

# *Sphagnum* moss moisture retention following the re-vegetation of degraded peatlands

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## ABSTRACT

Northern peatlands store approximately one-third of the World's soil carbon through the long-term accumulation of carbon as peat. However, when peatlands are exploited for *Sphagnum* moss and horticultural peat, they become degraded and large, persistent sources of atmospheric carbon dioxide. Recent advances in peatland restoration techniques have succeeded in the re-vegetation of *Sphagnum* moss on previously cutover surfaces. The long-term success of peatland restoration depends on the development of a sufficiently thick new peat layer that has ecohydrological and hydrophysical properties similar to natural peatlands. We determined these properties for an upper (0–4 cm) and lower (8–12 cm) peat layer in a recently restored peatland, a naturally re-vegetated cutover peatland, and a natural peatland in eastern Québec. The properties of the new peat layer differed significantly between the sites, especially for the lower layer samples. Lower samples for the natural and naturally re-vegetated sites had a bulk density of  $43 \pm 5$  and  $41 \pm 11 \text{ kg m}^{-3}$ , respectively, almost twice as high as the value for lower samples from the restored site ( $24 \pm 4 \text{ kg m}^{-3}$ ). *Sphagnum rubellum* capitula density ( $\rho_C$ ) was significantly higher ( $p < 0.05$ ) for the restored peatland ( $28\,726 \text{ \# m}^{-2}$ ) compared to the natural site ( $26\,050 \text{ \# m}^{-2}$ ). Residual moisture content at a soil water pressure of  $-200 \text{ mb}$  ( $\theta_r$ ) was significantly lower ( $p < 0.05$ ) for the restored site in comparison to the natural and naturally re-vegetated sites for the lower samples. This suggests that *S. rubellum* in a natural peatland is able to hold onto more moisture under increasing soil tension than the same species growing in a restored site likely due to its higher bulk density and relatively more decomposed state. We suggest that it is possible that *S. rubellum* growing in the harsher cutover peatland environment has possibly allocated more carbohydrates to vertical growth and as a consequence has a lower bulk density and poorer water retention. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS *Sphagnum*; ecohydrology; moisture retention; disturbance; restoration; peatland

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## INTRODUCTION

*Sphagnum* moss is a keystone species in peatlands, as it helps maintain a high water table position and decrease pH levels, thereby stimulating the development of peat bogs (Chirino *et al.*, 2006). Hayward and Clymo (1982) suggest that *Sphagnum* species likely store more carbon, in living tissue and as peat, than in any other plant genus in the world. Indeed, northern peatlands store approximately one-third of the world's soil carbon through the long-term accumulation of atmospheric carbon dioxide ( $\text{CO}_2$ ) as peat (Gorham, 1991). However, human disturbance such as drainage and peat extraction often switches peatlands to large, persistent sources of atmospheric  $\text{CO}_2$  (Waddington *et al.*, 2002) because of dramatic impacts to the hydrology of these ecosystems. The uppermost layer of peat (acrotelm) in natural peatlands is characterized by a high porosity, specific yield and saturated hydraulic conductivity. During extraction, the acrotelm is either dramatically altered or is removed altogether, resulting in a generally lower and 'flashier' water table position, limiting water availability for peatland vegetation (Price *et al.*, 2003). This is particularly

