



Original article

Initiation of *Sphagnum* moss hummocks in bogs and the presence of vascular plants: Is there a link?Rémy Pouliot^{a,*}, Line Rochefort^a, Edgar Karofeld^b, Caroline Mercier^c^aDépartement de phytologie, Centre d'études Nordiques, Pavillon Paul-Comtois, 2425 rue de l'Agriculture, Université Laval, Québec, Canada G1V 0A6^bInstitute of Ecology and Earth Sciences, University of Tartu, Lai 40, Tartu 51005, Estonia^cDépartement de biologie, Pavillon Alexandre-Vachon, 1045 avenue de la Médecine, Université Laval, Québec, Canada G1V 0A6

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ABSTRACT

Establishment of specific vascular plants and *Sphagnum* species, as well as asymmetrical competition and facilitation between the two types of plants are apparently important in the development of microtopography in peatlands. To determine whether peatland vascular plants can facilitate the initiation of *Sphagnum* hummocks, and consequently the differentiation of bog microtopography, we investigated the effects of vascular plant life form and structure on *Sphagnum* stem length and biomass. We showed that *Sphagnum* stem length and biomass were enhanced by low density of vascular plants and other introduced structures, which thus favoured hummock formation. Dense covers of vascular plants also promoted moss height growth, but the *Sphagnum* stems were etiolated and fluffy, their densities were too low and biomass was too small to initiate clear hummocks. We also showed that vascular plants contributed to microhabitats with stable temperatures and high relative humidity favourable to *Sphagnum* growth. Stress-gradient hypothesis, predicting that the relative frequencies of facilitation and competition events will vary inversely along abiotic stress gradients, could explain the nature of the interaction between mosses and vascular plants. At the onset of microstructures formation in peatlands, abiotic stress is probably more important and facilitation events could be frequent. Microclimatic effects of vascular plants may be essential for *Sphagnum* growth. Then, the presence of ericaceous shrubs or young trees enhances the microtopography by physically reinforcing the hummocks. During accentuation of microtopography, the positive interactions between *Sphagnum* mosses and vascular plants may be replaced by competition as abiotic stress declines. This study introduces new evidence for the role of vascular plants in the formation and maintenance of hummocks, especially under drier growing conditions.

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1. Introduction

Microtopography in *Sphagnum*-dominated peatlands can be described as a mosaic of peaty hummocks whose surfaces lie at least 20 cm above the highest annual water table, hollows characterised by shallow water table and frequent inundation, and more or less flat intermediate zones called lawns (Payette and Rochefort, 2001; Weltzin et al., 2001). The formation of mud-bottoms (Karofeld, 2004), fire (Benscoter et al., 2005), intermittent drought or inundation (Jeník and Soukupová, 1992), nest-building by ants (Luken and Billings, 1986; Lesica and Kannowski, 1998), herbivore impacts such as goose grubbing or reindeer trampling,

and plant interactions (e.g. Vitt et al., 1975; Malmer et al., 1994) can all accentuate the microtopography in bogs. However, throughout their vast distribution in boreal peatlands, the most striking common factor in the development of hummocks and hollows is the interaction between mosses and vascular plants.

Under certain conditions, vascular plants can facilitate *Sphagnum* growth (Vitt et al., 1975; Luken and Billings, 1986; Malmer et al., 1994; Fenton and Bergeron, 2006). Moreover, the abundance and distribution of hummocks, lawns and hollows – the microstructural units in peatlands – appear to be determined by the life forms and architecture of vascular plants (Malmer et al., 1994). Kenkel (1988) reports that the presence of microtopography in a Canadian poor fen can be related to the establishment and growth of *Sphagnum* mosses amongst the branches of *Chamaedaphne calyculata*, and a similar phenomenon involving *Calluna vulgaris* is reported from European peatlands (Clymo and Hayward, 1982). Vascular plants can also act as nurse plants for *Sphagnum* by creating wetter and more stable microclimates and

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Nomenclature

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consequently improving microhabitat conditions (Soro et al., 1999; Boudreau, 1999; Tuittila et al., 2000; Heijmans et al., 2002). Thus, vascular plants can promote *Sphagnum* growth by providing both scaffolding and protection (Rydin and Jeglum, 2006).

The coexistence of *Sphagnum* mosses and vascular plants is certainly not a system at equilibrium because the two components compete asymmetrically for light, water and nutrients (Malmer et al., 2003). If the environment changes such that vascular plant growth is favoured, the increase in both shade and litterfall will retard *Sphagnum* growth (Berendse et al., 2001; Pauli et al., 2002; Limpens et al., 2003). An increase in vascular plant cover can also cause lowering of the water table by augmenting evapotranspiration (Tomassen et al., 2003), increasing the risk of drought for *Sphagnum* mosses. On the other hand, *Sphagnum* has a higher cation exchange capacity than vascular plants (Clymo, 1963; Craigie and Maass, 1966) so that a number of vascular plant species are often excluded by asymmetrical competition for nutrients (Heijmans et al., 2002; Malmer et al., 2003). Moreover, *Sphagnum* creates an unsuitable environment for decomposers and thus slows down litter decomposition and reduces mineralisation, which is the main source of nutrients for vascular plants (Svensson, 1995).

The dynamic interplay between facilitation and competition in plant communities has been explored in hundreds of studies (Callaway, 2007). From these, a stress-gradient hypothesis has emerged, predicting that the relative frequencies of facilitation and competition events will vary inversely along abiotic stress gradients (Bertness and Callaway, 1994). Facilitation is much more common under severe abiotic stress and can improve the performance or fitness of beneficiary species (Callaway, 1995; Stachowicz, 2001; Bruno et al., 2003). Facilitation and competition events can occur simultaneously, and the effect of one species on another will depend upon which is the strongest interaction for the environment at a given time (Callaway and Walker, 1997; Holgrem et al., 1997). It seems unlikely that this “love–hate” relationship between facilitation and competition events can be avoided in the interactions between plants in the hummock formation.

To determine whether peatland vascular plants can facilitate the initiation of *Sphagnum* hummocks and, consequently, the differentiation of boreal bog microtopography, we conducted three experiments to investigate the effect of vascular plants on *Sphagnum* stem length and biomass. Our hypotheses were based on the complexity of the vascular plants in relation with arrangement of stems, roots or leaves (complexity of ericaceous shrubs > sedges or young trees) and the creation of microclimates by vascular plants. First, we predicted that increased physical support combined with a humid microclimate and a stable temperature would have a facilitating effect on the growth in length of *Sphagnum* mosses. Secondly, we hypothesised that an increase of vascular plant density would increase competition for light, therefore reducing the production of *Sphagnum* biomass and slowing down hummock initiation.

