Polytrichum strictum as a Nurse-Plant in Peatland Restoration

Elisabeth V. G. Groeneveld,[1] Ariane Massé,[1] and Line Rochefort[1,2]

Abstract

***Polytrichum strictum* is a pioneer plant frequently found on bare peat substrate after perturbations (fire, peat extraction). Can this moss facilitate the return of *Sphagnum* species or other boreal plants after disturbances? Field surveys of abandoned peatlands after peat extraction revealed that *Sphagnum* was always found in association with *P. strictum* carpets. We conducted field experiments in abandoned peatlands and showed that *P. strictum* carpets were able to keep *Sphagnum* fragments more humid than bare peat but only when the *P. strictum* carpets were not totally bone dry. In general, daytime temperatures beneath *P. strictum* carpets and fragments were reduced during the day and increased during the night compared to bare peat. *Polytrichum strictum* carpets acted as a seed trap, retaining more artificial seeds than bare peat. *Polytrichum strictum* can be a nurse-plant: after 16 months, vascular plants transplanted in the *P. strictum* carpet were healthier than the ones planted on bare peat. The use of *P. strictum* as a nurse-plant in boreal forest or peatland restoration is recommended for sites prone to frost heaving and with harsh microclimatic conditions.**

Key words: cutover peatlands, ecological restoration, facilitation, microclimate, milled vacuum-harvested peatland, pioneer species, recolonization, *Sphagnum*.

Introduction

Sphagnum mosses do not readily recolonize bare organic soils after fire or anthropogenic mechanical disturbance (Joosten 1995; Poulin et al. 2005). Former vacuum-harvested peatlands are hostile substrates, barren areas, and mostly devoid of *Sphagnum* mosses (Lavoie et al. 2005a). As *Sphagnum* is the main keystone plant of northern peatland ecosystems (Van Breemen 1995), it is judged necessary to reintroduce the peat mosses during restoration (Poschlod 1995; Rochefort 2000; Rochefort et al. 2003). Plant colonization of bare peat is severely curtailed for several reasons, including the absence of a seed bank of peatland species (Salonen 1987; Huopalainen et al. 1998), and limited concentration of critical nutrients such as phosphorus (Wind-Mulder et al. 1996). During summer, invading plants face poor hydrological conditions (Schouwenaars 1993; Price & Whitehead 2001; Price et al. 2003) and a harsh microclimate with potentially lethal temperatures (Sagot & Rochefort 1996; Price et al. 1998; Boudreau & Rochefort 1999). Although soil moisture conditions are improved in the spring and fall when the ditches of the former drainage system are blocked, the increased moisture, together with below-freezing temperatures, lead to frost heaving that can be devastating for newly established plants (Rietveld & Heidmann 1976; Gartner et al. 1986; Groeneveld & Rochefort 2002, 2005). In addition to frost heave, invading plants suffer from peat instability due to overland flow during snowmelt and wind blow (Anderson 1997; Campbell et al. 2002).

In spite of these difficult conditions, some tough pioneer plants are commonly found on postmilled sites such as cotton grasses, birches, and *Polytrichum* mosses (Tuitilla et al. 2000; see appendix 1 in Poulin et al. 2005; Lavoie et al. 2005*a*,*b*). *Polytrichum* species are pioneer mosses well adapted for growth on bare substrate after fire (Johnson 1981; Morneau & Payette 1989; Maltby et al. 1990; Corradini & Clément 1999) or on cutover bogs (Grosversnier et al. 1995; Lavoie et al. 2005*a*,*b*). Specialized leaves and an internal water conduction system allow *Polytrichum* mosses to photosynthesize at higher light levels and lower water content than do other mosses (Bayfield 1973; Callaghan et al. 1978; Silvola 1991). Resistance to burial and frost heave, as well as the ability to stabilize loose soil, allows *Polytrichum* mosses to colonize unstable substrates (Leach 1931; Birse et al. 1957; Collins 1969; Fenton & Lewis Smith 1982; Faubert & Rochefort 2002; Groeneveld & Rochefort 2005).

Once established, *P. strictum* appears to act as a nurse-plant, facilitating the growth of other species including *Sphagnum* (Buttler et al. 1996; Robert et al. 1999). Parker et al. (1997) demonstrated that *P. commune* increases drought survival of white spruce. Groeneveld and Rochefort (2005) demonstrated that *P. strictum* dramatically reduced the frost heaving of fir seedlings. Other suggested benefits include facilitation of seed germination, amelioration of the microclimate, and the prevention of crust formation, which could isolate diaspores

[1] Groupe de recherche en écologie des tourbières (GRET) et Centre d'études nordiques, Pavillon Paul-Comtois, Université Laval, Québec, Canada G1K 7P4
[2] Address correspondence to L. Rochefort, email line.rochefort@fsaa.ulaval.ca

from the soil water (Marsh & Koerner 1972; Grosvernier et al. 1995; Parker et al. 1997). However, the microclimate within a *P. strictum* carpet has not hitherto been characterized and the nursing functions of *Polytrichum* moss are poorly understood.

The objective of this study was to determine how *P. strictum* nurses *Sphagnum*. First, a systematic field survey on spontaneously revegetating abandoned peat fields was done to evaluate the presence of *Sphagnum* in relation to *P. strictum*. Second, a field experiment was designed to characterize the microclimate of a *P. strictum* carpet, in terms of irradiance, temperature, and moisture. Third, the role of *P. strictum* as a seed trap and as a nurse-plant facilitating plant survival and growth was also examined.

Methods

Field Survey on the Co-occurrence of *Polytrichum strictum* and *Sphagnum*

To verify if *Sphagnum* mosses were more likely to grow with *Polytrichum strictum*, two abandoned peat fields (30 × 400 m) were surveyed. The peat fields abandoned 10 years prior to investigation were chosen because they were spontaneously revegetating. The sites were located in Lac St-Jean, Québec (lat 48°47′N, long 72°10′W), in a 6,000-ha peatland. The sites were surrounded by natural peatlands at a distance of 30 m and diaspores, moss fragments, or seeds, could easily disseminate onto the bare beat. Systematic sampling surveys were carried out in 2000 to make sure that we sampled the whole peat field as opposed to random sampling. The distance between the sampling stations was set to 10 m across the width of each field and to 20 m along the length of each field and gave a total of 101 points sampled. At each sampling point, a water well was bored using an auger. The water table and the presence of *P. strictum* and *Sphagnum* were noted at each sampling point on the two abandoned peat fields five days after the wells were bored.

Nursing Effect Experiment

An important objective of this study was to test whether there was a causal–effect relationship for the observed *P. strictum–Sphagnum* association on spontaneously revegetating peat fields. An experimental design was used to characterize the microclimate generated by *P. strictum*, in terms of irradiance, temperature, and moisture and to evaluate the role of *P. strictum* as a seed trap for diaspores and as a nurse-plant facilitating plant growth. The experimental design was implemented in a peat field located near Rivière-du-Loup, Québec (lat 47°48′N, long 69°28′W), that was harvested by the vacuum method for approximately 10 years, and then abandoned in 1980. Spontaneous regeneration of plant cover on the abandoned peat fields has been poor likely due to the harsh microclimatic conditions. The site and experimental design are described in detail in Groeneveld and Rochefort (2005). In brief, three levels of *P. strictum* covers were tested for their nursing effect: (1) *P. strictum*–transplanted carpet; (2) *P. strictum* fragments—stems of *P. strictum* moss (average length = 7.9 cm) were harvested from a healthy colony and spread over the bare peat; and (3) no cover (bare peat). Straw has been shown to promote the growth of newly establishing bog vegetation (Price et al. 1998) and is used in the North American method of bog restoration. We tested the three levels of *P. strictum* cover in a factorial arrangement with straw (two levels: present, absent) applied at a rate of 3,000 kg/ha, in a complete randomized block design with six blocks. Each experimental unit measured 1.5 × 1.5 m and was separated by at least 1 m from its nearest neighbor. Although very sparse, all existing vegetation (including roots) and debris were removed from the blocks on the abandoned peat field, and the peat surface was smoothed with a garden rake before applying the treatments. The resulting smooth peat surface had the appearance of a freshly abandoned peat field. A wooden boardwalk was installed between the plots to minimize trampling. A variable number of treatments and blocks were used for the three different objectives of the study (Table 1). The experimental design was put into place in May 2000. Data were collected from 3 July 2000 to 16 October 2001.

