

Characterization of the fluxes and stores of water within newly formed *Sphagnum* moss cushions and their environment

Scott J. Ketcheson* and Jonathan S. Price

Department of Geography and Environmental Management, University of Waterloo, Waterloo, Ontario, Canada

ABSTRACT

Internal water storage and water exchanges that sustain hydration are critical for the physiological function of *Sphagnum* mosses that have recolonized cutover peatlands characterized by low soil–water pressures. The relative importance of water gains and losses for spontaneously regenerated *Sphagnum* moss cushions was addressed through investigation of the sensitivity of moss moisture dynamics to a range of environmental variables. Precipitation waters are poorly retained within the cushions, which indicated that rain event water can only be relied upon by the mosses for a short period. The relationship between water table depth and moisture content within moss cushions was strong when the water table was within 30 cm of the surface of the cutover peat but weakened as conditions became drier, as reflected by weakened upward hydraulic gradients in the unsaturated zone below the moss cushions. Calculation of a water budget between 19 May and 16 August 2006 for relatively wet and dry cushions, respectively, identified a water deficit of 28 and 44 mm. It is hypothesized that additional (small) sources of water during deficit conditions may be critical for maintaining physiological processes. Rewetting of the peatland by blocking drainage ditches created conditions more favourable for *Sphagnum* survival through increasing the moisture content and soil–water pressures within the remnant peat deposit although restoration efforts should aim to constrain the water table position to within the upper 30 cm. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS *Sphagnum* moss; moisture dynamics; peatland restoration; rewetting; unsaturated zone; hydrology

Received 13 December 2012; Revised 30 April 2013; Accepted 7 May 2013

INTRODUCTION

Sphagnum mosses are nonvascular plants that, in addition to meteoric water inputs, rely upon capillary retention and water flow in the spaces between individual plants (Hayward and Clymo, 1982) to sustain hydration of the photosynthesizing capitula (McNeil and Waddington, 2003). They are the primary peat-forming plants in northern peatlands (Kuhry and Vitt, 1996), which cover over 12% of Canada's total land area (Tarnocai, 2006). In cutover sites characterized by low (i.e. large negative number) soil–water pressures (Price, 1997), *Sphagnum* is unable to colonize spontaneously because it cannot generate the capillary forces sufficiently to extract water from the underlying peat substrate (Price and Whitehead, 2001). These dry conditions are commonly reported within disturbed bogs from many countries (Money and Wheeler, 1999). Price and Whitehead (2001) developed hydrological thresholds for *Sphagnum* recolonization on abandoned cutover sites by evaluating the conditions of the underlying

substrate in areas of the Cacouna bog (same site as in this study) that were (and were not) spontaneously recolonized by *Sphagnum* mosses. They concluded that *Sphagnum* recolonized where there was a high water table (mean position -24.9 ± 14.3 cm), volumetric water content greater than 50% and soil–water pressure greater than -100 mb. These areas were mostly in shallow ditches and low-lying areas within the site, where the site water table was closer to the surface.

Sphagnum mosses often initially recolonize cutover peatlands as isolated, hemispherical cushions that are closely tied to the moisture regime of the cutover peat substrate (Price and Whitehead, 2004) and the influence of the Ericaceae canopy (Farrick and Price, 2009; Heijmans *et al.*, 2001). The newly formed *Sphagnum* cushions are able to coalesce into larger carpets in wetter areas with the highest soil–water pressures. There appears to be a positive feedback in which the development of *Sphagnum* cushions protects the underlying substrate (already relatively wet) from evaporative demands, thus engineering its own environment (Price and Whitehead, 2004). Similarly, reintroduction of larger patches of intact *Sphagnum* communities during revegetation of cutover peatlands in Europe was favourable over smaller patches (Robroek *et al.*, 2009). Price and Whitehead (2004) found that soil

*Correspondence to: Scott J. Ketcheson, Department of Geography and Environmental Management, University of Waterloo, Waterloo, Ontario, Canada. E-mail: sjketch@uwaterloo.ca

moisture content beneath cushions was 5–14% higher than in bare cutover peat directly adjacent to it. Although these studies have documented the hydrological conditions required for *Sphagnum* moss recolonization and survival, no field-based studies that quantified the role of capillary rise from cutover peat versus water from precipitation on the moisture dynamics within moss cushions were found. In an undisturbed mire, Yazaki *et al.* (2006) used a hummock-scale mass balance approach to determine that the storage of precipitation water was important for the maintenance of moist conditions within *Sphagnum* moss hummocks. Because water is stored and transported primarily within the spaces between leaves and pendant branches (Hayward and Clymo, 1982), the arrangement of neighbouring plants can influence water dynamics within *Sphagnum* mosses (Proctor, 1982). Waddington *et al.* (2011) related differences in capitula density between *Sphagnum rubellum* mosses growing under varying hydrological conditions to water retention and bulk density. Further, the influence of water availability and species type on moss community architecture (Rydin, 1985; Schipperges and Rydin, 1998) can impact the fluxes and stores of water within *Sphagnum* moss cushions and between the moss cushions and their environment. Modelling work by Schouwenars and Gosen (2007) suggested that restricted vertical water transport within a *Sphagnum* moss layer increased vulnerability to water stress; however, unreliable measurements of soil–water pressure in the unsaturated zone limited the ability for proper characterization of the connectivity between the mosses and the underlying substrate. Therefore, it remains uncertain if the substrate is an important source or sink of water for the recolonized mosses.

The moisture exchanges at the moss–atmosphere interface are dominated by evaporation losses and precipitation inputs. However, small yet potentially critical sources of water, such as dewfall (Csintalan *et al.*, 2000), distillation (Carleton and Dunham, 2003) and vapour transport (Price *et al.*, 2009), may be physiologically important and could prevent desiccation. Carleton and Dunham (2003) found that under certain microclimatic conditions, condensation of upwardly transported vapour from within the moss matrix (distillation) hydrated the uppermost parts of forest (feather) mosses. Price *et al.* (2009) estimated that (upward) vapour flux in *Sphagnum* mosses was about 1% of capillary rise. Within *Sphagnum* moss cushions on cutover peat, Price and Ketcheson (2009) reported that temporal moisture variability increased with depth to the base of the cushion with smaller cushions generally exhibiting greater variability at common measurement depths. They hypothesize that the upper and lower parts of the larger cushions may be only weakly coupled, limiting vertical growth, and favouring lateral spreading and coalescing of cushions; however, water

exchanges between the base of the cushion and underlying peat substrate have not been well-characterized. Because rewetting of cutover peatlands will increase the water content of the cutover peat (Price, 1997), the direction and magnitude of water exchanges between *Sphagnum* cushions and the substrate could be affected. An increased understanding of the moisture dynamics within and exchanges of water between moss cushions and their surroundings is required. Consequently, the specific objectives of this study were to (1) characterize the distribution and variability of moisture within *Sphagnum* moss cushions that have developed over cutover peat, (2) identify potential water sources for the moss cushions and (3) compare substrate moisture and soil–water pressure conditions before and following rewetting.

Study area

The study site is an abandoned block-cut domed bog of the Low Boreal Wetland Region (National Wetlands Working Group, 1997) in Cacouna (47°53'N, 69°27'W), approximately 10 km northeast of Rivière-du-Loup, Québec, Canada. Mean annual precipitation (1971–2000) recorded at a meteorological station in Saint-Arsène (<2 km from study site) is 963 mm, 29% of which falls as snow (Environment Canada, 2003). Average monthly temperatures range from –10.9 °C in February to 16.5 °C in August (Environment Canada, 2003). Peat was harvested at Cacouna by using the traditional block-cut extraction technique, resulting in alternating sequences of narrow (2- to 4-m wide) baulks that were raised 0.5–1.0 m above the adjacent 10- to 12-m wide trenches when harvesting ceased in 1975. At the Cacouna bog, this topographical pattern occurred in parallel in an approximately north–south direction. The remnant peat is up to 4 m thick (Van Seters and Price, 2001), with average bulk density and specific yield values of 0.12 and 0.08 g cm⁻³, respectively (Price and Whitehead, 2001). Following agricultural encroachment and the development of roads and a railway line (Girard *et al.*, 2002), the Cacouna bog was reduced from an area of 210–148 ha and divided into two hydrologically distinct halves (Van Seters and Price, 2001). This study focused on a 55-ha section within the larger 80-ha southern half (see Ketcheson and Price (2011) for a full site description).

