover

Although *Sphagnum* spp. cover was not related to the growth of the study trees, it was negatively associated with the basal area and density of merchantable trees at the stand scale 15 years after treatment. The impact of *Sphagnum* spp. on surface soil conditions mainly affects the growth of trees that are rooted in the fibric layer (Simard et al. 2007, Saint-Denis et al. 2010). Because study trees were sampled among the biggest individuals of the plot at the time of thinning, they may have been sufficiently large and deeply rooted in the mineral soil that their growth was not related to *Sphagnum* spp. cover. However, by affecting the growth of the smallest trees and, eventually, that of the new seedlings, the dominance of *Sphagnum* spp. in the ground layer of some stands may have reduced the number of trees that reached 9 cm in dbh, resulting in a reduction of the basal area and density of merchantable trees at the stand scale 15 years after treatment.

The positive relationship between *Sphagnum* spp. and total stand density may result from the positive impact of this ground-cover type on germination (Ohlson and Zackrisson 1992, Groot and Adams 1994, Hörnberg et al. 1997) and spruce layering (Stanek 1961). Slow growth of trees in *Sphagnum* spp. mosses may also have resulted in slow self-thinning in high-density stands. Several of the subhydric stands with high *Sphagnum* spp. cover that we investigated in this study were probably paludified. In these stands, regeneration of black spruce is relatively abundant, but saplings tend to remain small because of unfavorable growth conditions (Saint-Denis et al. 2010, Lafleur et al. 2011). This high density of small trees associated with high *Sphagnum* spp. cover resulted in a total tree basal area that was not significantly different from that of the stands with low *Sphagnum* spp. cover.

TEI was not related to year-one *Sphagnum* spp. cover in the thinned plots, suggesting that the PCT impact on stand productivity was the same regardless of *Sphagnum* spp. cover at the time of thinning. Because PCT did not favor *Sphagnum* spp. expansion, it likely did not make *Sphagnum* spp. affect tree growth conditions worse when compared with unthinned plots. Therefore, a high cover of *Sphagnum* spp. had neither a negative nor a positive effect on TEI. Because the sensitivity to the impact of *Sphagnum* spp. on soil conditions is inversely proportional to root depth (Simard et al. 2007), as suggested by the absence of an effect of *Sphagnum* spp. on the growth of the study trees, we can hypothesize that part of the trees benefited from the increase in space, light, and soil resource availability associated with PCT even in stands with high *Sphagnum* spp. cover. However, because those stands were overall less productive, the growth increase due to PCT was lower than in the other stands.

Conclusion

PCT favored lichen expansion in xeric sites, but it had no effect on *Sphagnum* spp. cover, which was related to site moisture regime. In contrast to jack pine, the growth of the black spruce trees that were small at the time of thinning was lower in the sites with high lichen cover. This negative relationship was visible at the stand scale, where the positive effect of PCT on stand productivity was negatively related to the proportion of lichens in the ground layer 1 year after treatment. Although no relationship was established between *Sphagnum* spp. cover and the growth of the study trees in this study, *Sphagnum* spp. cover was negatively associated with the basal area and density of merchantable trees at the stand scale. These contrasting results between the two scales probably result from the size-dependent sensitivity of trees to *Sphagnum* spp. effects on the forest soil.

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