The Microclimate in a *Polytrichum strictum* Carpet. The microclimatic conditions generated under the following four different treatments were tested during July and August 2000: *P. strictum* carpet (without straw), *P. strictum* fragments (without straw), straw on bare peat, and bare peat (Table 1). Measures were taken successively during many sampling periods to do a fine-description *P. strictum* microclimate over the plant growing season.

Irradiance. Irradiance measures were taken in each treatment with a photometer (SunScan Analysis System Delta-T Devices Ltd., Cambridge, United Kingdom; 1-m-long probe containing 64 photodiodes). Measures were taken in midsummer on 14 July and in late-summer on 14 August 2000, under the following conditions: it was midday, there was at least 200 μmol m^{-2} second^{-1} of light and there were no abrupt changes from sunny to cloudy (Potter et al. 1996). In the bare peat treatment, the 1-m-long probe was placed on the peat surface across the center of each plot. Where there were fragments and straw, the probe was inserted beneath the cover in the center of the plot. For measures in the carpet, a long narrow furrow was cut approximately 15 cm from the edge of each carpet. When the probe was laid in the furrow, it was at the same height as the rhizoid coat of the *P. strictum* stems (where *Sphagnum* is often found growing). The surface of the probe was then covered with freshly clipped *P. strictum* so as to recreate the appearance of a natural carpet. This method is similar to that used by Keizer et al. (1985). Within each block, the order of data collection between experimental units was randomized.

Table 1. Name, purpose, and description of treatments used for field experiments on *Polytrichum strictum* as a nurse-plant at an abandoned vacuum-harvested bog near Rivière-du-Loup, Québec.

*Treatment Number**	*Treatment*		*Treatment Purpose*	*Treatment Description*
	P. strictum	*Straw*		
1	*P. strictum* carpet	Straw absent	To simulate a dense *P. strictum* colony	Squares of *P. strictum* were removed intact from naturally occurring colonies and transplanted into the experimental plots
2	*P. strictum* carpet	Straw present		As treatment 1, but with 3,000 kg/ha of straw spread over the carpet
3	*P. strictum* fragments	Straw absent	A treatment to simulate the reintroduction of plant material according to the usual North American restoration techniques	*P. strictum* fragments were clipped from a healthy colony and spread over each experimental plot of bare peat in a ratio of 1:10, which resulted fragments cover of approximately 75% of the bare peat
4	*P. strictum* fragments	Straw present		As treatment 3, but with 3,000 kg/ha of straw spread over the fragments
5	Bare peat	Straw absent	To test conditions on a surface left bare after harvesting	Bare peat
6	Bare peat	Straw present	To test the effect of a straw mulch compared to *Polytrichum* carpets	3,000 kg/ha of straw was evenly spread over bare peat

* Varying numbers of treatments and blocks were used for each experiment, as follows—microclimate experiment: treatments 1, 3, 5, and 6, and $n = 6$; seed trap experiment: treatments 1 and 5, and $n = 3$, $n = 6$; and nurse-plant experiment: treatments 1, 2, 3, 4, 5, and 6, and $n = 6$.

Air Temperature. Air temperature was measured every 30 minutes during three periods: 10–19 July, 23 July to 3 August, and 8–24 August 2000. StowAway dataloggers (Onset Computer Corporation, Pocasset, MA, U.S.A.) with external sensors were placed in each plot. The sensor was placed in the center of each plot within the rhizoids of the *P. strictum* carpet, beneath the fragments, on bare peat, or beneath the straw. One logger was placed per experimental unit, in each of the six blocks. Cumulative curves of the temperature differences between the treatments and bare peat were then calculated.

***Water Content of* Sphagnum.** For the moisture contents, we chose to use *Sphagnum* moss itself (individual stems with capitulum, hereafter called shoot) as a method for measuring the moisture provided by a *P. strictum* carpet. *Sphagnum* has no physiological mechanism to prevent water loss and therefore tends to be in equilibrium with its environment.

Sphagnum fuscum (Schimp.) Klinggr. was chosen for this measure. *Sphagnum fuscum* was harvested in the evening preceding its use, cut into 2.5-cm-long shoots then stored for 12 hours at 4°C. Prior to being inserted in the treatments, the *Sphagnum* shoots were saturated with bog water. Ten *Sphagnum* shoots per plot were placed at random locations within the *P. strictum* carpet, beneath the *P. strictum* fragments, on the bare peat, and beneath the straw. Because the *P. strictum* fragments had been spread in a 1:10 ratio (1 m^2 of collected material spread over 10 m^2), the *Sphagnum* shoots were not necessarily beneath fragments at every location. In the *P. strictum* carpets they were horizontally inserted in the zone where the stem was covered with the white tomentum. *Sphagnum* shoots were placed out once a week from July to August for a total of six time periods: 13–17 July, 18–20 July, 25–28 July, 1–4 August, 8–11 August, and 25–27 August 2000. The *Sphagnum* shoots were retrieved on rainless days, 3–5 days following their insertion. The order of retrieval was randomized within each block. The 10 *Sphagnum* shoots were collected, placed in a screw-top bottle (one bottle per shoot, 10 bottles per plot, but a mean value was retained for further calculation) and stored at 4°C for a maximum of 24 hours. The wet weight was then measured. Dry weight was determined following 24 hours of oven drying at 105°C and percent water content was calculated. A pluviometer was installed on the peat field and data were collected daily to calculate total precipitation for each experimental period.

***Polytrichum strictum* as a Seed Trap.** Studies with other moss species have shown that bryophyte carpets may act as seed traps and reduce the predation of large seeds (Van Tooren 1988). Abandoned peat fields are usually near natural peatlands, and diaspores dispersion from natural sites to peat field is frequent (Campbell et al. 2003). The purpose of this experiment was to determine if *P. strictum* carpets act as a facilitator for immigration by trapping diaspores as suggested by Parker et al. (1997), which we supposed should favor recolonization of the site afterward. The experiment was designed with the following assumption: all ground covers receive an equal amount of seed rain. After a given amount of time, more seeds will remain on some substrates than others because the substrates vary in their ability to retain the seeds. The suitability of *P. strictum* moss layer as a seed trap was tested using artificial seeds. Two different substrates were tested for seed retention: *P. strictum* carpet and bare peat.

Artificial seeds were constructed from chicken feather–dyed bright red and were used as a diaspore dispersion model. Real seeds were very fragile and difficult to manipulate and these artificial seeds had the advantage of being more durable and visible than real seeds. Forty artificial seeds were gently deposited (to simulate arrival by wind) on the bare peat and on the carpet. Artificial seeds measured around 30 mm long and wide and were comparable to real seed dimensions. The experiment was conducted on two different wind conditions: (1) strong wind on the 8 August 2000 ($n = 3$) and (2) light wind on 24 August 2000 ($n = 6$; for this second trial, 30 artificial seeds per plot were used). The number of artificial seeds remaining after 1 and 2 hours for the strong-wind conditions and after 4 hours for the light-wind conditions was counted.

