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The influence of past and present hydrological conditions on *Sphagnum* recolonization and succession in a block-cut bog, Québec

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Abstract:

This study of an abandoned cutover bog aims to understand the processes controlling moisture conditions that have led to distinct spatial patterns of *Sphagnum* recolonization, and also how substrate conditions may have changed since abandonment and the implications for plant establishment. Two (unreplicated) symmetrical $12 \times 3{\cdot}5$ m^2 quadrats either side of the centre-line of a block-cut trench were treated by removing all recolonized vegetation, including *Sphagnum*, from one quadrat (REMOV), examining *Sphagnum*-covered (SPHAG) peat in the other, and bare peat (BARE) in both. Average volumetric soil moisture contents θ in the peat (2 cm below the surface) of the SPHAG and REMOV substrates were similar (~86%), but greater than in BARE peat (~78%). In a location not manipulated for this experiment, where *Sphagnum* cushions have re-established on bare cutover peat, θ beneath the cushions was 5–14% greater than in bare cutover peat directly adjacent to it, indicating that cushions can regulate local substrate water storage, and benefit from it during periods of increased water demand. This may have assisted in the lateral expansion of *Sphagnum*. A loosely structured 0·5 to 1·0 cm thick organic litter layer (chiefly Ericaceae) overlying the BARE peat substrate slowed the rate of drying of bare peat in a laboratory sample. The laboratory tests found the capillary fringe to be up to 26 cm above the water table. The dry conditions and the larger pore structure of this litter layer hindered upward capillary flow and, therefore, plant water availability. In (occluded) ditches and low areas, the capillary fringe remained within 5 cm of the surface, and these locations supported the most complete *Sphagnum* cover. In slightly higher areas, where the capillary fringe was about 20 cm below the surface, and because of the leaf litter, capillary water supply to the surface is sufficiently restricted to limit *Sphagnum* recolonization. These locations may have to await lateral expansion of *Sphagnum* cushions to achieve a full cover. Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS peat; peatland; restoration; *Sphagnum*; capillary fringe; capillary barrier; hydrology; cutover bog

INTRODUCTION

In Canada, approximately 16 000 ha (approximately 0·02%) of peatlands have been exploited for horticultural peat (Keys, 1992), the majority located in southern Canada, where many peatlands have already been lost to agricultural and urban development (National Wetlands Working Group, 1988). Peat extraction by hand (block-cut) or mechanical (e.g. vacuum) techniques generally involves drainage and removal of the acrotelm, which in undisturbed systems provides essential self-regulating hydrological mechanisms (Ingram, 1978). This creates harsh hydrological and microclimatic conditions (Price *et al.*, 1998) generally unsuitable for *Sphagnum* regeneration (Rochefort, 2000).

Removal of the acrotelm exposes the underlying, formerly waterlogged peat, i.e. catotelm peat (Ingram, 1978). The smaller diameter pores characteristic of this more decomposed and compacted peat reduce water storage capacity (Beets, 1992; Schouwenaars and Vink, 1992), lower saturated hydraulic conductivity (Päivänen, 1973; Boelter, 1965), and increase capillary water retention (Boelter, 1968). After drainage, and

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with increasing time since abandonment, the peat matrix continues to change structurally due to primary consolidation, secondary compression, shrinkage (Schothorst, 1977; Price and Schlotzhauer, 1999; Van Seters and Price, 2002) and oxidation (Waddington and Price, 2000). This decreases water storage capacity, further contributing to deeper and more variable water tables (Schouwenaars, 1993; Price, 1996). Soil moisture declines rapidly during drier periods when the water table is low, since rates of upward capillary flow cannot keep pace with evapotranspiration demands at the peat surface (Price, 1997), further limiting water availability to plants, especially non-vascular *Sphagnum*.

The general conditions needed for *Sphagnum* to recolonize a bare cutover peat surface successfully include a high and stable water table (Campeau and Rochefort, 1996; Grosvernier *et al.*, 1997), high soil moisture (Sagot and Rochefort, 1996) and high pore-water pressures (Price, 1997). Specifically, Price (1997) has suggested that when pore-water pressure in peat falls below -100 cm the *Sphagnum* plants become incapable of extracting water from the peat. Price and Whitehead (2001) determined that recolonization of *Sphagnum* in a block-cut bog was rare where pore-water pressure dropped below -100 cm. For restoration purposes, retention of winter precipitation or snowmelt water is especially important to overcome deficiencies in water storage caused by alteration of the peat matrix (Price *et al.*, 2002).

Numerous studies have documented revegetation patterns in abandoned peatlands at different time scales, and include general observations of *Sphagnum* occurrence and prevailing hydrological conditions at the time of these surveys (e.g. Famous *et al.*, 1992; Meade, 1992; Mawby, 1995; Money, 1995; Lavoie and Rochefort, 1996; Girard, 1999). Few attempts, however, have been made to investigate how micro-scale hydrological processes may have directed *Sphagnum* succession since abandonment. Palaeoecological studies suggest that the soil condition many years after recolonization is not necessarily a good indicator of its state following abandonment (Robert *et al.*, 1999). The objective of this research, therefore, was to understand the processes controlling moisture conditions that have led to distinct spatial patterns of *Sphagnum* recolonization, how the substrate conditions may have changed since abandonment, and the implications for plant establishment. The approach here compared the hydrology on adjacent quadrats that were treated by removing *Sphagnum* cover from one quadrat to replicate the soil condition shortly after abandonment.

STUDY AREA

Cacouna peatland (47°52′N, 69°27′W), located approximately 10 km northeast of Rivière-du-Loup, is a domed bog of the Low Boreal Wetland Region (NWWG, 1988) in Québec, Canada. Climatic data from the St Arsène weather station (2 km from the study site) indicate that the climate is humid–continental with a mean annual total precipitation (1961–90) of 924 mm, with 27% of this precipitation falling as snow. The mean annual temperature (1961–90) is 3 °C, with mean temperatures in January and July of -12 °C and 18 °C respectively (Environment Canada, 1993).