2. Materials and methods

2.1. Field experiment

A field experiment was carried out over two years from 2006 to 2008 near Shippagan on the Acadian Peninsula, north-eastern New

Brunswick, Canada (47°43'53" N, 64°42'39" W), where annual mean temperature is 4.7 °C and annual mean precipitation is 1115 mm, of which 73% occurs as rain (Environment Canada, 2010). The site was a cutover peatland where trenches originally created by peat extraction have been spontaneously colonised by *Sphagnum* species (Robert et al., 1999). During the summer of 2004, six basins (15 m sides) were created in two different trenches by removing the vegetation and levelling the residual surface. *Sphagnum* mosses derived from the removed vegetation was then re-introduced. The protocol is described in detail by Landry and Rochefort (2009).

A randomised block design with six blocks (each within a half basin) and six treatments was used. The experimental units were 1.5 m squares. Selection criteria for the location of experimental units were *Sphagnum* cover \geq 75% and the absence of vascular plants and microtopography. The six treatments were randomly assigned to one of the selected experimental unit locations and consisted of 1) a control (no treatment); and the introduction of one of the following structures: 2) live *Eriophorum angustifolium* (Cyperaceae), 3) live *Eriophorum vaginatum* (Cyperaceae), 4) live *C. calyculata* (Ericaceae), 5) dead ericaceous shrubs, and 6) untreated wooden dowels, planted erect to imitate unbranched young trees. Water table depth relative to the ground surface was recorded at 24 dipwells installed within the basins on 16 occasions during the two growing seasons of the experiment. pH and electrical conductivity (corrected for H⁺ ions at 20 °C using the formula: $10^{-\text{pH}} \times 325/1000 \times 10^6$, Sjörs, 1950) were measured at the centre of each experimental block in July 2008 (pH/Ec/Tds/Temperature Tester, model HI98129, Hanna Instruments, Woonsocket, RI, USA).

Material for the living vascular plant treatments was hand-collected within the experimental site. Stems of *E. angustifolium* with at least one long (>5 cm) rhizome and several smaller ones were selected for Treatment 2. For Treatment 3, large tussocks of *E. vaginatum* were harvested whole and divided into patches 4–5 cm in diameter. The transplants of *C. calyculata* selected for Treatment 4 were 5–10 cm tall and had well-developed stem and root systems. For the dead ericaceous shrub treatment (Treatment 5), plants (mainly *Kalmia angustifolia*) were collected; their buds, leaves, flowers, seeds and roots were removed and the remaining stem systems were dried at 70 °C for 24 h. Although different species were used for treatments with live and dead ericaceous shrubs, the complexity of their stem structures was similar. The wooden dowels (Treatment 6) were 1.27 cm in diameter and about 30 cm long. For all treatments, the transplants or structures were placed ca. 10 cm apart within the central 1 m² of the experimental plot, such that initial cover was 20–25% for Treatments 2–5 (ericaceous shrubs and Cyperaceae) and around 1% for Treatment 6 (wooden dowels).

2.2. Greenhouse experiments

Two greenhouse experiments were conducted in two different greenhouse complexes at Laval University (Quebec City, Canada). Both experiments were of nine months' duration. The “Life form” greenhouse experiment ran from July 2007 to April 2008, and the “Life form plus vertical structure” greenhouse experiment from May 2008 to February 2009. Values presented with confidence limits in the account below are expressed as means \pm standard error.

The “Life form” greenhouse experiment was a repetition of field experiment under controlled conditions and tested the effect of vascular plant life form on the formation of *Sphagnum* hummocks. A randomised block design was used, with six blocks and the same six treatments as in the field experiment described above. The experimental units were plastic containers of plan dimensions

56 × 46 cm (44 cm deep), in which holes were drilled to maintain the water table at around –15 cm. Each container was filled with slightly humified *Sphagnum* peat (H2–H3 on the von Post scale) and the peat surface was rehydrated with distilled water and levelled. It was then completely covered with *Sphagnum* fibres (moss fragments with capitula, ca. 5 cm long) which had been harvested from a natural peatland in Quebec Province (46°45'57" N, 70°59'59" W) and carefully sorted to remove all vascular plants. Vascular plants were harvested from another natural peatland in Quebec Province (47°47'03" N, 69°28'34" W) and the selection, preparation and placement procedures for transplants were the same as for the field experiment (see above). The containers were watered three times a week with distilled water supplemented with a modified Rudolf solution (Faubert and Rochefort, 2002) until water overflowed from the holes. Temperature was 23.4 ± 0.2 °C for the 14-h photoperiod and 16.2 ± 0.1 °C at night, and relative humidity was $42.2 \pm 0.7\%$ (StowAway data loggers, Onset Computer Corporation, Pocasset, MA, USA).

After these simultaneous field and greenhouse experiments in which the same treatments were applied, a second greenhouse experiment ("Life form plus vertical structure") was conducted to investigate the effects of inert structures in more detail. A randomised block design was again used, this time with four blocks and nine treatments. The six previous treatments were repeated but the growth of live treatments was controlled, by cutting out stems as necessary, to maintain lower cover values than those attained in the "Life form" greenhouse experiment. Three new treatments were added to imitate unbranched young trees, as follows: 7) 40 wooden dowels of diameter 0.64 cm, 8) 10 wooden dowels of diameter 2.54 cm and 9) 40 smooth plastic straws of diameter 0.64 cm. The number of dowels or straws per experimental unit was adjusted to consistently offer a total surface contact area for *Sphagnum* mosses of around 80 cm² per cm increase in carpet thickness. The live vascular plants and dead ericaceous shrubs from the "Life form" greenhouse experiment were re-used, and the experimental setup was the same except that the plastic containers measured 61 × 41 × 42 cm. All experimental units were watered three times a week for the first five months. On each occasion, rainwater was applied until water emerged from the holes situated at –15 cm, then drainage down to –20 cm was allowed until the next watering. Thereafter, the frequency of watering was reduced to twice a week and the drainage level was set at –20 cm during watering and –25 cm at all other times, in order to control a fungal infection. Mean temperatures were 22.0 ± 0.1 °C for the 14-h photoperiod and 16.6 ± 0.1 °C at night, and mean relative humidity over a 24-h period was $66.8 \pm 0.3\%$ (Laval University greenhouse staff, unpublished data).

For both greenhouse experiments, artificial lights were turned on when the natural light dropped below 300 W m⁻² and initial pH and electrical conductivity values corrected for H⁺ ions at 20 °C (Sjörs, 1950) were measured for each block in a bulked sample containing peat from all experimental units.

2.3. Measurement of length, cover or frequency, and biomass of *Sphagnum* mosses

For each experimental unit of the field experiment, the cover of *Sphagnum* and vascular plants or structures was recorded in three randomly placed 25 × 25 cm quadrats after two years (in July 2008). The peat profile of restored peatland is characterised by a clear junction between the well-decomposed dark brown peat of the former catotelm which was at the surface before re-vegetation, and newly accumulated *Sphagnum* moss fibres (light brown to red and only slightly decomposed). The vertical distances from this junction to the capitula of ten individual *Sphagnum* stems per

quadrat were measured to determine length. Newly formed *Sphagnum* biomass was determined for two of the three quadrats per experimental unit by harvesting the *Sphagnum* moss fibres accumulated since restoration, removing vascular plants and litter, and drying to constant weight at 70 °C.

