Sphagnum establishment and expansion in black spruce (*Picea mariana*) boreal forests

Nicole J. Fenton, Catherine Béland, Sylvie De Blois, and Yves Bergeron

Abstract: Boreal forest bryophyte communities are made up of distinct colonies of feathermosses that cover the forest floor. In some black spruce (*Picea mariana* (Mill.) BSP) boreal forests, *Sphagnum* spp. establish colonies on the forest floor 30–40 years after the feathermosses, and ultimately expand to dominate the community. The mechanisms that permit the *Sphagnum* spp. to establish and expand are unknown. The objectives of this study were to examine the establishment and expansion substrates of *Sphagnum* spp., and the conditions correlated with colony expansion. Forty colonies, in six stands, of *Sphagnum capillifolium* (Ehrh.) Hedw. were dissected to determine their substrates, and the environmental conditions in which all colonies present were growing were measured. Coarse woody debris was the dominant establishment and early expansion substrate for *Sphagnum capillifolium* colonies. With age as the control factor, large colonies showed a significant partial correlation with canopy openness, and there were fewer individuals per cm^3 in large colonies than there were in small colonies. These results suggest that *Sphagnum* establishment in these communities is dependent on the presence of coarse woody debris, and expansion is linked to the stand break-up, which would allow an increase in light intensity, and rainfall to reach the colony. Consequently the community change represented by *Sphagnum* establishment and expansion is initially governed by a stochastic process and ultimately by habitat availability and species competition.

Key words: coarse woody debris, substrates, feathermosses, *Sphagnum capillifolium*.

Résumé : Dans les forêts boréales, les communautés de bryophytes sont composées d'agglomérations de mousses hypnacées qui couvrent le sol. Dans les pessières, (*Picea mariana* (Mill.) BSP) les sphaignes établissent des colonies sur le sol, 30 à 40 ans après les mousses hypnacées, et réussissent ultimement à dominer la communauté. Les mécanismes qui permettent cet établissement et étalement ne sont pas encore compris. Les objectifs de cette étude sont d'examiner les substrats d'établissement et d'expansion des sphaignes, ainsi que les conditions environnementales qui permettent leur étalement. Pour ce faire, 40 colonies de *Sphagnum capillifolium* (Ehrh.) Hedw., réparties sur six sites ont été disséquées afin de déterminer leurs substrats d'établissement, et les conditions environnementales présentes autour de toutes les colonies ont été mesurées. Le bois mort était le substrat dominant pour l'établissement et l'étalement des colonies. Quand l'âge des peuplements est contrôlé dans une corrélation partielle, les grandes colonies étaient corrélées positivement avec l'ouverture de la couronne, et il y avait moins d'individus par cm^3 dans les grandes colonies versus les petites colonies. Ces résultats suggèrent que l'établissement des sphaignes dépend de la présence de bois mort, et que l'étalement est corrélé avec l'ouverture du peuplement, phénomène qui permettrait à plus de lumière et de pluie d'atteindre les colonies. Par conséquent, l'établissement et l'expansion des colonies, qui représentent un changement dans la communauté, seraient gouvernées initialement par des processus stochastiques, et ultimement par la disponibilité d'habitat et la compétition.

Mots clés : bois mort, substrats, mousses hypnacées, *Sphagnum capillifolium*.

Introduction

Bryophytes play many roles in boreal forest ecosystems, influencing, among others, total net primary production (Gower et al. 1997; Bisbee et al. 2001) and soil respiration (O'Connell et al. 2003). They are also associated with paludification, where a coniferous forest on mineral soil is transformed into a treed peatland through tree diebacks caused mainly by the accumulation of a thick forest floor and waterlogging (Glebov and Korzukhin 1992; Fenton et al. 2005). Paludification is associated with a change in the bryophyte community, as *Sphagnum* spp. colonies establish

Received 16 August 2006. Published on the NRC Research Press Web site at http://canjbot.nrc.ca on 4 April 2007.

N.J. Fenton[1] and Y. Bergeron. UQAT-UQAM National Science and Engineering Research Council Industrial Chair, Université du Québec en Abitibi–Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, QC J9X 1C5, Canada.
C. Béland.[2] UQAT-UQAM National Science and Engineering Research Council Industrial Chair, Université du Québec en Abitibi–Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, QC J9X 1C5, Canada; McGill School of Environment, McGill University, Macdonald Campus 21, 111 Lakeshore Road, Ste. Anne de Bellevue, QC H9X 3V9, Canada.
S. DeBlois. McGill School of Environment, McGill University, Macdonald Campus 21, 111 Lakeshore Road, Ste. Anne de Bellevue, QC H9X 3V9, Canada.

[1] Corresponding author (e-mail: nicole.fenton@uqat.ca).

[2] Present address: Centre Universitaire de Formation en Environnement, Université de Sherbrooke 2500, boulevard de l'Université, Sherbrooke, QC J1K 2R1, Canada.

Can. J. Bot. **85**: 43–50 (2007) doi:10.1139/B06-148

and gradually overtop the previously dominant feathermosses (*Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis*; Reiners et al. 1971; Foster 1985; Boudreault et al. 2002).

