Sphagnum spore availability in boreal forests

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Abstract. The role of propagule availability in determining community composition is poorly understood, and is infrequently investigated for bryophytes. In addition the extent to which spore availability is limited by dispersal is unknown. If spore availability is not dispersal-limited, local and regional spore dispersal and wind availability may affect spore availability at any point. In this study, the abundance of *Sphagnum* spores was investigated within the context of a successional sequence where *Sphagnum* spp. invade a feather moss community in black spruce boreal forests of northwestern Québec, Canada. Spores were trapped and grown in a greenhouse to protonemal stage to estimate the abundance of spores within three sites that varied in *Sphagnum* abundance, and stand density (a surrogate for wind intensity). Sporophyte production was also investigated in one site where individual *Sphagnum* colonies could be distinguished. Spores were less abundant in sites with less ground cover of *Sphagnum* present in the community, although spores were trapped in all sites. Spore abundance was inversely correlated with local stand density, indicating that wind intensity may play a role in limiting dispersal. Sporophytes were produced in colonies that were larger and had greater access to light. These results suggest that *Sphagnum* invasion into young dense forests may be partially limited by spore dispersal, although the availability of germination substrates may also play an important role.

Keywords. *Sphagnum*, spore abundance, sporophyte abundance, boreal forest, dispersal, Québec, Canada.

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Habitat characteristics are often invoked to account for the presence or absence of a species within a community. However, the absence of a species in a community may also be due to an absence of reproductive propagules or the conditions necessary for their germination, i.e., aspects of the regeneration niche (Grubb 1977). While theories concerning the mechanics and establishment of bryophytes in a community is as of yet widely untested, asexual propagules are believed to play important roles in the maintenance and expansion of colonies (Laaka-Lindberg et al. 2003), while establishment of new colonies is believed to be dominated by spores. In the specific case of *Sphagnum*, evidence of sexual reproduction by spores has historically been rare (e.g., Clymo & Duckett 1986) and it has been demonstrated that *Sphagnum* can regenerate from stem fragments (Clymo & Duckett 1986). Therefore, it is possible that spores play little role in establishing colonies in new habitats, as fragments may be dispersed by animals or

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birds. However, there is growing evidence that sexual reproduction and establishment of new colonies by spores play an important role. Many genets have been found in close proximity and hybrid individuals have been identified (Cronberg 1996), many species not present before disturbance recruit after disturbance (Soro et al. 1999), and spores have been shown to germinate in field conditions (Sundberg & Rydin 2002).

Many factors influence spore availability at a given site, including the number of spores produced per individual, the number of individuals present locally and regionally, and the dispersal capacity of the spores. As sphagna are widely distributed in the boreal zone and produce numerous spores [18,000–200,000 per capsule (Sundberg 2005)], dispersal may be the most important factor affecting spore availability. Whether or not sphagna are actually dispersal-limited is as yet unclear. Spore dispersal is believed to be strongly leptokurtic to approximately 2 m (Cronberg 1991; Miles & Longton 1992), however over 50% of spores produced are unaccounted for in these studies, suggesting that many spores are dispersed outside the immediate area (Miles & Longton 1992; Söderstrom & Jonsson 1989; Sundberg 2005). Studies examining the diaspore rain have supported this assertion, as they have found species that are absent from the surrounding community (Marshall & Convey 1997; Ross-Davis & Frego 2004). Sundberg (2005) suggested that a point isolated from spore-producing colonies will receive spores from sources at a variety of distances, and that local sources will only dominate if the distance isolating the point from the closest source is relatively short (i.e., <1 km). Therefore the relative importance of local and regional spore sources, and thus the potential dispersal limitation of any individual species is yet unclear.

Dispersal agent availability is a factor that has not been explicitly addressed in previous studies. Wind is the main dispersal agent of terrestrial bryophyte spores (Cronberg 1991), and is likely to be unlimited in open environments, such as peatlands. However, within forested environments, or other habitats that are protected from the wind, the very local intensity of wind may limit spore dispersal and result in variable spore abundance across the landscape.