For the greenhouse experiments, the *Sphagnum* carpet in each experimental unit was allowed to establish for three months before the initial position of its surface was determined relative to a reproducible horizontal datum surface set above the rim of the container. This was done by measuring the vertical distance from the datum to the *Sphagnum* surface at 50 evenly distributed points and calculating a mean value. The surface height measurements were repeated after an interval of six months and the results were converted to *Sphagnum* length for each experimental unit by subtracting the mean value at the end of the experiment (after nine months of growth) from the initial mean value (obtained after three months of growth). As each set of surface height measurements was carried out, all cover beneath each reference mark was recorded so that the frequencies of *Sphagnum*, vascular plants and inert structures could be derived (point intercept method; Jonasson, 1988). At the end of each experiment, the plant biomass accumulated in each container since the beginning of the experiment was harvested, vascular plants and inert structures were removed, and the *Sphagnum* was dried to constant weight at 70 °C.

2.4. Temperature, relative humidity and irradiance monitoring

In the "Life form plus vertical structure" greenhouse experiment, data loggers were installed to measure temperature and relative humidity variations (microclimatic conditions) on the *Sphagnum* surface (HOBO[®] external temperature and relative humidity data loggers, model U23-002, Onset Computer Corporation, Pocasset, MA, USA). Only Treatments 1–5 and 7 were monitored, as these encompassed all of the structural variety under test. Hourly measurements were recorded throughout the six months from the end of the establishment period to the end of the experiment (180 days). Irradiance at the *Sphagnum* surface was measured manually at three locations within each experimental unit on a sunny day (no cloud during measurements, around noon), using a photometer (model LI-185B, GENEQ Inc., Montréal, QC, Canada).

2.5. Statistical analyses

The effects of the treatments on *Sphagnum* length and biomass (all experiments), and on cover or frequency of *Sphagnum* (field experiment and "Life form" greenhouse experiment), were analysed by conducting two-way ANOVAs for randomised block designs (using the GLM procedure available in SAS software; SAS Institute, 2003). Significant probability levels were set to $\alpha = 0.05$. All data were tested for homogeneity and normality and only the *Sphagnum* length data from both greenhouse experiments needed to be square-root transformed before analyses. *A-priori* contrasts based on the hypotheses (i.e. the complexity of vascular plants) were run for each experiment (see Tables 1–3 for details). The temperature, relative humidity and luminosity data from the "Life form plus vertical structure" greenhouse experiment were compared using protected LSDs (Least Significant Differences).

3. Results

3.1. Field experiment

During the two growing seasons of the experiment, the water table fluctuated between +1 and –18 cm relative to the ground surface (n = 16), pH ranged from 3.5 to 3.8 and corrected electrical

Table 1

Field experiment: results (*p*-values) of two-way ANOVAs and *a-priori* contrasts to evaluate the effects of vascular plants on *Sphagnum* length increment, biomass and cover when two growing seasons had elapsed after application of treatments. Values in bold type indicate significant differences ($p < 0.05$); d = diameter.

Source of variation	d.f.	Length	Biomass	Cover
Block	5	<0.01	<0.01	0.29
Treatment	5	<0.01	0.29	<0.01
Error	25			
Total	35			
Contrasts				
C1) Control vs. others	1	0.01	0.53	0.02
C2) <i>E. angustifolium</i> vs. <i>E. vaginatum</i>	1	0.15	0.27	<0.01
C3) <i>C. calyculata</i> vs. dead ericaceous shrubs	1	0.86	0.07	0.47
C4) <i>C. calyculata</i> vs. <i>Eriophorum</i> spp.	1	<0.01	0.24	<0.01
C5) Wooden dowels (d = 1.27 cm) vs. dead ericaceous shrubs	1	0.88	0.09	0.86

conductivity from 54 to 103 $\mu\text{S cm}^{-1}$. After two years of growth, 63 ± 7% of each experimental unit was covered by *Sphagnum* species belonging to Section Acutifolia (*Sphagnum flavicomans*, *Sphagnum fuscum* and *Sphagnum rubellum*) and 20 ± 5% by species belonging to Section Sphagnum (mainly *Sphagnum magellanicum*). Vascular plants (other than those used for treatments) had spontaneously colonised 8 ± 2% of each experimental unit (not significantly different between treatments; $p = 0.09$), and the cover of introduced live vascular plants had increased from the initial 20–25% to 31 ± 6% for *E. angustifolium*, 74 ± 5% for *E. vaginatum* and 25 ± 1% for *C. calyculata*.

The treatments had a significant positive effect on *Sphagnum* length, but a negative effect on *Sphagnum* cover (C1 in Table 1), that was mainly due to presence of *Eriophorum* species (Fig. 1). *Sphagnum* length was similar between *Eriophorum* species, even though *Sphagnum* cover was 145% lower beneath *E. vaginatum* than beneath *E. angustifolium* (C2). *Sphagnum* length was 25% higher in the presence of Cyperaceae (*Eriophorum* species) than with live ericaceous plants (*C. calyculata*), but its cover was 36% lower (C4). Other contrasts (C3 and C5) were not significant. *Sphagnum* biomass was unaffected by the treatments (Table 1).

3.2. "Life form" greenhouse experiment

The initial pH values ranged from 3.8 to 4.1, and corrected electrical conductivity from 50 to 146 $\mu\text{S cm}^{-1}$. The frequencies of transplanted live vascular plants increased with time, reaching 100 ± 0% for *E. angustifolium* and *E. vaginatum* and 74 ± 7% for *C. calyculata* by the end of the experiment. After nine months of

Table 2

"Life form" greenhouse experiment: results (*p*-values) of two-way ANOVAs and *a-priori* contrasts to evaluate the effects of vascular plants on *Sphagnum* length increment over six months, and biomass and cover after a growing period of nine months. Values in bold type indicate significant differences ($p < 0.05$); d = diameter.

Source of variation	d.f. ^a	Length	Biomass	Cover
Block	5	0.02	0.11	0.23
Treatment	5	0.01	<0.01	<0.01
Error	25			
Total	35			
Contrasts				
C1) Control vs. others	1	0.03	<0.01	0.01
C2) <i>E. angustifolium</i> vs. <i>E. vaginatum</i>	1	0.01	0.18	<0.01
C3) <i>C. calyculata</i> vs. dead ericaceous shrubs	1	0.02	0.02	0.34
C4) <i>C. calyculata</i> vs. <i>Eriophorum</i> spp.	1	0.03	<0.01	<0.01
C5) Wooden dowels (d = 1.27 cm) vs. dead ericaceous shrubs	1	0.05	0.87	0.48

^a d.f. error = 24 and d.f. total = 34 for length increment in "Life form" experiment.

Table 3

"Life form plus vertical structure" greenhouse experiment: results (*p*-values) of two-way ANOVAs and *a-priori* contrasts to evaluate the effects of vascular plants on *Sphagnum* length increment over six months and biomass after a growing period of nine months. Values in bold type indicate significant differences ($p < 0.05$); d = diameter.