damaging to *Sphagnum*, as *Sphagnum* mosses are non-vascular plants that require a constant supply of water (Price, 1997). *Sphagnum* moss has been observed to re-vegetate naturally on the remaining cutover peat following human disturbance at sites characterized by soil moisture  $>50\%$ , soil water pressure  $>-100 \text{ mb}$  and high water table (mean  $-29 \text{ cm}$ ) (Price and Whitehead, 2001). However, on many degraded cutover surfaces *Sphagnum* often cannot generate the capillary forces necessary to extract moisture from the peat as these conditions are lower than the required thresholds (Price, 1997). Lavoie and Rochefort (1996) noted that spontaneous regeneration of *Sphagnum* in block-cut peatlands was possible; however, this was only observed in areas where hydrological conditions appeared to be more favourable for moss regeneration. Spontaneous *Sphagnum* regeneration is much rarer in vacuum extracted peatlands, where a low water table level throughout the site prevents *Sphagnum* recolonization (Lavoie *et al.*, 2003). Vacuum harvested peatlands are characterized by a much flatter and regular surface, creating hydrological conditions that are typically less variable but more extreme than block-cut sites throughout the abandoned cutover peat surface (Price *et al.*, 2003). As such, these degraded peatlands usually require active restoration to allow the return of the more suitable hydrological conditions needed for

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*Sphagnum* survival, by blocking old drainage ditches and creating dykes to retain water on site (Price *et al.*, 2003; Rochefort *et al.*, 2003). Waddington *et al.* (2003) found that *Sphagnum* growing in these harsh hydrological conditions had a higher capitula density which they hypothesized was a mechanism to maintain high moisture contents due to the tighter arrangement of capitula.

While research has demonstrated that a peatland can return to a net sink for CO<sub>2</sub> within 3–5 years following *Sphagnum* re-vegetation (Waddington and Warner, 2001; Greenwood, 2005), it can be argued that a peatland can only be considered functionally 'rehabilitated' once the new re-vegetated *Sphagnum* moss and peat layer becomes thick enough to be a functional 'self-regulating' acrotelm. However, it is unknown whether *Sphagnum* mosses growing in the relatively harsher hydrological conditions of recovering human-disturbed peatlands are similar to natural peatlands. Here we determine the ecohydrological properties of *Sphagnum rubellum* moss following the re-vegetation of degraded peatlands and compare them with adjacent natural peatland moss properties. We chose *S. rubellum* as this hummock species is commonly used in the restoration of degraded peatlands. The degraded peatlands we examined included a peatland that has re-vegetated naturally following extraction using mechanized block-cutting (hereafter referred to as re-vegetated) and a peatland that was cutover using a vacuum harvest extraction process but due to harsher hydrological conditions (Price and Whitehead, 2001; Shantz and Price, 2006) required active restoration (hereafter referred to as restored) to re-vegetate the surface with *Sphagnum* moss. We hypothesized that *S. rubellum* growing in the restored peatland would be adapted to the harsher hydrological conditions and exhibit a higher capitula density, lower specific yield and higher moisture retention than the re-vegetated site and adjacent natural peatland.

## METHODOLOGY

This study was conducted at the Bois-des-Bel (BDB) and Cacouna Bog (CB) peatlands in the Bas-Saint-Laurent region of Québec, ~14 km east of Rivière-du-Loup (42°58'N, 69°25'W). BDB was the location of our natural and restored sites while CB was the location of our re-vegetated site. *S. rubellum* samples were collected from each peatland to determine the hydrophysical properties. In late May 2007, we took 7–23 high-resolution digital photographs of different plots of *S. rubellum* at each site to determine moss capitula density. We then removed three to five large peat blocks (50 × 25 × 30 cm<sup>3</sup>) of surface peat from each site. The peat blocks were frozen and returned to the Ecohydrology Laboratory at McMaster University for analysis of bulk density, specific yield, Von Post decomposition and moisture retention curves.