An 11-m wide, 180-m long trench within the Cacouna bog that exhibited structure and vegetation cover typical of this peatland was selected for study [herein referred to as the study trench (ST); Figure 1]. Well-decomposed catotelmic peat comprises all of the remnant peat deposit at the Cacouna bog and exhibits little spatial variability. For example, the average (geometric mean) saturated hydraulic conductivity within the ST was 4.5×10^{-4} cm s⁻¹,

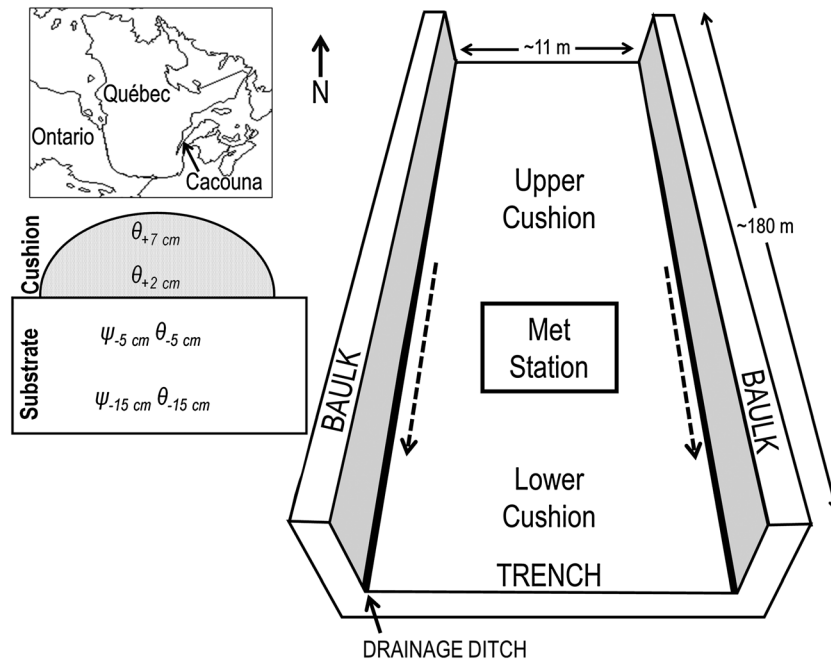


Figure 1. Location of the Cacouna bog and schematic representation of a baulk-trench topography and the relative location of the upper and lower cushion in the study trench. Dashed arrows indicate the direction of drainage. Cross-section indicates the relative location of measurements made both within and beneath the cushions.

whereas the site-wide geometric mean was $3.8 \times 10^{-4} \text{ cm s}^{-1}$ (Ketcheson and Price, 2011); hence, the substrate underlying the cushions in this study is characteristic for the peatland. Multiple *Sphagnum* moss cushions have recolonized on the surface of the remnant peat deposit within the ST, ranging in size from large (diameter = ~ 100 cm and height = ~ 40 cm) to small (diameter = ~ 15 cm and height = ~ 5 cm). The ST had a slope of 0.013 along its long axis (approximately north–south orientated), with *Sphagnum* prevalence and cushion size generally increasing in the lower (south) end of the trench, where conditions were more consistently moist. Cushions were dominated by *Sphagnum* species, most commonly *Sphagnum capillifolium* and *S. rubellum* in the upper portion of the trench and *S. capillifolium* and *Sphagnum magellanicum* in the lower end. Despite a number of distinguishable traits (Andrus, 1979; Cronberg, 1989), *S. capillifolium* and *S. rubellum* are often resolved as two taxa with partial morphological overlap within the group red *Acutifolia* species and, accordingly, exhibit morphological similarities (Cronberg, 1998). Ericaceous shrub species, predominantly Labrador tea (*Rhododendron groenlandicum*), leatherleaf (*Chamaedaphne calyculata*), sheep laurel (*Kalmia angustifolia*) and blueberry (*Vaccinium angustifolium*), proliferate both on the peat surrounding and beneath the moss cushions, with plant stems protruding out of the top of many of the cushions.

In October of 2006, peat dams were constructed throughout the southern section of the Cacouna bog that

consequently flooded the lower portions of some of the trenches (see Ketcheson and Price, 2011 for full description of the site rewetting). This study includes data from the summer prior to (2006) and following (2007) the site rewetting.

Field methods

Data were collected from 19 May to 16 August 2006 and 2007. Meteorological data were collected using a Campbell Scientific, Inc.™ data logger at a meteorological station established within the ST (Figure 1). Precipitation (P ; rainfall only) was automatically measured with a tipping bucket rain gauge (Texas Electronics TR-525) paired with an adjacent manual rain gauge for data checks. A net radiometer (REBS Q7.1) was installed in the centre of the ST 1.5 m above the surface of the remnant peat deposit, over a typical vegetation cover dominated by ericaceous vegetation and sporadic moss cushions, providing a representative measurement of the net radiation flux (Q^* ; J day^{-1}). Two soil heat flux plates (REBS HFT3) were installed (in the trench) at the meteorological station to provide measurements of ground heat flux (Q_G ; J day^{-1}), and temperatures were recorded using copper-constantan thermocouples in a profile within pooled water (2007 only) and paired with regular depth measurements for calculation of pool heat storage (Q_W ; J day^{-1}). Soil heat flux plates can underestimate the flux in organic soils because of poor contact between the plate and peat and the interruption of vapour flow (Halliwell and Rouse, 1987; Petrone *et al.*, 2004).

To minimize this, heat flux plates were installed carefully into a small pilot hole, ensuring a snug fit and good contact with the peat soils. The error associated with underestimation is assessed later.

Daily equilibrium evapotranspiration (ET_{eq}) was estimated using the Priestley and Taylor (1972) combination method where

$$ET_{eq} = \alpha \left[\frac{s}{(s+q)} \right] \left[\frac{(Q^* - Q_G - Q_W)}{L\rho} \right] \quad (1)$$

and where L is the latent heat of vaporization (J kg^{-1}), ρ is the density of water (kg m^{-3}), s is the slope of the saturation vapour pressure-temperature curve ($\text{Pa } ^\circ\text{C}^{-1}$) and q is the psychrometric constant (assumed to be $0.0662 \text{ kPa } ^\circ\text{C}^{-1}$ at 20°C). The α coefficient is the Priestley–Taylor coefficient of evaporability and represents the slope of the regression line relating actual (ET) to equilibrium (ET_{eq}) evapotranspiration. Individual α values were derived from lysimeters for each of the dominant surface and vegetation cover types at the Cacouna bog. This included five surface classes (open water, wet, moist, dry and forest) on the basis of field observations of vegetation cover, predominant moisture conditions and previous studies in the Cacouna bog that involved detailed vegetation surveys and aerial photograph interpretation (Van Seters and Price, 2001; Girard *et al.*, 2002). Moisture content within the lysimeters was measured at least weekly and compared with that of the adjacent area. Water was added or removed as required to maintain the moisture content in the lysimeter to within $\pm 5\%$ of the adjacent area. An aerielly weighted α value was derived for the Cacouna bog, which was used for the calculation of an aerielly averaged ET rate for the site. Petrone *et al.* (2004) quantified the ratio between the seasonal mean heat flux plate measurements in peat soils and calorimetric calculations of the total seasonal Q_G (Halliwell and Rouse, 1987) as 0.77 and 0.64 for cutover and restored peatland sites, respectively. Changing the Q_G values measured in the current study by $\pm 40\%$ changes the estimate of evapotranspiration by $\pm 2\%$.