The bog began to form approximately 9800 ± 100 years ago (Van Seters and Price, 2002) upon a clay substrate of low hydraulic conductivity deposited by the Goldthwait Sea (Dionne, 1977). The bog originally covered an area of 175 ha (Lavoie and Rochefort, 1996), but agricultural development and road building along the periphery has reduced the size of the peatland to 133 ha (Girard, 1999). A railway bisects the peatland roughly along a natural groundwater divide, which has subsequently compressed the underlying peat, creating a barrier that has separated the bog into two distinct hydrological sections, north and south (Van Seters and Price, 2001). The southern section of the bog (80 ha) was the focus of this study.

Harvesting of the southern area began in 1942 and was progressively abandoned from 1968 to 1972 (Girard, 1999). Approximately 88% (~70 ha) of the southern section of Cacouna bog was exploited for peat. The block-cut harvesting technique was used, leaving behind a landscape of alternating raised baulks and mined trenches. Residual peat within these sites, ranging from 1·5 to 4 m in depth, has subsided approximately 80 cm over time (Van Seters and Price, 2002) through oxidation and compression caused primarily by drainage.

Trees and ericaceous shrubs dominate the cutover surface, but *Sphagnum* recolonization is infrequent throughout the trenches, and absent from baulks (Lavoie and Rochefort, 1996; Girard, 1999). Less than 10% of the southern section was covered by *Sphagnum* in 1998, with *Sphagnum capillifolium, S. magellanicum* and *S. fallax* being the dominant species present (Girard, 1999). Bérubé and Lavoie (2000) conclude that this site is not returning to a functioning bog ecosystem.

The specific study sites comprise two mined trenches, hereafter referred to as the MAIN and EXPT trenches. Both are bounded by raised baulks that are 4–6 m wide and 0·6 m high. The MAIN trench is roughly 180 m long by 12 m wide. The EXPT trench is 80 m long by 10 m wide. Experimental observations in EXPT were confined to two $12 \times 3{\cdot}5\ m^2$ quadrats located in the south end of the trench (Figure 1).

Block-cut trenches within the peatland have a distinct microtopography characterized by a convex cross-sectional profile. These are labelled in Figure 1. The centre-skag (CS) is usually the highest point of this convex profile, which is then generally followed in decreasing altitude by the mid-skag (MS), lower skag (LS) and ditch edge (D). Lengthwise, the EXPT trench has an essentially flat profile that slopes gently to the north (topographic gradient 0·004).

The general dimensions, orientation and form of these sites are typical of this bog and other similar cutover peatlands in the area. However, the presence of recolonized *Sphagnum* mosses was typically greater in the trenches selected for observation than in other trenches (Girard, 1999). They were chosen specifically to observe the range of conditions where it was certain that *Sphagnum* could re-establish.

METHODS

The approach here compared the hydrology on adjacent quadrats, symmetrically located either side of the centre-skag of the EXPT trench (Figure 1). *Sphagnum* had recolonized on both sides, but was removed from the western half (REMOV). The idea behind REMOV was to replicate the soil condition shortly after abandonment. These data were compared with the INTACT eastern quadrat, where some locations were found to have a *Sphagnum* cover (SPHAG) and some locations did not (BARE). Shrub cover was removed from both quadrats—it was our intention to observe the differences caused by the presence or absence of *Sphagnum*, and the latter could not be removed without damaging the Ericaceae.

Because the experimental trench was atypical (more *Sphagnum* than most—see comments above), and because of the systematic patterns of *Sphagnum* distribution clustered in ditches and lower skag within all trenches (Price and Whitehead, 2001), replication was not attempted. In this sense, the experimental design suffers from pseudoreplication (Hurlbert, 1984); thus, the application of inferential statistics is avoided. Furthermore, it was not considered wise to exercise treatments within quadrats (i.e. treat small areas by removing *Sphagnum* in patches) because of potential microclimatic effects. However, the separation of treatments on either side of the trench opens the potential for differences in microclimate caused by aspect. Since the surface gradients were so small, and much less than microtopographic gradients, this was not considered important. Nevertheless, non-randomized samples can be subject to bias; thus, as noted above, statistical inferences are avoided.

Field instrumentation

Hydrological and microclimatic measurements were made from 9 May to 14 August 1998 (97 days). Meteorological data were collected at a meteorological station located in the south end of the MAIN trench. Precipitation P was measured with manual and tipping bucket rain gauges positioned 0·5 m above the cutover peat surface. Evapotranspiration was measured directly for *Sphagnum*-covered and bare cutover surfaces using lysimeters (see Van Seters and Price (2001) for details). Daily evapotranspiration E (mm day^{-1}) was estimated with the Penman–Monteith combination model as modified by Priestley and Taylor (1972), where

