

Sphagnum community change after partial harvest in black spruce boreal forests

Nicole J. Fenton*, Yves Bergeron

UQAT-UQAM National Science and Engineering Research Council Industrial Chair,
Université du Québec en Abitibi-Témiscamingue, 445 Boul. de l'Université, Rouyn-Noranda, Québec J9X 1C5, Canada

Abstract

In eastern Canada, boreal forests develop structural diversity in association with time since stand replacing fire. In some regions, this is associated with significant changes in the bryophyte community (*Sphagnum* moss invasion) and paludification (thick waterlogged forest floor development). The bryophyte community responds to opening of the canopy, and increasing moisture by replacement of slow growing species by faster growing *Sphagnum* spp. (e.g. *magellanicum*, *fallax*) that are dependent on constant hydration. Within a forest management context, partial harvest systems have been proposed as a strategy to maintain structural diversity, which is currently not accomplished with low retention systems. However, it is unknown whether these interventions will effectively accelerate community succession. The questions addressed in this study were: (1) is the composition of *Sphagnum* colonies in partially cut stands more similar to old-growth communities than in control, and low retention cut stands, (2) what aspects of harvest disturbance drive these changes, and (3) is the growth rate of *Sphagnum capillifolium* (an early successional shade tolerant species) different in partial versus low retention harvest systems? After harvest, *Sphagnum* patch size was reduced by 19.8% and 11.7% after low retention and partial harvest, respectively. While trends were not constant across three separate partial cut trials, the proportion of *Sphagnum magellanicum*, *Sphagnum fallax* and *Sphagnum fuscum* increased compared to controls and low retention 1–2 years after harvest. Models of percent *Sphagnum* cover indicated machinery track cover, percent cover of vascular plants, and patch depth were positive factors, while the influence of open canopy varied among species. Despite the inclusion of individual disturbance variables, the summary variable 'treatment' was significant in all models. Growth of *S. capillifolium* in partial cuts was intermediate to growth rates in control and low-retention cuts. Growth was positively influenced by slash cover and, contrary to the patch level, negatively influenced by track cover. These results indicate that partial harvest does represent an intermediate level of disturbance, as direct and indirect harvest effects were reduced, as was *Sphagnum* death. Change in composition 1 and 2 years after harvest indicates that partial harvests may effectively shift the bryophyte community towards an older community type and may thus be used to create landscape diversity. Long term trends and entire community compositions need to be assessed before this can be stated definitively. However, as paludified stands are less productive, the capacity of these partially harvested sites to produce merchantable timber is questioned.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Variable retention; Disturbance; Boreal forest; Bryophytes; *Sphagnum* growth

1. Introduction

Black spruce (*Picea mariana*) forests develop structural diversity in association with time since stand replacing fire (Lecomte et al., 2005; Lussier et al., 2002) and in the eastern boreal forest, where fire cycles are relatively long (Bergeron et al., 2001; Foster, 1985) these forests can dominate the landscape. With death of the initial post-fire tree cohort, the canopy opens, and new individuals are regenerated by layering (asexual reproduction of black spruce; Groot, 2002) and seed.

In some regions, including the Clay Belt of Quebec and Ontario, this is associated with significant changes in the bryophyte community (i.e. *Sphagnum* moss invasion) and paludification (thick waterlogged forest floor development; Fenton et al., 2005; Foster, 1985). This multi-layer, paludified forest structure represents a diverse habitat that supports rich bird (Drapeau et al., 2003), and bryophyte communities (Harper et al., 2003). Within the bryophyte community the gradient in canopy openness and paludification associated with time since fire results in a replacement series of sphagna, with *S. capillifolium* that dominates in young forests gradually being replaced by *S. magellanicum*, *S. fallax* and eventually *S. fuscum* (Fenton and Bergeron, 2006). These changes are a result of the increase in light and moisture availability at the forest floor,

* Corresponding author. Tel.: +1 819 762 0971 2312; fax: +1 819 797 4727.
E-mail address: nicole.fenton@uqat.ca (N.J. Fenton).

both of which are limiting growth factors (Gignac, 1992; Vitt, 1990) for the late successional *Sphagnum*, which are typically found in open bogs.

The complex structure of older forests is not created by low forest harvesting retention systems, in which stands are harvested before they reach this stage and are regenerated to even-age stands (Bergeron et al., 1999). Total cut and low retention systems alter existing vegetation via substrate damage and slash deposition (direct disturbance) and microclimatic change due to canopy removal (indirect disturbance; Nelson and Halpern, 2005; Fenton et al., 2003). While these harvesting systems partially mimic stand replacing disturbance, such as fire, they do not always result in a community similar to early successional communities (McRae et al., 2001).

Partial harvest systems have been proposed (e.g. Halpern et al., 2005; Bergeron et al., 1999) as a complementary strategy to low retention harvest in order to maintain some tree cover and have a less severe impact on the existing vegetation. Furthermore, partial harvesting encourages the rapid development of old-growth features such as structural diversity, and a more open canopy (Carey, 2003; Deal, 2001; Deans et al., 2003). In the specific case of black spruce forests on the Clay Belt, partial cuts have the possibility of recreating habitat associated with old forests by opening up the canopy (via stem removal) and raising the water table (via reduced precipitation interception and evapotranspiration; Roy et al., 2000). However, the efficacy of these modified silvicultural treatments in creating habitat conditions similar to older forests is unknown, as is the extent and rate at which the biological communities respond to these “new” old forest conditions.

This study forms part of a larger partial harvest trial where the effects of low retention and partial harvest on a variety of forest community components are being compared. The long-term goal is to determine whether the partial cut techniques applied (variable retention and diameter limit harvest) successfully recreate the habitat of old forests, and whether this habitat is used by a variety of forest species (e.g. birds, insects, lichens and bryophytes). As such it differs from most studies that examine the effect of forest harvest as compared to the pre-harvest condition (e.g. Fenton et al., 2003; Frisvoll and Prestø, 1997), rather than in comparison to a desired habitat type (c.f. Halpern et al., 2005; Carey, 2003).