Volumetric soil moisture (θ) and soil–water pressure (ψ) were monitored at two *Sphagnum* cushions located along a topographical gradient and situated atop the remnant cutover peat substrate within the south portion of the ST (Figure 1). Both cushions were greater than 60 cm in diameter and 12 cm in height and were enclosed on four sides (open at top and bottom) by a 60 cm \times 60 cm metal collar (to facilitate carbon flux measurements for an unrelated study). The focus of this study is on vertical

water fluxes, so the presence of the collar will not affect water flows within the cushions. Here, in the lower portion of the ST, the cushions have spread laterally covering patches of the cutover peat and were relatively flat-topped and irregularly shaped, presenting a small localized carpet. One cushion was dominated by *S. capillifolium* (with some *S. magellanicum*), which was located farther down the topographical gradient (south) within the ST where the shallow water table resulted in predominantly moist conditions at the surface (the ‘lower’ cushion). The other cushion was located approximately 100 m upslope (north) of the lower cushion (still within the ST) where conditions were generally drier and was dominated by *S. rubellum* (the ‘upper’ cushion; Figure 1). We recognize that the species and local conditions (e.g. water table) can affect the structure of the mosses hence their water relations (Rydin and McDonald, 1985; Titus and Wagner, 1984), so we caution that small variances in moisture in the mosses overlying the cutover peat reflect their inherent structure (McCarter and Price, 2012). This will be discussed later.

To quantify the relationship between the moisture regime of the moss cushion and that of the cutover peat substrate, measurements were made at two points within the moss (+7 and +2 cm) and the substrate (–5 and –15 cm), with sampling depths referenced to the moss–substrate interface (hence, –5 cm refers to a measurement point 5 cm below the interface; Figure 1). The +7 cm measurement point is approximately 5 cm below the surface of the moss cushion. θ was measured using Campbell Scientific Inc.TM water content probes (CS615) installed horizontally, each paired with a copper–constantan thermocouple, connected to a Campbell Scientific Inc.TM data logger and recording data every 20 min. Water content information is derived from the effect of changing dielectric constant on electromagnetic waves propagating along two 30-cm parallel stainless steel rods (Campbell Scientific, 1996). Probes were calibrated using the measured dielectric permittivity of the peat/air/water matrix in a mixing model expression (Roth *et al.*, 1990), which incorporates the individual dielectric permittivity of each medium and the influence of temperature, and soil porosity and geometry (cf. Kellner and Lundin, 2001). The standard error of the θ estimate associated with this technique is 0.05 (Kellner and Lundin, 2001). Tensiometers were installed within the peat substrate at depths of 5 and 15 cm beneath the base of the *Sphagnum* moss cushions. Soil–water pressure ψ was measured on a regular basis (approximately every 2 or 3 days, when possible) with a TensiometerTM pressure transducer accurate to ± 1 mb (1 cm water is \sim equal to 1 mb pressure). The water table beneath each cushion was monitored continuously using a Remote Data Systems Inc.TM water level monitoring device adjacent to a manual well for verification.

Additionally, manual measurements of θ , ψ and water table position were made daily or every other day in the 2006 and

2007 field seasons, beneath two additional, smaller *Sphagnum* moss cushions (dominated by *S. capillifolium* and *S. rubellum*) that had spontaneously recolonized on the upslope portion of the ST, where drier conditions were generally more prevalent. These cushions had a more hemispherical form than the upper and lower cushions described previously, with dimensions (length \times width \times height) of approximately $23 \times 26 \times 22$ and $29 \times 37 \times 16$ cm for the 'dry' and the 'wet' cushions, respectively. ψ measurements were made using L-shaped tensiometers installed at -5 and -12 cm beneath the cushions and were measured in the same manner as described above. θ measurements were made using a Campbell Scientific Inc. HydroSense™ soil–water measurement system (accuracy ± 0.03), and a calibration coefficient that was determined in the laboratory, on the basis of measurements using an independent measurement of water content and peat cores extracted from the Cacouna bog ($R^2 > 0.9$). Three replicate measurements were taken in the peat substrate surrounding each moss cushion, with θ averaged over the 12-cm probe length. Concurrent measurements of water table position were made using a manual well.

As an initial restoration measure, a series of peat dams were constructed within the Cacouna bog (Fall 2006), causing the site-average water table to rise by 32 cm (Ketcheson and Price, 2011). During the 2006 study period, standing water occupied a small ($< 5\%$) proportion of the site; however, in the 2007 study period, standing water covered 37% of the southern (rewetted) portion of the Cacouna bog (average depth = 24 cm), occupying some trenches along their entire length and others not at all. This resulted in flooding of many locations within the site where *Sphagnum* mosses had successfully recolonized prior to rewetting, including parts of the ST. Inundation of the upper and lower cushions occurred almost immediately as there was heavy rainfall on the day the dams were installed. This flooding persisted through the fall and winter and throughout the 2007 study period, precluding continued meaningful measurement and destroying the structure of the moss cushions before we were able to sample them for their physical properties.

Although the intention was to characterize the moisture relations in the upper and lower cushions before and after blocking the drainage ditches, this became pointless following their inundation in 2007. However, characterization of the cushion and substrate moisture and pressure conditions before and following rewetting was still possible at the smaller cushions that were manually monitored during both study periods, because they were not inundated.

RESULTS

Environmental variables

Less P was received during the summer of 2006 than 2007 resulting in a larger cumulative seasonal site water deficit

(precipitation minus evapotranspiration; $P - ET$) of -21 mm compared with -1 mm for 2007. ET rate from moss-covered surfaces (3.0 mm day $^{-1}$) was similar to the site-averaged ET rate (2.7 mm day $^{-1}$). The greatest number of days with rain events was in 2006 (67% of days); however, these were predominantly small rain events. Only one event exceeded 16 mm in 2006, which was a rain event that recorded nearly 60 mm of precipitation over a 4-day period. The wetter year, 2007, was dominated by large, less frequent precipitation events (46% of days), in which six separate events exceeded 16 mm. Precipitation for June and July 2006 and 2007 was 88% and 121% of the 30-year average (Environment Canada, 2003), and data checks made using manual rain gauges were within $\pm 10\%$ of the logging tipping bucket rain gauge.

Moisture dynamics within Sphagnum cushions

Data from the 2006 study period (19 May–16 Aug) demonstrate that water table variations (in response to precipitation inputs) produced a more distinct response in θ at the lower cushion (higher average water table) than at the upper cushion (lower average water table) (Figure 2). θ decreased upwards into the moss cushion, further from the water table. The average (\pm range) water table position relative to the interface at the upper cushion was -28 ± 5 cm, compared with -18 ± 5 cm at the lower cushion (Table I), which resulted in higher and more variable θ at all depths at the lower cushion (Figure 3). θ variability was greatest at the base of the lower cushion (θ_{+2}), indicated by the large standard deviation in Figure 3, as the lower cushion was influenced more strongly by variations in the position of the shallower water table. Conversely, the relatively dry upper cushion was less influenced by the position of the water table, as indicated by the lower and more stable θ .