Local sporophyte and spore production will strongly influence spore abundance, if it is dispersal-limited. Sporophyte production within a colony may be limited by spermatozoid dispersal, which is believed to be limited to tens of centimeters (Bisang et al. 2004); therefore, a colony must contain both male and female gametangia in order to produce sporophytes. Spatial clumping of colonies may favor the development of both sexes within a colony by the establishment of spores from neighboring colonies. In addition to limitations on fertilization, biotic (individual size) and abiotic (light, water) factors have been shown to influence sporophyte production in individual ramets (Rydgren & Økland 2002; Stark et al. 2000).

Within the boreal forest, several forest communities see a gradual establishment and expansion of *Sphagnum* spp. into the feather moss (*Pleurozium schreberi*, *Ptilium crista-castrensis*, *Hylocomium splendens*, *Ptilidium ciliare*) dominated community (Fenton et al. 2005; Viereck et al. 1993). *Sphagnum* capillifolium is the first *Sphagnum* to establish in the feather moss carpet (Fenton & Bergeron accepted) and is generally considered to be a dioicous or polyoicous species, but its sexual reproductive potential in these habitats is unknown. The dramatic expansion of *Sphagnum* spp. observed in stands over 100 years old, and the eventual invasion of *S. russowii*, *S. magellanicum* and *S. fallax* (Fenton & Bergeron accepted), is believed to be due to a change in the environment that favors the growth of *Sphagnum*. It may also be that dispersal limitation caused by a lack of local spores, and reduced wind in dense young stands lengthens establishment time of *Sphagnum* spp. in these forests.

The broad objective of this study was to determine the effect of local vs. regional spore dispersal and wind availability on spore abundance in black spruce stands. Specifically, we address three hypotheses: (1) there are fewer spores available in young stands with little *Sphagnum* compared to older stands with more *Sphagnum*; (2) because spore dispersal is predominantly local, spore abundance at a given point is correlated with *Sphagnum* cover and distance to reproductive colony, and is not correlated with wind intensity; and (3) sporophyte production is correlated with distance between colonies and with colony size and light availability.

The phenology of *Sphagnum* spore release has only been sporadically studied, and never in our region. However, based on Scandinavian studies, it can be expected that spore release would be later in shaded habitats such as forests where section *Acutifolia* dominates than in open peatlands where sections *Actuifolia* and *Cuspidata* are common (Cronberg, 1991; Sundberg 2002). Because the phenology of spore release of the species present within the communities was unknown for this habitat and region, variation in the date of spore release within a forest habitat was also examined.

Methods

Study Site. The study was conducted in the western boreal forest of Québec, Canada, within the black spruce (*Picea mariana*)-feather moss (*Pleurozium schreberi*) forest type (Grondin 1996). Specifically, the study took place within the Clay Belt of Québec 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 & Hardy 1977). 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, Québec (Environment Canada 2004). On the Clay Belt, forest stands on fine textured soils with light slopes tend to paludify over time, and dips are permanent peatlands. As a result, the regional cover of *Sphagnum* is high. Three sites (spread over 50 km) were chosen to represent a gradient in stand density and *Sphagnum* abundance. All three sites had only a light slope and a similar fine soil texture.

Annual spore production has been shown to vary with the climate of the proceeding summer (Sundberg 2002). Climate variables were collated from the data made available by the Meteorological Service of Environment Canada (2004). The weather station at Matagami (49°46′N, 77°48′W) was chosen, as it was the nearest station with a complete set of data available. Total volume of precipitation and number of degree-days (18°C) were determined for the last 30 years (mean 1971–2000), 2002, 2003, and 2004. Precipitation and degree-days varied widely between 2002 and 2004 (Fig. 1). In 2002, there was very little precipitation in August, while there was nearly double the number of degree-days. In contrast, 2003 had near normal precipitation, but very few degree-days in July. In 2004, July and August were wet and cold, while September was dry and warm.

Study Design and Data Collection. In 2003, five 100 m^2 square plots were established in each of three forest sites, as part of a larger study (**Table 1**). Basal area, a measure of stand density, was used as a surrogate for potential wind intensity, as there is less wind in denser stands. The dbh of all trees over 8 cm were measured and the basal area per hectare was calculated. In all three stands the cover of *Sphagnum* spp. was visually assessed, and the distances from the plot center to the three nearest colonies of *Sphagnum* of any species were measured in site 1, where there is little *Sphagnum* present in the bryophyte community.

