

# Soil water dynamics and hydrophysical properties of regenerating *Sphagnum* layers in a cutover peatland

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## Abstract:

The physical and hydrological conditions in extracted peatlands often act as barriers to the regeneration of the keystone peat-forming genus *Sphagnum*. Although previous work has suggested that *Sphagnum* mosses regenerating on cutover peat surfaces quickly become vulnerable to water stress as the thickness of the regenerated layer increases, uncertainties regarding the storage and transmission properties of this layer and how these might evolve over time have made this assertion difficult to evaluate. This study investigates the hydrophysical properties and hydrological behaviour of regenerating *Sphagnum* layers ranging from 3 to 43 years in age using both field and laboratory methods. The >40-year-old regenerated layers had significantly ( $p < 0.001$ ) higher bulk density and retention capacity in the 5-cm-thick basal layer directly overlying the cutover peat than the newer (<10 year old) regenerated layers. Capillarity was a much stronger control on surficial water content ( $\theta$ ) than precipitation, which was poorly retained in the *Sphagnum* canopy, suggesting that regulation of water table position is an effective method of controlling  $\theta$  as a means of optimizing productivity. In general, the  $\theta$  sustained at a given water table position decreased as regenerated layer thickness increased. Analysis of water table position relative to the former cutover peat surface in different areas of the site suggests that the soil water dynamics of the >40-year-old regenerated layers may be becoming increasingly similar to those of a natural bog peatland. Copyright © 2015 John Wiley & Sons, Ltd.

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## INTRODUCTION

The extraction of *Sphagnum* peat from bog peatlands is an important industry in certain regions of Canada, generating an estimated \$260 million dollars in annual revenue (Natural Resources Canada, 2014). *Sphagnum* peat is valued for its high water retention capacity among other properties and is produced within Canada primarily for use in horticultural growing substrates (Cleary *et al.*, 2005; Canadian Sphagnum Peat Moss Association, 2014). Peat extraction involves site drainage via ditching, the clearing of surface vegetation, and removal of the upper layers of peat. Prior to the 1970s, most peat was extracted by hand using traditional block-cutting methods, resulting in a landscape of wide, shallow extraction trenches separated by narrower baulks on which peat blocks were placed to dry. While this method is no longer used, a large number of cutover block cut sites still exist (Lavoie *et al.*, 2003). Modern peat extraction is mechanized, utilizing specialized

machinery to harrow and vacuum peat from the surface. This method requires a deeper and more extensive drainage network and profiling of surfaces to dry surficial peat layers and allow for vacuum harvesting equipment to be used on site. In both methods, the prevailing physical and hydrological conditions following extraction deter natural regeneration of the keystone peat-forming genus *Sphagnum* in most cases without active restoration (Price, 1996; Poulin *et al.*, 2005; Lavoie and Rochefort, 1996).

The need to address peatland losses in regions of intense extraction activity led to the development in the 1990s of methods for restoring abandoned sites to functional, carbon-accumulating ecosystems dominated by *Sphagnum* mosses (Rochefort, 2000; Rochefort *et al.*, 2003; Ferland and Rochefort, 1997). More recently, research has also focused on the potential of cutover peatlands as sites for growing *Sphagnum* biomass in order to produce material for horticultural substrates on a more sustainable basis (Gaudig, 2012; Pouliot *et al.*, 2015; Gaudig and Joosten, 2002). *Sphagnum* biomass has been found to be a suitable growing media substitute for 'white peat', the slightly decomposed *Sphagnum* peat currently used by the industry, for certain crops and applications (Emmel, 2008; Jobin *et al.*, 2014).

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The ability of non-vascular *Sphagnum* mosses to survive desiccation and to photosynthesize depends on their ability to maintain adequate moisture content at the capitula (Clymo and Hayward, 1982; McNeil and Waddington, 2003), a cluster of leaves and branches comprising the uppermost part of the plant. This, in turn, is controlled primarily by capillary flow through the underlying layers of peat and moss (Clymo and Hayward, 1982), with the vast majority of flow occurring between overlapping pendant branches and leaves along the outside of the stem (Proctor, 1982). Hyaline cells within the leaves hold water critical for structural support and the maintenance of photosynthetic processes (Clymo and Hayward, 1982). At soil water pressures between  $-200$  and  $-600$  cm, these cells will drain (Lewis, 1988; Clymo and Hayward, 1982) and photosynthesis will essentially cease (Gerdol *et al.*, 1996). In natural peatlands, the living mosses grow on layers of dead remains that become progressively more decomposed with depth (Clymo, 1984; Hayward and Clymo, 1982; Clymo and Hayward, 1982), creating a corresponding gradient in the hydraulic properties influencing the storage and transmission of water. By comparison, the hydrophysical properties of highly decomposed cutover peat can present a hostile environment for *Sphagnum* regeneration. Reduced specific yield in cutover peat relative to natural peatland surfaces can lead to low and highly variable water tables below cutover surfaces (Schouwenaars, 1993; Price, 1996). Furthermore, soil water pressures in cutover peat may be below the threshold at which the capillary forces generated by the mosses can extract enough water to offset evaporative losses, preventing recolonization of cutover surfaces (Price and Whitehead, 2001).

It has been suggested by some authors that *Sphagnum* is at increasing risk of water stress as it grows higher above the cutover surface due to low unsaturated hydraulic conductivity of the regenerated layers limiting upward water fluxes (Schouwenaars and Gosen, 2007; McCarter and Price, 2014). While some studies have examined the hydrological processes operating within *Sphagnum* hummocks (e.g. Yazaki *et al.*, 2006; Price and Whittington, 2010), the hydrophysical properties of *Sphagnum* layers are not well known, and only a few studies (Waddington *et al.*, 2011; Ketcheson and Price, 2014; McCarter and Price, 2014) have looked specifically at processes occurring in the context of regenerating cutover peatlands. The evolution of regenerating *Sphagnum* profiles also has not been well studied, and it is unknown how the water storage and transmission properties may change over time. This presents a barrier to creating optimal hydrological conditions in bog restoration and *Sphagnum* biomass production operations. An improved understanding of the soil water dynamics of regenerating *Sphagnum* in cutover peatlands is therefore

desirable. The specific objectives of this paper are the following: (1) to demonstrate differences in physical and hydraulic properties of *Sphagnum* profiles at different stages of regeneration; (2) to use differences in properties determined in the laboratory to explain the soil water dynamics within the profiles observed under field conditions, and; (3) to discuss potential implications for water management.

## METHODOLOGY

### *Study area*

Data were collected in a large cutover peatland located just south of Shippagan, New Brunswick ( $47^{\circ}40'N$ ,  $64^{\circ}43'W$ ; Figure 1). Mean annual air temperature in Shippagan is  $4.8^{\circ}C$ , and mean annual precipitation is 1077 mm, of which 69% falls as rain (Environment Canada, 2014). The site was extracted using traditional block-cut methods and, consequently, is characterized by an alternating baulk and trench structure. Trenches approximately 18 m wide are separated by approximately 5-m-wide and approximately 1-m-high baulks, with residual peat depths ranging from 0.6 to 1 m in the trenches (Robert *et al.*, 1999). Production operations at the site ceased in 1970, and no active restoration measures were taken at this time. In the trenches, but not the baulks, spontaneous regeneration of *Sphagnum* has occurred across most of the site. In this regard, the site differs from many other cutover block-cut peatlands in eastern North America (Poulin *et al.*, 2005), primarily at more continental locations. Natural *Sphagnum* regeneration has been found to be more common at block-cut than at vacuum-harvested sites as the landscape of block-cut peatlands offers a greater variety of microtopographic habitats (Price *et al.*, 2003; Triisberg *et al.*, 2011), although regeneration is generally limited to the wettest parts of the site (Price and Whitehead, 2001). Two sections of the site have been cleared and divided into plots for *Sphagnum* biomass production experiments dating from 2003 (Landry and Rochefort, 2009). The particular nature of this site, with regenerated *Sphagnum* layers of many different ages at the same location, presents an exceptional opportunity to study patterns of *Sphagnum* regeneration while controlling for the potentially confounding variables of climate and differences in peat substrate.