Both the upper and lower cushion θ responded to precipitation events and the accompanying water table fluctuations. The largest precipitation event of the 2006 study period occurred from 10 June to 14 June, totalling 61 mm of rain, with as much as 40 mm in 24 h (11 June). θ_{+7} at the lower cushion increased by 0.65, whereas θ_{+2} increased by 0.45 and reached saturation as the cushion became partially inundated by the rising water table (Figure 4). The maximum water table position beneath the upper cushion during the event was -11 cm, resulting in a more moderate increase in moss cushion θ (at θ_{+2}) of 0.1, whereas the substrate θ increased by over 0.15 at θ_{-5} (Figure 4). The top and bottom portion of both the upper and lower cushions (i.e. θ_{+2} and θ_{+7}) remained well connected throughout the 2006 study

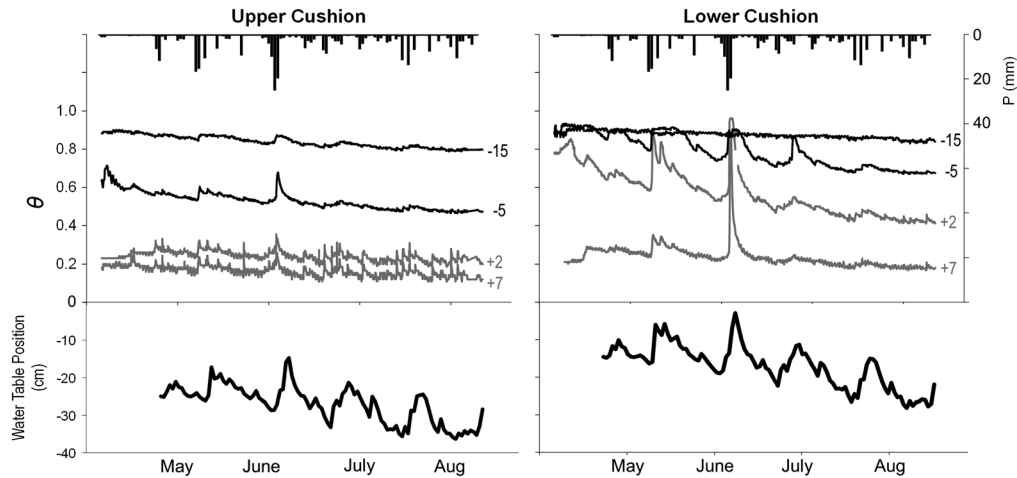


Figure 2. θ , water table and daily precipitation (P) at the upper (drier; left graph) and lower (wetter; right graph) moss cushion during the 2006 study period. Measurement location (relative to the substrate-moss interface) within the substrate (black lines) and the moss cushions (grey lines) are indicated on the figure.

Table I. Seasonal average θ , ψ (2006 only) and water table (2006 and 2007) at the upper and lower moss cushions.

Location	Measurement position (cm relative to cushion-substrate interface)	θ		Seasonal average water table (cm relative to cushion-substrate interface)		
		2006	2006	2006	2007	
Upper cushion	Moss	+7	0.16 (± 0.03)	-28 (± 5)	+12 (± 2)	
		+2	0.24 (± 0.02)			
	Substrate	-5	0.53 (± 0.05)			-10
		-15	0.84 (± 0.03)			-1
Lower cushion	Moss	+7	0.24 (± 0.06)	-18 (± 5)	+58 (± 2)	
		+2	0.58 (± 0.13)			
	Substrate	-5	0.79 (± 0.09)			-8
		-15	0.88 (± 0.02)			+13

No θ or ψ data are shown for 2007 because of the perpetually inundated state of the cushions following site rewetting; and values in brackets represent the standard deviation.

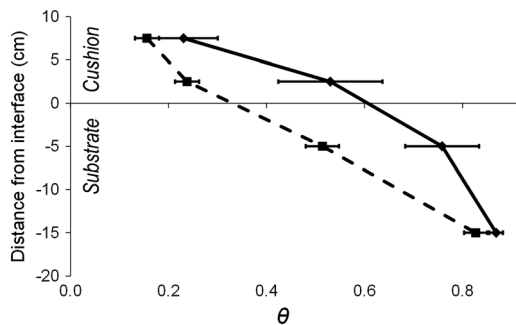


Figure 3. Seasonal θ at the upper (dashed line) and lower (solid line) cushion in 2006 (error bars represent the standard deviation).

period. The two θ measurement positions are two-way dependent and highly correlated ($r > 0.97$) within both cushions (data not shown).

Connectivity between *Sphagnum* cushions and the remnant peat substrate

Sphagnum cushions were generally well connected to the moisture regime of the cutover peat substrate when the position of the water table was between -5 and -20 cm (relative to the moss cushion-cutover peat substrate interface), as indicated by the relatively steep slope (0.02) of the linear regression relating θ to water table position (Figure 5 section A). In contrast, the slope was reduced (to 0.01) when the water table position was deeper than -20 cm (Figure 5 sections B and C). When the position of the water table dropped below -30 cm, the slope was further reduced (to < 0.001), and the coefficient of determination (R^2) dropped from greater than 0.7 to less than 0.01 (Figure 5 section D). In the unsaturated zone below the lower cushions, where the water table was generally closer to the surface, the vertical hydraulic

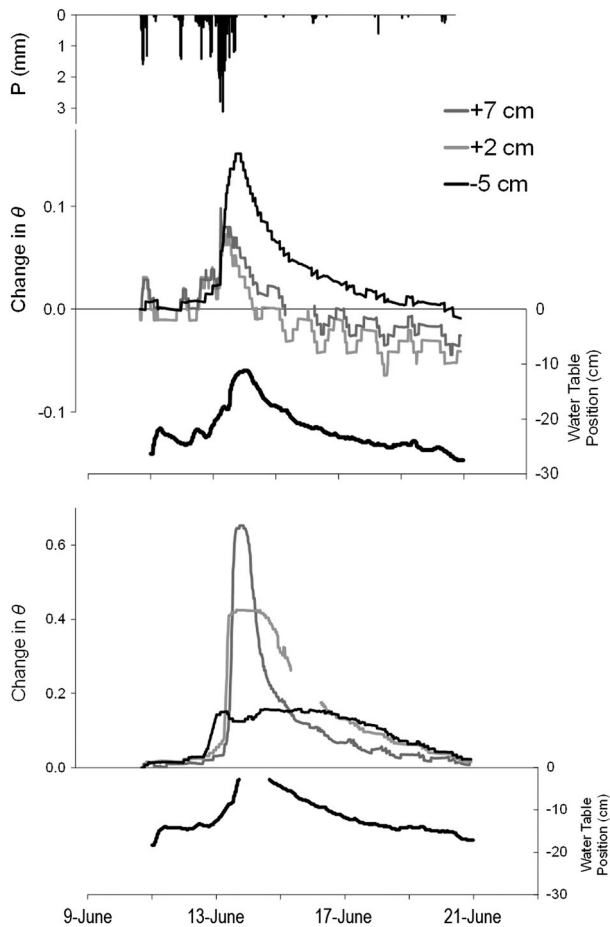


Figure 4. Water table and θ during a 61 mm precipitation (P) event during the 2006 study period at the upper cushion (top) and the lower cushion (bottom; bars represent precipitation). Note the different scale for change in θ on the upper and lower cushion plots. $\theta=0$ represents pre-event conditions.

gradients (Figure 5 inset) were consistently upwards (except during rain events) and increased during periods of higher water table (Figure 5 sections A and B). Hydraulic gradients below the upper cushion were much smaller and also upwards during wetter periods when the water table was higher (Figure 5 section C) but turned downwards during dry periods when the water table was low (Figure 5 section D).