In order to determine the phenology of spore abundance, 20 spore traps (see below) were exposed together in one plot at each site at approximately seven day intervals from July 24 to September 12, in 2003. In 2004, the experiment was repeated, however as results from 2003 indicated that spores were released in late August to early September, trapping began August 25 and ended on September 23. In addition, in order to correlate within-site variation in spore abundance with stand density and *Sphagnum* abundance, the 20 traps were spread out within each site with four spore traps exposed together in each of the in five plots. In both 2003 and 2004, a total of 60 spore traps placed in the same position were exposed in each site on the same day, per week.

Spore Trapping and Germination. The emergence method was used to determine the abundance of spores. Spores were trapped on 10 cm diameter petri plates filled with nutrient agar solution (modified from Parker Thompson's basal nutrient medium), which has previously been used with success in the germination of spores (Ross-Davis & Frego 2004). Plates were placed on the forest floor for approximately six hours on dry, sunny or variably cloudy days. Once plates were collected, they were placed in a greenhouse under ambient conditions for 3–5 weeks and surveyed for the development of protonemata under a dissecting microscope. Only *Sphagnum* protonemata were counted, which were easily distinguished from other developing protonemata by their thalloid form. They were not identified to

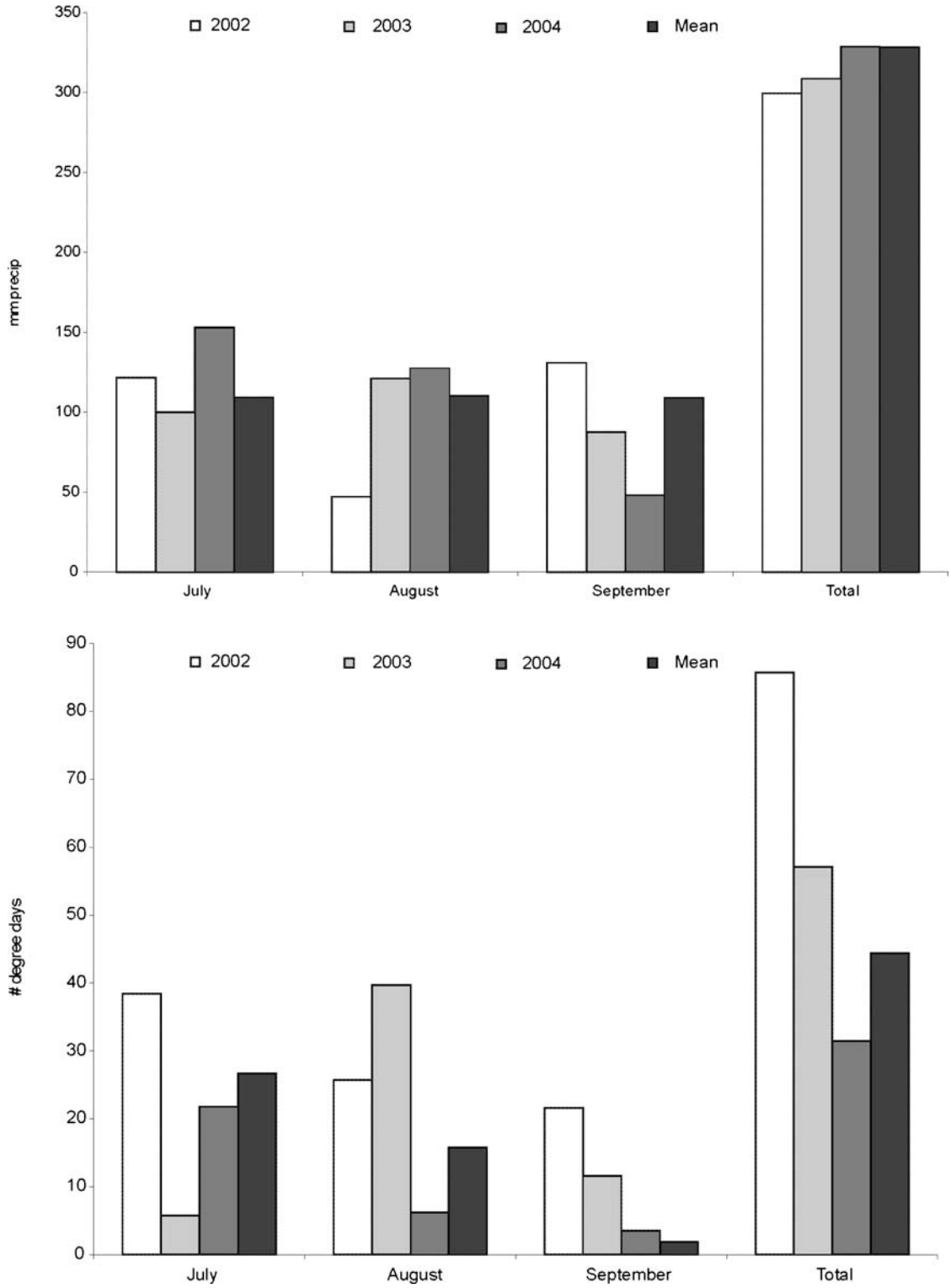

Figure 1. Precipitation (top) and degree-days (bottom) for Matagami, Québec for 2002, 2003, 2004 and the mean of 1971–2000. Precipitation is the total for year in millimeters, and degree-days are the sum of the temperature of all days over 18°C. Data is compiled from the Environment Canada database.

Table 1. Description of the three sites where studies were undertaken.

Variable	Site 1	Site 2	Site 3
Basal area (m^2/ha)	44.08±0.031	21.31±0.028	30.0±1.14
Open canopy (%)	43.67±2.48	67.40±2.51	62.72±2.60
Sphagnum cover (%)	10.14±1.49	62.6±4344	67.64±1.37

species, as we were interested in total *Sphagnum* spore abundance, and also because *Sphagnum* spp. grown in petri plates frequently develop unusual traits that prevent positive identification (Fenton pers. observ.). A limitation of the emergence method is that only spores that successfully germinate are counted; therefore spores whose germination requirements were not met will not be included in the census. However, as very high numbers of spores germinated we feel confident that this margin of error is relatively small.