Specifically this article examines the efficacy of partial (63–68% harvest of commercial stems) compared to low retention (100% harvest commercial stems) harvest by using the bryophyte community as an early indicator of compositional change towards an old growth state. In addition to community composition, growth of *S. capillifolium* was measured. While compositional changes may be less evident soon after harvest, effects on the growth of individuals are immediately measurable. *S. capillifolium* was chosen, as it was common in all sites and treatments.

Overall, this study addresses three main questions: (1) do partial harvests result in less damage and death to *Sphagnum* colonies than low retention harvest; (2) do partial harvests push community composition toward an older community composition compared to low retention harvest and which, if any,

aspects of disturbance are these changes related to; (3) is the growth rate of *Sphagnum capillifolium* (an early successional shade tolerant species) different in partial versus low retention harvest systems, and what aspects of the disturbance altered habitat is growth rate related to?

1.1. Study area

The Clay Belt of Ontario and Quebec is a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsin glaciation (Vincent and Hardy, 1977). In its northern portion, it is dominated by black spruce (*P. mariana*)-feather moss (*Pleurozium schreberi*) forests (type Grondin, 1996), and is particularly prone to paludification between fires due to its poorly drained clay dominated soil, low topographic relief, and moderately humid and cold climate [889.9 mm of precipitation annually; annual mean temperature 0.7 °C (Environment Canada, 2004)]. The dominant disturbance type is large fires that kill all above ground vegetation. Between 1850 and 1920 the fire cycle was ca. 135 years, and it has since increased to ca. 398 years (Bergeron et al., 2004), as a result the average age of the forests is in excess of 100 years. It lies just south of the Hudson Bay–James Bay Lowlands, the second largest peatland complex on the globe.

2. Methods

2.1. Sampling

This study takes part of a larger project to compare the effects of partial harvest and low retention-cut systems on ecosystem function, diversity and merchantable timber. Each site in the network consists of one block (each >50 ha) of each of three treatments: low retention-cut (cut with protection of regeneration and soils), partial harvest with variable retention, and control. Three sites were chosen for this study, from the network of 12 sites that were comparable in terms of clay dominated soil texture and light slope. All three sites were dominated by black spruce approximately 120 years after stand replacing fire. Within in this matrix, patches of different forest types were found, due to the large size of the sites (>150 ha each). The understory was dominated by bryophytes, with *Pleurozium schreberi*, *Dicranum polysetum*, *Hylocomium splendens*, *Ptilium crista-castrensis* *Sphagnum capillifolium*, *S. girgensohnii*, *S. russowii*, *S. fallax* and *S. fuscum*. *S. wulfianum* was occasionally found. Lichens *Cladina rangifera* and *C. stellaris* were also common. The herb layer was dominated by *Vaccinium* spp., *Trientalis borealis*, *Cornus canadensis*, *Gaultheria hispidula*, *Rhododendron groenlandicum*, and saplings of black spruce and balsam fir. Two of these sites, Fénélon and Puiseaux were harvested in the winter of 2003–2004, while the third, Gaudet, was harvested in the winter of 2002. The level of extraction varied among the three sites, from 63 to 69% of the stems in the partial harvest. All low retention harvest treatments removed all commercial stems (>9.9 cm DBH).

Table 1
Description of habitat tolerances of the species examined in detail in this study

Species	Shade	Position relative to water table	Growth form	Growth rate	Decomposition rate
<i>S. capillifolium</i>	Tolerant	High above	Hummock	Low	High
<i>S. magellanicum</i>	Intolerant	Low above	Low hummock-lawn	High	Moderate
<i>S. fallax</i>	Intolerant	Low above	Lawn	High	Moderate
<i>S. fuscum</i>	Intolerant	High above	High hummock	Low	Low

Shade tolerance is inferred from the frequency at which the species was found in shaded and un-shaded habitats. Position relative to water table indicates the habitat relative to the water table where the species are typically found. From Gignac (1992), Mulligan and Gignac (2001), Moore (1989), Johnson and Damman (1991) and Fenton unpublished data.

In the summer of 2004, three 20 m × 20 m (400 m²) plots were established per treatment in each site (i.e. a total of 9 plots per site, and 27 in total). An effort was made to capture the variability in forest structure within the 50 ha blocks of each treatment type, by widely spacing the three plots (generally >100 m), which were all located >50 m from an edge. Each 20 m × 20 m plot was surveyed for *Sphagnum* spp. patches, and at each patch that was found, the following measures were taken to describe the patch: species composition (percent cover of patch); size of patch (in m² calculated as the area occupied by a contiguous colony of *Sphagnum* spp.); depth of patch (in cm). Depth was measured in the center of each patch. In particularly large patches more than one depth measurement was taken, and they were averaged. The following direct or indirect disturbance variables were also measured at each patch: percentage of patch buried under slash; percentage crushed by machinery trails (hereafter track cover); and canopy openness (%; measured with a concave spherical densiometer). The percentage cover of vascular species (including tree saplings but not retained trees) growing within the patch was also measured as Malmer et al. (2003) indicated that they can accelerate *Sphagnum* growth by serving as a ladder or scaffolding (hereafter called “ladder species”). Some patches crossed the boundary of the plot, half of these patches (randomly selected) were included in the sampling. The area (m²) by species per patch was calculated by multiplying the percent cover of an individual species in a specific patch by the area of the entire patch. *Sphagnum* spp. species were determined in the field, except for difficult specimens, which were sampled and determined in the laboratory. *Sphagna* taxonomy follows Anderson (1990). *Sphagnum fallax* is treated in the large sense to include the different species of the *recurvum* complex.

Growth of *Sphagnum capillifolium* was measured in all three sites in the three treatment types. *S. capillifolium* was chosen for this study as it was consistently found in all sites, and is easily identifiable in the field. In a total of five patches per treatment per site, three cranked wires were installed in August 2004. Cranked wires are a widely used technique to measure *Sphagnum* growth (Clymo, 1970). The distance from the patch surface to the end of the wire is measured when they are installed, and again after a growth period, in this case 13 months. The difference in the length is the height of new biomass produced during the growth period. A cross bar is used to limit wire movement within the colony. *Sphagnum* growth was measured in September 2005.