### *Field data collection*

Data collection at the study site took place between 24 May and 13 August 2013. Seven plots were established in different areas of the study site for hydrological monitoring and hydrophysical analysis. Plot names denote the year in which regeneration began or was assumed to have begun. Three of these plots were in the spontaneously revegetated area of the site, assumed to have begun regeneration following the end of peat

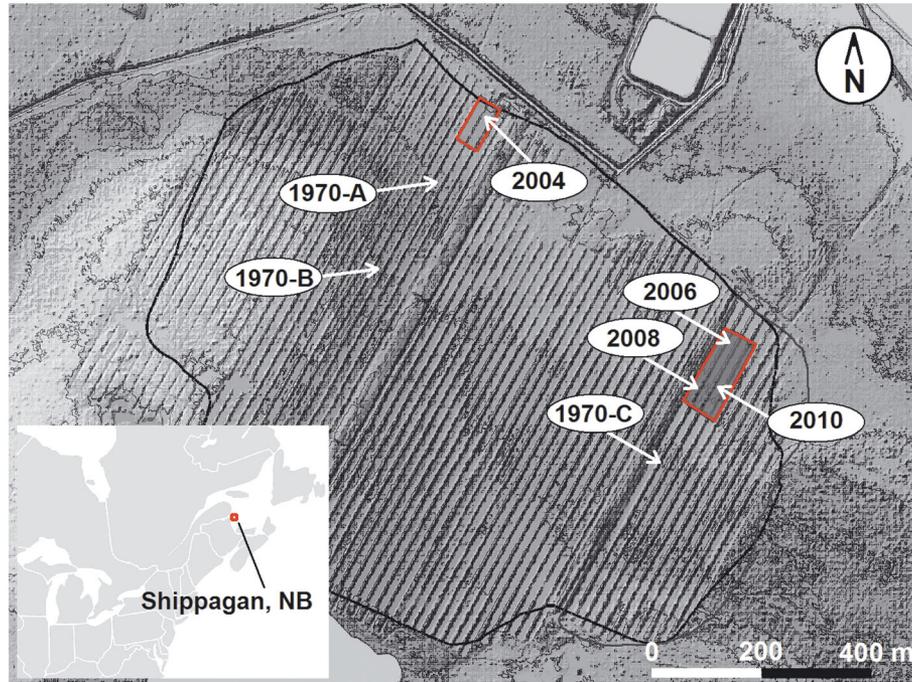


Figure 1. Map of study site showing locations of plots. Names of plots indicate the year in which *Sphagnum* regeneration began or was assumed to have begun. The two regions of the site within the coloured boxes are areas in which *Sphagnum* biomass production experiments have been occurring since 2004

production in 1970 (plots 1970-A, 1970-B, and 1970-C), and are collectively referred to here as SPONT. These had well-developed *Sphagnum* profiles (hereafter referred to simply as 'profiles') ranging from 23–40 cm in height above the former cutover peat surface. The other four plots were located within trenches where *Sphagnum* has regenerated on cleared cutover surfaces, having been artificially introduced for biomass production experiments over the period 2003–2012 (Landry and Rochefort, 2009). These plots had profile heights of 3–18 cm (plots 2004, 2006, 2008, and 2010) and are collectively referred to as EXPER. Profile heights and species composition within plots are shown in Table I. Each plot consisted of three replicate sub-plots in close proximity (<2 m) and of

apparent homogeneity in structure and species composition. Sub-plots were delineated by metal collars inserted into the profile to a depth of 40 cm, which were also used to measure productivity in a concurrent study not discussed in this paper. All sub-plots were flat and completely covered by regenerating *Sphagnum*. Most areas were characterized by a mix of *Sphagnum* species within section *Acutifolia* [*S. fuscum* (Schimp.) Klinggr., *S. rubellum* Wils., *S. flavicomans* (Sect. *Acutifolia*)], with significant presence of *S. magellanicum* Brid. at many locations. Nomenclature for *Sphagnum* species follows that of Anderson (1990). The relative proportion of species present within each sub-plot was estimated visually, while capitula density was estimated by counting

Table I. The average thickness of the regenerated layer and relative proportion of *Sphagnum* species present within the collars at each plot

Plot	Average layer thickness (cm)	<i>S. flavicomans</i>	<i>S. fuscum</i>	<i>S. magellanicum</i>	<i>S. rubellum</i>	Capitulum density (count · cm <sup>-2</sup> )
2004	16.2 (15–18)	0	0	43	57	2.07 ± 0.40
2006	9.8 (9–10.5)	0	36	8	56	2.44 ± 0.30
2008	3.2 (2.5–3.5)	9	6	50	35	1.97 ± 0.21
2010	3.7 (3–4)	42	0	20	39	2.64 ± 0.34
1970-A	30.0 (27–33)	0	16	54	30	1.58 ± 0.17
1970-B	33.3 (29–40)	97	0	0	3	2.68 ± 0.36
1970-C	23.7 (22–25)	0	0	2	99	3.31 ± 0.15

The range of measured layer thicknesses ( $n=9$  per plot) is also shown in brackets. Species proportions are shown as average spatial coverage across the three collars in percent. Percentages are rounded to two digits and may not add exactly to 100%. Spatial densities of capitula are shown ±SD.

the number of individuals within a 2-cm<sup>2</sup> quadrant of transparent graphing paper at 16 randomly selected locations within each plot (Table I). At some locations where there was minor presence of ericaceous shrubs or grasses within the sub-plots, the above-ground portion of the plant was clipped and replaced with cuttings of ericaceous branches or grass leaves, as appropriate, so as to maintain similar surface shading and to restrict latent energy exchanges to the moss surface. Cuttings were changed regularly and were removed from the surface during measurements. A system of boardwalks was constructed to prevent disturbance of *Sphagnum* profiles during measurements.

Each plot was instrumented with one central well containing a pressure transducer to record water table position (WT), and two weighing lysimeters at each plot were used in conjunction with data from a meteorological station to estimate plot-specific evaporation using the Priestley–Taylor method (Priestley and Taylor, 1972). WT measurements were corroborated by string-level measurements of the height of the *Sphagnum* surface in each collar relative to the top of the wells to generate WT values for each sub-plot. Two rain gauges, one manual and one automated, recorded precipitation input at the site. A portable WET-Sensor™ (Delta-T Devices, Cambridge, UK) time-domain reflectometry (TDR) device was used to measure the volumetric moisture content ( $\theta$ ) at the growing surface of each plot. During each measurement,  $\theta$  was sampled at five locations within each sub-plot and averaged across the three sub-plots to obtain a plot-scale  $\theta$  value for this layer. Two measurements were taken at each sampling location, one with the 6-cm-long probes inserted vertically to full depth and the other with the probes inserted down to a line drawn at half the probe length in order to generate  $\theta$  values for both the 0–6 cm and 0–3 cm depth layers. An alternative technique of inserting the WET-Sensor™ prongs at 45° to determine water content in the 0–3 cm layer was not used as it caused excessive disturbance to the surficial *Sphagnum* layers. TDR calibration curves for individual plots were developed using gravimetrically determined  $\theta$  and TDR-derived readings taken from *Sphagnum* samples of known volume as they dried, following the method of Topp *et al.* (1980). Separate calibrations were performed for the 0–6-cm layer and 0–3-cm layer measurements at each plot to account for differences resulting from the partial exposure of the probes to air. Plot-specific and layer-specific calibration curves were then applied to all readings from the WET-Sensor™.