$$E = \alpha \left(\frac{s}{s+q} \right) \frac{Q^* - Q_G}{L\rho} \tag{1}$$

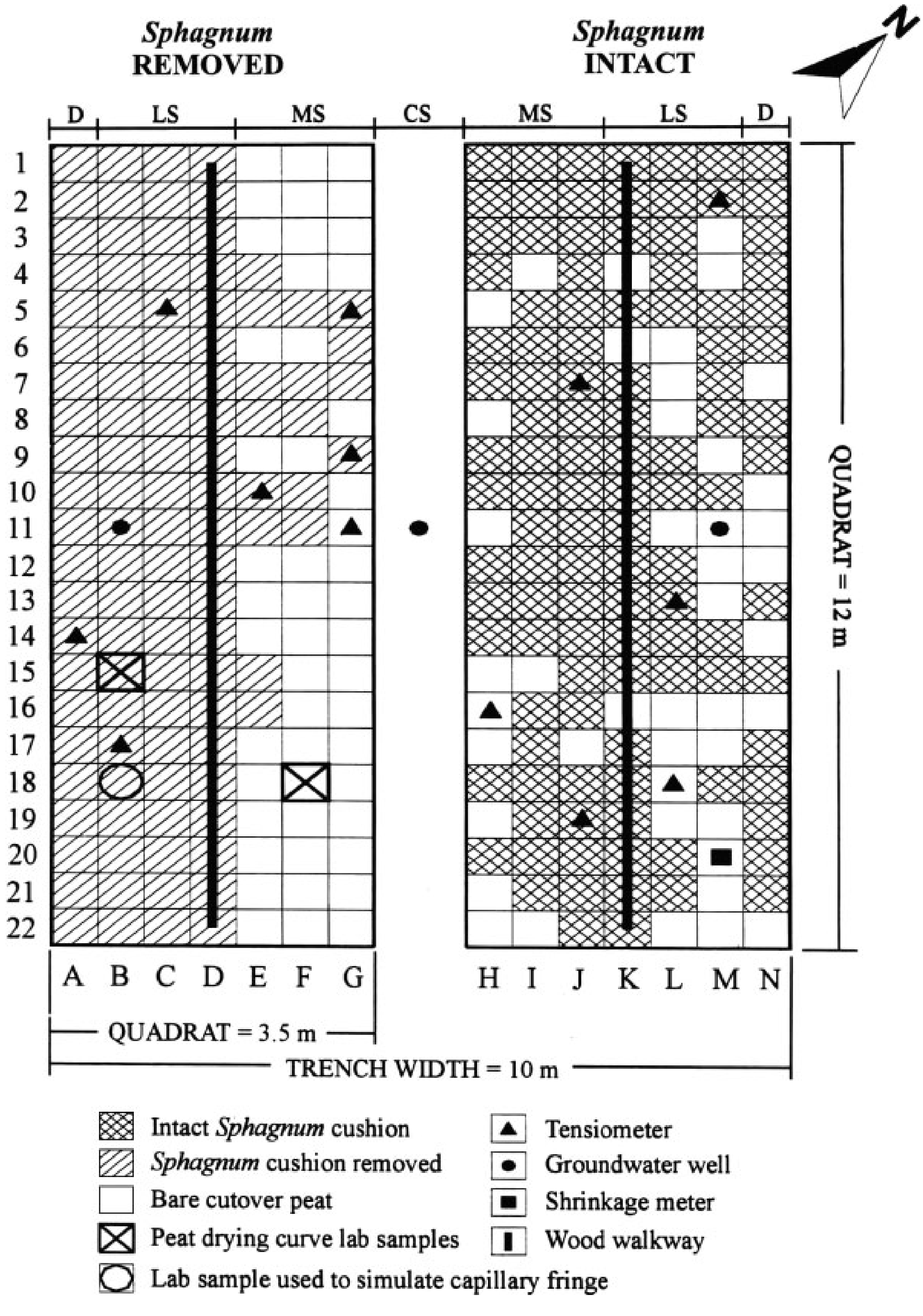

Figure 1. Experimental setup and patterns of *Sphagnum* distribution in the REMOV quadrat (left) and INTACT quadrat (right) of the EXPT trench. A cross-sectional profile across these quadrats is shown in Figure 3

and where L (J kg^{-1}) is the latent heat of vaporization, ρ (kg m^{-3}) is the density of water, s (Pa °C^{-1}) is the saturation vapour pressure–temperature curve, q is the psychrometric constant (0·0662 kPa °C^{-1} at 20 °C),

Q^* (J day^{-1}) is the net radiation flux, and Q_G (J day^{-1}) is the ground heat flux. In Equation (1), α is an empirical coefficient determined from the lysimeters. Q^* was recorded using two net radiometers positioned 1·5 m, one each above the *Sphagnum*–Ericaceae and bare peat–Ericaceae surfaces. The ground heat flux was measured with one soil heat flux plate 0·5 cm below the bare peat surface. Air temperature was measured with a shielded thermistor located 1 m above the peat surface.

Water table position was monitored in the EXPT trench approximately every 3 days using one transect of three wells (Figure 1). The well transect was installed perpendicular to the baulks, with wells positioned on the CS and 1·0 m from the edge of the east and west ditches (Figure 1). Wells were constructed from a 1·5 m PVC pipe (2·0 cm i.d.), slotted along their entire length, covered with 200 μm geotextile screen, and inserted into a pre-drilled (hand-augured) hole in the peat. All pipe intakes were above the peat–mineral interface. The altitude of the pipes was referenced to a common datum using standard surveying techniques. Field estimates of saturated hydraulic conductivity were conducted in early July using the hydrostatic time-lag method (bail test) of Hvorslev (1951) as described in Freeze and Cherry (1979).

Volumetric soil moisture θ and pore-water pressure ψ were measured at 2 cm below the peat surface using time domain reflectometry (TDR) and tensiometers at BARE (three sites), SPHAG (four sites) and REMOV sites (six sites) in the EXPT trench quadrats (Figure 1). TDR probes were a twin-probe design. The radius of influence of such a design of horizontally inserted probes 2 cm below a discontinuity (e.g. peat–air) is such that it encompasses approximately 95% of the relative dieletric permittivity of the material (e.g. peat) below the discontinuity (estimated from Ferré *et al.* (2001)). TDR probes (20 cm waveguides) were placed into dug pit walls, adjacent to L-shaped tensiometers, which were then backfilled with peat. Field measurements of θ were taken using a Tektronix™ model 1502B time domain reflectometer, calibrated in the laboratory (Whitehead, 1999) and ψ was measured with a Tensimeter™ pressure transducer accurate to ±1 mbar and adjusted to account for the height of the water column above the 1 cm o.d. porous ceramic cup (1 cm water is approximately equal to 1 mbar pressure). Soil moisture and ψ measurements at all sites were taken approximately every 3 days during the study period. Point samples of θ (0–4 cm depth) under *Sphagnum* cushions and adjacent bare cutover peat (within 5–10 cm of cushion) were also obtained from the MAIN trench using TDR (10 cm waveguide probe inserted into peat at a 23° angle).

Laboratory analysis

Dry bulk density ρ_B (g cm^{-3}) was determined gravimetrically using samples of the upper 3 cm of soil, as

$$\rho_B = \frac{M_{dry}}{V_{sat}} \tag{2}$$

where M_{dry} (g) is the dry sample mass (dried at 95 °C until mass remained constant) and V_{sat} is the saturated volume.