2.2. Analyses

The relative abundances of *S. capillifolium*, *S. magellanicum*, *S. fallax* and *S. fuscum* within patches were compared, as they differ in their microhabitat requirements from shade and desiccation tolerant to shade and desiccation intolerant, and shade intolerant and desiccation resistant (see Table 1) (Mulligan and Gignac, 2001; Gignac, 1992). Comparisons in variable values were made among treatments within a site, as differences in sites 50–100 km apart may have masked treatment differences. Within a site, plots were considered as the experimental unit as they were all over 100 m apart, and the community varies at a very fine scale (see Fenton and Bergeron, 2006). Differences in total *Sphagnum* cover, mean *Sphagnum* patch size, percentage of patch killed, depth of patch, mean percentage cover of each species in a patch, and mean area covered by a species in a patch, and in disturbance variables were tested with the non-parametric Kruskal–Wallis test (SPSS v.10), as the data were not normally distributed, and could not be normalised with a transformation.

Path analysis was used to determine the potential structure (including direction) of the relationships among the % cover of *Sphagnum* (total and relative cover of *S. capillifolium*, *S. fallax* and *S. fuscum*) and potential explanatory variables (natural log track cover, natural log slash cover, open canopy, ladder species cover, natural log patch depth, treatment and site). Path analysis (and partial correlation) was used instead of multiple regression as many of the explanatory variables were correlated. The variables included in each path analysis were selected from the list of potential variables based on strong partial correlations, indicating that they were still significant when the other variables were held constant. All sites were analysed together as this method is better equipped to deal with site as a covariable. A d-sep test (Shipley, 2000) was used to determine the likelihood that an *a priori* structure was correct. Partial correlation coefficients (or path coefficients) among the variables allowed us to determine the magnitude of direct and indirect effects. The percent of variation of the response variable explained by the selected explanatory variables was calculated using multiple regression (SPSS v.10).

Differences in growth (cm) among treatments were examined by GLM in SPSS v. 10, with natural log transformed (ln) growth, for normality. The interaction term between site and treatment was not significant. Regression was used to look at the effect of different habitat variables on growth, with ln live

Table 2
Mean (standard error) values for total area in *Sphagnum* patches and for different *Sphagnum* patch characteristics by site and treatment

Variable	Fénelon			Puisseaux			Gaudet		
	Control (12)	Partial-cut (24)	Low retention-cut (24)	Control (18)	Partial-cut (24)	Low retention-cut (24)	Control (17)	Partial-cut (51)	Low retention-cut (38)
Total <i>Sphagnum</i> area (m ²)	209.57 (115.81)	161.65 (71.39)	79.56 (47.97)	205.27 (20.82)	289.89 (31.56)	182.03 (21.80)	337.15 (54.82)	223.00 (50.26)	151.25 (17.44)
Patch size (m ²)	48.36 (30.10)	21.61 (9.62)	13.52 (6.39)	16.64 (5.54) a	39.28 (7.85) b	20.31 (4.25) ab	59.50 (25.52) b	15.80 (2.71) a	14.08 (2.78) a
Live patch size (m ²)	48.36 (30.10)	19.40 (8.37)	13.26 (6.41)	16.64 (5.54) a	36.24 (6.99) b	15.60 (3.06) a	59.50 (25.52) b	13.12 (2.34) a	11.94 (2.49) a
Percent <i>Sphagnum</i> patch killed	0.00	7.00 (4.26)	10.28 (5.92)	0.00 a	3.75 (2.32) ab	24.86 (4.77) b	0.00 a	10.78 (3.48) ab	16.05 (3.75) b
Mean depth of patch (cm)	38.79 (3.10)	31.74 (2.37)	31.26 (3.37)	48.53 (1.84)	46.26 (2.04)	47.22 (2.11)	57.53 (2.51) b	46.72 (2.61) a	52.54 (2.08) ab

The number in brackets after the treatment indicates the number of patches found in each treatment per site. Italics indicate significant differences among treatments within a site. Within a site, values for a variable that are followed by different letters are significantly different (a < b).

Sphagnum area, ln track cover, ln slash cover, and two dummy site and treatment variables, respectively. The critical value of *p* was 0.05 in all tests.

3. Results

3.1. Disturbance effect

Patch size varied greatly in all sites and treatments, but in the Gaudet and Fénelon sites total *Sphagnum* area, patch size and live patch size decreased from control, to partial cut, and to low retention (Table 2). While there was no significant difference, on average more *Sphagnum* was killed in low retention cuts than in partial cuts in Puisseaux and Gaudet; in Fénelon there was no difference between partial and low retention cuts and this may have been due to the smaller patch size at this site. In terms of the habitat (Table 3), the canopy was more open, and in Puisseaux and Gaudet more slash was deposited, on the *Sphagnum* patches in low retention cuts compared to partial cuts and controls.

3.2. Species composition

The composition of the patches varied among sites and treatments (Fig. 1). The relative abundance (percent cover) of *S. capillifolium*, *S. russowii*, *S. magellanicum*, *S. fallax*, and *S. fuscum* in each patch was examined. *S. capillifolium* dominated all sites and patches, but had significantly lower cover within patches in the partial cuts in all sites. *S. russowii* and *S. magellanicum* had varied responses, while *S. fallax* and *S. fuscum* had a greater percentage cover in partial cuts than in low retention cuts and controls in all three sites. When the actual area covered (in m²) is examined, the decrease in *Sphagnum* cover in the partial cut and low retention cuts is apparent (Fig. 2), as the cover of almost all species is lower in these treatments, if not statistically significant. The exception is Puisseaux, where the cover of all species was greater in partial cut compared to control and low retention cut treatments.