Three plots (2006, 2010, and 1970-C), taken to be representative of three different stages of regeneration, were fully instrumented with CS605 TDR probes (Campbell Scientific Canada Corp., Edmonton, Alberta) and tensiometers to quantify the moisture regime within and below the regenerated profile. TDR probes and

tensiometers were installed by excavating a face on one side of each collar and backfilling after installation. TDR probes were installed in the *Sphagnum* profile and cutover peat at 5-cm-depth intervals, measured down from the profile surface, in each collar at plots 2006, 2010, and 1970-C. At plot 2010, the probes were installed in the cutover peat only, as the *Sphagnum* profile was not thick enough to allow accurate measurement of  $\theta$  as a discrete layer using the CS605 probes. At the other two plots (2006 and 1970-C), probes were installed at 5-cm-depth intervals for an  $n$  of 3 at each plot and depth, with the exception that, due to equipment limitations, only one probe was installed for the 0–5-cm layer. This was justified as water content measurements in this layer were supplemented by WET-Sensor™ measurements. TDR probes were connected to dataloggers to record  $\theta$  of discrete soil layers at 30 min intervals. Tensiometers were installed in the cutover peat only at 2.5 and 7.5 cm below the cutover peat surface, as poor contact between the less-decomposed moss and the ceramic cups prevented direct measurement of the soil water pressure in the regenerated layer. Probe depths within the profile are reported relative to the growing surface, with positive numbers denoting the depth below the surface. Depths for probes located within the peat are given relative to the top of the cutover peat layer, with negative numbers denoting the depth below the cutover peat.

Direct precipitation was experimentally excluded from all plots during the 16-day period between 28 July and 13 August 2014, to evaluate the effect of the removal of this water source on surface moisture dynamics. This was accomplished using clear plastic sheets tented over the collars at each plot and attached to posts inserted into the peat. Plastic sheets were removed during measurements of  $\theta$  and other parameters. These sheets were approximately 80 cm above the collar surface and did not significantly alter air temperature and surface shading over the collar (see soil water dynamics in Results section).

Profiles at each plot were sampled for hydrophysical analysis using polyvinyl chloride rings 10 cm in diameter and 5 cm in height. After carefully cutting around the outside of the rings with scissors, the rings could easily slide down around a sample at a targeted depth. Samples were removed by cutting along the bottom of the ring. This system permitted the preservation of the *in situ* structure of the moss and partially decomposed plant matter during transport and laboratory analysis. Full profiles of the regenerated *Sphagnum* layer and the top layer of cutover peat were sampled, one from each of the three sub-plots in 5-cm increments at the end of the study season, providing three samples at each depth interval for all plots ( $n=99$  including peat and capitulum samples). Three additional 5-cm samples were taken from the surface layer of each plot, from which the top 2 cm

(roughly the capitulum) were later removed so that they could be analyzed as a distinct layer. This was accomplished by spraying samples with water and freezing to provide the necessary structural stability before cutting with a fine-toothed saw.

#### Laboratory analysis

The vertical saturated hydraulic conductivity ( $K_{\text{sat}}$ ), soil water pressure ( $\psi$ )–retention curve, unsaturated hydraulic conductivity– $\psi$  ( $K(\psi)$ ) curve, bulk density, and porosity of profile samples were determined in the laboratory. All samples were assessed for  $K_{\text{sat}}$ , bulk density, and porosity ( $n=99$ ), whereas analysis of retention and  $K(\psi)$  characteristics was restricted to select samples ( $n=48$ ; see following paragraph). All water used in these analyses was filtered by a reverse osmosis system.  $K_{\text{sat}}$  was measured using a Darcy permeameter. All samples were wrapped in plaster and sealed with paraffin wax around the sides before being placed in the permeameter so as to leave open a flow face on the top and bottom and eliminate preferential flow around the sides while preserving the structural integrity of the sample. Darcy's Law was used to calculate sample  $K_{\text{sat}}$  from the rate of

discharge across a known hydraulic gradient and flow face area. Bulk density was determined by oven-drying samples at 80 °C until they reached a stable mass. Porosity was estimated by placing ground soil samples of known mass in a known volume of kerosene to find the particle density by displacement, then calculating porosity as  $\left(1 - \frac{\text{particle density}}{\text{bulk density}}\right)$  following the liquid pycnometer method outlined by Blake and Hartge (1986).

The  $\psi$ –retention and  $K(\psi)$  curves were determined following the method of Price *et al.* (2008) at  $\psi$  of  $-3$ ,  $-6$ ,  $-12$ ,  $-20$ , and  $-30$  cm. Two samples from select depth intervals (0–2-cm capitulum layer, 0–5 cm, 5–10 cm, profile base, top 5 cm of cutover peat) at each plot were chosen for analysis, as equipment and time constrictions limited the number of samples that could be run simultaneously. Briefly, samples were placed on tension plates covered with 25  $\mu\text{m}$  pore size Nitex™ mesh which were connected to an Erlenmeyer flask beneath. This arrangement allowed the  $\psi$  of samples to be controlled by manipulating the height of the flask outlet below the tension surface, effectively creating a hanging column of water beneath the plate. A constant head was maintained within the flask by manually replacing water

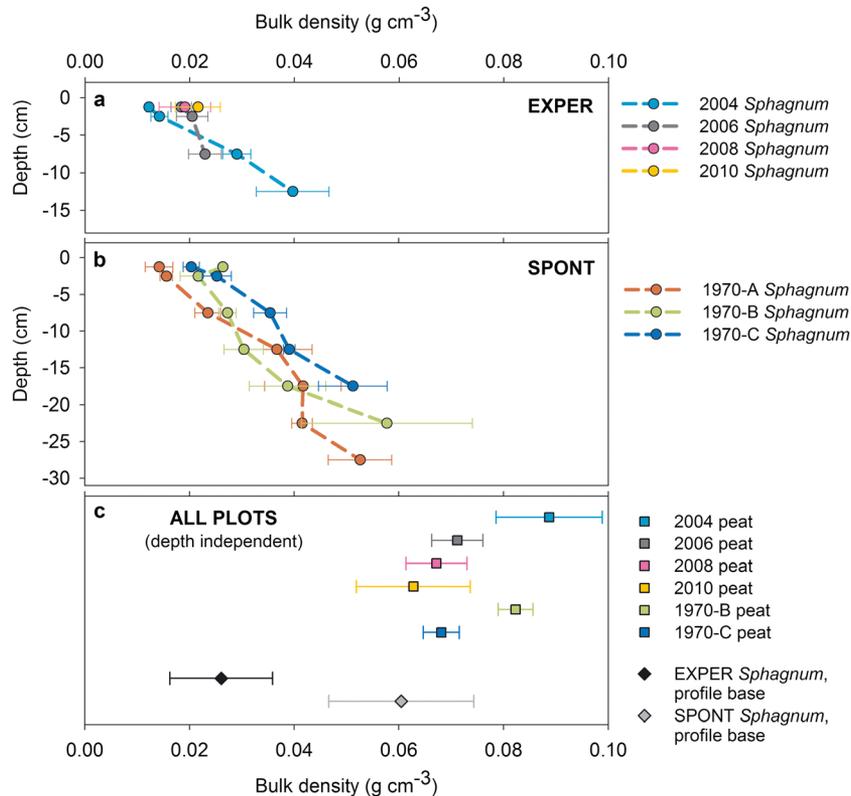


Figure 2. Bulk density depth profiles of regenerated *Sphagnum* profiles (a, b) and the upper 5 cm of remnant cutover peat for all sites (c),  $n=3$  for each point. Sampling of cutover peat samples at site 1970-A was prevented by high water table during sampling period. Error bars show  $\pm$ SD. As there is some variation in layer thicknesses, and because the profile surface was used as the 0-cm datum, data in (b) are only shown for plots and depths where there were no fewer than three samples. Data are shown independent of depth in (c) for cutover peat samples, along with the average bulk densities of the 5-cm *Sphagnum* layer directly overlying the cutover peat ('profile base') for both EXPER and SPONT plots ( $n=12$  and  $n=9$ , respectively)