Despite this important link with boreal forest dynamics, few studies have focused on *Sphagnum* spp. in forests, and most of the genus' known ecology is related to peatlands. However, in paludifying forests in Alaska, Labrador, and Ontario, *Sphagnum* spp. colonies have been documented as first occurring 80–90 years after high-severity fire, while the feathermosses establish shortly after canopy cover is re-established around 50 years after fire (Noble et al. 1984; Foster 1985; Taylor et al. 1987). The absence of *Sphagnum* spp. in these stands may be a function of propagule availability (in the case of *Sphagnum*, spores and unspecialized asexual propagules such as stem and branch fragments; Cronberg 1991; Sundberg and Rydin 2002), habitat tolerances, and interspecific interactions of juvenile and adult stages. In parallel studies (Fenton and Bergeron 2006*a*, 2006*b*), we have demonstrated that adult colonies of *Sphagnum capillifolium* (Ehrh.) Hedw. are capable of tolerating a wide variety of habitat conditions on the forest floor, and that spores are available in at least limited quantities even in areas where there are no or few *Sphagnum* spp. colonies. This suggests that habitat requirements during colony establishment may be the rate limiting step.

The regeneration niche (Grubb 1977) or the establishment conditions required for *Sphagnum* spp. colonization are generally unknown; however, in peatlands, phosphorus, nitrogen, and constant hydration have a positive effect on sphagna germination (Sundberg and Rydin 2002). Within forests, Noble et al. (1984) documented that *Sphagnum girgensohnii* Warnst. established in tree tip-ups, and Lawrence (1958) speculated on the role of animal urine in creating holes in the feathermoss carpet that allow *Sphagnum* spp. establishment.

The conditions that permit or encourage the expansion of these colonies at the expense of the feathermoss carpet are also unclear. *Sphagnum* spp. expansion was correlated with canopy openness in early successional stages (Fenton and Bergeron 2006*a*), and similarly Hayward and Clymo (1983) found that *S. capillifolium* growth was dependent on an optimum shade level, yet was independent of water-table depth. Competition from already established bryophytes has also been suggested as an important factor influencing *Sphagnum* spp. colony establishment and expansion, and some authors have suggested that varying colony density (i.e., number of individuals per cubic area) could be a way for bryophyte colonies to respond to interspecific competition (Rydin 1995; Frego 1996). Moreover, Rydin (1995) found that *Sphagnum* spp. horizontal colony expansion was positively related to colony density, and found increasing colony density with increasing height above the water table, suggesting high density may also be a strategy to counter desiccation.

This article therefore addresses two objectives: (*i*) to describe establishment substrate preferences for pioneer *Sphagnum* spp. in young black spruce (*Picea mariana* (Mill.) BSP) – feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) stands; and (*ii*) to examine colony expansion by defining the habitat requirements for *Sphagnum* spp. colony expansion in young stands, in terms of substrate and canopy opening as a proxy for microclimate; and by assessing the role of *Sphagnum* colony density in expansion.

Materials and methods

Study area

The study was conducted in the western boreal forest of Quebec (Canada) in the black spruce (*Picea mariana*) – feathermoss (*Pleurozium schreberi*) forest type (Grondin 1996). The study took place within the Clay Belt of Quebec and Ontario, a major physiographic region created by the deposits left by Lakes Barlow and Ojibway after their maximum extension during the Wisconsonian glaciation (Vincent and Hardy 1977; Fig. 1). Average annual temperature is 0.8 °C with an average of 856.8 mm of precipitation annually, recorded at the closest weather station, La Sarre, Quebec (available from Environment Canada's Web site, www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html, accessed 2004). On the Clay Belt, forest stands on fine-textured soils with light slopes tend to paludify over time, and low-lying basins are permanent peatlands. The main disturbances are large, severe fires that kill all aboveground vegetation. The fire cycle has been consistently increasing, from ca. 83 years prior to 1850 to ca. 325 years for the period 1920–1999 (Bergeron et al. 2001). Two *Sphagnum* species are pioneers in the process of paludification and are commonly found in young black spruce (*Picea mariana*) – feathermoss (*Pleurozium schreberi*) stands of the Clay Belt of Quebec and Ontario: *S. capillifolium*, and *S. girgensohnii* (Fenton and Bergeron 2006*a*). These species form dense or loose colonies on the predominantly feathermoss covered forest floor, and are capable of tolerating desiccating and shady conditions (Hayward and Clymo 1983; Gignac 1992). Nomenclature of sphagna follows Anderson (1990), and nomenclature of vascular plants follows Marie-Victorin (1995).

Sampling

Six stands, ranging from 50 to 182 years post-fire, were chosen within the study area (Table 1). No older stands were included, as after this stage it is difficult to distinguish individual monospecific *Sphagnum* colonies. All six stands had a canopy dominated by black spruce (*Picea mariana*), and an understory of scattered *Vaccinium angustifolium*, *V. myrtilloides* and *Ledum groenlandicum*. The bryophyte layer was a continuous carpet of feathermosses (*Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens*), with isolated and scattered *Sphagnum* spp. colonies. *Sphagnum* colonies were defined as contiguous groupings of *Sphagnum* individuals that were spatially distinct from the surrounding feathermoss carpet. Stand age (time since stand replacing fire) was established by verification of stand initiation map dates by dating basal cross-sections of a few dominant trees (for more details see Lecomte et al. 2006). At each of the stands, a 100 m transect was randomly established with the beginning at least 50 m from the nearest road, along which were delimited five 100 m^2 square-shaped plots, with at least 10 m between plots. Each 100 m^2 plot was subdivided into four 25 m^2 nested quadrats. The use of nested quadrats within 100 m^2 plots permitted the collection of environmental data that related specifically to the colo-

Fig. 1. Location of study area within in the province of Quebec. The ecoregions where the Clay Belt occurs are indicated, and may slightly overestimate the actual area.