To determine how substrates respond to air drying, peat block samples ($40 \times 34 \times 20$ cm^3) were collected, placed into plastic tubs of the same dimensions, sealed, and returned to the laboratory. One block had *Sphagnum* removed (as in REMOV field site), one was bare peat with the organic litter layer removed, and the third was bare peat with the organic layer intact (equivalent to BARE). Each substrate sample was fitted with two sets of tensiometers and TDR probes (20 cm waveguides), which were inserted horizontally into the peat (2 cm depth) through holes drilled in the tub wall. The holes were then sealed with silicone. A fully slotted PVC pipe (1·3 cm i.d.) was inserted to the full depth of the tubs to measure water table decline. To simulate rainfall under field conditions, water was sprinkled onto the peat over a 48 h period until the sample reached saturation (i.e. when the water table was at the surface). No additional water was added to the peat after the start of the experiment. Water table depth, θ, and ψ were measured approximately every 3 days.

The characteristics of the capillary fringe were determined in the laboratory with a 60 cm high rigid plastic cylinder (14·7 cm i.d.). The cylinder was pushed into the peat of the EXPT trench, progressively cutting the peat surrounding the sample to minimize compression. The cylinder was then removed, sealed and returned to the laboratory. The sample was instrumented with TDR and tensiometers at 2, 5, 10, 20, and 30 cm depths below the peat surface.

Sphagnum distribution and peat macrofossil analysis

A *Sphagnum* survey of the EXPT trench quadrats was conducted in 1998 using the point sampling method (Floyd and Anderson, 1987; Bonham, 1989). The presence of *Sphagnum* cushions touching an upright metal rod (1 cm diameter) was recorded every 0·5 m along seven longitudinal transects per quadrat (Figure 1).

Peat cores were obtained from the MAIN and EXPT trenches for macrofossil analysis to determine past patterns of vegetation occurrence arising from secondary succession. In the field, cores were sealed with cellophane wrap, followed by a layer of aluminium foil, and then returned to the laboratory and refrigerated at 4 °C. Two 5 cm thick slices were cut from peat cores on each side of the interface between residual and newly formed peat. The interface was identified by the darker colour characteristic of residual peat. A 0·5 to 1·0 cm litter layer was present at the interface of some samples. A 60 ml sub-sample was cut from the centre of each 5 cm peat slice, and botanical remnants from these samples were divided into the following groups: *Sphagnum*, other mosses, Cyperaceae, Ericaceae, trees, and other vegetation fragments. Residual peat samples provided a record of the botanical fragments left in place after exploitation (thus a potential source of diaspores), whereas botanical remnants in newly formed peat suggested which species may have first recolonized the cutover surface after abandonment (Robert *et al.*, 1999).

RESULTS

Water inputs and outputs

Daily precipitation and evapotranspiration for the Cacouna peatland from 9 May to 13 August 1998 (97 days) are presented in Figure 2a and b, respectively. Total precipitation P recorded during the same period was 218 mm. In 1998, precipitation in June and July was 83 mm and 102 mm, respectively, compared with long-term precipitation normals (1963–90) from St Arsène of 83 mm and 87 mm, respectively (Environment Canada, 1993). Rainfall totals measured by the tipping bucket and manual rain gauges in the bog were within 3% of each other. Average daily evapotranspiration (E) ranged from 1·9 to 3·8 mm day^{-1} in 1998. The α parameter (Equation (1)) determined with the soil lysimeters was 1·07 for *Sphagnum* cover, and 0·85 for bare peat (see Van Seters and Price (2001) for more details). The estimated average evapotranspiration for the EXPT trench was 2·8 ± 1·1 mm day^{-1}. Total evaporative water loss E was 285 mm, resulting in a net water deficit ($E - P$) of 67 mm for the study period.

No water loss from surface runoff occurred from the EXPT trench. Drainage ditches (D) were occluded in this section of the peatland, largely because of channel infilling by new vegetative growth, organic litter, and sediment (i.e. baulk slumping). The geometric mean hydraulic conductivity for EXPT trench peat ($n = 7$) was $1{\cdot}7 \pm 6{\cdot}3 \times 10^{-5}$ cm s^{-1}, indicating that groundwater movement was slow throughout the trench. The longitudinal hydraulic gradient was less than 0·001, and the transverse topographic gradients from CS to D approximately 0·1. Exchanges between bog groundwater and the regional aquifer were strictly limited because of the very low hydraulic conductivity of the underlying clay substrate ($K_s = 5 \times 10^{-8}$ cm s^{-1}).

Water table behaviour

Water table levels remained high throughout the summer, largely because of major precipitation events on 14 June (26·2 mm) and 10 July (35·6 mm) (Figure 2c). Patchy flooding occurred throughout the trench following these periods of rainfall, with the LS/D area of the REMOV quadrat becoming completely inundated with water. The water table remained relatively flat, and relative to the peat surface was typically deepest under the CS, followed by the MS, LS and D (Figure 3). The water table depth was lowest in mid-August, measuring approximately 44 cm, 38 cm and 27 cm, respectively, at the CENTER, EAST and WEST wells of the EXPT trench.