Source of variation	d.f.	Length	Biomass
Block	3	<0.01	0.16
Treatment	8	<0.01	<0.01
Error	18		
Total	29		
Contrasts			
C1) Control vs. others	1	0.07	0.06
C2) <i>E. angustifolium</i> vs. <i>E. vaginatum</i>	1	0.73 ^a	0.90 ^a
C3) <i>C. calyculata</i> vs. dead ericaceous shrubs	1	0.19	0.36
C4) <i>C. calyculata</i> vs. <i>Eriophorum</i> spp.	1	0.19 ^a	0.03^a
C5) Wooden dowels (d = 0.67 cm) vs. dead ericaceous shrubs	1	0.16	0.83
C6) Wooden dowels (d = 1.27 cm) vs. <i>E. angustifolium</i>	1	0.43	0.02
C7) Wooden dowels (d = 1.27 cm) vs. wooden dowels (d = 0.67 cm)	1	0.65	0.55
C8) Wooden dowels (d = 0.67 cm) vs. plastic straws (d = 0.67 cm)	1	0.39	0.95

^a Data were collected from only one experimental unit with *E. vaginatum* because of a fungal infection (infected experimental units were not included in the analyses) and are not statistically valid.

growth, the *Sphagnum* carpet was composed of 86 ± 4% *S. rubellum* and 11 ± 5% *S. magellanicum* (frequency values).

Sphagnum length was 76% higher when vascular plants or dowels were present (C1 in Table 2 and Fig. 2A) whereas *Sphagnum* biomass and frequency were respectively 28% and 12% lower in the presence of treatments (Fig. 2B and C), again largely because of the presence of *Eriophorum* species. Contrasts for *Sphagnum* length were more significant in the life form experiment than in the field experiment. That was reflected by a length in the presence of *E. vaginatum* double that in the presence of *E. angustifolium* (C2), 62% higher beneath live ericaceous shrubs than beneath dead ones (C3) and 57% greater under wooden dowels than in under dead ericaceous shrubs (C5). *Sphagnum* length was also 52% higher with live ericaceous shrubs than with *Eriophorum* species (C4), contradicting field results. *Sphagnum* frequency was 42% lower beneath *E. vaginatum* than beneath *E. angustifolium* (C2), confirming results observed in the field. However, contrary to field experiment, biomass was 21% lower under live ericaceous shrubs than under dead ones (C3). Biomass and frequency were also respectively 33% and 37% higher with live ericaceous shrubs than with *Eriophorum* species (C4).

3.3. "Life form plus vertical structure" greenhouse experiment

The initial pH varied from 3.6 to 3.8 and corrected electrical conductivity from 1 to 30 $\mu\text{S cm}^{-1}$. After nine months of growth, a *S. rubellum* carpet covered 97 ± 1% of each experimental unit (frequency) and the (controlled) frequencies of vascular plants were 53 ± 4% for *E. angustifolium*, 60% for *E. vaginatum* and 50 ± 1% for *C. calyculata*. All replicates of Treatment 8 (2.54 cm wooden dowels) and three experimental units of Treatment 3 (*E. vaginatum*) were lost due to a fungal infection, and so provided no data for inclusion in the analyses.

The presence of vascular plants, wooden dowels or plastic straws did not promote *Sphagnum* length or depress *Sphagnum* biomass or frequency as in the other two experiments (C1 in Table 3 and Fig. 3). Indeed, of the statistically valid comparisons, all indicated non-significant differences in *Sphagnum* length and only one (C6) identified a significant difference in *Sphagnum* biomass, which

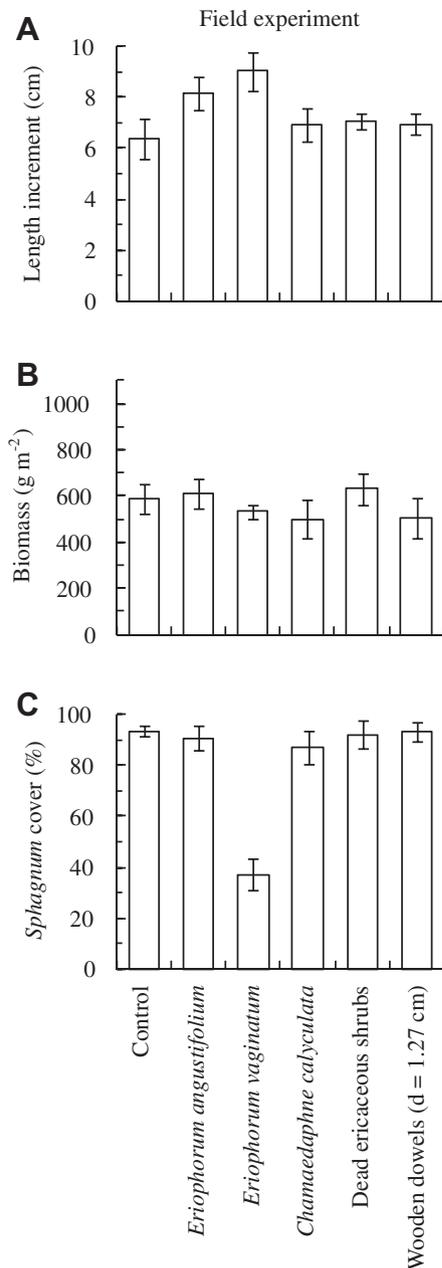


Fig. 1. Field experiment: effects of vascular plant treatments on A) *Sphagnum* length, B) *Sphagnum* biomass and C) *Sphagnum* cover when two growing seasons had elapsed after application of the treatments (mean \pm SE; n = 6 in all cases). See Table 1 for p-values of contrasts. d = Diameter.

was 20% lower with *E. angustifolium* than with wooden dowels (diameter 1.27 cm) offering approximately the same contact surface for *Sphagnum* mosses as the *Eriophorum* stems.

3.4. Temperature, relative humidity and irradiance monitored under structural treatments

Temperature at the *Sphagnum* surface was highest in treatments with zero (control) or sparse cover of introduced structures (dead ericaceous shrubs and wooden dowels; Fig. 4A). The highest hourly mean temperature was for the control treatment at noon (23.8 ± 0.2 °C), and the lowest was for Treatment 7 (0.64 cm diameter wooden dowels) at 6 a.m. (13.9 ± 0.1 °C). The daily