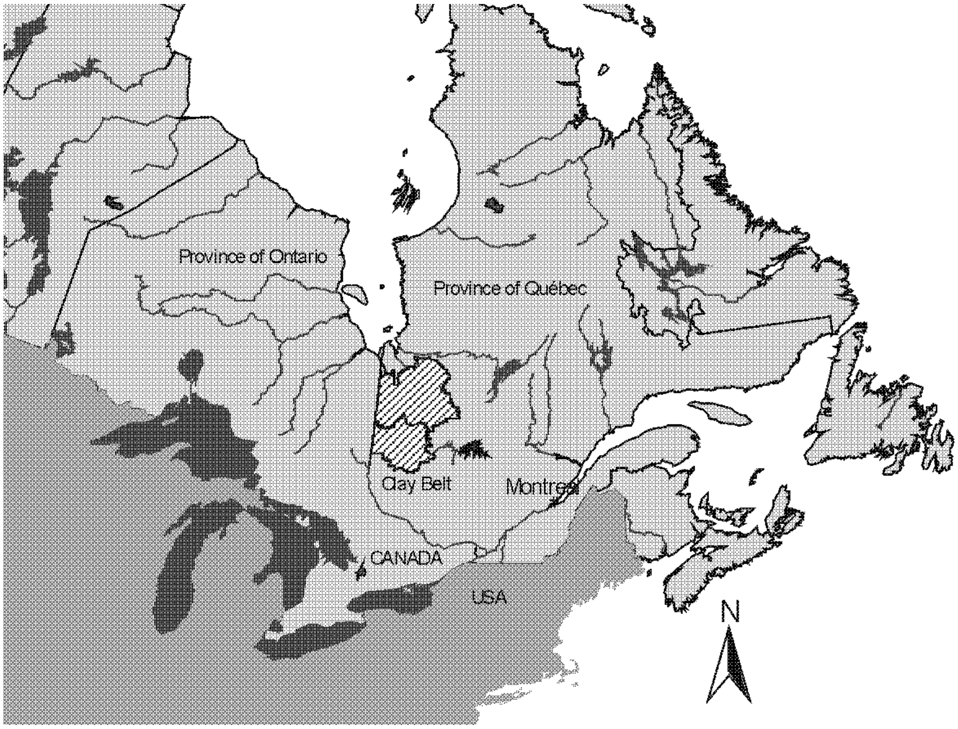


Table 1. Description of survey stands.

Stand	[a]Time since fire (years)	BA bS ($m^2 \cdot ha^{-1}$)	BA secondary species ($m^2 \cdot ha^{-1}$)	CWD (%)	Organic matter depth (cm)[b]	Exposed mineral soil (%)[c]	*Sphagnum* cover (%)[d]
D2	50	44.4±1.67	1.73±0.584[e]	14.17±1.39	19.9±1.4	0.83±0.35	9.5±2.4
N23	85	32.3±1.90	11.8±2.99[f]	17.31±2.39	16.6±1.3	0.6±0.20	9.7±4.9
S1	90	39.9±3.86	4.98±4.45[g]	5.73±1.80	19.7±1.5	2.97±1.14	21.8±4.4
N18	128	26.6±4.45	1.53±0.05[h]	13.58±2.15	33.6±3.0	1.81±0.54	15.4±5.2
W1	130	42.5±5.54	5.94±0.0[g]	5.73±2.49	29.9±2.4	0.56±0.34	11.0±3.2
D1	182	19.1±0.797	2.35±0.0[g]	31.1±2.82	31.0±2.0	1.86±0.74	23.7±5.9

Note: BA bS, basal area of black spruce; BA secondary species, basal area of the second most prominent species; % CWD, sum of the average coarse woody debris cover for all four decay classes within each 25 m^2 quadrat. All values are means with standard errors.

[a] Time since fire is an estimation of the age of the forest.

[b] Organic matter thickness as measured for each 25 m^2 quadrat.

[c] % exposed mineral soil for each 25 m^2 quadrat.

[d] % sphagnum cover is the cover of all *Sphagnum* species within each 25 m^2 quadrat.

[e] Balsam fir.

[f] Jack pine.

[g] Trembling aspen.

[h] Larch.

nies of *Sphagnum* that were studied. Within these plots three data sets were gathered.

The first data set examined establishment and expansion substrate preferences of *Sphagnum* colonies. A minimum of five colonies of *Sphagnum capillifolium* were sampled per stand (one per 100 m^2 plot), chosen to represent a range of colony sizes (m^2). *Sphagnum capillifolium* was chosen, as it was the most common species in these forests. At each colony, the canopy openness was measured above the colony centre, using a densiometer (a scored concave mirror). The colony was then cut into a grid (10 cm × 10 cm for small colonies, and 20 cm × 20 cm for large colonies), with a coordinate system over each colony, including in the grid the area of feathermosses immediately adjacent to the colony; length of colony was arbitrarily assigned as the longest axis. At each coordinate, the bryophyte species on the surface (i.e., feathermoss vs. sphagna), the height above the forest floor, depth of the colony from the surface to the bottom, and the substrate on which the bryophytes were growing were recorded. All substrates present were noted and a dominant substrate was determined. Substrates included coarse woody debris (CWD; downed wood greater than 5 cm in diameter), mineral soil, humus (organic material of unidentifiable origin), feathermosses (*Pleurozium schreberi*,

Table 2. General description of the sampled *Sphagnum* colonies.

	Area (m^2)	Depth (cm)	Height (cm)	Density ($g \cdot m^{-2}$)
Mean (SE)	0.56 (0.12)	30.1 (1.53)	20.22 (1.56)	0.027 (0.011)
Minimum	0.05	14.00	0.00	0.0057
Maximum	3.34	55.00	47.00	0.074

Hylocomiun splendens, *Ptilium crista-castrensis*), wood (sound wood attached to a living tree, i.e., roots). The percent cover of all potential substrates on the forest floor was assessed in each 25 m^2 quadrat order to compare their availability on the forest floor and their frequency as establishment substrates.