## Study areas

The BDB peatland is a 200 ha treed bog of which an 11.5 ha section was drained in 1972 and the upper 80 cm of peat was extracted from the site using the vacuum approach from 1973 to 1980. The site was then abandoned until 1999. The abandoned peatland was divided into 11 fields (30 × 300 m<sup>2</sup> each) and separated by drainage ditches running parallel (north–south) to the fields. In the autumn of 1999, ecosystem scale restoration commenced using the standard Canadian restoration technique as outlined in Rochefort *et al.* (2003). Initially, the peat surface was cleared of all vegetation and woody material that was present after abandonment. Drainage ditches were blocked and dykes (low-lying peat walls) were created to retain snowmelt. *Sphagnum* fragments were also introduced from a natural donor peatland, and a straw mulch cover applied at a rate of 3000 kg ha<sup>-1</sup> in order to protect the fragments. Lastly, phosphorus fertilizer was applied at a rate of 15 g m<sup>-2</sup> to enhance vascular plant colonization (Rochefort *et al.*, 2003). The cutover peatland was separated into two sections: a 7.5 ha restored section (westernmost eight peat fields) and a 1.8 ha cutover section (easternmost two peat fields) with a buffer strip left in-between the two sections. The restored section of the Bois-des-Bel peatland was further divided into four zones (1–4) and separated by dykes. Zones 2, 3 and 4 were restored in the fall of 1999, while zone 1 was restored in the fall of 2000. The average peat depths of the restored and cutover sites are 1.5 and 1.6 m, respectively, and the peatland is underlain by a layer of marine clay that hinders vertical flow through the base of the peat deposit. The dominant species found at Bois-des-Bel post-restoration include *Polytrichum* spp., ericaceous shrubs, *Eriophorum vaginatum* and *Typha latifolia*. Furthermore, *S. rubellum* was present at the restored site while *Picea mariana* and *Betula* spp. were present at the cutover site. Lavoie *et al.* (2001) provide further details on the site conditions and vegetation distribution within the undisturbed portion of the peatland. The natural portion of the peatland is located adjacent to the restored site.

The CB peatland was originally 210 ha but conversion to agricultural lands and construction of roads has reduced its total area to 172 ha (Girard, 2000). A railway constructed in the mid-1800s divides the peatland into north and south sections along a natural groundwater divide. Peat extraction for horticultural use began in 1942 using the block-cut method, and a series of trenches and raised baulk areas resulted from using this peat extraction method. Drainage ditches, created to facilitate peat extraction, were blocked naturally and manually (in 2006) by peat slumping after the peatland was abandoned in 1976 (Girard, 2000). The CB peatland has been naturally colonized by ericaceous shrubs and *S. rubellum* and *S. capillifolium*.

## Field measurements

*S. rubellum* capitula density (expressed as the number of capitula per m<sup>2</sup>) was determined at 18 natural sites

(BDB), 23 restored sites (BDB) and 7 re-vegetated sites (CB). High-resolution (8 megapixels) digital photographs were taken of 100 cm<sup>2</sup> *Sphagnum* quadrats, with a ruler as a scale in each photo. Photographs were analysed in a photo-editing program and used to provide a count of the number of capitula per 10 × 10 cm<sup>2</sup> quadrats. Photos that did not provide a clear view of capitula or could not yield 10 × 10 cm<sup>2</sup> quadrats were disregarded.

#### Laboratory measurements

In the laboratory, cylindrical peat 'pucks' (8 cm diameter, 4 cm deep) were randomly sub-sampled from the upper (0–4 cm) and lower (8–12 cm) depths of the frozen peat blocks. The peat 'pucks' were then stored in PVC cylinders (4 cm high) and a fine nylon mesh was attached to the bottom to minimize disturbance and soil loss from the samples.

We determined specific yield ( $S_y$ ) on a total of 49 peat 'pucks' (natural = 11, restored = 28, re-vegetated = 10) with approximately half of the samples from each of the upper and middle depths. The 'pucks' were thawed and then saturated from below by slowly filling a small tub containing the samples until water reached a level just below the top of the samples and allowing them to saturate for 24 h. Samples were then allowed to drain for 24 h and specific yield ( $S_y$ ) was calculated using the following equation:

$$S_y = \frac{(M_s - M_d)/\rho_w}{M_s/\rho_w} \quad (1)$$

where  $S_y$  (m<sup>3</sup> m<sup>-3</sup>) represents the specific yield (≤ porosity),  $M_s$  is the saturated weight of the sample,  $M_d$  is the weight of the sample after it was allowed to drain and  $\rho_w$  is the density of water, assumed to be 1 g cm<sup>-3</sup>.