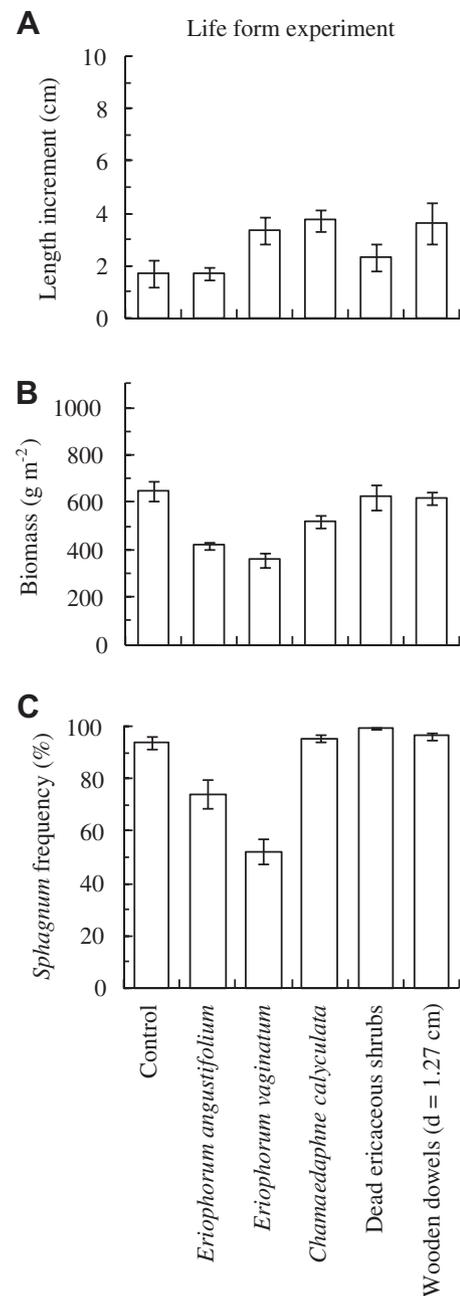


Fig. 2. “Life form” greenhouse experiment: effects of vascular plant treatments on A) *Sphagnum* length over six months; and B) *Sphagnum* biomass and C) *Sphagnum* frequency after a growing period of nine months (mean \pm SE; n = 6, except in control treatment where n = 5). See Table 2 for p-values of contrasts. d = Diameter.

temperature range exceeded 10.8 °C in average for 50% of the time in the treatments with dead ericaceous shrubs and wooden dowels, but for only 11% in average of the time beneath live vascular plants (Fig. 4B). Relative humidity at the *Sphagnum* surface was always lower than 90% in treatments with zero (control) and wooden dowels whereas it always exceeded 92% for other treatments (Fig. 4C). The highest hourly mean value of relative humidity was for the treatment with *E. angustifolium* at 1 a.m. ($95.9 \pm 0.2\%$), and the lowest value was for wooden dowels at 1 p.m. ($83.3 \pm 0.6\%$). The diurnal range of relative humidity exceeded 12.6% (wooden dowels) and 10.6% (control) for 50% of the time, but for only 6.7% of the time in average in the least variable treatments (*Eriophorum* species and dead ericaceous shrubs) (Fig. 4D). Significant shading of

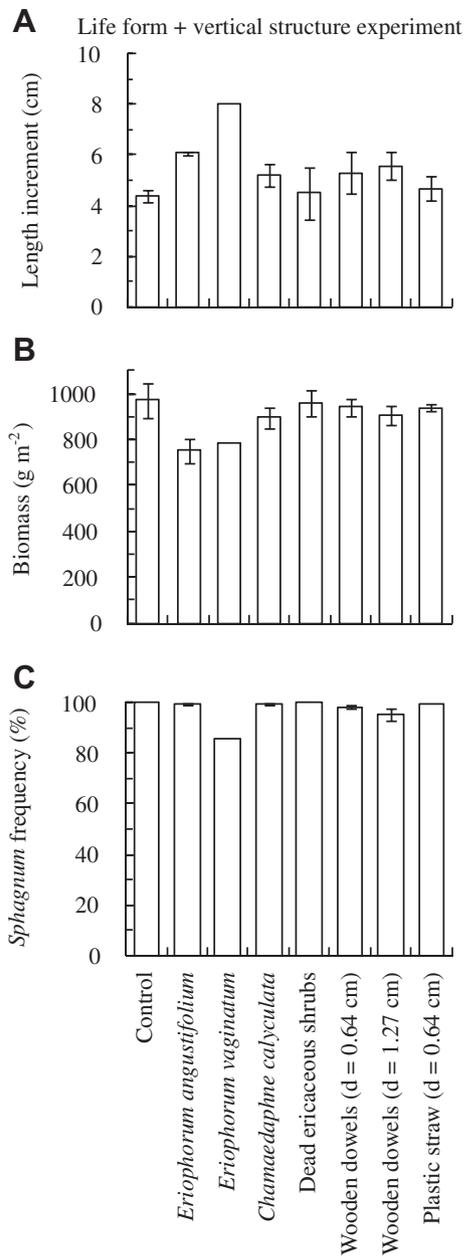


Fig. 3. “Life form plus vertical structure” greenhouse experiment: effects of vascular plant treatments on A) *Sphagnum* length B) *Sphagnum* biomass, and C) *Sphagnum* frequency after a growing season of nine months (mean \pm SE; $n = 4$ except for *E. vaginatum* where $n = 1$) Only one experimental unit with *E. vaginatum* was present at the end of the experiment. See Table 3 for p -values of contrasts. $d =$ Diameter.

the *Sphagnum* carpet occurred only beneath live vascular plants. In fact, irradiance in Treatments 1, 5 and 7 (control, dead ericaceous shrubs and inert structures) was almost double that beneath live ericaceous shrubs and Cyperaceae (389 ± 23 vs. $200 \pm 33 \mu\text{E m}^{-2} \text{s}^{-1}$).

4. Discussion

As expected, vascular plant structures generally promoted *Sphagnum* length until the vascular plants reached high density, at which stage the cover and biomass of *Sphagnum* declined. However, the effects of the different vascular plant life forms varied with the growing conditions of the experiments and did not exactly confirm

our hypotheses. Even though the duration of the two greenhouse experiments was the same, *Sphagnum* length and biomass were much higher (about double) in the “Life form plus vertical structure” experiment than in the “Life form” experiment. We believe that differences between experiments can be explained in terms of the prevailing abiotic conditions and the density of vascular plants.

4.1. Effects of vascular plant structures

Our results support the first part of the hypothesis of Malmer et al. (1994), which proposes that *Sphagnum* length should increase in the presence of ericaceous shrubs or other vascular plants with well-developed root and stem systems; but not the second part of the hypothesis that states that “clonal herbs with looser structures” should stabilise hollows and lawns rather than promote hummock formation. We found that a cover of Cyperaceae can favour *Sphagnum* length. In the field experiment, small *Sphagnum* hummocks formed around *Eriophorum* stems even though the water table was close to the surface for much of the year. As such a hummock increases in height, *Sphagnum* species of drier microhabitats (such as *S. fuscum* and *S. rubellum*) should colonise and contribute to the development, maintenance and accentuation of hummocks (Vitt et al., 1975). These species are better able to acquire water by capillarity as well as to retain it (Rydin, 1993) and have lower decomposition rates than hollow species (Johnson and Damman, 1993). The oxic zone thickness increases with the hummock height. Growth of ericaceous shrubs, which require a more oxygenated root environment than other bog plants, can be promoted. A firm matrix of roots and stems can thus be formed and that reinforces and supports *Sphagnum* growth. Certainly, in restored sites, the highest cover of ericaceous shrubs (>30%) is associated with the highest hummocks (Pouliot, 2011).