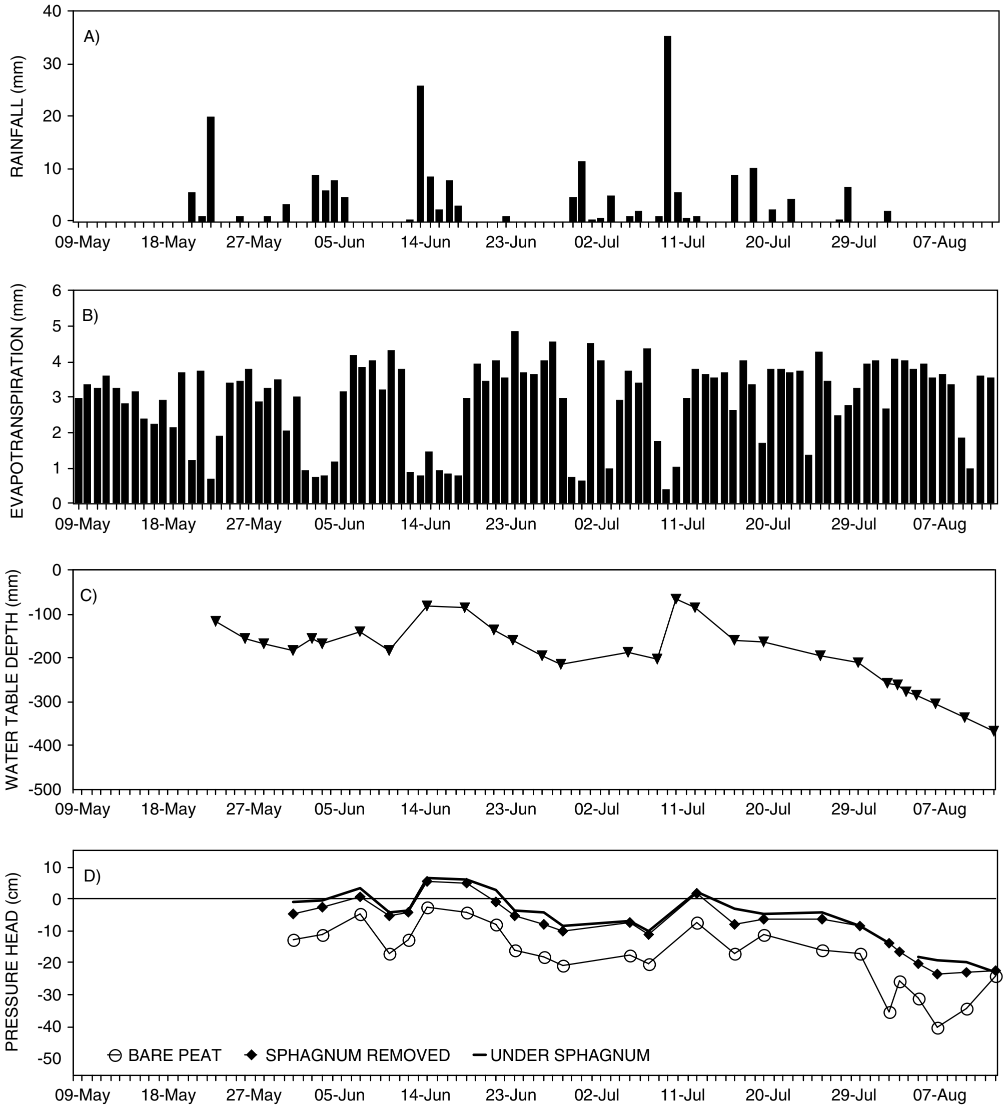

Figure 2. Rainfall, evapotranspiration, mean water table, and soil water pressure (at −2 cm depth) for the EXPT trench, 9 May to 13 August 1998

Spatial and temporal trends in volumetric soil moisture and pressure

TDR probes at BARE peat field sites did not function properly, but laboratory values indicate that the saturated volumetric soil moisture θ_s of this substrate was similar to field SPHAG and REMOV peat (mean $\theta_s = 91{\cdot}5\%$). Estimates of BARE θ were made on the basis of moisture characteristic curves ($\theta - \psi$) for BARE peat (Whitehead, 1999), using field values of ψ. The results indicate that in the EXPT trench the mean θ values in the SPHAG and REMOV substrates were similar (~86%), but greater than BARE peat (~78%) (Table I).

In the MAIN trench, the mean θ of peat under *Sphagnum* cushions was 5–14% greater than in adjacent bare cutover peat (measurement within 5–10 cm of cushion) throughout the study period (Figure 4). The difference in mean θ between these two peat substrates was most pronounced in the trench MS during August.

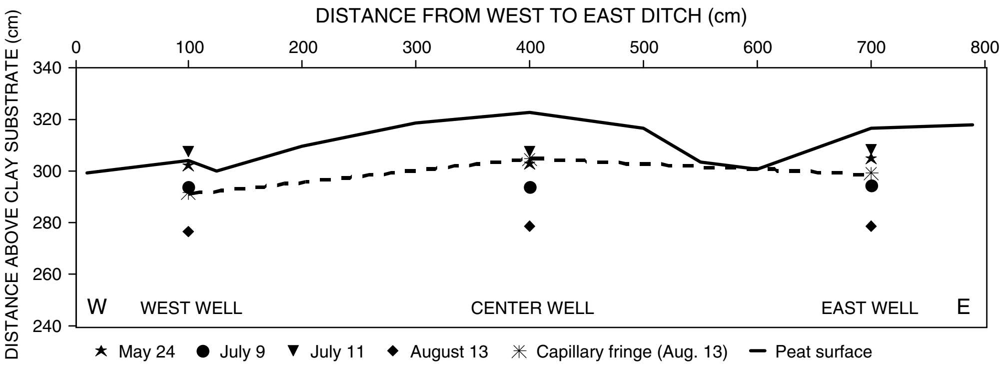

Figure 3. EXPT trench cross-sectional profiles of water table and capillary fringe (based on laboratory experiments; see Figure 6). Locations of wells are illustrated in Figure 1

Table I. Summary of mean volumetric soil moisture (by TDR) and pore-water pressure at −2 cm (+/− standard deviation) from 1 June to 13 August 1998

	Under *Sphagnum* (SPHAG)[a]	*Sphagnum* removed (REMOV)[a]	Bare peat (BARE)
Soil moisture (%)	86·6 (±4·0)	85·2 (±5·5)	77·8 (±8·0)[b]
Pore-water pressure (cm)	−5·9 (±8·4)	−7·4 (±9·2)	−18·4 (±10·7)
Bulk density[c]	0·10 (±0·03)	0·10 (±0·01)	0·11 (±0·01)

[a] Located predominantly in depressions.
[b] Derived from laboratory primary drying curves.
[c] A thin layer of fibric peat and litter-fall (∼0–1 cm depth) covered the BARE substrate.