Soil moisture retention curves were determined using seven peat 'pucks' for each of the two depths for all three sites using a methodology fully described by Klute (1986). Briefly, the frozen peat 'pucks' were thawed and saturated in de-aired water for 48 h prior to testing to achieve full saturation of the peat. The peat 'pucks' were then placed on top of a high flow 0.5 bar porous ceramic plate cell (effective pore size 6.0 μm, hydraulic conductivity 0.0000311 cm s<sup>-1</sup> and approximate porosity of 50% by volume) within a 5 bar pressure plate extractor (Model 1600, Soil Moisture Equipment Corp., Santa Barbara) and sealed. Various pressures were applied (–5, –10, –15, –20, –25, –30, –35, –40, –60, –80, –100, –120 and –200 mb) using a pressure manifold (±1% accuracy) (Model 700-3, Soil Moisture Equipment Corp. Santa Barbara). A water outflow tube was connected from the pressure extractor into a burette, which allowed outflow to be measured. Equilibrium of the samples at each pressure was reached when the outflow of water had ceased (generally 1–2 days). The peat 'pucks' were weighed prior to moisture extraction and after each pressure change once equilibrium was observed. The porous plate was sprayed with a fine mist of water after each

equilibrium point to re-establish the hydraulic contact between soil and porous plate. Cheese cloth was also attached to the bottom of the samples to ensure soil loss was minimized, to prevent the plates from clogging due to soil loss and to aid in maintaining hydraulic contact between the soil and porous plate (Klute, 1986). Volumetric water content ( $\theta$ ) at any given pressure ( $\psi$ ) was determined at equilibrium and soil water retention curves were developed.

The soil water retention model RETC (van Genuchten *et al.*, 1991) with van Genuchten's (1980) model to describe soil water retention curves was used to fit the observed moisture retention data. Curve fitting parameters  $m$ ,  $n$  and  $\alpha$  were estimated with RETC for  $\theta$  ( $\psi$ ) relationships, fitted through least square error analysis. The model was run with the empirical constant  $m = 1 - 1/n$ . The soil water content as a function of pressure head ( $h$ ) is given by:

$$\theta(h) = \theta_r + \frac{\theta_s - \theta_r}{[1 + (\alpha \times h)^n]^m} \quad (2)$$

where  $\theta_s$  is the saturated moisture content,  $\theta_r$  is the residual moisture content, and  $\alpha$ ,  $m$  and  $n$  are curve fitting parameters.

The bulk density of the peat 'pucks' used in the moisture retention experiment was determined by oven drying samples of known volume for 72 h at 70 °C. Dry mass was recorded and used to calculate bulk density. Porosity ( $\phi$ ) was calculated from the obtained bulk density and a particle density ( $\rho$ ) of 1.55 g cm<sup>-3</sup> based on the literature values for peat (Clymo, 1970). Von Post degree of decomposition was determined using a standard method (von Post, 1922). The peat samples were squeezed within a closed hand, and according to observations regarding the colour of the solution that was expressed between the fingers, the nature of the fibres, and the proportion of the original sample that remained in the hand, the soil sample was placed in one of ten classes (H1–H10).

## RESULTS

*S. rubellum* capitula density ( $\rho_C$ ) for upper *Sphagnum* samples was significantly higher ( $p < 0.05$ ) for the restored peatland ( $28\,726 \pm 3384 \text{ \# m}^{-2}$ ) when compared to the natural site ( $26\,050 \pm 5573 \text{ \# m}^{-2}$ ) (Table I).