***Polytrichum strictum* as a Nurse-Plant.** Species that benefit from the protection of various members of the *Polytrichum* genus include black spruce seedlings, white spruce seedlings, various woody plants, and *Sphagnum* mosses (Marsh & Koener 1972; Buttler et al. 1996; Filion & Morin 1996; Parker et al. 1997). We wanted to evaluate if *P. strictum* facilitates establishment of reintroduced plants, such as *Sphagnum*. As a proxy for time, we used fir (*Abies balsamea*) seedlings as a biological model for plant reintroduction in *P. strictum* carpet because we knew they would respond more quickly than waiting for the formation of *Sphagnum* cushions (4–5 years to develop). Fir seedlings were chosen because they were abundant on the site and easy to transplant. In each experimental unit, eight small fir seedlings were planted in the peat. Seedlings with only one shoot (no branches) and not more than two brown needles were transplanted. The average shoot length was 4.2 ± 0.6 cm, the average root length 9.9 ± 2.8 cm. Seedling health on a scale of 1–3 (1 = dead, 2 = intermediate, and 3 = healthy) was evaluated two and 11 months after planting, on 24 August 2000 and 29 May 2001. A final rating was given 16 months after the seedlings had been planted, on 16 October 2001. On this date a scale of 1–5 was used, with 1 = dead; 2 = almost dead, only a few living needles; 3 = intermediate, all leaves chlorotic or many leaves dead; 4 = almost healthy, only a few chlorotic or dead leaves; and 5 = perfectly healthy, all leaves bright green. Seedlings that were missing but had been noted as dead on a prior sampling date were considered dead; all other missing seedlings were excluded from the analysis.

Statistical Analyses

For the field survey on the presence of *Sphagnum*, a chi-square test was used to determine if *Sphagnum* was more likely to be found associated with *P. strictum* than by chance alone. All other statistical analyses were performed using the general linear models procedure of SAS (SAS Institute, Inc. 1988).

The Microclimate in a *Polytrichum strictum* Carpet. We used an analysis of variance (ANOVA) with sampling period as repeated factor to evaluate the effect of the four treatments on irradiance and soil moisture. A protected least significant difference was used to locate differences between treatment means once treatment effects were found significant. For the irradiance, the percent photosynthetically active radiation (PAR) transmitted through each cover was calculated and data were transformed (log [$x + 1$]) to normalize the distribution of the residuals. For the field experiment on water content a cubic transformation was necessary to reduce variance heterogeneity. Five data out of 144 were removed from the dataset because the percent moisture of *Sphagnum* came out negative because of an error in the initial weight of either the screw-top bottle or *Sphagnum*. To help interpret the variation in water content, we used total precipitations measured with the pluviometer installed on the abandoned peat field and daily temperature recorded with the dataloggers. We used records from dataloggers placed on the bare peat for the microclimate experiment to calculate average daily temperature between six and 18 hours for each experimental period. For the experimental period from 18–20 July, temperature data were available only for the first two days.

***Polytrichum strictum* as a Seed Trap.** Different ANOVAs were done for each seed count (because they included different total number of blocks) on each windy condition to compare percent seed remaining between *P. strictum* carpet and bare peat.

***Polytrichum strictum* as a Nurse-plant.** We used a factorial design to investigate the effect of *P. strictum* on plant growth and survival. We considered health index as a quantitative variable and thus calculate mean health index (MHI) for every treatment. Where there was no interaction between the main effects (*Polytrichum* cover, straw cover), a Tukey multiple comparison test was done on the means of each factor averaged over all the levels of the other factor (Sokal & Rohlf 1981). Where there was an interaction between the main effects, the Tukey multiple comparison test was limited to comparing the means of one factor within each level of the other factor.

Results

Co-occurrence of *Polytrichum strictum* and *Sphagnum*

Polytrichum strictum was present at 93 sampling points out of 101 on the abandoned peat fields. Where *P. strictum* was spontaneously revegetating, we found 31 sampling points where *Sphagnum* was also present. On the other hand, we found no point where *Sphagnum* grew alone ($\chi^2 = 3.85$, $p = 0.05$). When *Sphagnum* and *P. strictum* were absent, water table was relatively nearer the surface (Table 2). *Polytrichum strictum* and *Sphagnum* were associated where water table was intermediate and *P. strictum* was present alone at drier sampling points (Table 2).

Nursing Effect

The Microclimate in a *Polytrichum strictum* Carpet.

Irradiance. The amount of PAR passing through the *P. strictum* carpet was 5%, through the *P. strictum* fragments 24%, and 34% in the presence of the straw mulch ($ANOVA_{Treatment}$: $df = 3$, $F = 361.97$, $p < 0.0001$). Although the sampling period had a significant effect on PAR as it was measured at different times of the season, the difference between the treatments was similar for the two sampling periods ($ANOVA_{Time}$: $df = 1$, $F = 14.04$, $p = 0.002$; $ANOVA_{Time \times Treatment}$: $df = 3$, $F = 2.47$, $p = 0.105$). Average photosynthetic photon flux density reaching the surface was 38 for the carpet, 194 for the straw mulch, 309 for the fragments, and 677 μmol m^{-2} $second^{-1}$ for the bare peat.

Air Temperature. The temperature at the surface of the bare peat and beneath the *P. strictum* carpet, fragments, and straw are presented in Figure 1. Temperature data are presented as cumulative temperature curves, where the curve reflects the percent time when temperature is greater than that shown on the *y*-axis. The trends were similar for the three time periods; above 14–19°C, temperatures under the covers are generally cooler than those observed on bare peat. Cumulative temperature difference curves between the treatment and the bare peat is presented in Figure 1. Temperature reduction caused by the treatments is shown when the temperature difference is positive, and temperature increase caused by the treatments is shown when the temperature difference is negative. Below this same range, temperatures are generally warmer than those observed on bare peat. In general, the greatest temperature reduction compared to bare peat was observed at the highest temperatures (Fig. 1). In other words, amplitude of variation is lessened by the presence of *P. strictum* treatments when compared to bare peat surface temperature.

Table 2. Association between *Polytrichum strictum* and *Sphagnum* on an abandoned peat field spontaneously revegetating at Lac St-Jean, Québec, and the associate water level.*

	n	*Mean Water Table (cm)*
P. strictum present		
Sphagnum absent	62	−53.8 ± 0.6
Sphagnum present	31	−49.5 ± 1.7
P. strictum absent		
Sphagnum absent	8	−33.6 ± 4.0
Sphagnum present	0	No occurrence
Total	101	

**N* = number of sampling points where the genus was recorded, out of 101 points.

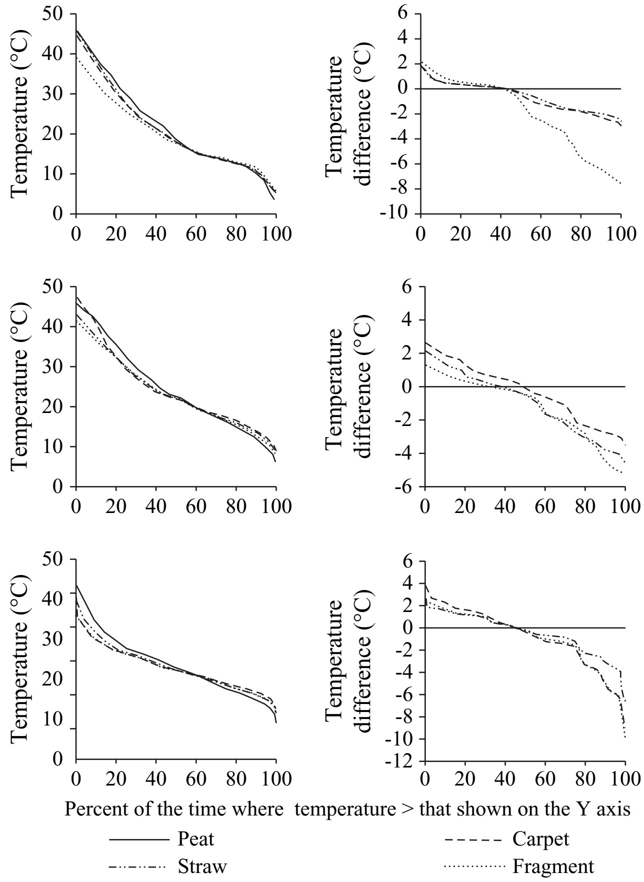

Figure 1. Temperature duration curves for surface temperature on an abandoned vacuum-harvested bog located near Rivière-du-Loup, Québec, from 10–19 July upper graphs, 23 July to 3 August middle graphs, and 8–24 August lower graphs. Temperature was measured on bare peat, and beneath a *Polytrichum strictum* carpet, between *P. strictum* fragments, and straw (left), and temperature difference between the three covers and bare peat was calculated (right).