The second data set was collected to examine the role of habitat factors in determining *Sphagnum* spp. colony size (surface area, m^2). A detailed habitat survey was carried out within each 25 m^2 quadrat, and canopy openness (with a densiometer), and tree basal area (by species) of all trees over 9 cm DBH were measured. To increase the sample size of large colonies, *Sphagnum* spp. colony size, and canopy openness data from two additional stands (Fénelon and Puisseau, unpublished data, 2005) initially sampled for a separate study were included. Colonies were selected from these two sites that fit the same profile as the colonies that were sampled in the primary data set.

Finally, the third data set consisted of samples from two colonies each of *Sphagnum* spp. (*S. girgensohnii*, *S. russowii* or *S. capillifolium*) and *Pleurozium schreberi* (the dominant feathermoss) randomly chosen in each quadrat. These were used to measure colony density in terms of mass rather than shoot number ($g \cdot cm^{-3}$). This measure was chosen because the masses of individual shoots of the species vary and the physical effect of the mass of adjoining colonies may affect the ability of *Sphagnum* spp. to spread. From each colony, 10 cm^3 samples were removed and the volume of each wet *Sphagnum* spp. and *P. schreberi* sample was measured, the samples were oven-dried over 24 h, the dry mass for each sample was recorded, and the density as grams (dry mass) per centimetre cubed was calculated. The surface area of the sampled bryophyte colonies was also measured.

Data analysis

The frequency of establishment substrates was calculated using the deepest point of each *S. capillifolium* colony as its presumed establishment point. χ^2 tests comparing observed and expected establishment substrate frequencies were performed. Expected substrate frequencies were calculated by multiplying the mean percent cover of each substrate type measured in the plots (coarse woody debris, basal area, feathermoss cover, and exposed mineral soil) by the total number of colonies observed (40). For example, as feathermosses covered 74% of the forest floor, if colony establishment substrates were randomly distributed it would be expected to find 74% of all the colonies or 29.6 colonies (40 × 0.74) established on feathermosses.

Colony expansion was analysed in terms of substrate (first data set) and habitat conditions (second data set). Expansion substrates were determined to be all substrates above the deepest point, which was previously identified as the establishment substrate; these expansion substrates were expressed as a percent frequency. The mean depth of colonies among different establishment substrates was compared using ANOVA (SPSS version12). The relationships between colony size (natural log transformed for normality) and habitat conditions (canopy openness) and colony depth were analysed with Pearson's correlations (ρ, SPSS version 12.0). Partial correlations, with age as the controlling factor, were also calculated to take into account the correlation between stand age and canopy openness. The data set was subsequently divided at the median point for colony size (0.48 m^2) and the analyses were repeated for the two groups (small (<0.48 m^2) and large (>0.48 m^2) colonies) to see if small and large colonies had different relationships with these variables. To increase the number of large colonies in the data set, the data from Fénelon and Puisseaux (unpublished data, 2005) were included, and as there were no data on the basal area of the trees in these plots, only canopy openness could be analysed. Similarly, correlation coefficients (Pearson's ρ and partial correlations) were calculated between colony density (third data set) and explanatory variables (colony size, tree basal area, canopy openness, feathermoss density). The critical value of p in all tests was 0.05.

Results

Sphagnum colonies

Surface area varied among the 40 sampled colonies in the 6 stands, from 0.05 m^2 to 3.34 m^2 with an average of 0.56 m^2 (Table 2). Average maximum colony depth was 30.1 cm (range 14–55 cm); average length and width for the colonies were, respectively, 0.76 m and 0.53 m; and the average height of the colony above the surrounding forest floor, based on the highest point for each colony, was 20.22 cm, ranging from 0 cm to 47 cm.

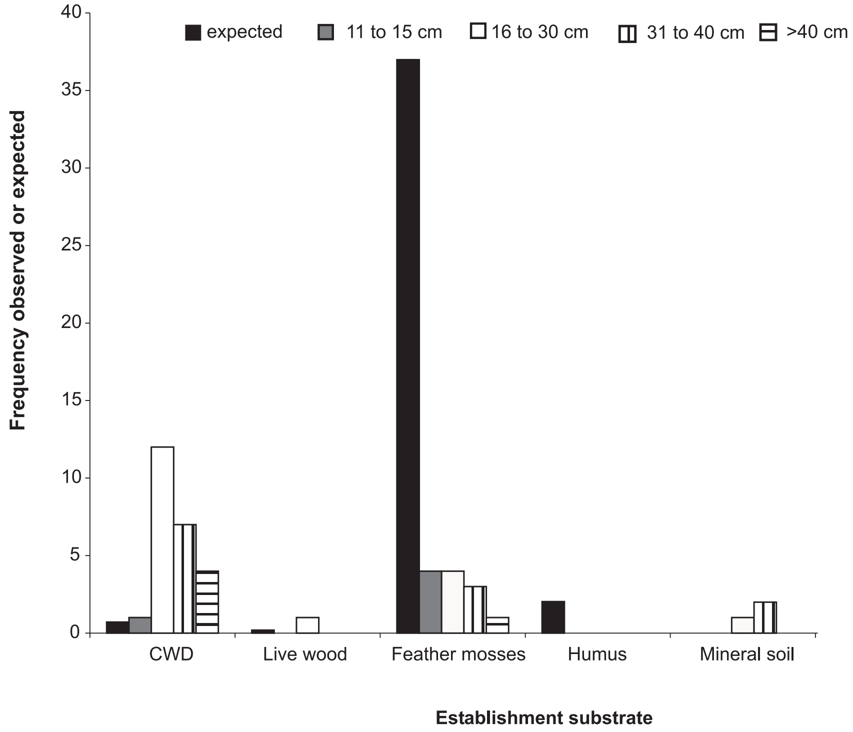
Sphagnum capillifolium colony establishment