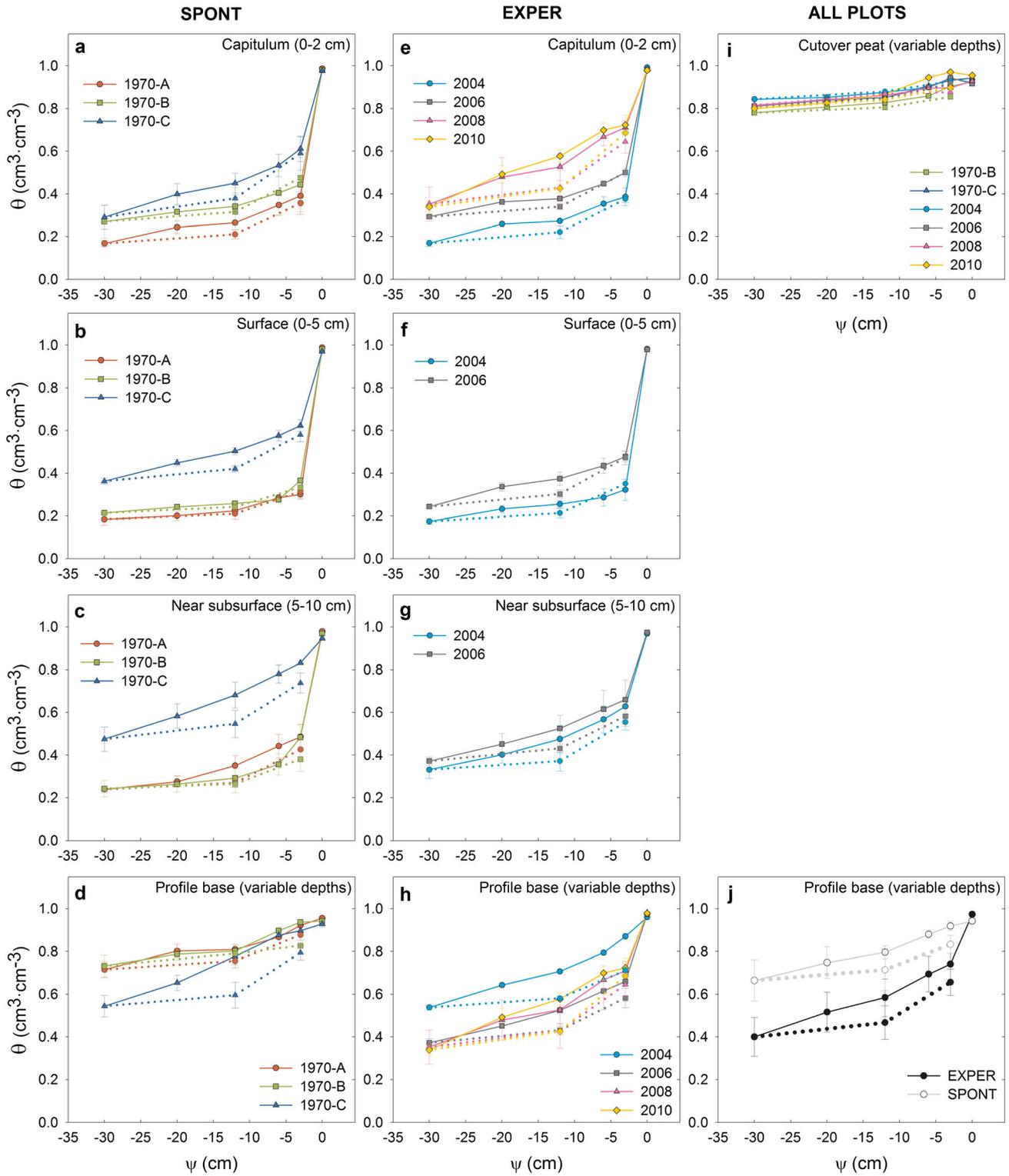


Figure 3. (a-j) Retention curves for samples taken from different profile depth intervals at each plot ( $n = 2$  for all points except cutover peat values, where  $n = 1$ ). (j) shows group average retention curves for EXPER and SPONT ( $n = 6$  per point). The profile base in (d), (h) and (j) refers to the 5-cm layer directly overlying the former cutover peat surface at each plot. Values for  $\psi = 0$  were derived from sample porosity using the liquid pycnometer method. Solid lines and dotted lines indicate drying and wetting curves, respectively. Error bars show  $\pm$ SD in  $\theta$

lost to overflow or evaporation. The flask outlet height was set relative to the midpoint of the sample to achieve the desired average value of  $\psi$  within the sample. Samples were weighed daily and allowed to equilibrate at a given  $\psi$  until masses stabilized ( $<1 \text{ g} \cdot \text{day}^{-1}$  change), at which point  $\theta$  for that  $\psi$  was determined gravimetrically.  $K(\psi)$  was measured once all samples had equilibrated to a given  $\psi$ .  $K(\psi)$  measurements used a second Nitex<sup>TM</sup>-covered tension disc placed on top of the sample, connected to a reservoir which was maintained at a constant head value equivalent to the equilibrated  $\psi$  at the top of the sample. The beaker outlet was then lowered by half the height of the sample, maintaining the same average  $\psi$  within the sample and inducing a constant discharge at a hydraulic gradient of 1. After equilibrating for an hour, the rate of discharge was measured to determine  $K(\psi)$  using Darcy's Law. All discharge measurements retained for analysis had  $r^2 > 0.9$ .

Groups of samples were compared statistically using  $t$ -tests for independent samples, with an alpha value of 0.05 and without the assumption of equal group variance. Where more than two groups were compared simultaneously, one-way analysis of variance was used with Tukey's HSD post hoc tests and alpha of 0.05. Statistical analyses were performed in IBM SPSS Statistics 20.0 (IBM Corp, 2011). Sample sizes were adequate for most comparisons; however, the time intensity of the retention and  $K(\psi)$  methods limited the number of samples that could be processed, thereby preventing a rigorous statistical comparison of these parameters between individual plots.

## RESULTS

### Hydrophysical properties

The bulk density of all profiles followed a clear increasing trend with depth below the surface (Figure 2).

There were no significant differences in bulk density between SPONT and EXPER in the top 5 cm ( $p > 0.1$ ; average  $0.021 \pm 0.005$  and  $0.018 \pm 0.005 \text{ g} \cdot \text{cm}^{-3}$  for SPONT and EXPER, respectively). However, SPONT had significantly greater ( $p < 0.001$ ) bulk densities in the 5-cm layer directly overlying the cutover peat (average  $0.061 \pm 0.013 \text{ g} \cdot \text{cm}^{-3}$ ) compared with the same layer at EXPER (average  $0.026 \pm 0.009 \text{ g} \cdot \text{cm}^{-3}$ ). The terms 'profile base' and 'basal layer' are used interchangeably to refer to this layer throughout the remainder of this paper. Peat samples had the highest average bulk density at  $0.073 \pm 0.012 \text{ g} \cdot \text{cm}^{-3}$ , significantly higher ( $p < 0.001$ ) than that of *Sphagnum* samples at all depths.

The  $\psi$ - $\theta$  relation for all tested depth intervals is shown in Figure 3. Water retention capacity for  $\psi < 0$  was higher in the basal layer than in the overlying layers at all plots, although the capitulum (0–2 cm) layer had a higher retention capacity than the 0–5 cm layer at four of the five plots with profile heights exceeding 5 cm. The capitulum layer at EXPER plots 2008 and 2010 had significantly ( $p < 0.05$ ) higher retention capacity than all other plots at  $\psi$  between  $-3$  and  $-20$  cm, but approached comparable values of  $\theta$  at  $\psi = -30$  cm (Figure 3a, e). Retention at  $\psi = -30$  cm, the lowest measured pressure, was significantly ( $p < 0.001$ ) higher in the basal layer at SPONT (average  $0.66 \pm 0.10$ ) when compared with the same layer at EXPER (average  $0.40 \pm 0.09$ ), and both groups had higher retention in the basal layer relative to the surface (0–5 cm) layer (Figure 3j). There were no apparent differences in retention between SPONT and EXPER in the surface (0–5 and 5–10 cm) layers, with the exception of plot 1970-C, which had higher  $\theta$  than other plots across the measured range of  $\psi$ .