3.3. Relationship between *Sphagnum* cover, composition, disturbance, and habitat variables

The models describing the relationship between *Sphagnum* cover and the explanatory variables were only significant for total *Sphagnum* area and percentage cover of *S. capillifolium*, *S. fallax* and *S. fuscum*. The relationship between total *Sphagnum* area, percentage cover of individual species and disturbance and habitat variables was relatively consistent (Table 4). The measured direct (only track cover, slash was not significant) and indirect effects (open canopy) of the harvest treatments were both significant in the majority of the models. Track cover tended to be positively related to and higher cover of *S. capillifolium*, *S. fallax* and *S. fuscum*, while open canopy was positively correlated with *S. fallax* and negatively correlated with *S. capillifolium* and *S. fuscum* cover. In addition to the measured effects of harvest, the summary variable “treatment” was significantly partially correlated with the response variable

Table 3
Mean (standard error) values for different variables characterizing the habitat in which patches were found, by site and treatment

Variable	Fénelon			Puisseaux			Gaudet		
	Control	Partial-cut	Low retention-cut	Control	Partial-cut	Low retention-cut	Control	Partial-cut	Low retention-cut
Percentage of patch on track	0.00	13.20 (5.99)	22.78 (8.82)	0.00 a	23.75 (7.16) b	20.57 (5.98) b	0.00 a	28.33 (5.63) b	16.62 (5.31) a
Percentage of patch under slash	0.00	6.60 (3.90)	1.39 (1.39)	0.00 a	2.92 (2.21) a	17.88 (4.46) b	0.00 a	0.20 (0.20) a	15.81 (3.83) b
Percentage open canopy above patch	64.87 (2.39) a	90.10 (2.47) b	90.47 (3.58) b	66.37 (2.53) a	82.67 (3.07) b	97.49 (0.66) c	51.60 (4.90) a	84.46 (2.21) b	96.66 (1.56) c
Percentage ladder spp. cover in patch	54.62 (8.59)	32.29 (5.52)	34.44 (7.55)	50.27 (3.54) b	43.75 (5.91) ab	33.28 (5.62) a	45.88 (5.53)	47.55 (4.59)	49.14 (3.96)

Italics indicate significant differences among treatments within a site. Within a site, values for a variable that are followed by different letters are significantly different (a < b < c).

in all the models, although the indirect effects were generally larger than the direct effects. Depth of patch was always positively correlated with patch area and percent cover of all the species; percentage cover of ladder species had the largest direct effect in the models for total *Sphagnum* area and *S. capillifolium*. ‘Site’ had the largest direct effect in the *S. fuscum* model.

3.4. Growth in height of *S. capillifolium*

Overall, growth of *S. capillifolium* differed by site and treatment, with no interaction between the two terms. Growth was, overall, greatest in Fénelon and lowest in Puisseaux, with Gaudet intermediate, although there was no significant difference in growth between Puisseaux and Gaudet for any of the treatments (Fig. 3). In terms of treatment, plants in control plots grew significantly more than those in the partial and low retention cuts, and while the difference was not significant, plants in partial cut plots grew at rates intermediate to control and low retention cut plots.

Multiple regression indicated that growth was positively influenced by cover of slash (0.243 β coefficient), and negatively affected by machinery tracks on the patch (−0.221 β coefficient); treatment type was also significant (control 0.501 β coefficient, partial cut 0.250 β coefficient; $p < 0.001$; R^2 0.272).

4. Discussion

4.1. Disturbance effect

As has been indicated in previous studies (Halpern et al., 2005; Carey, 2003; Deal, 2001), partial and low retention harvests created a gradient of disturbance severity, as perceived by the bryophyte community. Both direct substrate disturbance (cover of machinery track, slash deposition) and indirect disturbance via microclimatic change caused by canopy removal were lower in the partial cut compared to the low retention harvests for at least two of three sites for each variable. As a consequence, there was more *Sphagnum* death in the low retention cut than the partial cut harvests.

4.2. Patch composition and disturbance and habitat variables

Despite the fact that only 1–2 years had passed since harvest, in all sites the community had changed in response to treatment. Compared to the control the partial cut harvests had a community composition (relative abundance of species; Fig. 1) that was closer to that which is found in older forests (Fenton and Bergeron, 2006), i.e. reduced cover of *Sphagnum capillifolium* and increased cover of *S. fallax* and *S. fuscum*. Similar results for the vascular plant, fungi, and bird communities were found less than 5 years after variable retention thinning in the Pacific Northwest (Carey, 2003). The low retention harvests had a community that more closely resembled a community in a younger forest, as did the control.