Sporophytes. The abundance of sporophytes was assessed in site 1, where *Sphagnum* was not the dominant ground cover and individual colonies could be determined. Each colony of *Sphagnum* within the five 100 m^2 quadrats was examined and the species present identified; the canopy cover above the colony was determined with a densiometer, and the distance to the three nearest neighbor colonies was measured. Where sporophytes were found, they were counted within three randomly placed 10×10 cm squares per 1 m^2 of *Sphagnum*.

Analyses. Spore abundance for each plate was determined and placed into one of four classes: 0, 1–10, 11–50, >50, and the median value of each category was used in subsequent analyses, i.e., 0 (class 0), 5 (class 1–10), 30 (class 11–50), 80 (class >50). Mean spore abundance (the number of spores trapped) and standard error were calculated for each site, each week in 2003 and each plot in 2004. The data were checked for normality and heteroscedascity, and differences in means among weeks within a site were established with analysis of variance (ANOVA) followed by Bonferroni's post-hoc tests.

Pearson's correlations were calculated between 2004 spore abundance (abundance) and local *Sphagnum* abundance, *Sphagnum* proximity (site 1 only) and stand density during high and low abundance weeks (September 1 and 17, respectively) at landscape (all sites) and local (each site separately) scales. In order to separate the effects of correlated explanatory variables (e.g., *Sphagnum* abundance and total basal area are negatively correlated), partial-correlations were calculated between spore abundance and total basal area, *Sphagnum* cover, mean distance to neighboring colony, and minimum distance to neighboring colony. This approach allows the separation of the effects of total basal area (wind) from amount of *Sphagnum* (local dispersal) despite their correlation.

The characteristics of colonies with and without sporophytes and their habitat conditions were compared with t-tests. Pearson's correlation was used to calculate the relationship between sporophyte density in colonies that were reproductive and internal resource availability (colony area and height) and external resource availability (light and mean and minimum distances to neighboring colonies). The critical level of p was 0.05 in all tests.