***Water Content of* Sphagnum.** The effect of *P. strictum* carpet, *P. strictum* fragments, and straw on moisture varied from period to period ($ANOVA_{Date \times Treatment}$: $df = 15$, $F = 2.66$, $p = 0.002$) and was influenced by the temperature and precipitations (Fig. 2). When experiencing dry and warm spells (see first two periods of July of Fig. 2), *Sphagnum* stems in all treatments were equally dry, the average water content over both periods for all the treatments being 22%. On the other hand, when it is hot but some moisture is available from precipitation (see the two periods at end of July and beginning of August of Fig. 2), *P. strictum* or straw treatments all have a fairly similar effect in improving moisture condition at the air peat interface when compared to bare peat: ranging from 35 to 53% compared to 12% in July and from 95 to 165% compared to 31% in August. During moist periods (see the last two observation periods of August of Fig. 2), water content in *Sphagnum* for all treatments are higher (in the range of 400–700%), but still all treatments (*P. strictum* or straw additions) tend to provide more moisture at the interface air–peat.

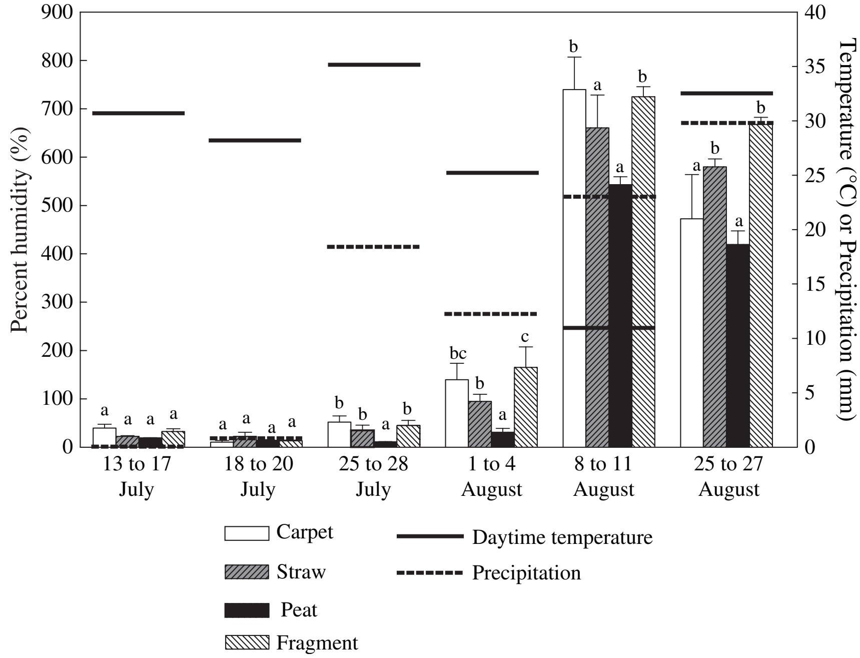

Figure 2. Average daily temperature (from 6–18 hours), total precipitation, and mean water content (±SE) of stem sections of *Sphagnum fuscum* placed in a *Polytrichum strictum* carpet, between *P. strictum* fragments, and in straw, or on the bare peat surface of an abandoned vacuum-harvested bog located near Rivière-du-Loup, Québec, during six measurement periods. Identical letters identify mean water content that did not differ statistically between treatments ($p \leq 0.05$) for a specific time interval.

***Polytrichum strictum* as a Seed Trap.** For the seed retention test during strong-wind condition, after one hour significantly more seeds were retained on the carpet (94%) than on the bare peat (52%) ($\text{ANOVA}_{\text{Treatment}}$: $df = 1$, $F = 48.48$, $p = 0.02$; Fig. 3a). After two hours, the difference was even greater, with 90% retention on the carpet and 43% retention on the bare peat ($\text{ANOVA}_{\text{Treatment}}$: $df = 1$, $F = 100.00$, $p = 0.001$). When the trial was repeated during light-wind conditions, more seeds were retained on the carpet (94%) than on bare peat (86%), but this difference was not significant ($\text{ANOVA}_{\text{Treatment}}$: $df = 1$, $F = 4.12$, $p = 0.1$; Fig. 3b).

***Polytrichum strictum* as a Nurse-plant.** Two months after planting, seedlings growing in the *P. strictum* carpet (mean health index = 2.85) were significantly less healthy than seedlings growing in the bare peat (MHI = 3.0), regardless of the presence of straw ($\text{ANOVA}_{\text{Polytrichum}\times\text{Straw}}$: $df = 2$, $F = 0.91$, $p = 0.4$; $\text{ANOVA}_{\text{Polytrichum}}$: $df = 2$, $F = 3.55$, $p = 0.04$), but still, the effect of *P. strictum* is minim (Fig. 4a). The health of seedlings planted in the fragments was intermediate (2.95) and did not differ significantly from the two others. Straw had no significant effect on fir health ($\text{ANOVA}_{\text{Straw}}$: $df = 1$, $F = 0.73$, $p = 0.4$; straw: MHI = 2.97; no-straw MHI = 2.9).

Eleven months after they were planted, seedling health and survival were affected only by the presence of straw ($\text{ANOVA}_{\text{Straw}}$: $df = 1$, $F = 9.2$, $p = 0.006$; Fig. 4b). Seedlings were significantly healthier and less likely to die when planted in straw (MHI = 2.63) compared to when there was no straw independently of the presence of *P. strictum* carpet (MHI = 2.4; $\text{ANOVA}_{\text{Polytrichum}\times\text{Straw}}$: $df = 2$, $F = 1.07$, $p = 0.4$; $\text{ANOVA}_{\text{Polytrichum}}$: $df = 2$, $F = 2.15$, $p = 0.1$).

Sixteen months after they were planted, seedling health and survival was significantly affected by the ground cover; the survival of seedlings differed depending on the level of *P. strictum* and the presence of straw ($\text{ANOVA}_{\text{Polytrichum}\times\text{Straw}}$: $df = 2$, $F = 4.89$, $p = 0.02$; $\text{ANOVA}_{\text{Polytrichum}}$: $df = 2$, $F = 1.4$, $p = 0.3$; $\text{ANOVA}_{\text{Straw}}$: $df = 1$, $F = 5.85$, $p = 0.02$; Fig. 4c). Seedlings planted in the *P. strictum* carpet were healthy regardless of the presence of straw (carpet MHI = 3.4; carpet + straw MHI = 2.9). On the other hand, seedlings planted in fragments fared better when also covered with straw (fragment MHI = 2.7; fragments + straw MHI = 3.7), as did seedlings planted in bare peat (bare peat MHI = 2.0; straw MHI = 3.4). When comparing the three levels of *P. strictum* in absence of straw, seedlings were healthier when planted in *P. strictum* carpet (Fig. 4c).