Ecological impact of restoration (rewetting)

Blocking the drainage network at the Cacouna bog resulted in flooding of much of the lower lying portions of the site (i.e. trenches), where most of the *Sphagnum* mosses had spontaneously recolonized prior to rewetting. Inundation killed many of the established moss cushions, including the upper and lower cushions from this study. However, the smaller cushions that had recolonized drier areas further upslope within the ST were also monitored in 2006 and 2007. At these cushions, the water table was higher in 2007

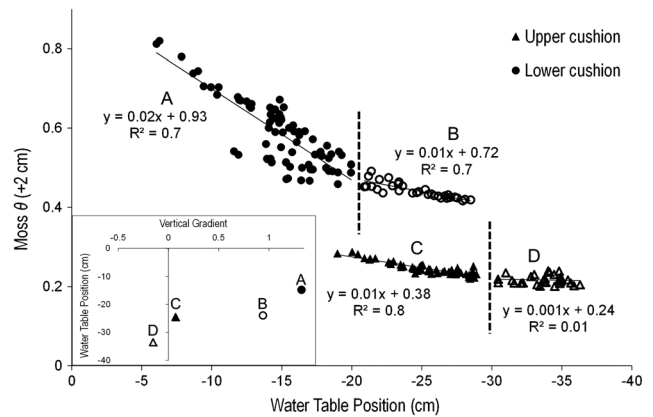


Figure 5. The relationship between water table (relative to the moss cushion-cutover peat substrate interface) and θ_{+2} (within the cushion) at the upper and lower cushions. Open symbols represent θ when it becomes less dependent upon the position of the water table (B and D for the lower and upper cushions, respectively) and solid symbols represent conditions when θ is responsive to changes in water table (A and C for the lower and upper cushions, respectively). Dashed vertical lines distinguish between these trends. Note that these cut-off points were determined from visual inspection of the dataset. The inset figure illustrates the average vertical hydraulic gradients measured beneath the cushions under the corresponding average water table position. Positive values indicate upward gradients (i.e. from the substrate to the cushion).

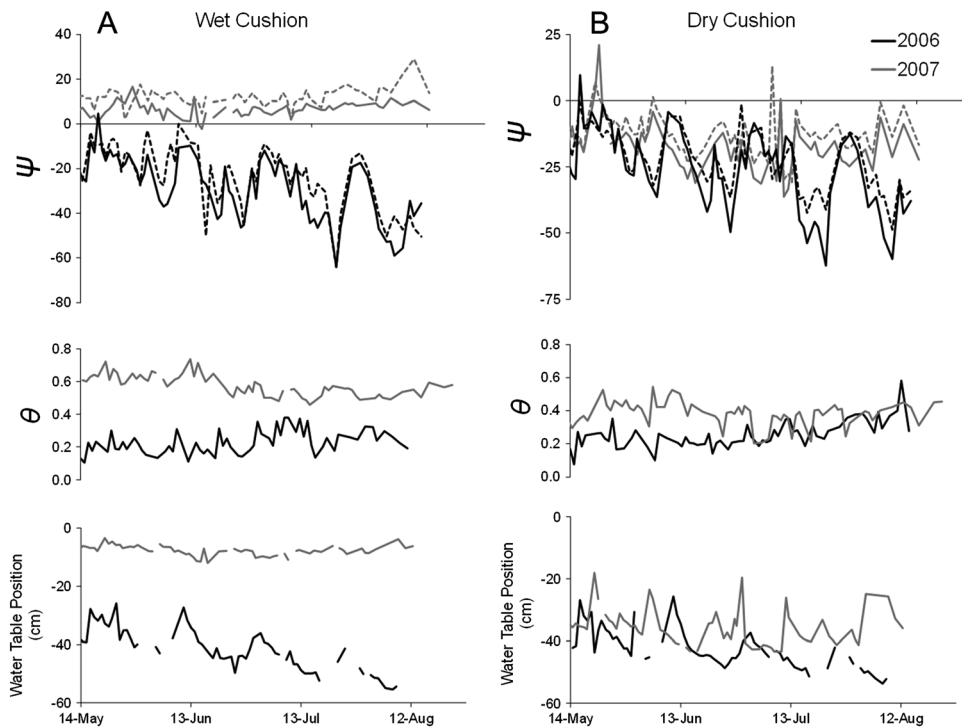
than in 2006, and its depth below the surface depended on the cushions' topographic position within the trench. θ , ψ and water table position were comparable beneath two selected cushions prior to rewetting (Table II); however, the cushion that was situated in a topographically lower position within the ST (the wet cushion) was impacted more by the rewetting than the cushion located further upslope in the trench (the dry cushion) (Figure 6). The average seasonal water table position at the wet cushion increased by 34 cm, whereas the water table increased by 7 cm at the dry cushion. Accordingly, both ψ and θ increased proportionately more at the wet cushion compared with at the dry cushion (Table II and Figure 6).

DISCUSSION

Precipitation was poorly retained within the moss cushions. The upper cushion returned to pre-event moisture conditions much more rapidly (within ~2–3 days) than the lower cushion (~7 days; Figure 4). Although some of this effect is caused by the overall site drainage (i.e. lower areas drain later), the rapid stabilization of θ within both the upper and lower moss cushions indicates that rain events provide water that persists in the mosses for only about a week. Because water inputs from precipitation were shed rapidly from both the upper and lower cushion, the water table position, when close to the surface, exhibited a stronger control on the moisture dynamics within both cushions than precipitation inputs. For example, moisture content

Table II. Seasonal average ψ , θ (averaged over 0 to -12 cm) and water table at two *Sphagnum* moss cushions within the study trench at the Cacouna bog.

	Wet cushion diameter = ~ 33 cm; height = ~ 16 cm		Dry cushion diameter = ~ 25 cm; height = ~ 22 cm		Change	
	2006	2007	2006	2007	Wet cushion	Dry cushion
ψ (mb)	-5 cm	-28	7	-26	+35	+8
	-12 cm	-24	12	-22	+36	+10
$\theta_{0-12\text{ cm}}$	0.23	0.58	0.25	0.39	+0.35	+0.14
Water table	-42	-8	-43	-36	+34	+7

Figure 6. θ , ψ and water table position at two *Sphagnum* moss cushions in the study trench prior to (2006) and following (2007) rewetting. The wet cushion (A) was situated in a topographically lower position within the study trench compared with the dry cushion (B).

within the lower cushion (θ_{+2} and θ_{+7}), where the water table is close to the surface, responded more strongly than θ within the upper cushion (water table farther from surface) to a common precipitation event (hence, approximately the same precipitation water input; Figure 4). Moisture content beneath the upper cushion (i.e. θ_{-5}) appeared to respond more strongly than at the lower cushion; however, θ_{-5} reached saturation at the lower cushion, which constrained changes in θ during the precipitation event. Despite the poor retention of precipitation waters, θ_{+7} at both moss cushions was sustained during extended dry periods with low water table and infrequent precipitation (Figure 2). This was sufficient for critical physiological processes at the photosynthesizing capitula, because these mosses sustained a moist-to-touch

surface and healthy appearance that is indicative of higher rates of carbon fixation (Wagner and Titus, 1984) and increased *Sphagnum* growth rates (McNeil and Waddington, 2003).

Numerical simulations of water flow between the moss cushion and the cutover peat substrate were not possible because reliable estimates of unsaturated hydraulic conductivity are not available. However, the direction and magnitude of vertical hydraulic gradients measured beneath the cushions indicates that water fluxes were occurring from the substrate to the mosses at the lower cushion (Figure 5 inset), except during and immediately following rain events when event water was percolating downwards. Water fluxes remained in the upward direction even under conditions of relatively deep water table at the

lower cushion, albeit reduced gradients indicate smaller magnitude fluxes of water, which is in agreement with the concurrent reduced dependence of cushion θ on water table position (Figure 5). At the upper cushion, however, downward gradients indicate some movement of water from the cushion to the substrate when conditions are very dry (deep water table). Nonetheless, given the strong connectivity within both cushions ($r > 0.97$ between θ_{+2} and θ_{+7}) and considering the relatively stable θ_{+7} and θ_{+2} at the upper cushion (Figure 3), it seems that upward capillary transport of water within the cushion and water retention near the moss capitula is sufficient to hold water against the soil–water pressures observed within the substrate in this study. The moisture regime observed at the cushions in this study are within the range of values reported for 11 *Sphagnum* moss cushions measured at the Cacouna bog by Price and Ketcheson (2009) ($n = 72$ measurements at each of four depths), including the observation of stable θ near the surface of the moss cushion. Price and Ketcheson (2009) reported the lowest value of standard deviation in the uppermost part of the moss cushions where θ remained relatively stable, and McNeil and Waddington (2003) observed similar moss moisture profiles. A similar range of θ was observed within a transplanted *Sphagnum* moss cover in a restored peatland (Cagampan and Waddington, 2008) as well as within *Sphagnum* cushions in a natural peatland (Yazaki *et al.*, 2006).