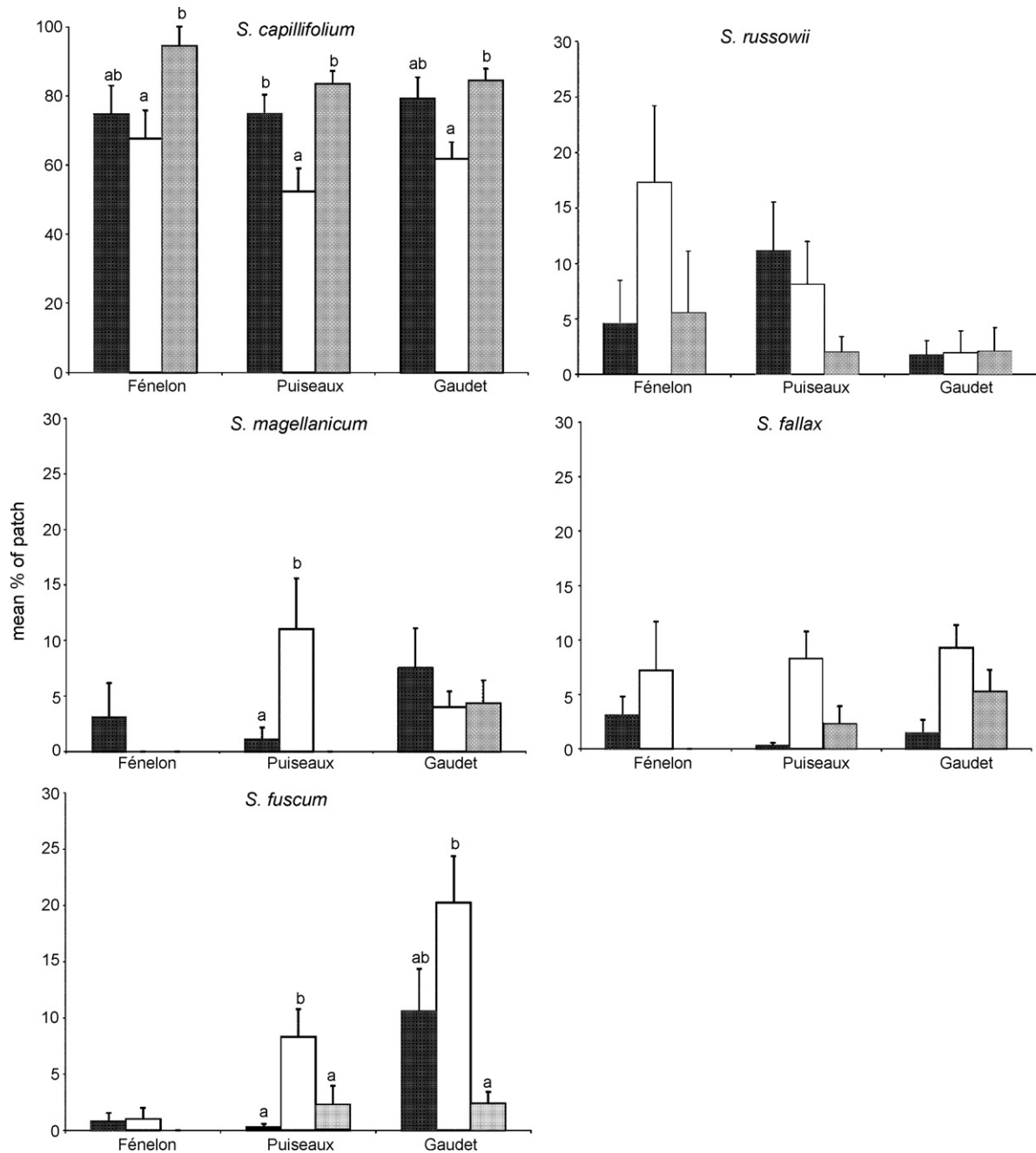


Fig. 1. Percent of cover of species in each patch per site and treatment type. Values are means + standard error. Bars within a site with a different letter are significantly different. Black, control; white, partial harvest; grey, low retention cut.

However, when actual surface area of *Sphagnum* species within patches was examined, both the partial cut and low retention harvests had smaller surface areas of the late successional species, as defined in Section 1 and Table 1 (Fig. 2), and the process of successional change is not yet advanced. Initial changes in relative cover suggest that partial cuts may in fact be efficient in pushing sites to a community similar to that found in older forests. However, longer term studies should be completed to document that the actual rate of change is faster than what would have occurred if the stands were allowed to develop naturally (i.e. develop an open canopy and paludify) and had not been harvested.

While the changes in relative abundance of the species appeared to match their known habitat requirements, correlations between species abundance and the disturbance-altered habitat variables were less clear. Surprisingly direct disturbance (machinery track cover) had a positive influence on total *Sphagnum* area overall, and in *S. capillifolium* and *S. fuscum*. *S. capillifolium* and *S. fuscum* are both high hummock species that form tight colonies and are therefore able to tolerate dry conditions (Schipperges and Rydin, 1998; Hayward and Clymo, 1983). This characteristic may allowed them to develop new colonies, or expand existing colonies, onto the newly created, frequently dry, surfaces of the machinery tracks.