Discussion

Nursing Effect

We found that *Polytrichum strictum* is able to spontaneously recolonize abandoned peat fields. On the other hand, *Sphagnum* seems to only colonize microsites where *P. strictum* is present. We conclude that when

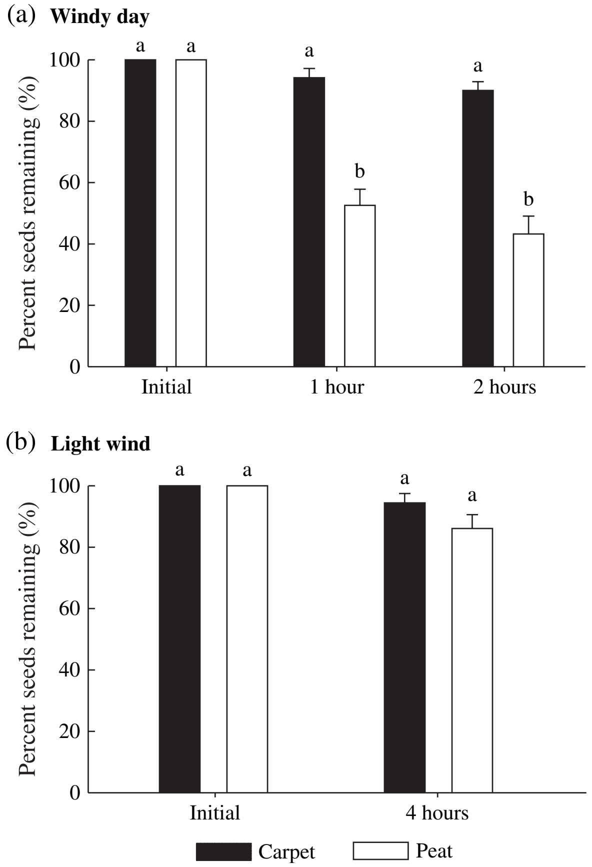

Figure 3. Mean percent artificial seeds remaining (±SE) on a *Polytrichum strictum* carpet and on the bare peat surface of an abandoned vacuum-harvested bog located near Rivière-du-Loup, Québec, during (a) windy day on 8 August 2000 and (b) light wind day on 24 August 2000. Identical letters identify mean percent seeds remaining that did not differ statistically between treatments ($p \leq 0.05$). Analyses were performed separately for each time interval.

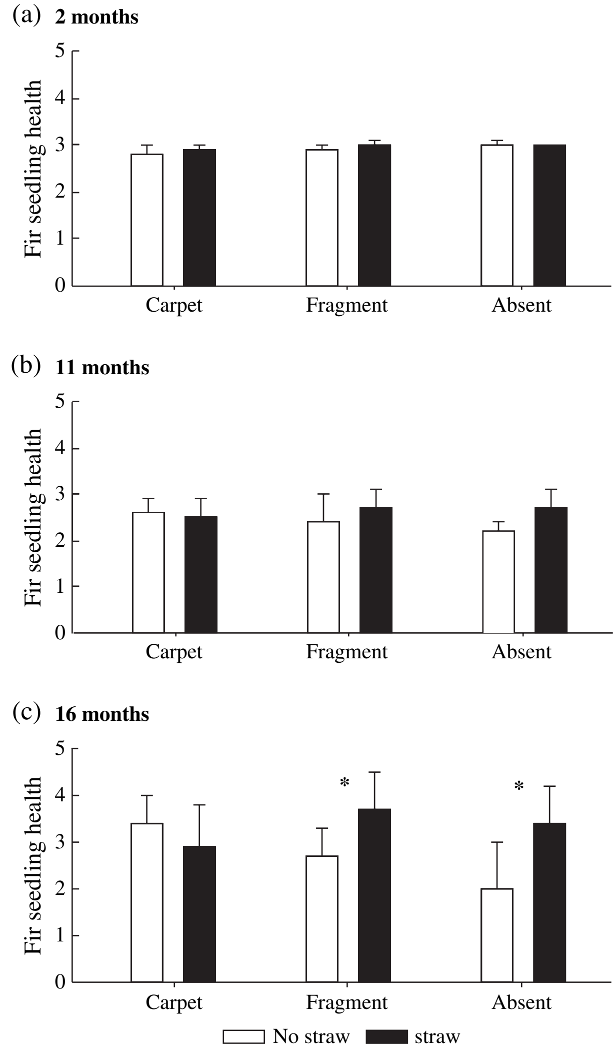

Figure 4. MHI (±SE) of fir seedlings planted on an abandoned vacuum-harvested bog near Rivière-du-Loup, Québec. (a) Two months after plantation, Tukey main effects for *Polytrichum*: carpet = a, fragments = ab, absent = b. Tukey main effect for straw: absent = a, present = a. (b) Eleven months after plantation, Tukey main effects for *Polytrichum*: carpet = a, fragments = a, absent = a. Tukey main effect for straw: absent = a, present = b. (c) Sixteen months after plantation, $ANOVA_{Polytrichum \times Straw}$: $p = 0.02$. Asterisk (*) indicates a significant difference between levels of straw. Health indexes for (a) and (b) 1 = dead, 2 = intermediate, 3 = healthy and for (c) 1 = dead, 2 = almost dead, 3 = intermediate, 4 = almost healthy, 5 = healthy.

a *P. strictum–Sphagnum* association is found, *Sphagnum* benefits from the presence of *P. strictum.* In general, nurse-plants offer many benefits to the beneficiaries, including reduction of temperature extremes, amelioration of light conditions, improved moisture availability, soil stabilization, increased nutrient availability, and predator protection (Latheef & Ortiz 1984; Gill & Marks 1991; Valiente-Banuet & Ezcurra 1991; Callaway 1992; Belsky 1994; Suzán et al. 1996; Martinez & Moreno-Casasola 1998; Raffaele & Veblen 1998).

The Microclimate in a *Polytrichum strictum* Carpet.

Irradiance. The amount of PAR transmitted within the *P. strictum* carpet, fragments, and straw was reduced compared to the bare peat. This reduction in light could explain, in part, the association found between *Sphagnum* and *P. strictum* in the field. In fact, a reduction in light, ranging from 38 to 80% has been found to favor *Sphagnum* growth (Sonesson et al. 1980; Murray et al. 1989*b*; Rochefort & Bastien 1998).

Although *Sphagnum* requires a certain minimum of light to grow, exposure to high light levels can reduce the photosynthetic capacity (Harley et al. 1989; Murray et al. 1993). As long as the light compensation point is reached, *Sphagnum* will be able to grow in the shade. On the bare peat, PAR will often be above light saturation levels, causing photoinhibition. Thus, in a context of

Sphagnum establishment during peatland restoration, a microclimate with shade could be important because the whole *Sphagnum* individual is exposed to light compared to a natural colony were only the capitulum is exposed.

Air Temperature. Our results demonstrate that the presence of *P. strictum* is able to create a cooler microclimate for *Sphagnum*. Knowing that high temperatures may limit the growth of *Sphagnum* by increasing evaporation and respiration, and reducing photosynthesis and destroying plant cells, *P. strictum* can play an important role as companion to *Sphagnum* by keeping it cooler (Harley et al. 1989; Balagurova et al. 1996; Sagot & Rochefort 1996; Riis & Sand-Jensen 1997). Many studies have shown that nurse-plants can promote the establishment of beneficiary species by reducing soil temperatures. For example, on highly disturbed bare pit heaps, Richardson (1958) describes how a layer of moss and lichens nursed a graminoid by decreasing the soil temperature up to 10°C. This effect has also been documented for mosses and vascular plants in peat bogs, the Sonoran Desert, and sand dunes (Franco & Nobel 1988, 1989; Nobel 1989; Suzán et al. 1996; Martinez & Moreno-Casasola 1998; Boudreau & Rochefort 1999; Marcoux 2000).

The optimal temperature for *Sphagnum* photosynthesis varies by species and climatic conditions. The optimal temperature for *S. squarrosum*, *S. angustifolium*, and *S. warnstorfii* is near 20°C; between approximately 13 and 30°C, at least 75% of maximal photosynthesis was maintained (Harley et al. 1989). According to Kurets et al. (1993), above 30°C, the carbon balance for *S. fuscum* became negative. In this study, the *P. strictum* carpet reduced maximum temperatures during the day. Potential *Sphagnum* mosses growing in *P. strictum* carpets would spend more time in the ideal temperature window than *Sphagnum* growing on bare peat. At night, temperatures were on average higher beneath the *P. strictum* carpet than on bare peat; maximal nightly increase being 3.8°C. The carpets increase the nighttime temperatures by reducing radiative and convective heat loss.