One unpredicted result was that *Sphagnum* length was favoured by the wooden dowels which we used to imitate young trees. It appears that the roughness of the wood was sufficient to promote upward growth of the moss regardless of dowel density provided. In natural ecosystems, young trees also present branches and roots, increasing anchor points for *Sphagnum* mosses. In restored sites and sites with spontaneous re-vegetation after peat extraction, young trees are often found in the centres of tall *Sphagnum* hummocks (personal observation). Thus, it seems that the effectiveness of the erect structures tested in promoting *Sphagnum* length arises from the ability of these mosses to use all available protruding structures to support their upward growth.

4.2. Creation of microclimates by vascular plants

The presence of vascular plants maintains high levels of relative humidity, prevents extremes of temperature, limits diurnal ranges of relative humidity and temperature, and reduces light intensity at the *Sphagnum* surface. Even dead ericaceous shrubs are sufficient to elevate relative humidity by restricting air movement and increasing the thickness of the boundary layer. Therefore, it is not surprising that *Sphagnum* length increased when vascular plants or structures were introduced in our experiments. Under conditions of moderate vascular plant cover ($\sim 50\%$), shade is sufficient to protect the *Sphagnum* without impeding hummock formation by blocking almost all light. For example, Murray et al. (1993) found that total *Sphagnum angustifolium* length was 2–3 times higher in shaded plots than in control plots that lacked vascular plants, and that photoinhibition of photosynthesis can be observed even at moderately high light intensities. Thus, the microclimates created by vascular plant covers provide optimal growth conditions for *Sphagnum* species, principally by reducing irradiance and water losses (Harley et al., 1989), and consequently maintaining high

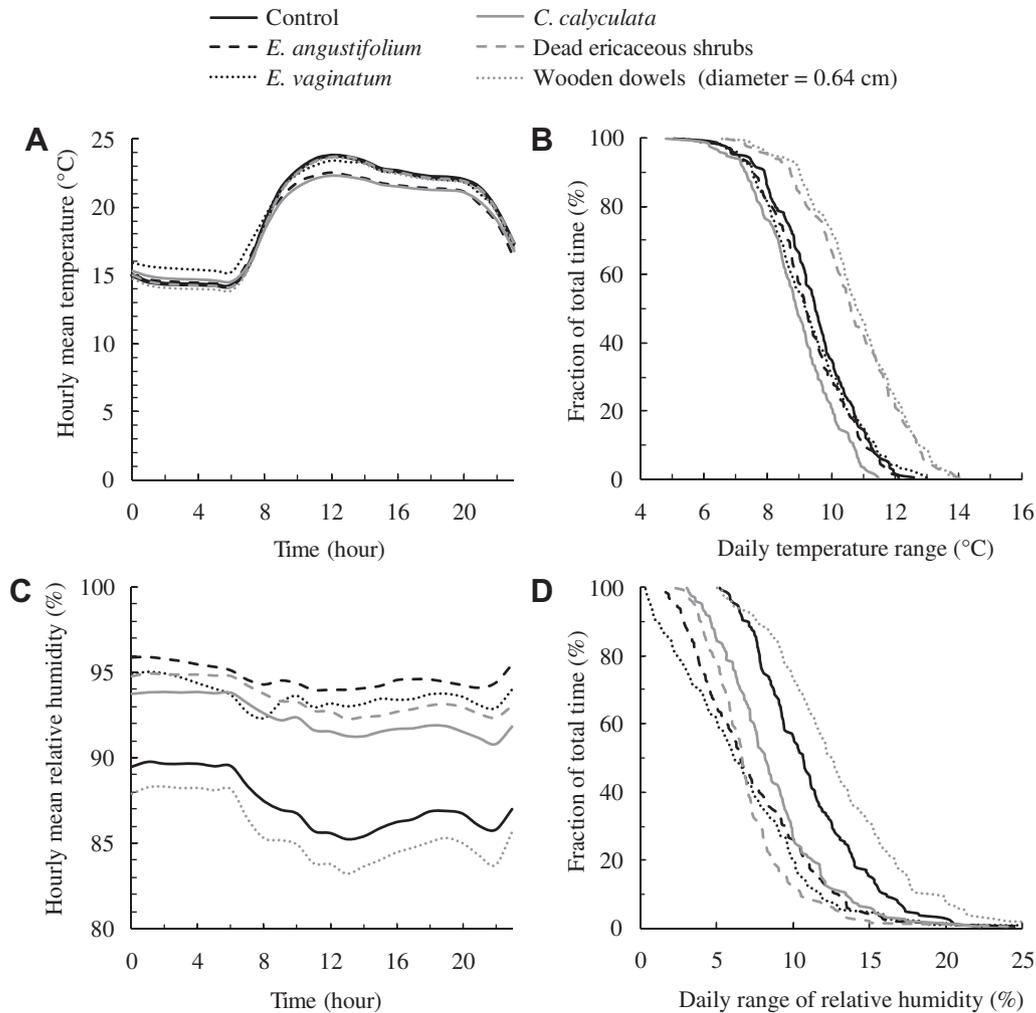


Fig. 4. “Life form plus vertical structure” greenhouse experiment: effects of vascular plant treatments on A) hourly mean temperature, B) cumulative curves for daily temperature range, C) hourly mean relative humidity and D) cumulative curves for daily range of relative humidity; $n = 180$ in all cases. The cumulative curves show the percentage of the 180 days of data logger operation on which the range of temperature or relative humidity indicated by the abscissa was attained or exceeded. $d =$ Diameter.

relative humidity. On the other hand, increased shading under very dense covers of vascular plants (as in the “life form” experiment) tends to impede hummock formation because the *Sphagnum* stems become etiolated and fluffy, they grow less densely, and the rate of biomass declines.

Large *Sphagnum* length recorded in the “Life form plus vertical structure” greenhouse experiment are probably attributable to a 60% higher relative humidity than in the other greenhouse experiment. *Sphagnum* growth increases with temperature if the water supply is not limiting (Dorrepaal et al., 2004; Breeuwer et al., 2008), but a period of drought impacts negatively on *Sphagnum* growth, even under cool conditions, and few species can survive excessive drying (Clymo, 1973; Sagot and Rochefort, 1996). Therefore, it seems likely that the low relative humidity in the greenhouse during the “Life form” experiment furnished ambient conditions of water stress under which more favourable microclimates for *Sphagnum* growth have been created by the presence of vascular plants. On the other hand, the combination of high relative humidity with similar temperatures in the greenhouse during the “Life form plus vertical structure” experiment provided optimal growth conditions for *Sphagnum* and vascular plants were not needed for the initiation or modification of surface structure. This hypothesis is supported by the observation that some of the hummocks which formed in the “Life form plus vertical structure”

experiment collapsed when the relative humidity level was reduced in connection with greenhouse maintenance work, apparently because there were no vascular plants to strengthen the hummocks and prevent peat compaction as suggested by Malmer et al. (1994). Thus, the usefulness of vascular plants in facilitating *Sphagnum* hummock formation seems to be particularly dependent on relative humidity.