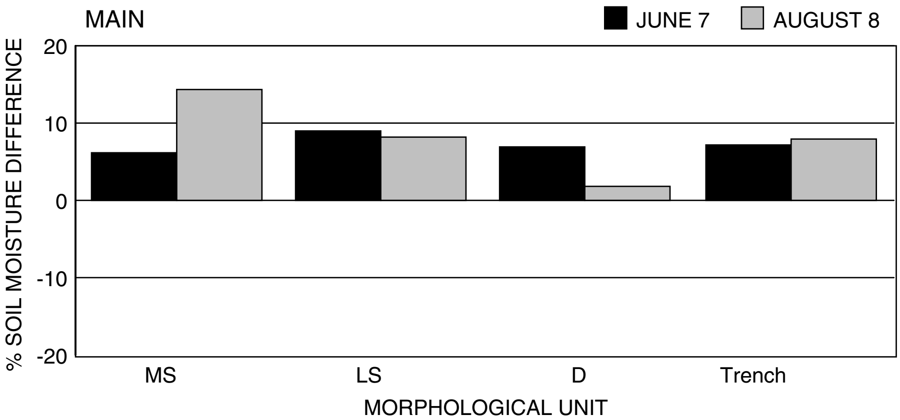

Figure 4. Differences in mean volumetric soil moisture (0–4 cm depth) between *Sphagnum* covered and bare cutover peat in the MAIN trench, June and August 1998. The average for MS, LS and D are labelled 'Trench'

Pore-water pressure ψ, measured at 2 cm below the surface, tended to mimic fluctuations in the water table for all substrates in the EXPT trench (Figure 2). Mean ψ of BARE peat was lower throughout the summer compared with the SPHAG and REMOV substrates (Table I).

Laboratory results

Peat monoliths with an intact *Sphagnum* cover (SPHAG) and with *Sphagnum* removed (REMOV) dried more quickly than bare peat with an undisturbed litter cover (BARE) (Figure 5). REMOV ψ reached -100 cm before the BARE cutover peat.

In the peat column experiment, the zone of capillary saturation increased in thickness as the water table fell deeper into the peat profile (Figure 6). Air began to enter saturated pores (i.e. soil moisture began to drop) 2 cm, 5 cm, 10 cm, 20 cm and 30 cm below the peat surface when ψ equalled -2 cm, -4 cm, -15 cm, -26 cm and -21 cm respectively. The capillary fringe ensured that the zone of saturation remained within 30 cm of the peat surface, even when the water table descended below 50 cm.

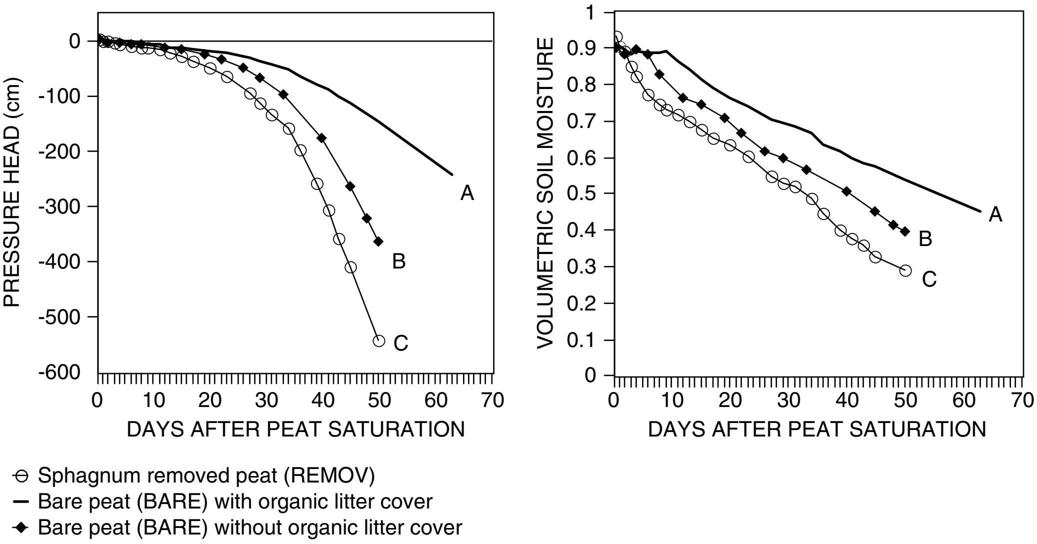

Figure 5. Pore-water pressure (left) and volumetric soil moisture (right) changes (-2 cm) in a container of peat with (A) bare peat with an approximately 1 cm thick undisturbed organic litter cover, (B) similar peat but without a litter layer, and (C) bare peat from which a *Sphagnum* cover was removed (REMOV)

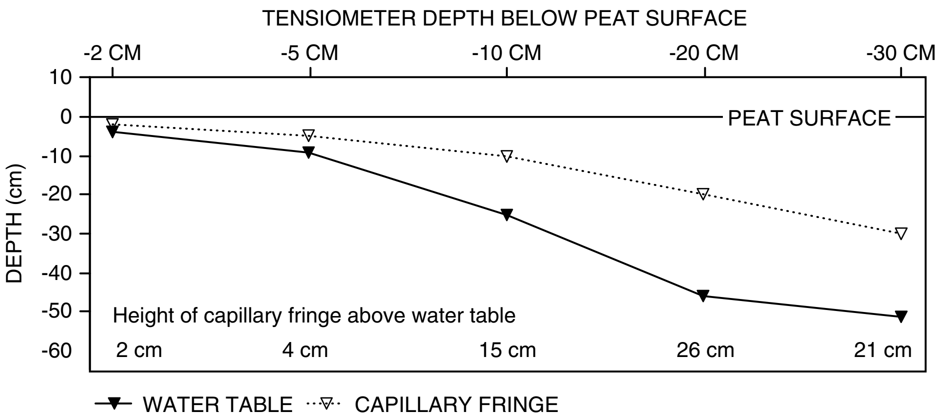

Figure 6. Capillary fringe height above the water table in a peat column. Note that the height of the capillary fringe is equal to the pressure head at which significant volumes of air began to appear in soil pores (i.e. air-entry pressure)

Sphagnum distribution and peat macrofossil analysis

The patterns of *Sphagnum* distribution before cushions were removed tended to be more aggregated in the west (REMOV) quadrat compared with the INTACT quadrat (Figure 1). However, both quadrats had approximately 70% of their total area covered by *Sphagnum*. Most recolonized *Sphagnum* in the REMOV quadrat was present on the LS or D (84%), whereas coverage was fairly uniform between the LS/D (52%) and MS (48%) of the INTACT quadrat. Quadrat areas having most *Sphagnum* growth (A1–D22 and I1–L22 in Figure 1) were found to be in topographically lower areas (see cross-sectional profile in Figure 3). No *Sphagnum* was found on either the CS or baulks.