Notable differences existed in the nature of the fluxes and stores of water within the upper and lower cushions in this study. The average water table position at the upper cushion was deeper (–28 cm) than at the lower cushion (–18 cm) (Table I), which resulted in differing moisture availability at each cushion, as indicated by weaker hydraulic gradients and lower θ at the upper cushion. Consequently, the moisture regime of the upper cushion appeared to be unaffected by the moisture conditions within the underlying substrate during dry periods with deep water tables (Figure 5). Restricted water storage losses from the upper cushion (Figure 7) resulted in a fairly constant θ throughout the study period (Figure 2), indicating that the water storage within the cushion is

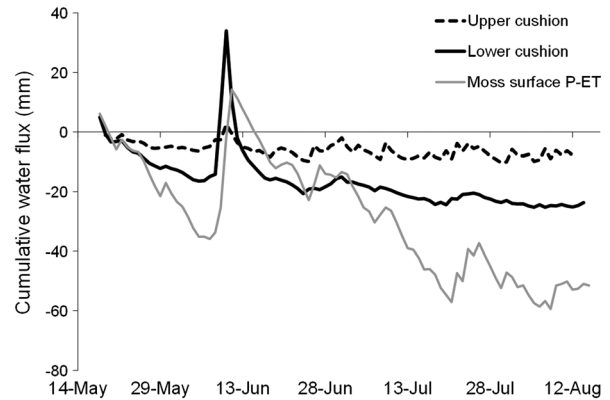


Figure 7. Cumulative water storage at the upper and lower cushions, and the net water flux at the moss surface ($P - ET$) in 2006. Negative water fluxes indicate loss of water storage from the cushions.

only slightly depleted between rain events and throughout the summer months (Table 3), which experienced a water deficit in 2006. The lower cushion, however, displays a more prominent trend of decreasing θ throughout the season (Figure 7), especially at θ_{+2} (Figure 2), indicating a greater loss of internal water from cushion storage (Table III). Here, water losses from the cushion exceed the rate of replenishment from atmospheric sources and upward conductance from the substrate. The moisture regime of the lower cushion is characterized by limited water retention and constrained water redistribution, whereas the upper cushion appears to have increased water retention and maintains a more uniform vertical water distribution (Figure 3). Minor differences in moisture regime dynamics could be attributed, in part, to slight structural differences between the two cushions that occurred as a consequence of both the prevalent moisture conditions (i.e. wet vs dry; e.g. Waddington *et al.*, 2011; Waddington *et al.*, 2003) and/or differences related to the *Sphagnum* species composition of the cushions (e.g. Hayward and Clymo, 1982; Rydin, 1986); however, characterization of the physical properties of the moss cushions was not possible because of their inundation (as discussed previously).

Table III. Components of the *Sphagnum* moss cushion water budget, seasonal average vertical hydraulic gradient and the estimated minimum unsaturated hydraulic conductivity necessary [$K(\psi)_{\text{MIN}}$] to meet the water demand at the surface of the moss cushions (in the absence of other water sources and passive water conservation mechanisms).

Cushion	$P - ET$	$\Delta S_{\text{cushion}}$	q	Average vertical gradient	$K(\psi)_{\text{MIN}}$
	(mm)	(mm)	(mm)	(mm day ⁻¹)	(m s ⁻¹)
Upper	–52	–8	44	0.006	9.6×10^{-7}
Lower	–52	–24	28	1.17	3.0×10^{-9}

$P - ET$, precipitation minus evapotranspiration.

Water balance of *Sphagnum* cushions

Time series θ data within the cushions permits calculations of one dimensional (vertical) water flux dynamics using mass balance on the basis of the volumetric water content changes in a moss layer of known volume (cf. Yazaki *et al.*, 2006). This requires that the sample volume change is negligible, which is a reasonable assumption given the small moisture fluctuations in cushions (Yazaki *et al.*, 2006). Also, lateral fluxes of water within the cushions were ignored, because they are minimal considering the flat centre areas within the *Sphagnum* cushions (Yazaki *et al.*, 2006), our upper and lower cushions being low (12 cm) and broad (>60 cm).

An estimation of the seasonal (19 May to 16 August 2006) water budget was determined for each cushion, where

$$P - ET + q + \varepsilon = \Delta S_{\text{cushion}} \quad (2)$$

where q is the net water flux between the substrate and the moss cushion and $\Delta S_{\text{cushion}}$ is the water storage change within the moss cushion. $\Delta S_{\text{cushion}}$ was calculated daily as the summation of the change in θ_{+2} and θ_{+7} multiplied by the thickness of the moss layer (0–5 cm for θ_{+2} and 5–12 cm for θ_{+7}). ε is the residual term, which incorporates much smaller probable sources of water such as dewfall, distillation and vapour transport, as well as measurement error. Because P , ET and $\Delta S_{\text{cushion}}$ were quantifiable, the water budget equation can be used to calculate the net water flux, q .

Average ET rates from moss-covered surfaces (3.0 mm day^{-1}) were higher than the average daily P and resulted in a water deficit ($P - ET$) of -52 mm (Figure 7) between 19 May and 16 August. In response to this, there was a change (decrease) in soil–water storage ($\Delta S_{\text{cushion}}$) of -8 and -24 mm over the season within the upper and lower cushions, respectively (Figure 7), on the basis of a decrease in average volumetric water content, θ , of 0.13 and 0.43, respectively (Figure 2). Consequently, water fluxes (q) of 44 and 28 mm to the upper and lower cushion, respectively, are required to satisfy the water budget (Table III). Considering the predominance of upward pressure gradients in the substrate (Figure 5), it is hypothesized that some of this flux is satisfied by upward water movement from the unsaturated cutover peat. However, on the basis of Darcy's law using literature values of unsaturated hydraulic conductivity of cutover bog peat (at zero matric potential, or saturation) of $2.7 \times 10^{-8} \text{ m s}^{-1}$ (Schlotzhauer and Price, 1999) and hydraulic gradients observed here (as displayed in Figure 5, inset), the measured water deficit is at least an order of magnitude larger than the calculated Darcy flux at the upper cushion. Accordingly, to balance the water budget with the observed hydraulic gradients at the upper cushion, the unsaturated hydraulic conductivity must be at least $3.0 \times 10^{-9} \text{ m s}^{-1}$. This is an

order of magnitude lower than the value for cutover peat reported by Schlotzhauer and Price (1999; Table 3), and here, the cutover peat, in its unsaturated state, probably had an even lower unsaturated hydraulic conductivity value that was insufficient to provide the requisite water supply to balance the water budget. It is possible that the mosses are relying upon additional sources of water such as dew and distillation (discussed in the succeeding texts), but the importance of these sources is uncertain in light of potential errors in the water budget.