The principle that environmental conditions determine the importance of vascular plants for the initiation and development of hummock–hollow patterning in bogs is consistent with some observed differences in the characteristics of natural bogs between different climatic zones. The hyperoceanic climate of South Patagonia supports bogs that are dominated by a single *Sphagnum* species (*S. magellanicum*), which can form all microforms from hollows to tall hummocks, and vascular plants are not ubiquitous (Kleinebecker et al., 2007; Grootjans et al., 2010). In contrast, under temperate continental climates such as those of the boreal forest biome, hummock tops are almost always covered by an association of *Sphagnum* mosses and vascular plants with well-developed root and stem systems, such as ericaceous shrubs (e.g. Vitt et al., 1975; Damman and Dowhan, 1981; Andrus, 1986). Here, the shady and moist microclimates created by vascular plants can be important for the upward growth of *Sphagnum* (and thus for hummock evolution) under the drier climatic conditions, as in the older

greenhouse complex with low (ca. 42%) and poorly stabilised relative humidity which hosted our “Life form” greenhouse experiment. In other words, it seems that vascular plant structures are an enhancing factor for hummock formation, rather than a prerequisite as Malmer et al. (1994) have suggested. Vascular plants may or may not be essential to the development of bog microtopography, depending upon the climate.

4.3. Interactions between vascular plants and *Sphagnum* mosses

Positive interactions between plants contribute substantially to the formation of hummock elements within peatland microtopography. Ericaceous shrubs and young trees in particular, but also Cyperaceae, provide internal structure (skeletons) for hummocks. The growth of vascular plants increases the availability of structures and therefore living space for other species, which amounts to a form of ecological engineering according to Jones et al. (1997). Vascular plants, especially Cyperaceae, also act as nurse species during the initiation of hummocks, insofar as they modify abiotic conditions beneath their leaves. For example, in a fen restoration project, bryophytes regenerated most successfully in the shade provided by *Scirpus cyperinus* (Graf and Rochefort, 2008). Thus, facilitation events according with the stress-gradient hypothesis (Bertness and Callaway, 1994), such as ecological engineering and nursing by vascular plants, are particularly important for the establishment and length of *Sphagnum* mosses during the earliest stages of microstructures formation, when abiotic stresses are still dominant.

Negative interactions between plants that occur during the formation of microtopography must also be considered as potential influences on hummock development. *Sphagnum* mosses are autogenic engineers in peatland ecosystems because they acidify the environment, alter water relations, capture nutrients early in their terrestrial cycles, and immobilise these in slowly decomposing peat (Svensson, 1995; Malmer et al., 2003). This means that only the presence of *Sphagnum* mosses can reduce the potential for growth and reproduction of vascular plants. In order to keep pace with the elongation of *Sphagnum* stems, the vascular plants must adopt growth strategies that effect continuous upward movement of meristems and frequent formation of adventitious roots, which reinforces hummock structure. The presence of vascular plants also improves conditions for *Sphagnum* growth by reducing abiotic stress, and this in turn increases competition between *Sphagnum* and vascular plants for water, light and nutrients, the principal resources that plants strive to secure in peatlands (Malmer et al., 2003). On the other hand, an increase in vascular plant cover will reduce the accessibility of both light and water to *Sphagnum* mosses, and thus impede its growth, by increasing shade (Berendse et al., 2001; Pauli et al., 2002; Malmer et al., 2003) and intensifying evapotranspiration and water table drawdown (Tomassen et al., 2003). However, interspecific competition amongst mosses or vascular plants is likely to operate during the development of microtopography in natural peatlands and should also be considered in this context (not possible in our experiments). In summary, once the plants are sufficiently well established that the frequency at which they experience abiotic stress declines, competition becomes extremely important in the initiation and subsequent development of microtopography. In this situation, small changes in abiotic conditions can change the course of microstructure evolution by favouring the growth of one species or species group over others.

4.4. Conclusion

The growth in length of *Sphagnum* stems is promoted by the structures of *Eriophorum* species, ericaceous shrubs or imitation

young trees when vascular plant cover is moderate (~50%) and abiotic conditions are sub-optimal. An increase in the cover of vascular plants allows moss stems to continue increasing in length but precludes high stem densities and substantially reduces biomass. Consequently, hummocks cannot form beneath dense vascular plant covers. During the earliest stages of microstructure initiation, the favourable microclimates beneath the leaves of vascular plants are probably more important for *Sphagnum* growth than the physical support offered by their roots or stems. Later, the presence of ericaceous shrubs or young trees is necessary to strengthen and thus prevent collapse of hummocks as they increase in size during microtopography enhancement. Positive interactions such as facilitation of *Sphagnum* growth by vascular plants may be superceded by competition when the moss becomes sufficiently established, and competitive interactions contribute in various ways to microtopography accentuation. In fact, as in many other plant communities (Callaway, 1995), both facilitation and competition contribute to driving the evolution of microstructures. Our study cannot answer the “chicken-and-egg” question of whether vascular plants or *Sphagnum* mosses arrive first, but it provides strong evidence for the usefulness of vascular plants in the formation and maintenance of hummocks, especially in drier continental climates.

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References

- Andrus, R.E., 1986. Some aspects of *Sphagnum* ecology. *Can. J. Bot.* 64, 416–426.
- Benscoter, B.W., Wieder, K., Vitt, D.H., 2005. Linking microtopography with post-fire succession in bogs. *J. Veg. Sci.* 16, 453–460.
- Berendse, F., van Breemen, N., Rydin, R., Buttler, A., Heijmans, M.M.D., Hoosbeek, M.R., Lee, J.A., Mitchell, E., Saarinen, T., Vasander, H., Wallén, B., 2001. Raised atmospheric CO₂ levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bog. *Global Change Biol.* 7, 591–598.
- Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193.
- Boudreau, S., 1999. Restauration de tourbières exploitées, abandonnées et recolonisées par diverses communautés végétales. M. Sc., Université Laval, Québec, Canada, 93 pp.
- Breeuwer, A., Heijmans, M.M.P.D., Robroek, B.J.M., Berendse, F., 2008. The effect of temperature on growth and competition between *Sphagnum* species. *Oecologia* 156, 155–167.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125.
- Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78, 1958–1965.
- Callaway, R.M., 1995. Positive interactions among plants. *Bot. Rev.* 61, 306–349.
- Callaway, R.M., 2007. *Positive Interactions and Interdependence in Plant Communities*, first ed. Springer, New York.
- Clymo, R.S., 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. *Ann. Bot. Lond.* 27, 309–324.
- Clymo, R.S., 1973. The growth of *Sphagnum*: some effects of environment. *J. Ecol.* 61, 849–869.
- Clymo, R.S., Hayward, P.M., 1982. The ecology of *Sphagnum*. In: Smith, A.J.E. (Ed.), *Bryophyte Ecology*. Chapman and Hall, London, pp. 229–289.
- Craigie, J.S., Maass, W.S., 1966. The cation-exchanger in *Sphagnum* spp. *Ann. Bot. Lond.* 30, 153–154.