The degree of daytime temperature reduction depended on climatic conditions. In mid-August, the daytime temperature on bare peat ranged between 30 and 42°C; it was 6.3°C cooler on average in the *P. strictum* carpet than on the bare peat. We hypothesize that the abundant rainfall permitted *P. strictum* to remain with open leaves (Bayfield 1973), thus reducing daytime temperatures compared to bare peat. The opposite situation occurred in the end of July, when it was very hot and dry. During this time, it was on average 4.0°C cooler under the straw than on the bare peat. On the other hand, it was 2.7°C hotter in the carpet than on the bare peat. *Polytrichum strictum* likely folded its leaves up to reduce water loss, thus increasing the exposure of *Sphagnum*, or in this case, the temperature sensor, to elevated temperatures.

***Water Content of* Sphagnum.** *Sphagnum* plants must remain hydrated to photosynthesize. In as little as 2–4 days, plants may die following complete desiccation. Plants that survive may regain photosynthetic function but at a much reduced rate (Skre & Oechel 1981; Schipperges & Rydin 1998). Our results confirm the existence of a moister microclimate in the *P. strictum* carpet, fragments, and straw treatments. The presence and amplitude of this microclimate depends on the daytime temperature and precipitation.

A minimum of precipitation was necessary for the different covers to create an environment moister than the bare peat. In the almost complete absence of precipitations with high temperatures (13 and 18 July 2000), none of the covers offered a moister environment in comparison to bare peat. Estimates of the compensation water content of mosses, below which the net carbon exchange is negative, vary from 62 to 225% (Skre & Oechel 1981; Schipperges & Rydin 1998), depending on both species and environmental conditions. In mid-July the water content was well below 62%, the lowest moisture compensation point cited in literature. Buttler et al. (1998) showed in an experimental setup that microclimatic conditions under plastic mulch may compensate for a low water table for the growth of *Sphagnum*. However, during severe drought conditions like we experienced in mid-July, mulch or nurse-plants by themselves without any hydrological remediation cannot supply sufficient moisture to *Sphagnum*.

With lower temperatures and higher precipitation toward the end of July and beginning of August, water content of *Sphagnum* mosses was significantly higher in the carpet, straw, and fragments treatments compared to bare peat. Murray et al. (1989*a*) found that the optimal range for photosynthesis in *Sphagnum* moss is 600–1,000%. Other authors have found optimal ranges of 400–2,500% for various species (Schipperges & Rydin 1998), 725% for *S. subsecundum* (Skre & Oechel 1981), and 600–1,000% for *S. fuscum* (Silvola & Aaltonen 1984). In this study, *Sphagnum* was within its optimal range of water content for photosynthesis more often in the *P. strictum* carpet, fragments, and straw treatments, than on bare peat. In fact, for most of August, the water content of *Sphagnum* in the carpet was above 400%, well within the moisture range required for *Sphagnum* photosynthesis. Nurse-plants have been found to increase soil moisture in many environments including harvested peatlands, shrub lands, deserts, and disturbed bare pit heaps (Richardson 1958; Valiente-Banuet & Ezcurra 1991; Salonen 1992; Raffaele & Veblen 1998). Many studies have shown that the more humid conditions beneath vegetation or other protective covers were favorable to the growth of *Sphagnum* (Salonen 1992; Buttler et al. 1996; Price et al. 1998; Rochefort & Bastien 1998; Boudreau & Rochefort 1999).

***Polytrichum strictum* as a Seed Trap.** Diaspores dispersion from natural sites to abandoned peat fields is an important source of moss fragments or seeds (Campbell et al. 2003). Parker et al. (1997) suggest that *P. commune* may help other plants establish by capturing their seeds and allowing them to germinate. In this study we present evidence that a *P. strictum* carpet captures more artificial seeds than bare soil. This is similar to Van Tooren (1988) who determined that the bryophyte layer in a chalk grassland acts as a seed trap, accumulating large numbers of seeds. Mallik et al. (1984) also showed that bryophyte layers in heathlands can contain large numbers of viable seeds. Other nurse-plants with a flat, cushion growth form have been noted as seed traps for wind-dispersed seeds (Griggs 1956; Kikvidze 1993). Welden (1985) explains how nurse-plants reduce wind velocity, thus allowing the deposition of fine wind-born materials, which potentially could include seeds.

Once the diaspores have been trapped by a nurse-plant, they are offered a protected environment in which to germinate and grow. However, not all plants grow better in a bryophyte carpet. *Polytrichum commune* has been found to inhibit the growth of other heathland plants (Corradini & Clément 1999). *Polytrichum formosum* has been shown to reduce soil mineralization, probably caused by an allelopathic effect (Rozé 1987). This aspect needs to be further investigated in relation to *Sphagnum* fragment or spore germination although the co-occurrence of *Sphagnum* mosses and *P. strictum* in spontaneously revegetating abandoned peat fields points to the contrary.

***Polytrichum strictum* as a Nurse-plant.** Once diaspores have been captured by a *P. strictum* carpet, they must survive and grow. The third objective of this study was to evaluate growth and survival within *P. strictum* carpets using fir seedlings as a plant reintroduction model. Two months after planting, seedlings growing in *P. strictum* carpet were less healthy than the ones growing on bare peat. This was likely due to the transplantation shock of seedlings in the *P. strictum* carpet. Indeed, the seedlings were inserted deeper within the carpet to reach firm soil and that method could have been more stressful than just planting on bare peat. Sixteen months after planting, we found that seedlings growing in *P. strictum* carpets or under straw mulch were healthier than the ones growing on bare peat. Thus, we propose that *P. strictum* carpets create a more favorable microenvironment for bog plant growth.

Nutrient competition could potentially reduce the growth of plants taking shelter in the *P. strictum* carpet. Phosphorus is the element most likely to be limiting because it is scarce in postharvested bogs (Wind-Mulder et al. 1996). However, a study by Chapin et al. (1987) revealed that *Sphagnum* moss, which may be nursed by *Polytrichum*, had a much higher rate of phosphate absorption than *Polytrichum*, which helped it survive when developing within a *Polytrichum*-dominated environment. In other cases, nurse-plants can actually increase the amount of nutrients available to the beneficiary (Walker & Chapin 1987; Belsky 1994). For example, a study by Gartner et al. (1986) showed that *Eriophorum* seedlings growing in the protection of moss mats had higher nitrogen and phosphorus concentrations than seedlings growing in frost boils. Because a light phosphorus fertilizer was applied at the beginning of our experiment, nutrient competition was unlikely.

Many authors have recently suggested that nurse-plants may hasten the reestablishment of a typical peatland flora (Buttler et al. 1996; Boudreau & Rochefort 1999; Robert et al. 1999; Marcoux 2000; Tuitilla et al. 2000). In this paper we demonstrated that (1) *Sphagnum* is present only where *P. strictum* was spontaneously recolonizing abandoned bare peat surfaces; (2) a *P. strictum* carpet can generate microclimatic conditions favorable for the proliferation of *Sphagnum*; and (3) *P. strictum* may play a role as a diaspore trap and a nurse-plant by improving plant establishment. As discussed in Groeneveld and Rochefort (2005) on *P. strictum* and peat stability, straw mulch used in restoration may be the best option for protecting *Sphagnum* because it does not compete for water and may release nutrients as it decomposes. However, it degrades rapidly, for most part within three years, and on windy sites it may blow away. On sites where peat instability is a problem and longer-term protection of *Sphagnum* is needed, facilitation by *P. strictum* carpets is an interesting aid to restoration.

Implications for Practice

- The use of *Polytrichum strictum* as a nurse-plant in boreal forest or peatland restoration is recommended for sites prone to frost heaving and with harsh microclimatic conditions.
- Establishing a *P. strictum* carpet is simple. Simply spreading moss fragments collected from a bog where *P. strictum* is present, naturally occurring among the *Sphagnum* layer, lightly fertilizing with phosphorus, and covering with a straw mulch is sufficient to ensure a continuous *P. strictum* carpet within a year.
- To the best of our knowledge, *P. strictum* mosses should be reintroduced at the same time as *Sphagnum* mosses when restoring cutover bogs as a warranty against potential adverse climatic conditions.