The most frequently observed establishment substrate was CWD (coarse woody debris; Fig. 2), which was present in 72.5% of colonies. Most colonies had at least some CWD as their establishment substrate. In contrast, the expected frequency of CWD as substrate was low at less than 5%. Mineral soil and live wood were also more frequently observed than would be predicted by their availability on the forest floor, whereas feathermosses were under-represented. CWD was the most frequent substrate at all establishment depths, except in the shallowest colonies (11–16 cm) where feathermosses were the most frequent substrate. χ^2 analysis indicated that the frequency of the substrates differed significantly from the expected distribution ($\chi^2 = 710.59$, $p < 0.001$).

Sphagnum colony expansion

Feathermosses and coarse woody debris were the two dominant expansion substrates beneath *S. capillifolium* colonies, with 42.1% and 37.0% of recorded values, respectively

Fig. 2. Observed and expected frequencies of establishment substrates for *Sphagnum capillifolium* colonies at different depths (cm). Expected values were calculated based on percent cover of the substrate types observed on the forest floor. χ^2 analysis indicated that the frequency of the substrates differed significantly from the expected distribution ($\chi^2 = 710.59$, $p < 0.001$).



(Table 3). Humus (9.3%), mineral soil (7.1%), and charcoal (3.8%) were the other substrates. In three cases *S. capillifolium* was found to be expanding over an older *Sphagnum* colony. Interestingly, the importance of these substrates varied between shallow and deep colonies or portions of colonies, as the mean depth for the feathermoss substrate was 15.3 cm, whereas the mean depth for the other substrates was over 20 cm. There was a significant positive relationship between the natural log of colony area and colony depth ($\rho = 0.636$, $p < 0.001$; Fig. 3*a*).

There was no partial correlation between canopy openness (surrogate for microclimate) and colony size (natural log transformed), with age as the control variable ($\rho = 0.049$, $p < 0.901$). When small ($<0.48\ \mathrm{m}^2$) and large ($>0.48\ \mathrm{m}^2$) colonies are analysed separately, small colonies showed no significant partial correlation between the natural log of colony size and canopy openness ($\rho = 0.090$, $p < 0.690$; Fig. 3*b*), but there was a significant partial correlation for large colonies ($\rho = 0.614$, $p < 0.003$). There was an apparent light threshold at 20% canopy openness, as no colonies were found in areas where the canopy openness was below this value.

Sphagnum colony density

Sphagnum spp. colony surface area and colony density were not correlated ($\rho = -0.094$, $p < 0.231$; Fig. 4*a*); however, the very large colonies were less dense than the rest.

Sphagnum spp. colony density was correlated with environmental conditions, with a significant correlation between *Sphagnum* colony density and quadrat basal area (Pearson's $\rho = 0.253$, $p < 0.0001$; Fig. 4*b*), and canopy openness (Pearson's $\rho = -0.272$, $p < 0.0001$; not shown). However, when partial correlations with age as the control variable are calculated, both become less significant ($\rho = 0.136$, $p < 0.085$ and $\rho = -0.141$, $p < 0.074$, respectively). Interestingly, there was a significant positive correlation between *Sphagnum* colony density and feathermoss density ($\rho = 0.525$, $p < 0.001$; Fig. 4*c*) that is little changed when partial correlations are calculated with age as the controlling factor ($\rho = 0.494$, $p < 0.001$).

Table 3. *S. capillifolium* expansion substrate frequency and mean depth.

Substrate	Overall frequency (%)	Mean depth ± SE
CWD	37.0	21.39±0.75 b
Charcoal	3.8	20.00±1.93 ab
Humus	9.3	20.54±1.66 b
Feathermosses	42.1	15.39±0.62 a
Mineral soil	7.1	22.88±1.13 b
Sphagnum	0.6	11.00±3.79

Note: Differences in mean depths, as determined by ANOVA (F 10.13, $p < 0.0001$), are indicated by letters, with a < b. Because of the small number of samples, *Sphagnum* was not included in the ANOVA; CWD, coarse woody debris.

Discussion

Colony establishment

CWD was the dominant establishment substrate within the colonies examined in this study (Fig. 2). CWD may be the most suitable habitat for *S. capillifolium* spores, as it pro-

Fig. 3. Relationships between colony area (m^2) and (A) colony depth (cm) and (B) canopy openness (%). Correlation coefficients are indicated on each graph. In (B) partial correlations, with age as the control factor, are indicated for large (>0.48 m^2) and small (<0.48 m^2) colonies.