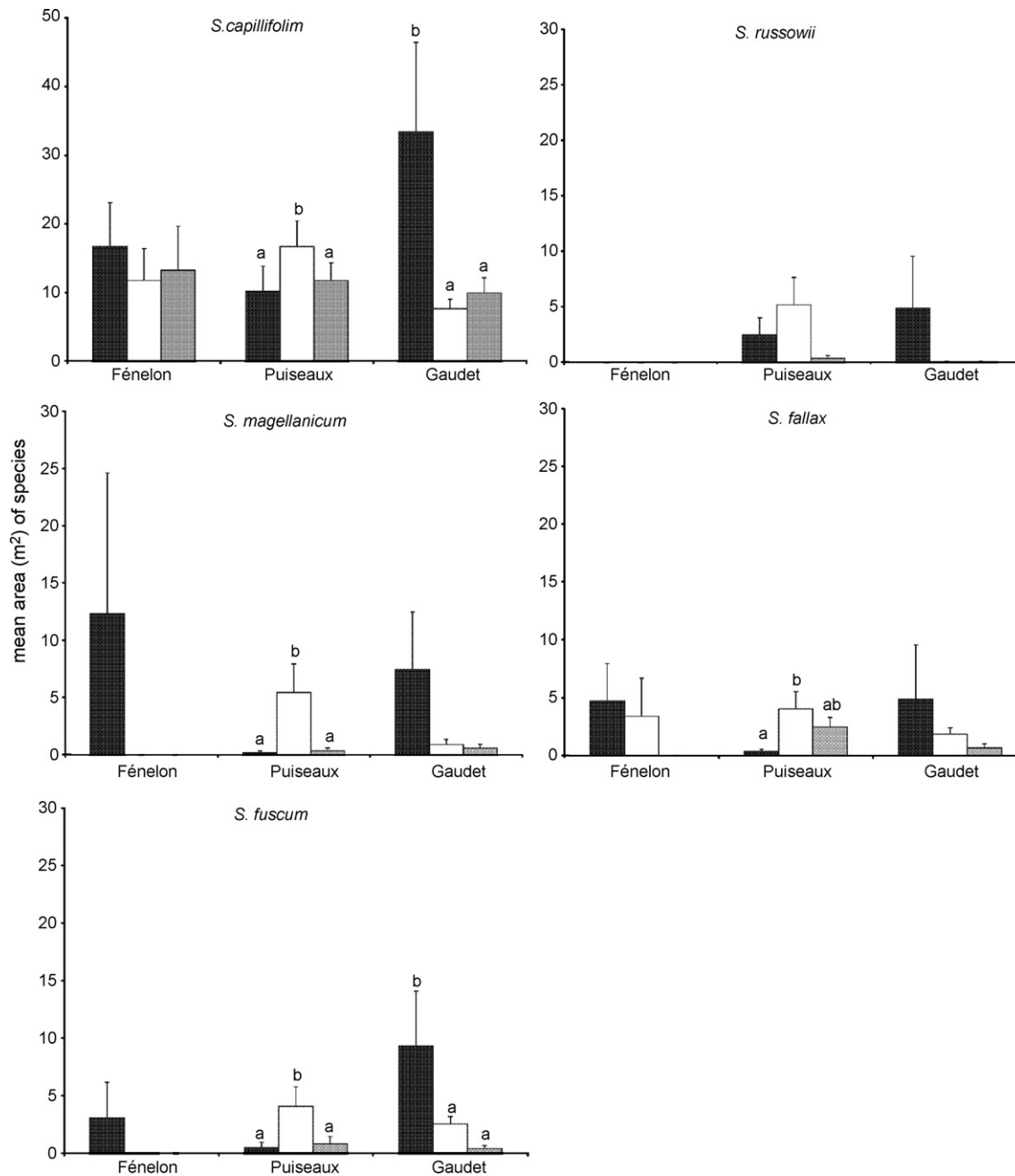


Fig. 2. Area (m²) of species per site and treatment type. Values are means + standard error. Bars within a site with a different letter are significantly different. Black, control; white, partial harvest; grey, low retention cut.

Open canopy had a negative influence on the relative abundance of *S. capillifolium*, as would be expected of the shade tolerant species (Gignac, 1992), but the negative impact of open canopy on the late successional *S. fuscum*, which typically grows in well illuminated high hummocks in bogs (Gignac, 1992), is surprising. It may be due to the physiological shock of the colony being suddenly exposed to new conditions, and if so it may be only temporary, as the individuals develop new growth beneath the colony surface (e.g. Coates and Duckett, 1986).

In addition to the measured effects of harvest (machinery track, slash deposition, and canopy opening), the variable

“treatment” was also significant in all of the models. The fact that the summary variable treatment was significant, despite the fact that individual factors characterizing the disturbance associated with the treatment were taken into account suggests that there are aspects of the treatment effect that were not captured in these individual variables. These other factors might include an altered water balance, or changes in canopy cover at a scale not included in the analysis.

In addition to the factors associated with harvest, patch depth, cover of ladder species and site were significant factors. While it is generally accepted that *Sphagnum* patches spread clonally by vertical and horizontal growth (Hayward and

Table 4

Direct (due only to the factor) and indirect (due to interactions with other factors) coefficients (which indicate effect), error and total correlation for factors influencing ln total *Sphagnum* area, ln % cover *S. capillifolium*, % *S. fallax*, and % *S. fuscum* within patches as determined by path analysis

Variable	Direct	Indirect	Error	Total
ln Total <i>Sphagnum</i> area, p 0.827, R^2 0.340				
ln Track cover	0.255	-0.0160	0.132	0.107
Ladder cover	0.488	0.0325	0.0605	0.541
ln Depth	0.204	0.0497	0.0923	0.346
Treatment	-0.077	0.163	0.0141	0.072
Percent ln <i>S. capillifolium</i> , p 0.998, R^2 0.359				
ln Track cover	0.171	-0.0504	0.0466	0.074
Open canopy	-0.100	-0.0770	0.0120	-0.035
Ladder cover	0.442	0.0889	0	0.529
ln Depth	0.255	0.171	0.0353	0.391
Treatment	0.044	-0.0685	0.0105	-0.035
Site	0	0.180	0.0918	0.088
Percent ln <i>S. fallax</i> , p 0.779, R^2 0.023				
ln Track cover	0.015	0.0467	0.0327	0.029
Open canopy	0	0.055	0.0479	0.103
ln Depth	0.097	0.0295	0.00853	0.118
Treatment	0.063	0.00308	0.002	0.064
Site	0.064	0.0488	0.00681	0.106
Percent ln <i>S. fuscum</i> , p 0.996, R^2 0.203				
ln Track cover	0.097	-0.0865	0.0065	0.017
Open canopy	-0.155	0.00095	0.007	-0.163
Ladder cover	0.137	0.0885	0.0115	0.214
ln Depth	0.127	0.166	0.0359	0.257
Treatment	-0.034	-0.0587	0.0363	-0.129
Site	0.198	0.0757	0	0.273

All included factors were significant. The likelihood that the structure was correct is indicated by a p value for each model, and the percentage of the variability explained (as determined by multiple regression) by R^2 .

Clymo, 1983) the fact that depth positively influenced not only total *Sphagnum* area but also the relative cover of all three species suggests that their capacity to occupy space is augmented by the depth of the patch. This is potentially due to increased water retention volume, which would limit evaporation stress. Furthermore, the substantial indirect effect

of patch depth (particularly via the cover of ladder species, not shown) results in depth being a dominant factor.

The cover of vascular plant species that may act as ladders for *Sphagnum* was the most important factor in the model of *Sphagnum* area, and *S. capillifolium* cover. These vascular plants may be influencing the patches via both shading of the patch, and physical support of *Sphagnum* individuals. Light shading of bryophytes by slash in low retention cuts has been shown to be beneficial in a variety of forest habitats as it attenuates the increase in solar radiation (Fenton et al., 2003; Olsson and Staaf, 1995), and vascular plants growing in bogs are generally believed to not offer competition for light to *Sphagnum* if total cover is less than 60% (Heijmans et al., 2002). Therefore the vascular plants growing in the *Sphagnum* patches may be allowing individuals to tolerate the sudden change in light intensity, and indeed individuals shaded by ericaceous shrubs had a denser green pigmentation (Fenton pers. obs.). In addition to the shading effect, the vascular plants may be providing a physical support that allows the *Sphagnum* to grow at a faster rate. As cushion species sphagna generally grow vertically, but lack any type of internal support mechanism, they depend on colony density to remain upright (Hayward and Clymo, 1983). With the presence of ladder species, they may be able to grow vertically at a lower density, limiting the need for energy expensive asexual budding to increase patch density.