Bulk density was found to be positively correlated with water retention capacity of samples at  $\psi < 0$  (Figure 4). The relationship between these parameters was best approximated by a linear function at  $\psi = -30$  cm and by

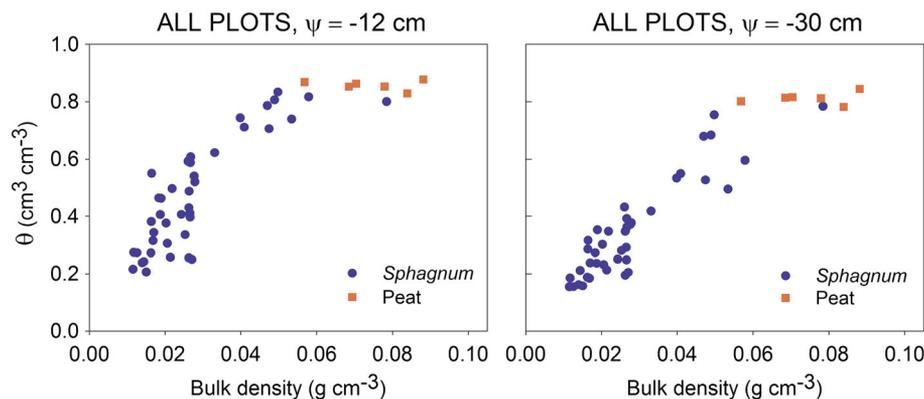


Figure 4. Relationship between bulk density and volumetric water content at tension for all samples. Water contents at two tension levels are shown here as typical examples of this relationship. Samples tended to follow a linear relationship at  $\psi = -30$  cm and semi-logarithmic relationship at all other measured  $\psi$

a semi-logarithmic function at all higher  $\psi$ . After scaled log transformation of  $\theta$  for the aforementioned  $\psi$  values,  $r^2$  of the bulk density– $\theta$  relationship was  $>0.77$  across the

range of  $\psi$  tested. Peat samples showed virtually no variation in the slope of the bulk density–retention curve throughout this  $\psi$  range.

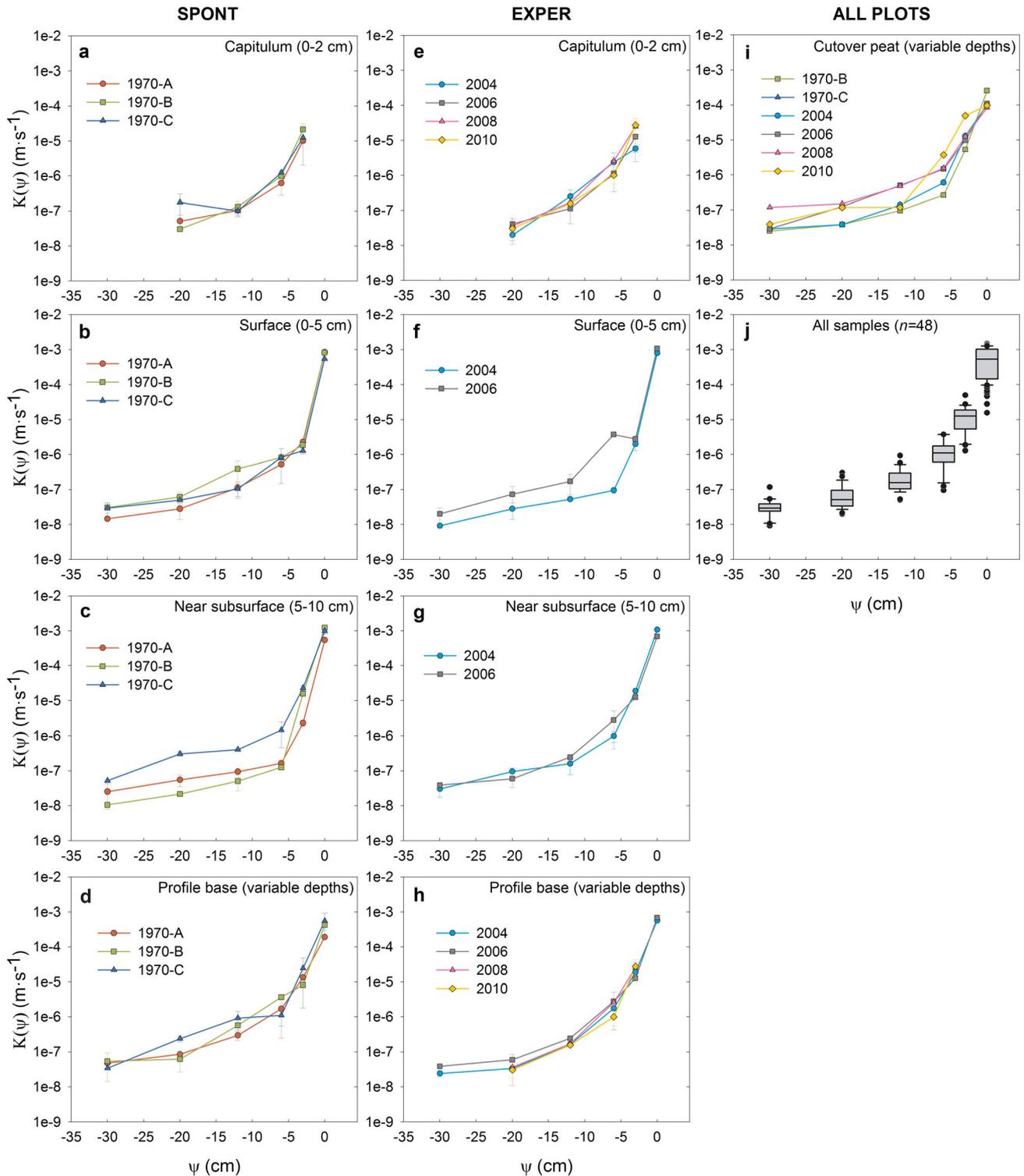


Figure 5. (a–j) Unsaturated hydraulic conductivity ( $K(\psi)$ ) for samples under soil water pressures in the range of 0 to  $-30$  cm ( $n=2$  for all points except cutover peat values, where  $n=1$ ). The profile base in (d) and (h) refers to the 5-cm layer directly overlying the former cutover peat surface at each site.  $K(\psi)$  values for  $\psi=0$  are the saturated hydraulic conductivities measured in a Darcy permeameter. Error bars represent  $\pm$ SD in  $K(\psi)$ . Box plots of data from all samples, showing 25th, 50th, and 75th percentiles as well as outliers, are shown in (j) to demonstrate the pattern of variability in  $K(\psi)$  across samples

The  $K_{\text{sat}}$  and porosity of samples showed less distinct patterns of variation with depth.  $K_{\text{sat}}$  was lower in the basal layer than at the top of the profile at all plots, although there was substantial variability at most depth intervals.  $K_{\text{sat}}$  values are shown in Figure 5 as  $K(\psi)$  at  $\psi=0$ . Values for *Sphagnum* samples ranged from  $1.5 \times 10^{-3}$  to  $6.6 \times 10^{-5} \text{ m} \cdot \text{s}^{-1}$  (average  $7.1 \times 10^{-4} \text{ m} \cdot \text{s}^{-1}$ ) while peat samples had average values nearly an order of magnitude lower (average  $1.0 \times 10^{-4} \text{ m} \cdot \text{s}^{-1}$ ) than surficial *Sphagnum* samples.  $K_{\text{sat}}$  was weakly negatively correlated with bulk density ( $r^2=0.53$ ). Porosity for all samples was very high, ranging from 0.91 to 0.99, and tended to decrease with depth. Peat samples had a slightly lower average porosity ( $0.93 \pm 0.01$ ) than *Sphagnum* samples (average  $0.97 \pm 0.02$ ).

$K(\psi)$  curves for all tested samples are shown in Figure 5.  $K(\psi)$  dropped by an average of four orders of magnitude between  $\psi=0 \text{ cm}$  (saturation) and  $\psi=-30 \text{ cm}$ . Despite there being differences between samples in other properties, samples tended to follow a similar relationship between  $\psi$  and  $K(\psi)$ , with about one and a half orders of magnitude variability between all samples at any given  $\psi$  (Figure 5j). The implications of this are explored further in the Discussion section.