- Damman, A.W.H., Dowhan, J.J., 1981. Vegetation and habitat conditions in Western Head Bog, a southern Nova Scotian plateau bog. *Can. J. Bot.* 59, 1343–1359.
- Dorrepaal, E., Aerts, R., Cornelissen, J.H.C., Callaghan, T.V., van Logtestijn, R.S.P., 2004. Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. *Global Change Biol.* 10, 93–104.
- Environment Canada, May 2010. Canadian climate norms 1971–2000. http://www.climat.meteo.gc.ca/climate_normals/index_f.html.
- Faubert, P., Rochefort, L., 2002. Response of peatland bryophytes to burial by wind-dispersed peat. *Bryologist* 105, 96–104 (see Erratum in *Bryologist* 105, 299).
- Fenton, N.J., Bergeron, Y., 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. *J. Veg. Sci.* 17, 65–76.
- Graf, M.D., Rochefort, L., 2008. Moss regeneration for fen restoration: field and greenhouse experiments. *Restor. Ecol.* 18, 121–130.
- Grootjans, A., Iturraspe, R., Lanting, A., Fritz, C., Joosten, H., 2010. Ecohydrological features of some contrasting mires in Tierra del Fuego, Argentina. *Mires Peat* 6. http://www.mires-and-peat.net/map06/map_06_01.htm Art. 1. Online.
- Harley, P.C., Tenhunen, J.D., Murray, K.J., Beyers, J., 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.
- Heijmans, M.M.P.D., Klees, H., Berendse, F., 2002. Competition between *Sphagnum magellanicum* and *Eriophorum angustifolium* as affected by raised CO₂ and increased N deposition. *Oikos* 97, 415–425.
- Holgre, M., Scheffer, M., Huston, M.A., 1997. The interplay of facilitation and competition in plant communities. *Ecology* 78, 1966–1975.
- Jeník, J., Soukupová, L., 1992. Microtopography of subalpine mire in the Krkonose Mountains, the Sudetes. *Preslia* 64, 313–326.
- Johnson, L.C., Damman, A.W.H., 1993. Decay and its regulation in *Sphagnum* peatlands. *Adv. Bryol.* 5, 249–296.
- Jonasson, S., 1988. Evaluation of the point intercept method for the estimation of plant biomass. *Oikos* 52, 101–106.
- Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78, 1946–1957.
- Karofeld, E., 2004. Mud-bottom hollows: exceptional features in carbon-accumulating bogs? *Holocene* 14, 119–124.
- Kleinebecker, T., Hölzel, N., Vogel, A., 2007. Gradients of continentality and moisture in South Patagonian ombrotrophic peatland vegetation. *Folia Geobot.* 42, 363–382.
- Kenkel, N.C., 1988. Spectral analysis of hummock–hollow pattern in a weakly minerotrophic mire. *Plant Ecol.* 78, 45–52.
- Landry, J., Rochefort, R., 2009. Site expérimental de culture de sphaigne, Shippagan, Nouveau-Brunswick. Rapport d'activité 2003–2008. Chaire de recherche industrielle du CRSNG en aménagement des tourbières. Groupe de recherche en écologie des tourbières/Peatland Ecology Research Group, Université Laval, Québec.
- Lesica, P., Kannowski, P.B., 1998. Ants create hummocks and alter structure and vegetation of a Montana fen. *Am. Midl. Nat.* 139, 58–68.
- Limpens, J., Berendse, F., Klees, H., 2003. N deposition affects N availability in interstitial water, growth of *Sphagnum* and invasion of vascular plants in bog vegetation. *New Phytol.* 157, 339–347.
- Luken, J.O., Billings, W.D., 1986. Hummock-dwelling ants and the cycling of microtopography in an Alaskan peatland. *Can. Field Nat.* 100, 69–73.
- Malmer, N., Svensson, B.M., Wallén, B., 1994. Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobot.* 29, 483–496.
- Malmer, N., Albinsson, C., Svensson, B.M., Wallén, B., 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos* 100, 469–482.
- Murray, K.J., Tenhunen, J.D., Nowak, R.S., 1993. Photoinhibition as a control on photosynthesis and production of *Sphagnum* mosses. *Oecologia* 96, 200–207.
- Pauli, D., Peintiger, M., Schmid, B., 2002. Nutrient enrichment in calcareous fens: effects on plant species and community structure. *Basic Appl. Ecol.* 3, 255–266.
- Payette, S., Rochefort, L., 2001. *Écologie des tourbières du Québec-Labrador*, first ed. Presse de l'Université Laval, Québec.
- Pouliot, R., 2011. *Initiation du gradient de buttes et de dépressions dans les tourbières ombrotrophes boréales*. PhD thesis, Université Laval, Quebec City, Canada.
- Robert, É.C., Rochefort, R., Garneau, M., 1999. Natural revegetation of two block-cutting post-mined peatlands in eastern Canada. *Can. J. Bot.* 77, 447–459.
- Rydin, H., Jeglum, J.K., 2006. *The Biology of Peatland*, first ed. Oxford University Press, Oxford.
- Rydin, H., 1993. Mechanisms of interactions among *Sphagnum* species along water-level gradients. *Adv. Bryol.* 5, 153–185.
- Sagot, C., Rochefort, L., 1996. Tolérance des sphaignes à la dessiccation. *Cryptog. Bryol. Lichénol.* 17, 171–183.
- SAS Institute, 2003. *Language Guide*. Release 9.1. SAS Institute, Inc, Cary, NC.
- Sjörs, H., 1950. On the relation between vegetation and electrolytes in North Swedish mire waters. *Oikos* 2, 241–258.
- Soro, A., Sundberg, S., Rydin, H., 1999. Species diversity, niche metrics and species associations in harvested and undisturbed bogs. *J. Veg. Sci.* 10, 549–560.
- Stachowicz, J.J., 2001. Mutualism, facilitation, and the structure of ecological communities. *BioScience* 51, 235–246.
- Svensson, B.M., 1995. Competition between *Sphagnum fuscum* and *Drosera rotundifolia*: a case of ecosystem engineering. *Oikos* 74, 205–212.
- Tomassen, H.B.M., Smolders, A.J.P., Limpens, J., Lamers, L.P.M., Roelofs, J.G.M., 2003. Expansion of invasive species on ombrotrophic bogs: desiccation of high N deposition. *J. Appl. Ecol.* 41, 139–150.
- Tuittila, E.-V., Rita, H., Vasander, H., Laine, J., 2000. Vegetation patterns around *Eriophorum vaginatum* L. tussocks in a cut-away peatland in southern Finland. *Can. J. Bot.* 78, 47–58.
- Vitt, D.H., Crum, H.A., Snider, J.A., 1975. The vertical zonation of *Sphagnum* species in hummock–hollow complexes in northern Michigan. *Mich. Bot.* 14, 190–200.
- Weltzin, J.F., Harth, C., Bridgman, S.D., Pastor, J., von der Harr, M., 2001. Production and microtopography of bog bryophytes: response to warming and water-table manipulations. *Oecologia* 128, 557–565.