Consideration of the errors associated with the cushion water balance equation (Equation 2) must be based on relative terms in the absence of a standard against which to quantify absolute error (Van Seters and Price, 2001). Estimates of ET were based upon the Priestley–Taylor (1972) method that is both widely used and appropriate for this application when used in combination with a site-specific calibration factor (Drexler *et al.*, 2004). Although we recognize potential errors in measurement of Q^* and Q_G in the Priestley–Taylor (1972) method, their calibration to measured ET in the lysimeters means any inconsistencies (e.g. caused by sensor error) are compensated for in the calibration process; thus, errors in ET are mainly associated with lysimeter error. Lysimeters were situated in representative moss cushions, and although weighing accuracy was good ($\pm 0.02 \text{ mm}$), we recognize errors occur when the monolith wetness differs from the surroundings (Allen *et al.*, 1991). Nonetheless, lysimeter accuracies are often better than 0.05 mm (Howell *et al.*, 1991). In this study, ET rates from moss-covered surfaces represent an average of triplicate lysimeter measurements; seasonal losses from individual lysimeters were within 15% of one another. Rainfall measured in the tipping bucket and manual rain gauge had a randomly distributed difference of $\pm 10\%$, which, although dependent upon the local rainfall intensity and timescale (Ciach, 2003), is within the typical accuracy range of approximately $\pm 15\%$ for such instruments (Habib *et al.*, 2001). The gauges were located in between (within $\sim 50 \text{ m}$ of) the cushions, the latter being fully exposed (i.e. no overhead vegetation except for a sparse layer of ericaceous shrubs). Estimates of $\Delta S_{\text{cushion}}$ probably have relatively little error as the absolute θ probe accuracy is within $\pm 5\%$ and the change in θ used to calculate $\Delta S_{\text{cushion}}$ will therefore be a fraction of this (Campbell Scientific, 1996).

The residual term ($q + \varepsilon$) incorporates these errors, which may or may not cancel out. In this case, ε was 85% and 54% of $P - ET$ for the upper and lower cushions, respectively. Although it is possible that a significant component of these relatively large unexplained differences could be caused by error, additional sources of water from dew, distillation and soil–water flux from the cutover peat almost certainly comprise some of it.

The potential role of small-scale water sources on moss cushion moisture dynamics

The methodology of a parallel experiment (not reported here) involved removing the ericaceous shrubs from several *Sphagnum* moss cushions within the Cacouna bog. These mosses quickly desiccated and whitened, becoming dry and brittle to the touch; a phenomenon previously observed by McNeil and Waddington (2003). However, field observations during the 2007 study period indicate that these cushions regained colour and elasticity and were moist to the touch in the early morning hours (and following precipitation events), returning to their desiccated state typically before noon. It is hypothesized that overnight dewfall is, under the right meteorological conditions, partially responsible for this rejuvenation of mosses, although this occurrence was still observed on mornings following nights when atmospheric conditions (relative humidity and temperature) were not conducive to dewfall. Water gains to boreal feather mosses have also been attributed to overnight condensation of upward fluxes of vapour (distillation) thereby hydrating the uppermost parts of the mosses (Carleton and Dunham, 2003). It is, however, controlled by the vapour flux, which Price *et al.* (2009) suggest is only ~1% of the total water flux, but which may be critical physiologically when moisture availability is limited. Although small, these water sources (dewfall and distillation) could represent a physiologically critical supply of water to the capitula, especially during a period of water deficit.

Rewetting and moss survival

The presence of cushions in the southern portion of the trench proves that conditions were already inherently suitable for moss recolonization prior to rewetting. Raising the water table by ditch-blocking increased ψ and θ within the remnant peat (Figure 6). The degree to which ψ and θ within the substrate are affected depends on the surface topography and the level of peat decomposition, which affects pore-size distribution, hence water retention and capillary rise. Regardless, the higher water table caused an increase in ψ and θ in the substrate beneath the moss cushions (Figure 6), which creates favourable conditions for photosynthesis (McNeil and Waddington, 2003; Strack and Price, 2009). Given the weak connectivity between the mosses and the underlying substrate at low water tables (Figure 5), rewetting must raise the water table within the remnant peat to within 30 cm of the cutover peat surface to re-establish a good capillary connection that favours water fluxes to *Sphagnum* cushions. The connection strength between the remnant peat deposit and the new mosses is in part a function of the characteristics of the cutover peat (e.g. bulk density, pore-size distribution and botanical composition) as well as the *Sphagnum* species. As previously noted, species with tighter structure (thus smaller average pore diameter) are able to impart a stronger capillary force and more effectively withhold water from (reduce water loss to) the cutover substrate.

CONCLUSIONS

The position of the water table exhibited a strong control on the moisture regime of the *Sphagnum* moss cushions; however, this relationship weakened when ψ and θ in the peat substrate beneath the cushion decreased as the water table dropped. Specifically, in the moss cushions measured for this study, the moisture regime within the cutover peat substrate had a reduced influence on cushion θ at water table positions deeper than -20 cm, with no influence at water table positions deeper than -30 cm. Under these dry conditions often found in cutover peatlands, the newly formed *Sphagnum* mosses are likely relying upon atmospheric (rain and dew) and internal (capillary transport and storage) water inputs over the water table within the remnant peat deposit as a source of water for critical physiological functions. However, precipitation waters are poorly retained within the cushions in this study, indicating that rain event water can likely only be relied upon by the mosses for a short period following precipitation events. Observations indicated that dewfall and/or distillation was capable of rejuvenating desiccated moss cushions, which justifies consideration of potentially important small sources of water for the mosses. Further quantification of these small-scale water fluxes is required. Additionally, future studies with replication and parameterization are required to investigate the impact of moss architecture (e.g. pore size and species composition) on the cushion moisture regime.

Intense field-based measurements coupled with parameterization of the unsaturated hydraulic properties of the mosses and cutover peat should facilitate future modelling of water fluxes within spontaneously regenerated *Sphagnum* mosses in cutover peatland ecosystems. In the current study, restoration (rewetting) efforts created conditions more favourable for *Sphagnum* survival through increased soil moisture and soil-water pressure; however, future rewetting efforts should strive to obtain a more uniform impact throughout the peatland. Water table fluctuations should be constrained within the upper 30 cm of the cutover peat surface to ensure sufficient water fluxes to *Sphagnum* cushions.

ACKNOWLEDGEMENTS

We thank Andy Baird, Bjorn Robroek and an anonymous reviewer for constructive comments on an earlier draft of this manuscript. Field and lab support from Nathalie Brunet, Sean Bryant, Mike Christie, Antonio DiFebo, Dave Fox, Janine Gilbert, Joseph Lance and Peter Whittington is gratefully acknowledged. This research was supported by the Natural Science and Engineering Research Council (NSERC) Industrial Research Chair (Rochefort) and Discovery Grant (Price) programs.