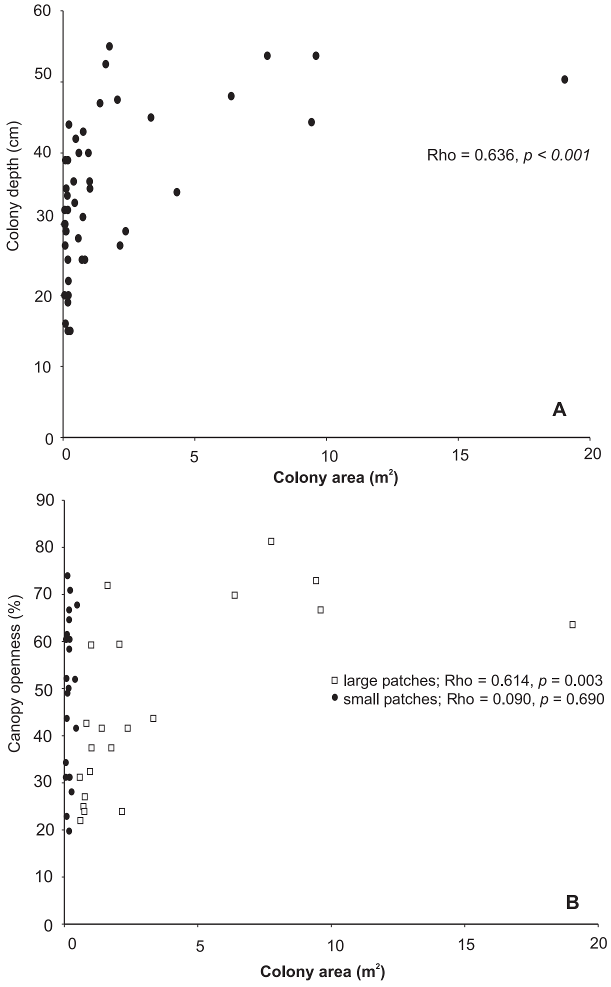
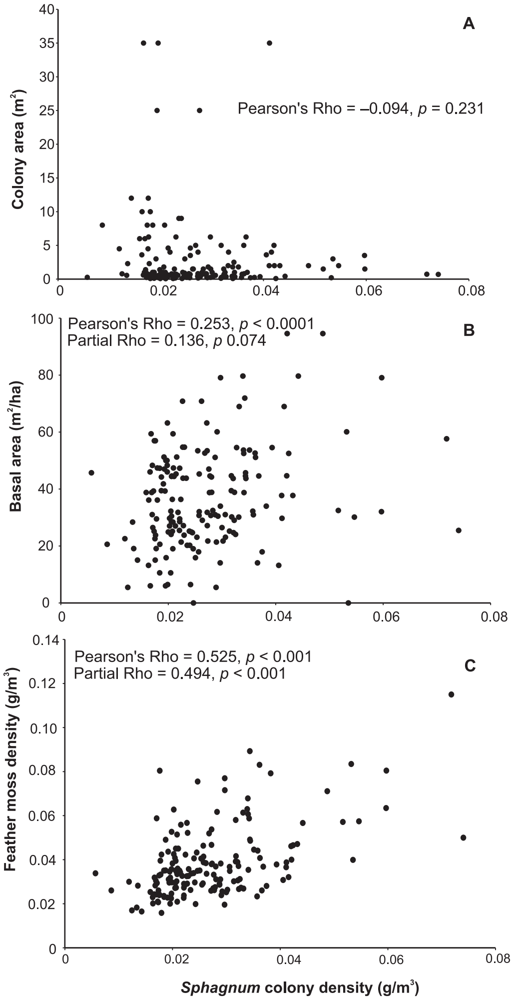


Fig. 4. Relationships between *Sphagnum* colony density ($g \cdot cm^{-3}$) and (*a*) *Sphagnum* colony area (m^2), (*b*) tree basal area ($m^2 \cdot ha^{-1}$), and (*c*) feathermoss density ($g \cdot cm^{-3}$). Correlations are indicated on the graph;. In partial correlations age was used as the control factor.



vides a habitat with constant humidity and nutrients (Ganjegunte et al. 2004), two of the potential limiting factors to spore establishment (Sundberg and Rydin 2002). CWD might also permit the newly developing colony to temporarily escape interspecific competition from the dominant feathermosses. The small number of colonies established on mineral soil suggests that the mechanism of establishment on the Clay Belt differs from that described by Noble et al. (1984) where *S. girgensohnii* established in the pits created by treefall. This may in part be due to the shallow roots of black spruce (Greene et al. 2004) that expose less mineral soil when they fall, compared with the deeper-rooted white spruce.

The near restriction of establishing colonies to CWD suggests that substrate availability, at least during the early stages of stand development, may be the limiting factor for establishment of *Sphagnum* spp. in these forests, as spores are available (Fenton and Bergeron 2006*b*). CWD abundance is high immediately after stand-replacing disturbance, and then decreases until the self-thinning stage, where it begins to increase again (Hély et al. 2000; Harper et al. 2005). In the very early stages of stand initiation *Sphagnum* spp. establishment may be limited by microclimate, as the open canopy creates a very hot and dry environment (Foster 1985; Taylor et al. 1987) that may not be favourable to spore germination. Then, once the canopy is closed, a lack of CWD may limit *Sphagnum* establishment, until the self-thinning stage (70–80 years post-fire; Taylor et al. 1987) when CWD once again becomes available. This may partly explain why *Sphagnum* is rarely found in relatively young (i.e., less than 60 years post fire) black spruce stands (Foster 1985; Taylor et al. 1987; Boudreault et al. 2002). A similar mechanism is reported in the late post-fire establishment of eastern white cedar (*Thuja occidentalis*; Simard et al. 2003). These hypotheses need to be tested experimentally.

Feathermosses were rarely an establishment substrate for *S. capillifolium*. This may have been due to the poikilohydric nature of these species, as they would not provide constant humidity for germinating spores. Alternatively, the colonies may prevent spore germination in some manner, as Sundberg (2000) similarly found that *Sphagnum* spores were generally unable to germinate within established *Sphagnum* colonies.