4.3. Growth in height of *S. capillifolium*

The growth rate of *Sphagnum capillifolium* varied widely among sites and treatments from an average of over 3.7 cm (from August 2004 to September 2005) in the control of Fénelon to less than 0.5 cm in the clear cut at Puiseaux. These rates are similar to what has been documented for *S. capillifolium* in other studies that vary from 1.6 cm per year to 5.0 cm per year (Asada et al., 2003; Gunnarsson et al., 2002). While Roy et al. (2000) found no variation in *Sphagnum* growth rate among low retention cut and control plots (potentially due to confounding of species), the growth rate of the individuals in the partial cuts were intermediate to those of the control and low retention cuts, but varied among sites from nearly identical to the low retention cut at Fénelon to nearing the rate of control at Gaudet. As Gaudet is the site where two years have passed since treatment, this may suggest that the plants in the partial cut recover faster than those in the low retention cut. However, due to the lack of replicates at the site level, these observations will have to be confirmed in the future.

The growth rate of *S. capillifolium*, a shade tolerant species (Gignac, 1992) responded positively to slash cover, which confirms the positive role of moderate slash levels in attenuating extreme light levels after forest harvest (Peterson, 1999; Olsson and Staaf, 1995). The negative partial correlation of machinery tracks suggests that at the individual level damage by tracks has a negative effect, which contrasts with the patch level relative abundance. This undoubtedly reflects the impact of individuals that were actually damaged by the machinery

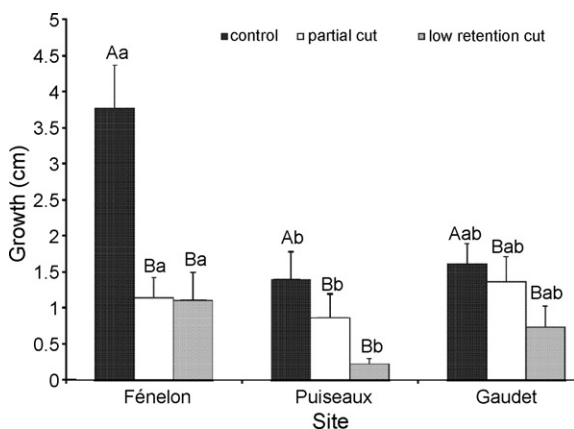


Fig. 3. Growth (cm) of *Sphagnum capillifolium* among sites and treatments. Black, control; white, partial harvest; grey, low retention cut. Letters indicate significant differences in growth; capital letters among sites for a given treatment, and lower case letters among treatments within a site.

compared to the space created by the machinery tracks. The positive influence of both control and partial cut treatments reflects that in two of the three sites (Puisseaux and Gaudet) the growth rate of individuals in partial cuts was intermediate to the control and low retention treatments. Again, as for the cover of species within patches as shown by path analysis, treatment was a significant variable despite the inclusion of the measured effects.

The model of *S. capillifolium* growth explains, however, only a relatively small percentage of the variation in the data set. Two additional factors that influence *Sphagnum* growth may be responsible for part of the unexplained variance: night-time temperature and nutrient deposition via throughfall and stem flow. Low night-time temperatures retard *Sphagnum* growth (Gerdol et al., 1998) and the lack of forest cover may have resulted in lower temperatures in the low retention cuts compared to partial cuts. Similarly, *Sphagnum* species are dependant on aerial deposition of nutrients, and are capable of extracting >90% (Malmer et al., 2003) of available nutrients present in water falling from above. The removal of the canopy undoubtedly reduced the nutrient input to the patches, and may have lowered their growth rate.

4.4. Conclusions

The *Sphagnum* community in black spruce forests on fine textured soils in the Clay Belt of Quebec and Ontario are good indicators of water table position and canopy openness, as they responded to the change in conditions created by forest harvest in 1–2 years after treatment. The composition of the bryophyte community in stands that have been harvested also indicate the effect of partial and low retention cuts not only on the bryophyte community but also on the level of paludification, as indicated by the composition of the bryophyte community. These results indicate that, at least in the initial post-harvest stage, the partially harvested stands are developing a community typical of an old paludified stand. Therefore, including partial harvests in management plans on this landscape may help preserve biodiversity, however, only widespread macroscopic species were examined here, and it is not yet clear whether created habitat will succeed in recruiting smaller species that are potentially dispersal limited. Furthermore as paludified stands have reduced productivity, it also indicates that partial harvest of these stands may not create productive forests in the immediate future (Lecomte et al., 2005).

Acknowledgements

Catherine Béland, Hervé Béscand, and Maude Beauregard provided valuable field assistance. Comments from two anonymous reviewers improved the manuscript. Funding for this project was provided by the UQAT-UQAM National Science and Engineering Research Council Industrial Chair (NSERC), an NSERC scholarship, the Lake Abitibi Model Forest and by an NSERC partnership grant with Forest industries and the Canadian Forest Service.