REFERENCES

- Allen RG, Pruitt WO, Jensen ME, 1991. Environmental requirements of lysimeters. In: Allen, R.G., Howell, T.A., Pruitt, W.O., Walter, I.A., Jensen, M.E. (Eds.), ASCE Specialty Conference on 'Lysimeters for Evapotranspiration and Environmental Measurements'. ASCE, Honolulu, Hawaii, pp. 444.
- Andrus RE. 1979. *Sphagnum subtile* (russow) warnst. and allied species in North America. *Systematic Botany*, **4**(4): 351–362.
- Cagampan JP, Waddington JM. 2008. Net ecosystem CO₂ exchange of a cutover peatland rehabilitated with a transplanted acrotelm. *Ecoscience*, **15**(2): 258–267.
- Campbell Scientific, 1996. CS615 water content reflectometer instruction manual. Campbell Scientific Inc.
- Canada E, 2003. Climate normals. Environment Canada.
- Carleton TJ, Dunham KMM. 2003. Distillation in a boreal mossy forest floor. *Canadian Journal of Forest Research*, **33**: 663–671.
- Ciach GJ. 2003. Local random errors in tipping-bucket rain gauge measurements. *Journal of Atmospheric and Oceanic Technology*, **20**(5): 752–759.
- Cronberg N. 1989. Patterns of variation in morphological characters and isoenzymes in populations of *Sphagnum capillifolium* (ehrh.) hedw. and *S. rubellum* wils. from two bogs in southern Sweden. *Journal of Bryology*, **15**(4): 683–696.
- Cronberg N. 1998. Population structure and interspecific differentiation of the peat moss sister species *Sphagnum rubellum* and *S. capillifolium* (*Sphagnaceae*) in northern Europe. *Plant Systematics and Evolution*, **209**(3–4): 139–158.
- Csintalan Z, Takács Z, Proctor MCF, Nagy Z, Tuba Z. 2000. Early morning photosynthesis of the moss *Tortula ruralis* following summer dew fall in a Hungarian temperate dry sandy grassland. *Plant Ecology*, **151**(1): 51–54.
- Drexler JZ, Snyder RL, Spano D, U KTP. 2004. A review of models and micrometeorological methods used to estimate wetland evapotranspiration. *Hydrological Processes*, **18**: 2071–2101.
- Farrick KK, Price JS. 2009. Ericaceous shrubs on abandoned block-cut peatlands: implications for soil water availability and *Sphagnum* restoration. *Ecohydrology*, **2**: 530–540.
- Girard M, Lavoie C, Thériault M. 2002. The regeneration of a highly disturbed ecosystem: a mined peatland in southern Québec. *Ecosystems*, **5**: 274–288.
- Habib E, Krajewski W, Kruger A. 2001. Sampling errors of tipping-bucket rain gauge measurements. *Journal of Hydrologic Engineering*, **6**(2): 159–166.
- Halliwell DH, Rouse WR. 1987. Soil heat flux in permafrost: characteristics and accuracy of measurement. *Journal of Climatology*, **7**(6): 571–584.
- Hayward PM, Clymo RS. 1982. Profiles of water content and pore size in *Sphagnum* peat and their relation to peat bog ecology. *Proceedings of the Royal Society of London B*(215): 299–325.
- Heijmans MMPD, Arp WJ, Berendse F. 2001. Effects of elevated CO₂ and vascular plants on evapotranspiration in bog vegetation. *Global Change Biology*, **7**(7): 817–827.
- Howell TA, Schneider AD, Jensen ME, 1991. History of lysimeter design and use for evapotranspiration measurements. In: Allen, R.G., Howell, T.A., Pruitt, W.O., Walter, I.A., Jensen, M.E. (Eds.), ASCE Specialty Conference on 'Lysimeters for Evapotranspiration and Environmental Measurements'. ASCE, Honolulu, Hawaii, pp. 444.
- Kellner E, Lundin L-C. 2001. Calibration of time domain reflectometry for water content in peat soil. *Nordic Hydrology*, **32**(4–5): 315–332.
- Ketcheson SJ, Price JS. 2011. The impact of peatland restoration on the site hydrology of an abandoned block-cut bog. *Wetlands*, **31**(6): 1263–1274.
- Kuhry P, Vitt DH. 1996. Fossil carbon/nitrogen ratios as a measure of peat decomposition. *Ecology*, **77**(1): 271–275.
- McCarter CPR, Price JS. 2012. Ecohydrology of *Sphagnum* moss hummocks: mechanisms of capitula water supply and simulated effects of evaporation. *Ecohydrology*. DOI: 10.1002/eco.1313
- McNeil P, Waddington J. 2003. Moisture controls on *Sphagnum* growth and CO₂ exchange on a cutover bog. *Journal of Applied Ecology*, **40**(2): 354–367.
- Money RP, Wheeler BD. 1999. Some critical questions concerning the restorability of damaged raised bogs. *Applied Vegetation Science*, **2**: 107–116.
- National Wetlands Working Group, 1997. The Canadian Wetland Classification System – Second Edition. University of Waterloo, Waterloo, Ontario.
- Petrone RM, Price JS, Waddington JM, von Waldow H. 2004. Surface moisture and energy exchange from a restored peatland, Québec, Canada. *Journal of Hydrology*, **295**(14): 198–210.
- Price JS. 1997. Soil moisture, water tension, and water table relationships in a managed cutover bog. *Journal of Hydrology*, **202**: 21–32.
- Price JS, Edwards TWD, Yi Y, Whittington P. 2009. Physical and isotopic characterization of evaporation from *Sphagnum* moss. *Journal of Hydrology*, **369**(175–182): .
- Price JS, Ketcheson SJ, 2009. Water relations in cutover peatlands. In: AGU (Ed.), Carbon Cycling in Northern Peatlands, pp. 277–287.
- Price JS, Whitehead GS. 2001. Developing hydrologic thresholds for *Sphagnum* recolonization on an abandoned cutover bog. *Wetlands*, **21**(1): 32–40.
- Price JS, Whitehead GS. 2004. The influence of past and present hydrological conditions on *Sphagnum* recolonization and succession in a block-cut bog, Quebec. *Hydrological Processes*, **18**: 315–328.
- Priestley CHB, Taylor RJ. 1972. On the assessment of surface heat flux and evaporation using large-scale parameters. *Monthly Weather Review*, **100**(2): 81–92.
- Proctor MCF (Ed.), 1982. Physiological Ecology: Water Relations, Light and Temperature Responses, Carbon Balance. Bryophyte Ecology. Chapman and Hall, London, 333–381 pp.
- Robroek BJM *et al.* 2009. *Sphagnum* re-introduction in degraded peatlands: the effects of aggregation, species identity and water table. *Basic and Applied Ecology*, **10**(8): 697–706.
- Roth K, Schulin R, Flüher H, Attinger W. 1990. Calibration of time domain reflectometry for water content measurement using a composite dielectric approach. *Water Resources Research*, **26**(10): 2267–2273.
- Rydin H. 1985. Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna*. *Oikos*, **45**: 374–379.
- Rydin H. 1986. Competition and niche separation in *Sphagnum*. *Canadian Journal of Botany*, **64**(8): 1817–1824.
- Rydin H, McDonald AJS. 1985. Tolerance of *Sphagnum* to water level. *Journal of Bryology*, **13**: 571–578.
- Schipperges B, Rydin H. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. *New Phytologist*, **140**(4): 677–684.
- Schouwenaars JM, Gosen AM. 2007. The sensitivity of *Sphagnum* to surface layer conditions in a re-wetted bog: a simulation study of water stress. *Mires and Peat*, **2**: 1–19.
- Strack M, Price JS. 2009. Moisture controls on carbon dioxide dynamics of peat-*Sphagnum* monoliths. *Ecohydrology*, **2**: 34–41.
- Tarnocai C. 2006. The effect of climate change on carbon in Canadian peatlands. *Global and Planetary Change*, **53**: 222–232.
- Titus JE, Wagner DJ. 1984. Carbon balance for two *Sphagnum* mosses: water balance resolves a physiological paradox. *Ecology*, **65**(6): 1765–1774.
- Van Seters TE, Price JS. 2001. The impact of peat harvesting and natural regeneration on the water balance of an abandoned cutover bog, Quebec. *Hydrological Processes*, **15**: 233–248.
- Waddington JM, Lucchese MC, Duval TP. 2011. *Sphagnum* moss moisture retention following the re-vegetation of degraded peatlands. *Ecohydrology*, **4**(3): 359–366.
- Waddington JM, Rochefort L, Campeau S. 2003. *Sphagnum* production and decomposition in a restored cutover peatland. *Wetlands Ecology and Management*, **11**(1): 85–95.
- Wagner DJ, Titus JE. 1984. Comparative desiccation tolerance of two *Sphagnum* mosses. *Oecologia*, **62**(2): 182–187.
- Yazaki T, Urano S-i, Yabe K. 2006. Water balance and water movement in unsaturated zones of *Sphagnum* hummocks in Fuhrengawa Mire, Hokkaido, Japan. *Journal of Hydrology*, **319**: 312–327.