Colony expansion

The expansion of *S. capillifolium* colonies at deeper points over CWD supports the hypothesis that CWD provides a competition-free habitat for the initial small colony (Table 3). One reason *S. capillifolium* may ultimately be able to expand over the feathermosses is due to the elevated position of the *Sphagnum* mosses, which would allow them to smother the feathermosses. The lower growth rates of feathermosses compared with sphagna (Williams and Flanagan 1998; Bisbee et al. 2001) may also explain why they were rarely found to have overtopped *S. capillifolium*. The cases where feathermosses were able to overtop *Sphagnum* spp. may represent habitats that were too dark even for the shade-tolerant *S. capillifolium* (Hayward and Clymo 1983; Gignac 1992).

Overall, *Sphagnum* (*S. capillifolium* and *S. girgensohnii*) colonies established in stands with at least 20% canopy openness (Fig. 3), which appears to constitute a threshold for colony establishment and subsequent expansion, although the broad range of light conditions under which *Sphagnum* was found to grow (20% to 80% canopy openness), suggests that above this threshold, light is not a limiting factor.

Previous studies (Foster 1985; Taylor et al. 1987; Boudreault et al. 2002) have generally shown a positive relationship between canopy openness and *Sphagnum* spp. cover. The relative photosynthetic capacities of *Sphagnum* spp. and *Pleurozium schreberi* (Williams and Flanagan 1998), suggest that *Sphagnum* spp. are able to increase their photosynthetic rate at high incident light levels, while *P. schreberi* reaches its maximum photosynthetic rate at low light levels. However, in our study only large *Sphagnum* colonies (greater than the median 0.48 m^2) showed a positive relationship between *Sphagnum* spp. colony size and canopy openness. The lack of relationship between colony size and canopy openness in the small colonies may indicate that while colonies are able to establish in a wide range of light conditions, their expansion past a minimum size is dependent on high incident light levels.

Colony density

There was no significant relationship between *Sphagnum* spp. patch density and patch surface area, possibly because there were few large colonies, which tended to have lower density compared to small colonies (Fig. 4). High density in small colonies may be an adaptation to tolerate adverse growth conditions such as low humidity or competitive pressure from surrounding species (Rydin 1985, 1995). High-density colonies have branches and capitula packed tightly together, which would maximize water retention within the colony, and reduce colony roughness (Hayward and Clymo 1983). Similarly, a more tightly packed *Sphagnum* spp. colony may better resist invasion by the surrounding species (Rydin 1995). Large colonies may have lower densities than small colonies because they are able to grow faster as a result of more favourable substrate, light, or moisture conditions, or because they have grown large enough that competition is no longer a threat to colony survival. Low densities would be an advantage for a colony, as it would increase the stem and leaf area exposed to incoming radiation, resulting in more photosynthetically active surfaces compared with high densities.

Sphagnum density was positively correlated with tree basal area (Fig. 4). This may be due to the fact that tree basal area is negatively correlated with incident light and precipitation on the forest floor, which would in turn promote *Sphagnum* growth. *Sphagnum* colony density and canopy opening were negatively correlated, suggesting that the increased light availability associated with canopy opening resulted in increased growth rates.

Conclusions

In previous studies we have shown that the factor limiting the presence of *S. capillifolium* in black spruce stands on the Clay Belt of Quebec and Ontario is not habitat limitation of the adults (Fenton and Bergeron, in preparation.), nor is it predominantly due to spore availability (Fenton and Bergeron 2006*b*). The importance of CWD as an establishment substrate as demonstrated by this study, suggests that the regeneration niche (Grubb 1977) and stochastic establishment factors may be the driving force of succession in this community. Several other bryophyte communities in coniferous forests have been shown to be at least partially controlled by the regeneration niche and stochastic establishment factors such as the feathermoss patterns in coniferous forests (Lloret 1994; Frego and Carleton 1995*a*, 1995*b*; Frego 1996). Subsequent to colonization, the apparent control of colony expansion by environmental factors suggest that once *Sphagnum* spp. are established in the community, successional changes in the forest environment switches the control of the community pattern from establishment to habitat and competitive factors. This supports the hypothesis of Rydin (1997) that early successional communities are dominated by stochastic and establishment factors, as lower community richness reduces the chance of interspecific interactions, whereas richer, late-successional communities are controlled by habitat and competitive interactions resulting from the greater chance of interspecific interactions.

Acknowledgments

Discussions with Kate Frego, Nicolas Lecomte, and Sonia Légaré greatly enhanced the article. Bruce Bagnell provided valuable support during *Sphagnum* identification. Funding for this project was provided by the Université du Québec en Abitibi-Témiscamingue – Université du Québec à Montréal. 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. doi:10.2307/3243612.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. **31**: 384–391. doi:10.1139/cjfr-31-3-384.

Bisbee, K., Gower, S., Norman, J., and Nordheim, E. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia, **120**: 261–270.

Boudreault, C., Bergeron, Y., Gauthier, S., and Drapeau, P. 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. Can. J. For. Res. **32**: 1080–1093. doi:10.1139/x02-027.

Cronberg, N. 1991. Reproductive biology of *Sphagnum.* Lindbergia, **17**: 69–82.

Fenton, N.J., and Bergeron, Y. 2006*a*. Facilitative succession in boreal black spruce forests driven by changes in available moisture and light. J. Veg. Sci. **17**: 65–76. doi:10.1658/1100-9233(2006)017[0065:FSIABB]2.0.CO;2.