#### Soil water dynamics under field conditions

The study period was characterized by higher than average seasonal precipitation, receiving 227 mm more than would be expected from the 30-year (1981–2010) mean for the 82-day period between 24 May and 13 August (Environment Canada., 2014). More than two-thirds of seasonal precipitation was received in five events  $>30 \text{ mm}$  in size, and nearly a quarter was from a single 100 mm event on 26–27 July. Evaporation, determined using the Priestley–Taylor method for each individual plot, was exceeded by precipitation by  $>110 \text{ mm}$  at all

plots. Soil water pressures measured by tensiometers set in the cutover peat at plots 2006, 2010, and 1970-C remained above  $-15 \text{ cm}$  for the entire study season, and WT fluctuations were mostly constrained to within 40 cm of the surface. The presence of the plastic sheeting above the collars during the 16-day rainfall exclusion experiment reduced incoming photosynthetic photon flux density (PPFD, measured for a concurrent carbon study) at the collar surface by an average of  $222 \pm 92 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  and had no measurable effect on air temperature ( $n=20$ ). Although it is likely that evaporation dynamics were affected slightly by the exclusion structures through a decrease in wind velocity over the collars, the reduction in light intensity was assumed to have been too small to have had a meaningful influence on moss physiological condition or collar evaporation dynamics, as this represented a roughly 9% reduction in PPFD from typical cloud-free mid-day conditions of approximately  $2500 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ .

Plots exhibited very different responses to WT in  $\theta$  at the surface (0–3 cm) layer (Figure 6). This is evident from the fact that the plots span different regions of the WT– $\theta$  graph, implying different surface layer water contents for the same range of WT. WT was significantly correlated with surficial  $\theta$  at all plots at the 0.05 level (Pearson's correlation coefficient, two-tailed test of significance). The slope of the linear regression for each of these plots represents the change in  $\theta$  per unit change in WT and can be taken as an indication of the degree to which surface moisture dynamics are linked to WT. Slopes are given in parentheses in Figure 6 as the percent increase in  $\theta$  per cm rises in WT. The newly regenerated plots 2008 and 2010 showed a much stronger WT– $\theta$  response (greater slope) than all other plots, and 1970-C had a higher WT– $\theta$  slope than the other SPONT plots. Plots 2008 and 2010 also showed the highest absolute  $\theta$  values of all plots when WT was within 20 cm of the surface. At plots 2004, 1970-

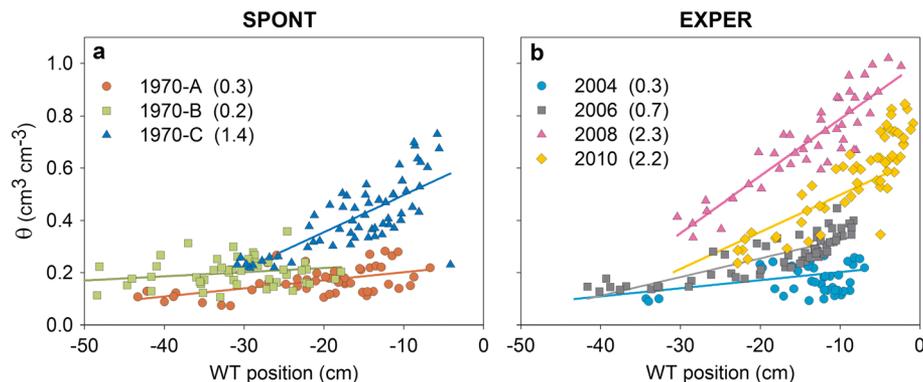


Figure 6. Relationship between volumetric moisture content in the surface (0–3 cm) layer ( $\theta$ ) and water table position (WT) relative to the growing surface for (a) SPONT and (b) EXPER *Sphagnum* profiles. Moisture content values were determined using a calibrated portable TDR device. All relationships were significant at the 0.05 level (Pearson's correlation coefficient, two-tailed test of significance). Slopes are shown in parentheses as the percent change in  $\theta$  per cm change in WT

A, and 1970-B, which had profile heights ranging from 16 to 40 cm, slopes approaching zero indicated that changes in WT did not greatly influence  $\theta$ . The response in  $\theta$  appeared to be non-linear at plots 2006, 2010, and 1970-C and suggested that the effect of WT on  $\theta$  may diminish as WT decreases.

Time series of  $\theta$  generated by the static TDR probes inserted in the profiles at 2006, 2010, and 1970-C revealed that  $\theta$  in the near-surface layers responded differently to precipitation events at different plots (Figure 7). At plots 2006 and 1970-C, the response of  $\theta$  within the profile to WT was much stronger when WT was within approximately 10 cm of the surface (Figure 8). A series of precipitation events between 3.5 and 12 mm in size failed to produce a clear response in near-surface  $\theta$  at these plots when WT was at its seasonal low (Figure 7b, c; day-of-year 185 to 200), despite producing a clear response in WT. Near-surface  $\theta$  remained high during a 16-day period where direct precipitation was excluded from all plots using tented plastic sheeting (day-of-year 209 to 225).  $\theta$  could be seen to closely mirror WT at these plots. At plot 2010, the profile was not sufficiently thick for a TDR inserted horizontally to measure profile  $\theta$  without being

influenced by the  $\theta$  of the cutover peat, and so the roaming WET-Sensor™ was used to measure near-surface  $\theta$ . However, the inherent variability and lower timescale resolution of this measurement technique made it difficult

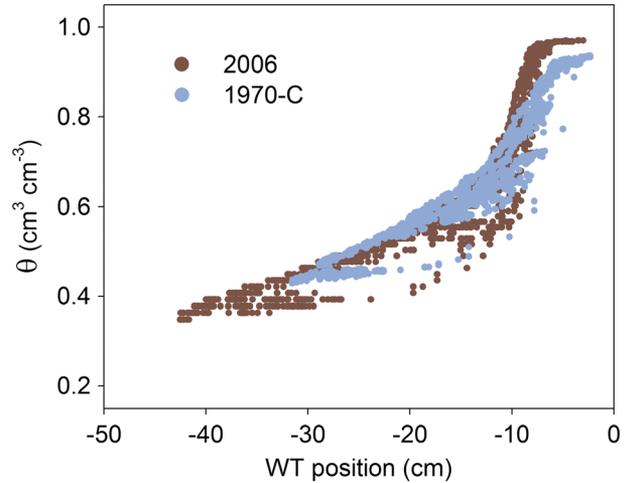


Figure 8. Water table position versus volumetric water content ( $\theta$ ) measured by TDRs 2.5 cm below the growing surface (representing roughly the 0–5 cm layer of the regenerated profile) at two plots