References

- Anderson, L.E., 1990. A checklist of *Sphagnum* in North-America north of Mexico. *Bryologist* 93, 500–501.
- Asada, T., Warner, B., Banner, A., 2003. Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia. *Bryologist* 106, 516–527.
- Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. *For. Chron.* 75, 49–51.
- Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., Lesieur, D., 2001. Natural fire frequency for the eastern canadian boreal forest: consequences for sustainable forestry. *Can. J. Forest Res.* 31, 384–391.
- Bergeron, Y., Gauthier, S., Flannigan, M., Kafka, V., 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* 85, 1916–1932.
- Carey, A.B., 2003. Biocomplexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. *Forestry* 76, 127–136.
- Clymo, R.S., 1970. The growth of *Sphagnum*: methods of measurement. *J. Ecol.* 58, 13–49.
- Coates, D., Duckett, J., 1986. Regeneration of *Sphagnum*. *N. Phytol.* 102, 589–614.
- Deal, R.L., 2001. The effects of partial cutting on forest plant communities of western hemlock - Sitka spruce stands in southeast Alaska. *Can. J. For. Res.* 31, 2079.
- Deans, A., Malcolm, J., Smith, S., Carleton, T., 2003. A comparison of forest structure among old-growth, variable retention harvested and clearcut peatland black spruce (*Picea mariana*) forests in boreal northeastern Ontario. *For. Chron.* 79, 579–589.
- Drapeau, P., Leduc, A., Bergeron, Y., Gauthier, S., Savard, J.P., 2003. Bird communities in old lichen-black spruce stands in the Clay Belt: problems and solutions regarding forest management. *For. Chron.* 79, 531–540.
- Environment Canada, 2004. http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html.
- Fenton, N.J., Frego, K.A., Sims, M., 2003. Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. *Can. J. Bot.* 81, 714–731.
- Fenton, N., Lecomte, N., Légaré, S., Bergeron, Y., 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. *For. Ecol. Manag.* 213, 151–159.
- Fenton, N.J., Bergeron, Y., 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. *J. Veg. Sci.* 17, 65–76.
- Foster, D., 1985. Vegetation development following fire in *Picea mariana* (Black spruce) - Pleurozium forests of south-eastern Labrador, Canada. *J. Ecol.* 73, 517–534.
- Frisvoll, A., Prestø, T., 1997. Spruce forest bryophytes in central Norway and their relationship to environmental factors including modern forestry. *Ecography* 20, 3–18.
- Gerdol, R., Bonora, A., Marchesini, R., Pancaldi, S., 1998. Growth response of *Sphagnum capillifolium* to nighttime temperature and nutrient level: mechanisms and implications for global change. *Arc. Alp. Res.* 30, 388–395.
- Gignac, D., 1992. Niche structure, resource partitioning and species interactions of mire bryophytes relative to climatic and ecological gradients in western Canada. *Bryologist* 95, 406–418.
- Grondin, P., 1996. Écologie forestière. In: Bérard, J.A., Côté, M. (Eds.), *Manuel de foresterie*. Le Presse de l'Université Laval, Québec, pp. 133–279.
- Groot, A., 2002. Is uneven-aged silviculture applicable to peatland black spruce (*Picea mariana*) in Ontario, Canada? *Forestry* 75, 437–442.
- Gunnarsson, U., Malmer, N., Rydin, H., 2002. Dynamics or constancy in *Sphagnum* dominated mire ecosystems? A 40-year study. *Ecography* 25, 685–704.
- Halpern, C., McKenzie, D., Evans, S.A., Maguire, D., 2005. Initial responses of forest understories to varying levels and patterns of green-tree retention. *Ecol. App.* 15, 175–195.
- Harper, K., Boudreault, C., DeGrandpré, L., Drapeau, P., Gauthier, S., Bergeron, Y., 2003. Structure, composition, and diversity of old-growth black spruce

- boreal forest of the Clay Belt region in Québec and Ontario. Environ. Rev. 11, S79–S98.
- Hayward, P., Clymo, R., 1983. The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water table depth. J. Ecol. 71, 845–863.
- Heijmans, M., Klees, H., Berendse, F., 2002. Competition between *Sphagnum magellanicum* and *Eriophorum angustifolium* as affected by raised CO₂ and increased N deposition. Oikos 97, 415–425.
- Johnson, L.C., Damman, A.W.H., 1991. Species-controlled *Sphagnum* decay on a south Swedish raised bog. Oikos 61, 234–242.
- Lecomte, N., Simard, M., Bergeron, Y., Larouche, A., Asnong, H., Richard, P.J.H., 2005. Effects of fire severity and initial tree composition on understory vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. J. Veg. Sci. 16, 665–674.
- Lussier, J.-M., Morin, H., Gagnon, R., 2002. Évolution de la structure diamétrale et production ligneuse des pessières noires issues de coupe et de feu. Can. J. For. Res. 32, 526–538.
- Malmer, N., Albinsson, C., Svensson, Y., Wallen, B., 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. Oikos 100, 469–482.
- McRae, D.J., Duchesne, L.C., Freedman, B., Lynham, T.J., Woodley, S., 2001. Comparisons between wildfire and forest harvesting and their implications in forest management. Environ. Rev. 9, 223–260.
- Moore, T.R., 1989. Growth and net production of *Sphagnum* at 5 fen sites, subarctic eastern Canada. Can. J. Bot. 67, 1203–1207.
- Mulligan, R.C., Gignac, D.L., 2001. Bryophyte community structure in a boreal poor fen: reciprocal transplants. Can. J. Bot. 79, 404–411.
- Nelson, C.R., Halpern, C., 2005. Short term effects of timber harvest and forest edges on ground-layer mosses and liverworts. Can. J. Bot. 83, 610–620.
- Olsson, B., Staaf, H., 1995. Influence of harvesting intensity of logging residues on ground vegetation in coniferous forests. J. App. Ecol. 32, 640–654.
- Peterson, J., 1999. The effects of forest harvest on bryophyte recolonization in a mixed forest in New Brunswick. M.Sc. Thesis. Department of Biology, University of New Brunswick, Saint John.
- Roy, V., Ruel, J.-C., Plamondon, A., 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. For. Ecol. Manag. 129, 253–267.
- Shipley, B., 2000. Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations, and Causal Inference. Cambridge University Press, Cambridge.
- Schipperges, B., Rydin, H., 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. N. Phytol. 140, 677–684.
- Vincent, J., Hardy, L., 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. Geogr. Phys. Quat. 31, 357–372.
- Vitt, D., 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. Bot. J. Linn. Soc. 104, 35–59.