Fenton, N.J., and Bergeron, Y. 2006*b*. *Sphagnum* spore availability in boreal forests. Bryologist, **109**(2): 173–181.. doi:10.1639/0007-2745(2006)109[173:SSAIBF]2.0.CO;2.

Fenton, N., Lecomte, N., Légaré, S., and Bergeron, Y. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. For. Ecol. Manage. **213**: 151–159.

Foster, D.R. 1985. Vegetation development following fire in *Picea mariana-Pleurozium* forests of Southeastern Labrador, Canada. J. Ecol. **73**: 517–534.

Frego, K.A. 1996. Regeneration of four boreal bryophytes: colonization of experimental gaps by naturally occurring propagules. Can. J. Bot. **74**: 1937–1942.

Frego, K., and Carleton, T. 1995*a*. Microsite conditions and spatial pattern in a boreal bryophyte community. Can. J. Bot. **73**: 544–551.

Frego, K., and Carleton, T. 1995*b*. Microsite tolerance of four bryophytes in a mature black spruce stand: reciprocal transplants. Bryologist, **98**: 452–458. doi:10.2307/3243584.

Ganjegunte, G.K., Condron, L.M., Clinton, P.W., Davis, M.R., and Mahieu, N. 2004. Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. For. Ecol. Manage. **187**: 197–211.

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. doi:10.2307/3243564.

Glebov, F., and Korzukhin, M. 1992. Transitions between boreal forest and wetland. *In* A systems analysis of the global boreal forest. *Edited by* H. Shugart, R. Leemans, and G. Bonan. Cambridge University Press, Cambridge. pp. 241–266.

Gower, S., Vogel, J., Norman, J., Kucharik, C., Steele, S., and Stow, T. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. **102**: 29029–29041. doi:10.1029/97JD02317.

Greene, D.F., Noël, J., Bergeron, Y., Rousseau, M., and Gauthier, S. 2004. Recruitment of *Picea mariana, Pinus banksiana* and *Populus tremuloides* across a burn severity gradient following wildfire in the southern boreal forest of Quebec. Can. J. For. Res. **34**: 1845–1857. doi:10.1139/x04-059.

Grondin, P.. 1996. Écologie forestière. *In* Manuel de foresterie. *Edited by* J.A. Bérard and M. Côté. Les Presses de l'Université Laval, Quebec. pp. 133–279.

Grubb, P. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. (Camb.), **52**: 107–145.

Harper, K.A., Bergeron, Y., Drapeau, P., Gauthier, S., and De-Grandpré, L. 2005. Structural development following fire in black spruce boreal forest. For. Ecol. Manage. **206**: 293–306. doi:10.1016/j.foreco.2004.11.008.

Hayward, P.M., and Clymo, R.S. 1983. The Growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. J. Ecol. **71**: 845–863.

Hély, C., Bergeron, Y., and Flannigan, M.D. 2000. Coarse woody debris in Southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Can. J. For. Res. **30**: 674–687. doi:10.1139/cjfr-30-5-674.

Lawrence, D. 1958. Glaciers and vegetation in south-eastern Alaska. Am. Sci. **Summer**: 89–122.

Lecomte, N., Simard, M., and Bergeron, Y. 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of north western Quebec, Canada. Écoscience, **13**(2): 152–163.

Lloret, F. 1994. Gap colonization by mosses on a forest floor: an experimental approach. Lindbergia, **19**: 122–128.

Marie-Victorin, F. 1995. Flore Laurentienne. 3^{e} ed. Les presses de l'Université de Montréal, Montréal, Que.

Noble, M.G., Lawrence, D.B., and Streveler, G.P. 1984. *Sphagnum* invasion beneath an evergreen forest canopy in southeastern Alaska. Bryologist, **87**: 119–127. doi:10.2307/3243117.

O'Connell, K., Gower, S., and Norman, J. 2003. Net ecosystem production of two contrasting boreal black spruce forest communities. Ecosystems (N.Y.), **6**: 248–260. doi:10.1007/s10021-002-0202-9.

Reiners, W., Worley, I., and Lawrence, D. 1971. Plant diversity in a chronosequence. Ecologist, **52**: 55–69.

Rydin, H. 1985. Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna.* Oikos, **45**: 374–379. doi:10.2307/3565573.

Rydin, H. 1995. Effects of density and water level on recruitment, mortality and shoot size in *Sphagnum* populations. J. Bryol. **18**: 439–453.

Rydin, H. 1997. Competition among bryophytes. Adv. Bryol. **6**: 135–168.

Simard, M.J., Bergeron, Y., and Sirois, L. 2003. Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. Can. J. For. Res. **33**: 672–681. doi:10.1139/x02-204.

Sundberg, S. 2000. The ecological significance of sexual reproduction in peat mosses (*Sphagnum* sp.). Comprehensive Summaries of Uppsala. Dissertations from the Faculty of Science and Technology 581. Acta Universitatis Upsaliensis, Uppsala, Sweden.

Sundberg, S., and Rydin, H. 2002. Habitat requirements for establishment of *Sphagnum* spores. J. Ecol. **90**: 268–278. doi:10.1046/j.1365-2745.2001.00653.x.

Taylor, S., Carleton, T., and Adams, P. 1987. Understory vegetation change in a *Picea mariana* chronosequence. Vegetatio, **73**: 63–72.

Vincent, J., and Hardy, L. 1977. L'évolution et l'extinction des lacs glaciaires Barlow et Ojibway en territoire québécois. Geogr. Phys. Quat. **31**: 357–372.

Williams, T., and Flanagan, L. 1998. Measuring and modelling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*. Plant Cell Environ. **21**: 555–564. doi:10.1046/j.1365-3040.1998.00292.x.