Acknowledgments

This study was funded by the Natural Sciences and Engineering Research Council of Canada and by industrial partners who are members of the Canadian Sphagnum Peat Moss Association. We extend our deepest thanks to the research assistants who participated in data collection during the study. We are also thankful to Stéphanie Boudreau, Monique Poulin, and many graduate colleagues for their helpful comments on the manuscript.

LITERATURE CITED

Anderson, P. 1997. Fire damage on blanket mires. Pages 16–28 in J. H. Tallis, R. Meade, and P. D. Hulme, editors. Blanket mire degradation: causes, consequences and challenges. The Macaulay Land Use Research Institute, Aberdeen, United Kingdom.

Balagurova, N., S. Drozdov, and S. Grabovik. 1996. Cold and heat resistance of five species of *Sphagnum*. Annales Botanici Fennici **33:**33–37.

Bayfield, N. G. 1973. Notes on the water relations of *Polytrichum commune* Hedw. Journal of Bryology **7:**607–617.

Belsky, A. J. 1994. Influence of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. Ecology **75:**922–932.

Birse, E. M., S. Y. Landsberg, and C. H. Gimingham. 1957. The effects of burial by sand on dune mosses. Transactions of the British Bryological Society **3:**285–301.

Boudreau, S., and L. Rochefort. 1999. Établissement de sphaignes réintroduites sous diverses communautés végétales recolonisant les tourbières après l'exploitation. Écologie **30:**53–62.

Buttler, A., P. Grosvernier, and Y. Matthey. 1998. Development of *Sphagnum fallax* diaspores on bare peat with implications for the restoration of cut-over bogs. Journal of Applied Ecology **35:** 800–810.

Buttler, A., B. Warner, P. Grosvernier, and Y. Matthey. 1996. Vertical patterns of testate amoebae (Protozoa: Rhizopoda) and peat-forming vegetation on cutover bogs in the Jura, Switzerland. New Phytologist **134:**371–382.

Callaghan, T. V., N. J. Collins, and C. H. Callaghan. 1978. Photosynthesis, growth and reproduction of *Hylocomnium splendens* and *Polytrichum commune* in Swedish Lapland-Strategies of growth and population dynamics of tundra plants. 4. Oikos **31:**73–88.

Callaway, R. M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. Ecology **73:**2118–2128.

Campbell, D. R., C. Lavoie, and L. Rochefort. 2002. Wind erosion and surface stability in abandoned milled peatlands. Canadian Journal of Soil Science **82:**85–95.

Campbell, D. R., L. Rochefort, and C. Lavoie. 2003. Determining the immigration potential of plants colonizing disturbed environments: the case of milled peatlands in Québec. Journal of Applied Ecology **40:**78–91.

Chapin, F. S. III., W. C. Oechel, K. Van Cleve, and W. Lawrence. 1987. The role of mosses in the phosphorus cycling of an Alaskan (USA) black spruce forest. Oecologia **74:**310–315.

Collins, N. J. 1969. The effects of volcanic activity on the vegetation of Deception Island. British Antarctic Survey Bulletin **21:**79–94.

Corradini, P., and B. Clément. 1999. Growth pattern and modular reiteration of a hardy coloniser *Polytrichum commune* Hedw. Plant Ecology **143:**67–76.

Faubert, P., and L. Rochefort. 2002. Response of peatland mosses to burial by wind-dispersed peat. The Bryologist **105:**96–103.

Fenton, J. H. C., and R. I. Lewis Smith. 1982. Distribution, composition and general characteristics of the moss banks of the maritime Antarctic. British Antarctic Survey Bulletin **51:**215–236.

Filion, J., and H. Morin. 1996. Spatial distribution of black spruce regeneration 8 years after fire in Quebec boreal forest. Canadian Journal of Forest Research **26:**601–610.

Franco, A. C., and P. S. Nobel. 1988. Interactions between seedlings of *Agave deserti* and the nurse-plant *Hilaria rigida*. Ecology **69:** 1731–1740.

Franco, A. C., and P. S. Nobel. 1989. Effect of nurse-plants on the microhabitat and growth of cacti. Journal of Ecology **77:**870–886.

Gartner, B. L., F. S. Chapin III, and G. R. Shaver. 1986. Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. Journal of Ecology **74:**1–18.

Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. Ecological Monographs **61:** 185–203.

Griggs, R. F. 1956. Competition and succession on a Rocky Mountain Fellfield. Ecology **37:**8–20.

Groeneveld, E. V. G., and L. Rochefort. 2002. Nursing plants in peatland restoration: on their potential use to alleviate frost heaving problems. Suo **53:**73–85.

Groeneveld, E. V. G., and L. Rochefort. 2005. *Polytrichum strictum* as a solution to frost heaving in disturbed ecosystems: a case study with milled peatlands. Restoration Ecology **13:**74–82.

Grosvernier, P., Y. Matthey, and A. Buttler. 1995. Microclimate and physical properties of peat: new clues to the understanding of bog restoration processes. Pages 435–449 in B. D. Wheeler, S. C. Shaw, W. J. Fojt, and R. A. Robertson, editors. Restoration of temperate wetlands. John Wiley & Sons Ltd., Chichester, United Kingdom.

Harley, P. C., J. D. Tenhunen, K. J. Murray, and J. Beyers. 1989. Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia **79:**251–259.

Huopalainen, M., E. S. Tuittla, J. Laine, and H. Vasander. 1998. Seed and spore bank in a cut-away peats twenty years after abandonment. International Peat Journal **8:**42–51.

Johnson, E. A. 1981. Vegetation organization and dynamics of lichen woodland communities in Northwest Territories, Canada. Ecology **62:**200–215.

Joosten, J. H. J. 1995. Time to regenerate: long-term perspectives of raised bog restoration with special emphasis on paleoecological studies. Pages 379–404 in B. D. Wheeler, S. C. Shaw, W. J. Fojt, and R. A. Robertson, editors. Restoration of temperate wetlands. John Wiley & Sons Ltd., Chichester, United Kingdom.

Keizer, P. J., B. F. Van Tooren, and H. J. During. 1985. Effects of bryophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. Journal of Ecology **73:**493–504.

Kikvidze, Z. 1993. Plant species associations in alpine-subnival vegetation patches in the Central Caucasus. Journal of Vegetation Science **4:**270–302.

Kurets, V. K., A. V. Talanov, E. G. Popov, and S. N. Drozdov. 1993. Light-temperature dependencies of apparent photosynthesis and dark respiration in *Sphagnum*. Russian Journal of Plant Physiology **40:**704–708.

Latheef, M. A., and J. H. Ortiz. 1984. Influence of companion herbs on *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) on collard plants. Journal of Economic Entomology **77:**80–82.

Lavoie, C., K. Marcoux, A. Saint-Louis, and J. S. Price. 2005*a*. The dynamics of a cotton-grass (*Eriophorum vaginatum* L.) cover expansion in a vacuum-mined peatland, southern Québec, Canada. Wetlands **25:**64–75.

Lavoie, C., A. Saint-Louis, and D. Lachance. 2005*b*. Vegetation dynamics on an abandoned vacuum-mined peatland: five years of monitoring. Wetlands Ecology and Management **13:**621–633.

Leach, W. 1931. On the importance of some mosses as pioneers on unstable soils. Journal of Ecology **19:**98–102.

Mallik, A. U., R. J. Hobbs, and C. J. Legg. 1984. Seed dynamics in *Calluna-Arctostaphylos* heath in North-Easter Scotland. Journal of Ecology **72:**855–871.

Maltby, E., C. J. Legg, and M. C. F. Proctor. 1990. The ecology of severe moorland fire on the North York Moors: effects of the 1976 fires, and subsequent surface and vegetation development. Journal of Ecology **78:**490–518.