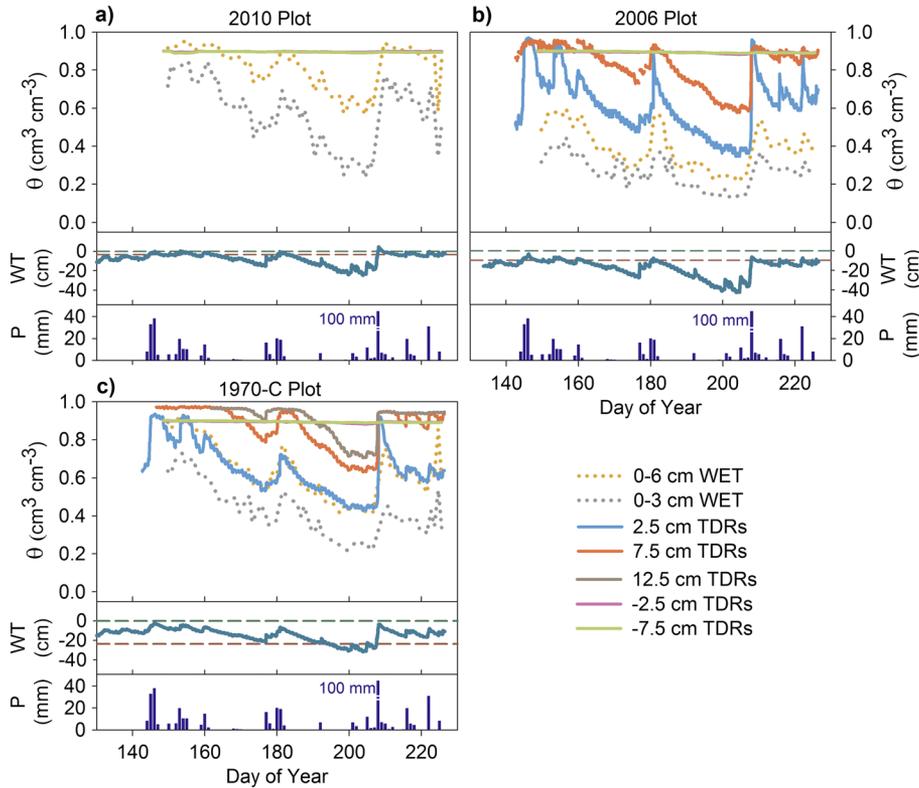


Figure 7. Compound figures showing changes in moisture content with depth, WT position, and precipitation over time for three different plots: (a) 2010, (b) 2006 and (c) 1970-C. Values for each plot are averaged across three replicate profiles at each site. Measurements include both *in situ* TDRs (solid lines;  $n = 3$  for all values except 2.5-cm depth where  $n = 1$ ) and WET-sensor portable TDR (dotted lines;  $n = 15$ ). TDR depths relative to profile surface indicated by positive numbers, and negative numbers indicate depth below cutover peat interface. Changes in WT are shown with dashed green and red horizontal lines representing the profile surface (0-cm WT datum) and former cutover peat surface, respectively (profile heights differ between plots; Table I). Direct precipitation was excluded experimentally from each of the plots between day-of-year 209 and 225

to establish the response to precipitation at plot 2010. WET-Sensor<sup>TM</sup>  $\theta$  measurements (representing the 0–6-cm layer) agreed well with 2.5-cm depth TDR readings at plot 1970-C (representing the 0–5-cm layer) but were systematically approximately 20% lower than the 2.5-cm TDR readings at plot 2006. The reason for this is unclear.

## DISCUSSION

In general, the hydrophysical properties of the regenerated profiles show that the greatest differences between SPONT and EXPER plots occur closer to the profile base. This is most likely due to the fact that at SPONT, where plots were assumed to have begun regenerating >40 years before data collection, decomposition and compression from the weight of overlying layers have compacted the moss fibre. More decomposed and compacted plant matter generally possesses a greater abundance of small pore sizes (Boelter, 1968), imparting a stronger capillary force. This has resulted in a higher bulk density and water retention capacity, and slightly lower  $K_{\text{sat}}$ , at SPONT compared with the same layer at the <10-year-old EXPER plots. Whereas an abrupt transition in hydrophysical properties exists at the interface between the regenerating layer and the cutover peat at EXPER, at SPONT, the basal layer is approaching levels of bulk density and retention capacity comparable with the cutover peat (Figure 2). Interestingly, plot 2004 showed a basal layer bulk density and retention capacity only slightly lower than that of the SPONT plots, suggesting that perhaps some degree of compaction and decomposition had already taken place after only 9 years of growth.

Cutover peat samples had higher average bulk density and greater retention capacity than *Sphagnum* samples. While *Sphagnum* profiles exhibited a wide range of  $\theta$  in the field, the TDR probes at the three instrumented plots show that  $\theta$  variance within the cutover peat was remarkably small and that this layer remained close to saturation for the entire study season (Figure 7). Peat samples also showed little variance in  $\theta$  across the range of  $\psi$  tested in the laboratory (Figure 3i), which encompassed the  $\psi$  range observed in the field within peat at similar depths (seasonal minimum of  $-14$  cm within instrumented plots 2006, 2010, and 1970-C). Regenerating *Sphagnum* at plots 2008 and 2010, consisting of only a thin (3–4 cm) layer directly overlying the cutover peat, maintained the highest average surface  $\theta$  over the study period. This would suggest that at these plots, the water stored in the cutover peat can be easily accessed by capillary flow to maintain photosynthesis, at least within the relatively narrow range of  $\psi$  observed in the field.

Direct precipitation appeared to be poorly retained within the upper regenerating layer. This is supported by field observations of  $\theta$  in the near-surface layer at plots 2006 and 1970-C, which showed very little response to substantial (up to 12 mm) precipitation events during periods of lower WT (Figure 7b, c; day-of-year 185 to 200). When WT was within about 20 cm of the surface, near-surface  $\theta$  mirrored the position of the water table very closely. Furthermore, logging TDR probes at the 2.5-cm depth level showed clear hysteretic loops on a  $\theta$ –WT graph and a relatively narrow variance in  $\theta$  for a given WT, suggesting the strong predominance of WT as a control on near-surface  $\theta$  (Figure 8). This said, it has been demonstrated that small (<1 mm) atmospheric inputs of water such as dewfall can be crucial to maintaining metabolic processes during highly water-limiting conditions (Csintalan *et al.*, 2000; Strack and Price, 2009), which were not observed in this study. The 16-day period of precipitation exclusion for all plots in this study, during which mosses remained healthy and productive, shows that *Sphagnum* can maintain adequate moisture for photosynthesis in the absence of direct precipitation inputs for at least this long, although it is noted that WT was also near its seasonal high during the first several days of this period. The large variations in  $\theta$  observed within the profiles during this period can thus be attributed exclusively to WT fluctuations and evaporation, in the absence of significant atmospheric inputs of water.

While WT dynamics were closely tied to near-surface (0–3 cm)  $\theta$  at plots 2008 and 2010, the effect of WT on  $\theta$  in this layer tended to diminish with increasing profile height. Plot 2006, with a regenerated layer thickness of 10 cm, showed a  $\theta$ –WT relationship that was clear but weaker (had a lower slope) than that of plots 2008 and 2010 (Figure 6b). At plots 2004, 1970-A, and 1970-B, the regenerated layers were >15 cm thick and the  $\theta$ –WT relationship slopes approached horizontal, indicating that WT was a relatively poor predictor of  $\theta$  in the near surface at these plots. Plot 1970-C was an important exception to this pattern.

The profile at plot 1970-C was notably different from the other well-developed *Sphagnum* profiles in that surface moisture dynamics were more strongly affected by WT than at any other plots besides 2008 and 2010, especially in relation to the other plots at SPONT where all profiles exceeded 20 cm in height. Samples from 1970-C also had a greater water retention capacity than other plots in the 0–5 and 5–10 cm profile depth intervals across the range of  $\psi$  tested (Figure 3b, f) and had higher average bulk density than the other SPONT plots throughout the regenerated profile (Figure 2). This may be attributable to the fact that this plot had both a significantly ( $p < 0.01$ ) higher density of capitula (average  $3.31 \text{ cm}^{-2}$ ) and a greater proportion of *S. rubellum* Wils. (98.5%) than all other plots (Table I).

This area of the peatland also had a visually distinctive regenerated surface relative to other areas of the site, with a denser appearance, more even surface contour, and very little ericaceous plant cover. It is well established that hummock species are able to remain productive at higher elevations above the water table than lawn or hollow species due to the greater capillarity afforded by tighter spacing of individuals (Luken, 1985; Rydin, 1993; Hayward and Clymo, 1982). *Sphagnum rubellum* has also been found to have a higher water retention capacity than *S. magellanicum* (McCarter and Price, 2012), a species that was present at most plots in varying proportions. While the heterogeneous array of species at most plots and the small number of plots in this study made it difficult to isolate the effects of individual species on soil water dynamics, it appears very likely that the differences in hydrophysical properties and WT connectivity observed at 1970-C are attributable to the particular community architecture of the dense *S. rubellum* Wils. carpet that has developed there. Although all other plots where the regenerated layer thickness exceeded 15 cm had reduced WT connectivity and generally low near-surface  $\theta$ , plot 1970-C demonstrated that WT connectivity and capillarity of regenerating *Sphagnum* layers are not simply a function of age but are controlled by factors such as species composition and community architecture as well.