Macrofossil analysis indicated that *Sphagnum* was the most abundant botanical remnant found in residual (i.e. cutover) peat and in newly formed peat of both MAIN and EXPT trenches (Table II). Ericaceae (*Ledum* and *Chamaedaphne*) were slightly more prevalent in EXPT, and sedge (*Eriophorum* spp.) more important in newly formed EXPT peat. Moss (*Polytrichum strictum*) remnants were only found in both new and residual peat from the MAIN trench.

DISCUSSION

Hydrological conditions

Although a groundwater mound occurred in the residual peat dome of Cacouna (see Van Seters and Price (2002)), the trench-scale water table was essentially flat (Figure 3). The water table fluctuated uniformly in response to atmospheric fluxes. For example, 1 day after the largest recorded rainfall of the summer (10 July: = 35·5 mm), the water table increased uniformly at all wells in the EXPT trench (Figure 3). Whereas the longitudinal topographic gradient was small (0·004), the transverse (i.e. east to west) topographic gradients from CS to D were relatively large (~0·1), so lateral drainage was potentially 100 times more effective. Consequently, the water table across the trench was flat (Figure 3). Groundwater flow along (and therefore out of) the trench was negligible; thus, decreases in the water table elevation were mainly due to evapotranspiration ($E - P = 65$ mm). Discharge measurements and a water balance of the whole peatland system substantiate the predominance of evaporative water losses (Van Seters and Price, 2001).

An extended dry period in August led to a steady decline in the water table. Laboratory estimates of capillary fringe height (Figure 6), however, suggest that the zone of capillary saturation remained closer to the peat surface during this time. When applied to field water table data, inferred values of the capillary fringe show that the top of the capillary saturated zone at the CENTER, EAST and WEST wells of the EXPT trench on 13 August were 18 cm, 17 cm and 12 cm below the peat surface respectively (Figure 3). Thus, in the ditch area (D), the capillary fringe remained within ~5 cm of the surface, whereas in the CS zone it lay close

Table II. Botanical remnant composition of residual and newly formed peat from the EXPT, MAIN and BAULKLESS trenches

Trench	Vegetation component (mean percentage volume)					
	Sphagnum	Moss[a]	Sedge[b]	Ericaceae shrub	Tree	Other
EXPT						
Residual peat	58·3	0	2·3	27·5	12·0	0
Newly formed peat	57·5	0	18·0	24·5	0	0
MAIN						
Residual peat	57·4	9·6	1·6	23·1	7·9	0·4
Newly formed peat	51·3	28·3	0	20·1	0·1	0

[a] Predominantly *Polytrichum strictum*.
[b] Predominantly *Eriophorum* spp.

to 20 cm. The zone of capillary saturation increased in thickness as the water table descended (Figure 6), probably because at depth there is older, more compacted peat, where a greater fraction of smaller pores is present. Variations in peat pore size distribution can produce a capillary fringe ranging from 20 to 40 cm in thickness (Boelter, 1966; Romanov, 1968; Päivänen, 1973; Prévost *et al*., 1997). The high capillary fringe increases the responsiveness of water table fluctuations (Gillham, 1984).

The SPHAG (intact cushions) and REMOV (cushions removed) substrates of the EXPT trench quadrats maintained high θ and ψ throughout the study period (Table I), because these substrates were mostly located in low-lying areas (A1–D22 and I1–L22; Figure 1) characterized by shallow water tables and a substantial capillary fringe (Figure 3). Bare cutover peat (BARE) was generally in topographically higher areas of the EXPT trench. θ and ψ at BARE sites were lower than values observed for the other two substrates (Table I). Although the water table was lower at these elevated BARE peat sites, the presence of a thick capillary fringe (Figure 6) resulted in a capillary saturated zone that remained within ~20 cm of the peat surface throughout the summer (Figure 3), suggesting that a strong connection remained with the upper peat layers. However, the laboratory experiment showed that BARE peat lost moisture more slowly to the atmosphere than the REMOV substrate (Figure 5). The macrofossil analysis indicated the BARE substrate was covered with a thin layer of organic material (0–1 cm depth) that was either a remnant of debris left over from the harvesting process, or leaf matter from ericaceous shrubs and trees (or both). The dry conditions and the larger pore structure of this litter layer acted as a mulch to hinder upward capillary flow, thus slowing moisture transfer from the underlying BARE peat to the surface (Figure 5). However, because of the more elevated surface and greater depth to water table in the MS and CS areas, one expects the equilibrium pressure profile to result in a lower pressure–moisture status. This was indeed the case. Without the litter layer this would have been more extreme.

In the MAIN trench, measurements of θ in bare peat directly beside *Sphagnum* cushions removed the elevation effect characterizing differences between BARE and SPHAG sites at the EXPT trench. At MAIN, mean θ remained higher under *Sphagnum* compared with adjacent bare cutover peat (Figure 4), suggesting that cushions themselves reduce water loss from the peat. A larger pore structure (poor capillarity), coupled with the ability of *Sphagnum* cushions to increase their surface albedo and reflect incident radiation (Ingram, 1983; Bragg, 1995), provided underlying peat with some protection against evaporative losses. Moreover, *Sphagnum* that is not saturated is not an efficient evaporating surface (Price, 1991).