Results

Spore Abundance. Spore abundance was low in August 2003, and peaked in all sites in September 2003 and 2004 (**Figs. 2A, B**). In addition to the temporal variation, spore abundance also varied spatially across the landscape. Fewer spores were trapped in site 1 compared to sites 2 or 3; spore abundance also varied within sites and within plots.

In 2004, spore abundance on September 1 (high abundance) in all sites was correlated with *Sphagnum* abundance (**Table 2**). In contrast spore abundance on September 17 (low abundance) was correlated with basal area. At a smaller spatial scale within individual sites, spore abundance was not correlated with *Sphagnum* cover or basal area in sites 1 or 2. However, spore abundance on September 23 was correlated to the minimum distance to a reproductive *Sphagnum* patch in site 1. In site 3, the pattern was similar to the pattern observed in all sites combined.

Sporophytes. Of the 49 *Sphagnum* colonies found within the 500 m^2 surveyed in site 1, 43 were *S.*

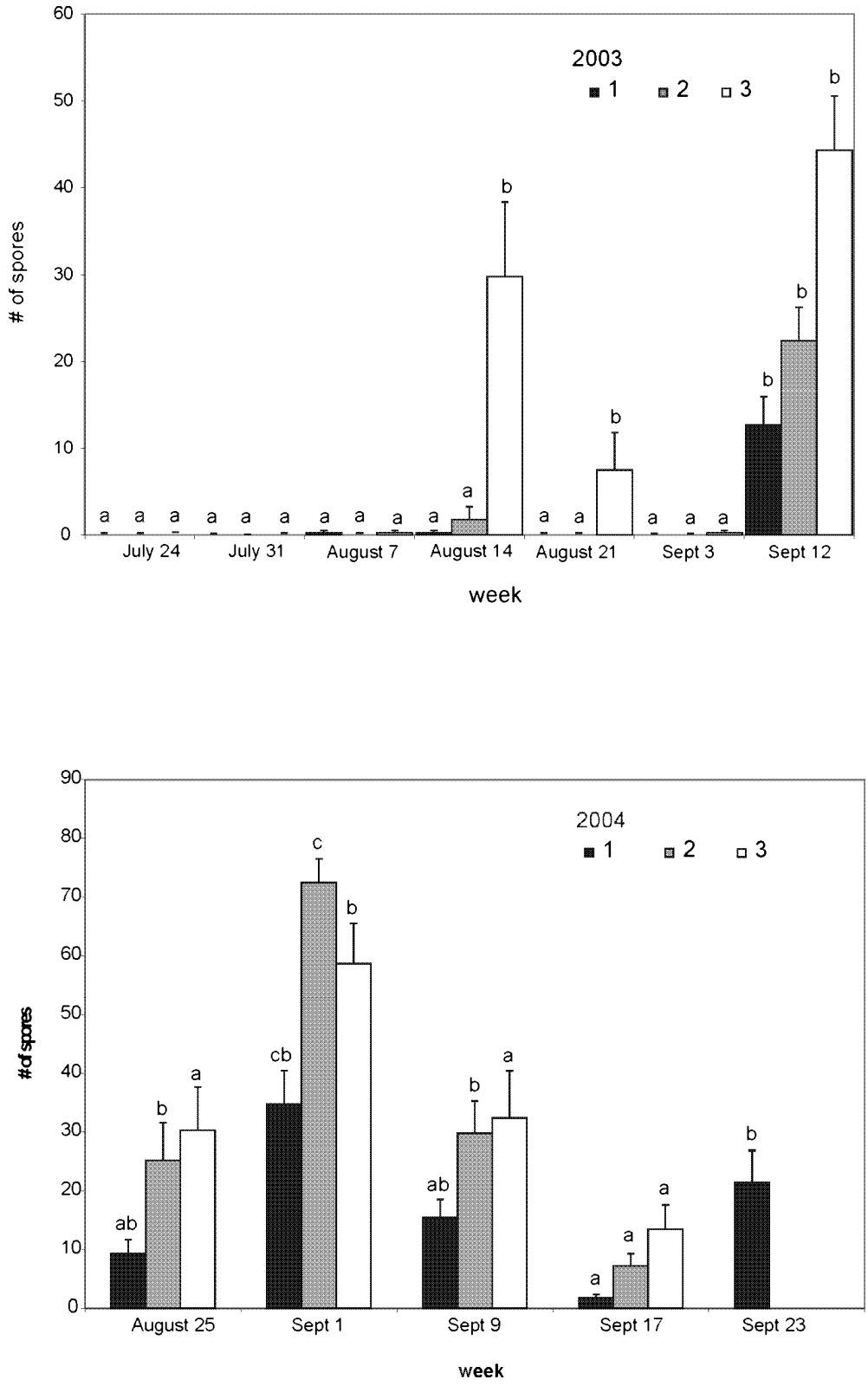

Figure 2. Mean and standard error of spore abundance in three sites for each sampling date in 2003 (top) and 2004 (bottom). Within a site, dates with a different letter are significantly different a<b<c.

Table 2. Partial correlation (R^2, p value) between spore abundance and habitat characteristics for high (1 Sep) and low (17 Sep) abundance weeks in 2004. Distances between colonies were only measured at site 1, where discreet colonies were visible. Partial correlations are between spore abundance and the listed variable, while the other variables are held constant.

Site	Variable	Spore abundance	
		High	**Low**
1	Mean distance to *Sphagnum* colony	0.0491(0.842)	−0.417 (0.076)
	Minimum distance to *Sphagnum* colony	0.247(0.307)	**-0.471(0.042)**
	Mean basal area	0.0810(0.742)	0.213(0.383)
	Mean *Sphagnum* cover	0.0918(0.709)	0.346(0.147)
2	Mean basal area	−0.119(0.639)	**-0.432(0.05)**
	Mean *Sphagnum* cover	**-0.479(0.044)**	−0.154(0.506)
3	Mean basal area	0.323(0.177)	−0.293(0.210)
	Mean *Sphagnum* cover	−0.103(0.674)	−0.296(0.205)
All sites	Mean basal area	0.045(0.737)	**-0.248(0.052)**
	Mean *Sphagnum* cover	**0.286(0.029)**	0.0535(0.680)