Marcoux, K. 2000. Les invasions de la linaigrette (*Eriophorum vaginatum* L.): aide ou frein à la restauration des tourbières? M. Sc. thesis. Université Laval, Sainte-Foy, Québec, Canada.

Marsh, W. M., and J. M. Koerner. 1972. Role of moss in slope formation. Ecology **53:**489–493.

Martinez, M. L., and C. P. Moreno-Casasola. 1998. The biological flora of coastal dunes and wetlands: *Chamaecrista chamaecristoides* (Colladon) I. and B. Journal of Coastal Research **14:**162–174.

Morneau, C., and S. Payette. 1989. Postfire lichen spruce woodland recovery at the limit of the boreal forest in northern Québec. Canadian Journal of Botany **67:**2770–2782.

Murray, K. J., P. C. Harley, J. Beyers, H. Walz, and J. D. Tenhunen. 1989*a*. Water content effects on photosynthetic response of *Sphagnum* from the foothills of the Philip Smith Mountains, Alaska. Oecologia **79:**244–250.

Murray, K. J., J. D. Tenhunen, and J. Kummerow. 1989*b*. Limitations on *Sphagnum* growth and net primary production in the foothills of the Philip Smith Mountains, Alaska. Oecologia **80:**256–262.

Murray, K. J., J. D. Tenhunen, and R. S. Nowak. 1993. Photoinhibition as a control on photosynthesis and production of *Sphagnum* mosses. Oecologia **96:**200–207.

Nobel, P. S. 1989. Temperature, water availability, and nutrient level at various soil depths—consequences for shallow-rooted desert succulents, including nurse-plant effects. American Journal of Botany **76:**1486–1492.

Parker, W. C., S. R. Watson, and D. W. Cairns. 1997. The role of hair-cap mosses (*Polytrichum* spp.) in natural regeneration of white spruce (*Picea glauca* (Moench) Voss). Forest Ecology and Management **92:**19–28.

Poschold, P. 1995. Diaspore rain and diaspore bank in raised bogs and implications for the restoration of peat-mined sites. Pages 471–494 in B. D. Wheeler, S. C. Shaw, W. J. Fojt, and R. A. Robertson, editors. Restoration of temperate wetlands. John Wiley & Sons Ltd., Chichester, United Kingdom.

Potter, E., J. Wood, and C. Nicholl. 1996. SunScan Canopy Analysis System. User manual. SS1-UM-1.05 (version 1.05). Delta-T Devices Ltd., Cambridge, United Kingdom.

Poulin, M., L. Rochefort, F. Quinty, and C. Lavoie. 2005. Spontaneous revegetation of mined peatlands in eastern Canada. Canadian Journal of Botany **83:**539–557.

Price, J. S., A. L. Heathwaite, and A. J. Baird. 2003. Hydrological processes in abandoned and restored peatlands: an overview of management approaches. Wetlands Ecology and Management **11:**65–83.

Price, J. S., L. Rochefort, and F. Quinty. 1998. Energy and moisture considerations on cutover peatlands: surface microtopography, mulch cover and *Sphagnum* regeneration. Ecological Engineering **10:**293–312.

Price, J. S., and G. S. Whitehead. 2001. Developing hydrologic thresholds for *Sphagnum* recolonization on an abandoned cutover bog. Wetlands **21:**32–40.

Raffaele, E., and T. T. Veblen, 1998. Facilitation by nurse shrubs of resprouting behavior in a post-fire shrubland in northern Patagonia, Argentina. Journal of Vegetation Science **9:**693–698.

Richardson, J. A. 1958. The effect of temperature on the growth of plants on pit heaps. Journal of Ecology **46:**537–546.

Rietveld, W. J., and L. J. Heidmann. 1976. Direct seeding of Ponderosa Pine on recent burns in Arizona. Research note RM-312. U.S.D.A. Forest Service, Washington, D.C.

Riis, T., and K. Sand-Jensen. 1997. Growth reconstruction and photosynthesis of aquatic mosses: influence of light, temperature and carbon dioxide at depth. Journal of Ecology **85:**359–372.

Robert, E., L. Rochefort, and M. Garneau. 1999. Natural revegetation of two block-cut mined peatlands in eastern Canada. Canadian Journal of Botany **77:**1–13.

Rochefort, L. 2000. *Sphagnum*—a keystone genus in habitat restoration. The Bryologist **103:**503–508.

Rochefort, L., and D. F. Bastien. 1998. Réintroduction de sphaignes dans une tourbière exploitée: évaluation de divers moyens de protection contre la dessiccation. Ecoscience **5:**117–127.

Rochefort, L., F. Quinty, S. Campeau, K. W. Johnson, and T. J. Malterer. 2003. North American approach to the restoration of *Sphagnum* dominated peatlands. Wetlands Ecology and Management **11:** 3–20.

Rozé, F. 1987. Effets comparés de différentes litières sur la minéralisation et la nitrification nettes de l'azote dans un sol de lande haute. Revue d'écologie et de Biologie du Sol **24:**273–282.

Sagot, C., and L. Rochefort. 1996. Tolérance des sphaignes à la dessiccation. Cryptogamie: Bryologie et Lichénologie **17:**171–183.

Salonen, V. 1987. Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. Holarctic Ecology **10:**171–174.

Salonen, V. 1992. Effects of artificial plant cover on plant colonization of a bare peat surface. Journal of Vegetation Science **3:**109–112.

SAS Institute, Inc. 1988. SAS Proprietary Software Release 6.12 TS020. SAS Institute, Inc., Cary, North Carolina.

Schipperges, B., and H. Rydin. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytologist **140:**677–684.

Schouwenaars, J. M. 1993. Hydrological differences between bogs and bog-relicts and consequences for bog restoration. Hydrobiologia **265:**217–224.

Silvola, J. 1991. Moisture dependence of carbon dioxide exchange and its recovery after drying in certain boreal forest and peat mosses. Lindbergia **17:**5–10.

Silvola, J., and H. Aaltonen. 1984. Water content and photosynthesis in the peat mosses *Sphagnum fuscum* and *S. angustifolium*. Annales Botanici Fennici **21:**1–6.

Skre, O., and W. C. Oechel. 1981. Moss functioning in different taiga ecosystems in interior Alaska. Oecologia **48:**50–59.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2nd edition. W.H. Freeman and Company, New York.

Sonesson, M., S. Persson, K. Basilier, and T. A. Stenström. 1980. Growth of *Sphagnum riparium* Ångst. in relation to some environmental factors in the Stordalen mire. Ecology of a subarctic mire. Ecological Bulletin **30:**191–207.

Suzán, H., G. P. Nabhan, and D. T. Patten. 1996. The importance of *Olneya tesota* as a nurse-plant in the Sonoran Desert. Journal of Vegetation Science **7:**635–644.

Tuittila, E.-S., H. Rita, H. Vasander, and J. Laine. 2000. Vegetation patterns around *Eriophorum vaginatum* L. tussocks in a cut-away peatland in southern Finland. Canadian Journal of Botany **78:** 47–58.

Valiente-Banuet, A., and E. Ezcurra. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse-plant *Mimosa luisana* in the Tehuacan Valley, Mexico. Journal of Ecology **79:**961–971.

Van Breemen, N. 1995. How *Sphagnum* bogs down other plants. Tree **10:**270–275.

Van Tooren, B. F. 1988. The fate of seeds after dispersal in chalk grassland: the role of the bryophyte layer. Oikos **53:**41–48.

Walker, L. R., and F. S. Chapin III. 1987. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology **67:**1508–1523.

Welden, C. 1985. Structural pattern in alpine tundra vegetation. American Journal of Botany **72:**120–134.

Wind-Mulder, H., L. Rochefort, and D. H. Vitt. 1996. Water and peat chemistry comparisons of natural and post-harvested peatlands across Canada and their relevance to peatland restoration. Ecological Engineering **7:**161–181.