During drier periods (August), *Sphagnum*-covered peat maintained an even greater θ than surrounding bare peat, with θ differences between the two substrates being most pronounced in the MS (14%), followed by the LS (8%) and D (2%) (Figure 4). As the water table falls deeper into the peat, its responsiveness eventually decreases (Ahti, 1974; Mannerkoski, 1985), as moisture loss occurs primarily from the unsaturated zone (Price, 1997). Consequently, θ declined more rapidly in higher sections of the trench (e.g. MS), where water tables were generally deepest (Figure 3), and were unable to sustain flow to the unsaturated zone, compared with low-lying areas (e.g. LS and D). The hydrological benefits (higher mean θ and ψ) afforded by *Sphagnum* cover should be expected in the EXPT trench. However, this was masked by differences caused by elevation.

Influence of hydrological conditions on Sphagnum *recolonization and succession*

The recolonization of *Sphagnum* overexploited peatland surfaces is a long-term process that may involve several micro- and macro-successional phases, which are guided by the edaphic, hydrological and ecological processes operating within the trench–baulk system (e.g. Smart *et al*., 1989; Robert *et al*., 1999). In both EXPT trench quadrats, most *Sphagnum* regrowth was present in depressions (e.g. REMOV quadrat A1–D22; scattered depressions throughout INTACT quadrat I1–L22; Figure 1). The dominant component of newly formed peat (i.e. the pioneer species horizon) in the EXPT trench was *Sphagnum* (Table II), implying that the starting conditions for recolonization throughout the trench were initially wet. *Sphagnum* probably recolonized depressions shortly after abandonment (Ferland and Rochefort, 1997; Groot, 1998; Price *et al*., 1998), given that peat in these areas had higher soil moisture, pore-water pressure (Table I) and water tables (Figure 3).

At topographically higher locations the conditions were less favourable for *Sphagnum*. While the litter layer (currently) present at these sites reduces moisture loss by evaporation, and θ and ψ of the substrate are higher than they otherwise might be, any *Sphagnum* diaspore translocated there must contend with a reduced moisture flow caused by the litter layer. That is, the litter layer, while providing the benefits of a mulch to underlying soil and perhaps vascular plants rooted there, has been an impediment to the establishment of non-vascular species that must establish on top of it, and which rely on capillary moisture supply. However, since *Sphagnum* is present (albeit less frequently) at higher sections of the EXPT trench (e.g. E4–G11; H1–H22 and M1–N22; Figure 1) some micro-sites formerly provided favourable conditions for *Sphagnum* re-establishment. The pattern of distribution (Figure 1) suggests this occurred through both *in situ* establishment of plants (cushions isolated from those in LS and D) and, mostly, from lateral expansion of previously established LS and D communities.

If fairly uniform hydrological conditions existed after abandonment (e.g. see SPHAG and REMOV; Table I), and physical properties of the different substrates were similar (as suggested by similar ρ_B), then the present patterns of *Sphagnum* distribution in the EXPT trench may have become established entirely through random diaspore dispersal. If *Sphagnum* were to establish randomly and cover the EXPT trench peat at a mean rate of 5% per growing season (e.g. see Campeau and Rochefort (1996)), then one would expect the trench now to have acquired a completely developed moss carpet given that about 30 years have passed since abandonment. Since *Sphagnum* coverage is still very incomplete, factors other than time must be responsible for determining the present recolonization patterns. This study suggests that non-uniform conditions of wetness, initially associated with trench morphology, have an important effect, and this is complicated by subsequent changes in the nature of the abandoned surface. Organic debris spread during harvesting and the rapid establishment of Ericaceae and trees resulted in the establishment of a litter layer at the interface of old and new peat that breaks the capillary connectivity of the peat with the surface. This was not a problem for sphagna in lower areas (e.g. D and LS) because of more frequent inundation and a generally higher level of saturation. These areas have already been shown to be preferred sites of *Sphagnum* recolonization (Girard, 1999; Price and Whitehead, 2001). However, in raised areas associated either with local microtopography or with the convex morphological profile, the litter layer may be more hostile to spores and retard their establishment. A potential successional pathway for *Sphagnum* at raised locations within the EXPT trench may have been through the lateral expansion of previously established cushions. *Sphagnum* initially recolonized the most hydrologically suitable locations (LS and D). The expansion of *Sphagnum* cushions by spreading of pendant branches and stems over adjacent areas of hydrologically unsuitable peat ameliorated the moisture status of adjacent bare peat (Figure 4), allowing them to spread. Given the absence of *Sphagnum* on CS and baulks, it seems that the colonization of these sites will have to wait for lateral expansion to take its course.

Sphagnum recolonization of the EXPT trench is an ongoing process that occurs slowly over time. However, the influence of more extreme inter-annual variability in this process cannot be ignored. A peat substrate presenting harsh hydrological conditions in one season may become suitable for recolonization in a succeeding season that is exceptionally wet. In a wet season, *Sphagnum* re-establishment and growth may be substantial (Joosten, 1995; Ferland and Rochefort, 1997). Once established, *Sphagnum* cushions modify local hydrological conditions to their own benefit and maintain higher θ compared with adjacent bare peat substrates, especially during drier periods (Figure 4). Essentially, *Sphagnum* develops an ecological momentum that allows established cushions to persevere in drier areas where surrounding substrates normally would not present favourable hydrological conditions for survival.

CONCLUSIONS

Block-cut harvesting of the Cacouna bog has left a landscape of varying microtopography and a cutover surface consisting of previously waterlogged catotelmic peat. Although the structure and water retention properties of this peat can present harsh hydrological conditions to invading diaspores, these hydrophysical properties do not appear to hinder *Sphagnum* recolonization in areas where near-saturated conditions prevail. After abandonment, *Sphagnum* seems to have readily recolonized EXPT trench depressions and the lower skag, where the high capillary fringe helped to maintain saturation under moisture tension at or near the peat surface in summer.

At more elevated locations, where the recolonization of *Sphagnum* has been delayed, a litter layer comprising mostly leaves of ericaceous plants restricts the water loss from the surface, and thus further hinders the establishment of diaspores that may be randomly translocated there. *Sphagnum* cushions that initially colonized lower parts of the system increased the moisture status of its substrate, allowing it to spread laterally. However, the presence of isolated *Sphagnum* cushions growing at higher, drier locations, demonstrates that conditions at some of these sites may be suitable in some seasons.

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