capillifolium, including all 17 (39.5%) of the colonies with sporophytes. The remaining patches were *S. wulfianum* (3) and *S. girgensohnii* (3). Compared to the *S. capillifolium* colonies without sporophytes, reproductive colonies were significantly larger and taller (**Table 3**). In contrast, sporophyte density on an individual patch was not correlated with colony size (not shown). Reproductive colonies were also associated with significantly more open canopy (**Table 4**). Reproductive and non-reproductive colonies did not differ in their proximity to neighboring *S. capillifolium* colonies, however the correlation between sporophyte density and mean and minimum distance to a neighboring colony was close to significant (R^2 0.290 p=0.073; R^2 0.306 p=0.058, respectively).

Discussion

Spores. The lower spore abundance in site 1 compared to sites 2 and 3, and the correlation between *Sphagnum* abundance and spore abundance indicate that local dispersal influences spore abundance during peak periods (**Fig. 2, Table 2**). Within site 1, spore abundance was also strongly influenced by local dispersal as the spore abundance was negatively correlated with the minimum distance to other *Sphagnum* colonies. The lack of a correlation with basal area during the peak period of spore abundance may suggest that most spores are produced locally and when local production is high, reduced wind capacity (because of closed tree canopies) does not detectably limit spore abundance. However, the negative correlation with basal area at low overall spore abundance suggests that when local spore production is low, reduced wind capacity yields a detectable reduction in total spore rain. The difference in dispersal timing of local and regional spores may be related to either differences in dispersal phenology among species (Sundberg 2002) or in environmental variables (Rydgren & Økland 2002) within forest stands and across the region. These results support the hypothesis that abundance is relatively limited in young stands with little *Sphagnum* present due to the predominantly local dispersal of spores.

In site 1, the negative correlation between spore

Table 3. Characteristics of patches with and without sporophytes in site 1. Values are means and standard errors, and values followed by different letters are significantly different, a<b.

	No sporophytes	Sporophytes
Sphagnum colony area (m^2)	21.88 ± 0.008 a	2.83 ± 1.2 b
Sphagnum colony height (m)	0.122 ± 0.0015 a	0.202 ± 0.0022 b

Table 4. Habitat conditions of colonies with and without sporophytes in site 1. Values are means and standard errors. Values followed by different letters are statistically different.