An analysis of the observed range of WT relative to the regenerating *Sphagnum*–cutover peat interface at each plot (Figure 9) revealed that at SPONT, WT remained above the cutover peat for  $81 \pm 8\%$  of the study season, whereas at EXPER, WT was above the cutover peat for only  $30 \pm 25\%$  of the time. Although this cannot be used as evidence that seasonal WT has increased over the time period of regeneration as data on initial conditions are lacking, the fact that the site was abandoned after extraction and that drainage ditches remained active during this time implies

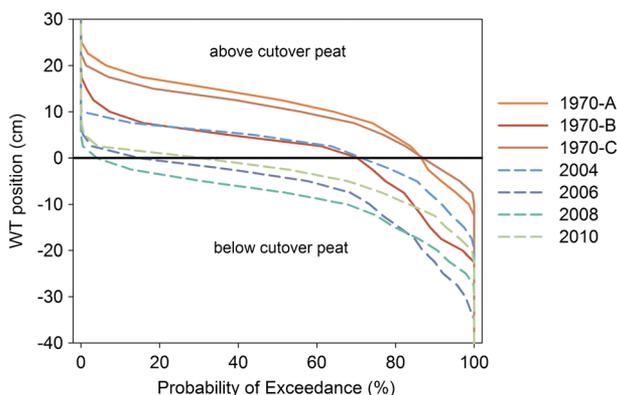


Figure 9. Probability of exceedance of a given water table position on the y-axis over the study period. The interface between the old cutover peat and the regenerating moss layer (black horizontal line) is used as the 0-cm datum for all plots, with positive values signifying water tables above the interface

that it is unlikely that WT was above the cutover surface at the start of regeneration. If it is indeed the case that seasonal WT has increased at SPONT, one possible interpretation is that spontaneously regenerated areas are able to constrain WT fluctuations largely to within the regenerated moss profile as a result of the hydrophysical properties of the regenerated layers, and in particular the increased retention capacity of the profile base. Several studies (Lucchese *et al.*, 2010; McCarter and Price, 2014; McNeil and Waddington, 2003) have identified this as a significant target for bog restoration, because once WT fluctuations are constrained entirely to within the regenerated layer, the hydrological regime of the plots functions much more similarly to that of a natural bog peatland. There are two main feedback processes which could account for this observation. Firstly, as the retention capacity of the profile base increases and  $K_{\text{sat}}$  decreases (albeit only slightly), a greater proportion of precipitation is retained in the regenerated layer. Secondly, there may be an evaporation-limiting feedback (Waddington *et al.*, 2014) occurring, whereas the thickness of the regenerated layer increases, the vertical  $K(\psi)$  decreases as the upper layers dry, limiting upwards transfer of water and thus reducing evaporative losses. A combination of these two processes could account for the perceived increase in seasonal WT at SPONT.

The relationship between  $\psi$  and  $K(\psi)$  between samples did not exhibit as much variability as expected (Figure 5j), given the substantial variation in other hydrophysical properties. This was surprising given the large differences in  $\theta$  between samples at a given  $\psi$ , as hydraulic conductivity is often assumed to be a function of  $\theta$  as explained by differences in water-filled pore diameter and pore connectivity for a given level of saturation (Buckingham, 1907). The relationship between  $\theta$  and  $K(\psi)$  for all samples as a group was quite weak, with an average  $r^2$  across all tensions of 0.16. This presents two possible interpretations. One is that as  $\psi$  decreases, the connectivity between the remaining saturated pores decreases more rapidly in some samples than in others (or flowpath tortuosity increases more rapidly, or a combination of the two). In the peat samples for example, which maintained  $\theta > 0.77$  throughout the analysis, it may be that the largest pores which drain at  $\psi$  of  $-3$  to  $-12$  are capable of transmitting much more water than those pores which are only slightly smaller due to dramatically lower connectivity between these pores. This would account for the fact that  $K(\psi)$  values for peat are within an order of magnitude of values for surficial *Sphagnum* samples at the lowest levels of  $\psi$  despite having a water content  $>50\%$  higher. An alternative explanation is that a large proportion of the water remaining in the samples at lower pressures was immobile, such as that stored in hyaline cells, and that differences in  $\theta$  between samples at a given  $\psi$  are

attributable primarily to differences in immobile water content rather than mobile water content. This would explain the similarity in  $K(\psi)$  across samples, while differences in  $\theta$  could result from differences in the bulk volume of hyaline cells within a sample. This latter conjecture is supported by the data of Waddington *et al.* (2011). We propose that these differences in retention and  $K(\psi)$  derive from differences in species morphology and capitula density, although no known studies to date have specifically examined this proposition. Regardless of the explanation, the results show that  $K(\psi)$  in regenerating moss layers drops precipitously between 0 and  $-30$  cm  $\psi$ , corresponding to an approximate 30-cm WT decline below a given point within the profile.

### CONCLUSION

This study presents novel data on the hydrophysical properties and hydrological behaviour of regenerating *Sphagnum* layers of a range of different ages. Although the data are insufficient to conclude that *Sphagnum* regeneration on cutover surfaces follows a standard pattern of evolution across different species, climates, and peatland management strategies, they point to a pattern of structural development whereby the bulk density and water retention capacity of the layers directly overlying the cutover peat increase over time. Both of these properties were significantly ( $p < 0.001$ ) greater in the basal layer at the older SPONT plots than in the same layer at EXPER, presumably because the longer period of growth has allowed more time for decomposition and compaction of the moss. The relatively higher bulk density and retention capacity of the 9-year-old 2004 plot compared with the other EXPER plots suggest that the development of this water-retaining basal layer may proceed more quickly than previously thought. The ability of the basal layer to hold more water against tension may be an important mechanism for maintaining capillary flow during periods of low WT. The evolution of moss properties with time reflects local conditions including hydrological setting, climate, and regional ecological processes. Different climates and peatland management strategies will likely influence the rate of *Sphagnum* establishment on cutover surfaces. Nonetheless, the authors believe this work highlights hydrological processes within the regenerated layer and underlying peat that are likely to occur under a range of different settings.

Direct precipitation was poorly retained in the *Sphagnum* canopy and near surface. Changes in WT position were strongly correlated with  $\theta$  in the near surface at all plots, and this along with the relatively narrow variance in the TDR-derived water contents for a

given WT suggests that capillarity was a much stronger control on surficial  $\theta$  than precipitation. Six of the seven plots demonstrated a pattern whereby the surficial  $\theta$  that was sustained at a given WT decreases as the thickness of the regenerated layer increases. Plot 1970-C was an exception to this trend, and while this area may or may not be unique within this peatland or other cutover sites, it shows that community architecture and species composition have the potential to be more influential than layer thickness in determining profile capillarity. The  $K(\psi)$  curves observed here demonstrated the rapid ( $>4$  orders of magnitude) reduction in  $K(\psi)$  that occurs as soil water pressures drop to  $-30$  cm.

The data shown here strongly support the conclusion that WT is an effective regulator of near-surface  $\theta$  in regenerating *Sphagnum* in block-cut peatlands when WT is within 30 cm of the surface and possibly at lower positions as well. The data of Ketcheson and Price (2014) also support this conclusion. This implies that regulation of WT through subsurface irrigation, a method that is currently under investigation in eastern Canada (L. Rochefort, pers. comm.), is an effective means of optimizing hydrological conditions for *Sphagnum* biomass production, even when WT is below the cutover peat surface. The potential increase in WT at SPONT as compared with EXPER may be indicative of the evolution of SPONT plots at this site towards a hydrophysical structure that at some future point would be able to fully constrain WT to within the regenerated profile, which several studies (Lucchese *et al.*, 2010; McCarter and Price, 2014; McNeil and Waddington, 2003) have identified as a critical criterion for hydrological restoration as well as net carbon sequestration in restored bog peatlands. Future work should integrate soil water dynamics with  $\text{CO}_2$  measurements and attempt to quantify the resilience of regenerating *Sphagnum* in cutover environments to more highly water-limiting conditions in order to establish both optimal and limiting hydrological conditions for *Sphagnum* biomass production. A numerical modelling approach using the hydrophysical parameters described here may prove useful in these regards.

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