	No sporophytes	Sporophytes
Mean distance to *Sphagnum* colony (m)	1.71 ± 0.261 a	2.54 ± 0.614 a
Minimum distance to *Sphagnum* colony (m)	0.948 ± 0.210 a	1.78 ± 0.579 a
Open canopy (%)	21.88 ± 1.12 a	27.80 ± 1.74 b

abundance and distance to a *Sphagnum* colony during the low density week suggests that the spores trapped on September 1 may not have been locally produced, but rather dispersed from the surrounding region, and that local dispersal occurred on September 23. This is supported by observation that the sporophytes in site 1 were only slightly dehisced on September 1 (Fenton pers. observ.). The lack of any correlation between spore density and *Sphagnum* abundance or stand density within site 2 is interesting. Other factors must be determining local dispersal of spores.

Overall, fewer spores were trapped in 2003 than in 2004 (**Fig. 2**). Sundberg (2002) found that the production of sporophytes and spores was positively correlated with the amount and distribution of precipitation the summer before, due to gametangial production that takes place at that time. August 2003 was considerably wetter and warmer than August 2002, which may have resulted in the production of more gametangia, and therefore more spores the following fall (**Fig. 1**).

Sphagnum spores were released in late summer and early fall (**Fig. 2**) approximately one month later than what has been previously recorded for these species (Cronberg 1991; Sundberg 2002). This may be due to lower levels of light in forests compared to open peatlands, which would increase sporophyte development time during the summer or, later snow melt, which would result in a later fertilization period.

Sporophytes. Reproduction (sporophyte and spore production) is energetically expensive for the parent gametophyte plant (Ehrlèn et al. 2000), and may be limited to individuals with the internal resources (i.e., ramet size) and access to external resources (e.g., available light) to undertake reproduction (Rydgren & Økland 2002). *Sphagnum capillifolium* colonies with sporophytes were larger, taller, and received more sunlight because of more open tree canopies than colonies without sporophytes (**Table 4**), suggesting that the limitations observed at the individual level in *Dicranum polysetum* (Ehrlèn et al. 2000) and *Hylocomium splendens* (Rydgren & Økland 2002) also apply at the colony level in *S. capillifolium* in this environment. As a consequence, the relatively limited spore abundance in site 1 may not only be limited by lack of *Sphagnum* within the community, but also by reduced sporophyte production by the colonies present due to a lack of resources.

Despite the relatively limited spore abundance within site 1, nearly 40% of colonies contained sporophytes. The high number of sporophytes present within an environment where each colony is isolated from each other by approximately 1 m is surprising as *S. capillifolium* is generally listed as dioicous, and dioicous bryophytes are generally believed to be mate-limited (Bisang et al. 2004). The ability of these colonies to be fertilized suggests that *S. capillifolium* is polyoicous in this environment, as suggested by Cronberg (1991) and Pujos (1993). An alternative explanation is that each colony is established by several spores. *Sphagnum capillifolium* may show a pattern of multiple spore establishment followed by genet exclusion as the colony grows (Cronberg 1996), which would permit both male and female individuals to temporally co-exist within a single colony. However, determining which of these possibilities is correct is beyond the scope of this study.

CONCLUSIONS

Spore abundance was at least partially determined by local production of spores, however spores were also available via regional dispersal. Therefore, the long interval observed in the establishment of *Sphagnum* spp. into the feather moss carpet that is on the Clay Belt of Québec and Ontario may be partially due to dispersal limitation. Sites with no or very few *Sphagnum* colonies will depend on the relatively low number of spores that are dispersed regionally. A

second limit to spore abundance in these sites may be a size and resource limitation on sporophyte production on the colonies that do establish within the closed forest. Therefore, the rapid expansion of *Sphagnum* documented in these stands approximately 150 years after fire may be partially related to the gradual opening of the forest stand during this period, allowing greater local sporophyte and spore production, and increased regional dispersal. However, gametangia production was not observed in this study, nor was spore germination and establishment assessed, and these processes should be further investigated to determine the relative roles of gametangia production, spore availability and germination site availability in *Sphagnum* establishment within the feather moss carpet.

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