Lower samples from the re-vegetated and natural sites had a higher degree of decomposition ( $H = 4\text{--}5$ ) than the restored site ( $H = 2$ ) (Table I), with restored site samples more loosely packed and with better preserved *Sphagnum* remains than samples from the other two sites. Upper *Sphagnum* samples were mostly between undecomposed and almost undecomposed for the three sites. The samples from the natural and restored sites showed a higher presence of small leaves and fragmented branches than the samples from the re-vegetated site. The restored and natural sites also demonstrated the presence

Table I. Hydrophysical properties of the two surface peat layers at the three study sites (mean  $\pm$  standard deviation).

	$S_y$ ( $\text{m}^3 \text{m}^{-3}$ )	$\rho_b$ ( $\text{kg m}^{-3}$ )	$\phi$ (%)	$\rho_c$ ( $\# \text{m}^{-2}$ )	$H$
Upper (0–4 cm)					
Natural	$0.47 \pm 0.06$	$24 \pm 3$	$98.4 \pm 0.2$	$26050 \pm 5573$	n/a
Restored	$0.52 \pm 0.08$	$19 \pm 3$	$98.8 \pm 0.2$	$28726 \pm 3384$	n/a
Re-vegetated	$0.54 \pm 0.07$	$20 \pm 1$	$98.7 \pm 0.1$	$27743 \pm 3670$	n/a
Lower (8–12 cm)					
Natural	$0.22 \pm 0.01$	$43 \pm 5$	$97.2 \pm 0.3$	n/a	4
Restored	$0.36 \pm 0.06$	$24 \pm 4$	$98.5 \pm 0.3$	n/a	2
Re-vegetated	$0.33 \pm 0.08$	$41 \pm 11$	$97.4 \pm 0.7$	n/a	4–5

of *Polytrichum* mosses, which appeared more frequently in the restored site samples.

Bulk density ( $\rho_b$ ) was significantly higher for lower samples (8–12 cm) in comparison to upper (0–4 cm) samples for each of the sites ( $p < 0.05$  for restored and  $p < 0.01$  for natural and re-vegetated sites) (Table I). However, the difference was much smaller between upper and lower samples for the restored site. Lower samples for the natural and re-vegetated sites had a  $\rho_b$  of  $43 \pm 5$  and  $41 \pm 11 \text{ kg m}^{-3}$ , respectively, almost twice as high as the value for lower samples from the restored site ( $24 \pm 4 \text{ kg m}^{-3}$ ). Values were closer among the sites for the upper samples, ranging from  $19 \pm 3 \text{ kg m}^{-3}$  for the restored site to  $24 \pm 3 \text{ kg m}^{-3}$  for the natural site. Bulk density was also statistically different between the three sites for upper as well as lower samples ( $p < 0.05$  for upper and lower samples).

Porosity ( $\phi$ ) was significantly higher for upper samples for all sites ( $p < 0.001$  for re-vegetated,  $p < 0.01$  for natural and  $p < 0.05$  for restored site). Porosity was significantly different among the three sites for upper as well as lower samples ( $p < 0.05$  for upper and lower samples, Table I).

Specific yield ( $S_y$ ) was greater for upper samples in comparison to lower samples for all three sites ( $p < 0.01$  for natural, restored and re-vegetated sites) (Table I).  $S_y$  for the lower samples was greater for the restored and naturally re-vegetated sites ( $0.36 \pm 0.06$  and  $0.33 \pm 0.08$ , respectively) in comparison to the natural site ( $0.22 \pm 0.01$ ) ( $p < 0.05$ ). Greater values were observed for the upper samples, with values ranging from  $0.47 \pm 0.06$  for the natural site to  $0.54 \pm 0.07$  for the naturally re-vegetated site.

Soil moisture retention characteristics for lower samples (8–12 cm below the surface) differed greatly between the restored site and the other two sites (Figure 1a). Residual moisture content at a soil water potential of  $-200 \text{ mb}$  ( $\theta_r$ ) was significantly lower ( $p < 0.05$ ) for the restored site ( $13.7 \pm 1.3\%$ ) in comparison to the other two sites (Figure 1a and Table II). VWC at  $-100 \text{ mb}$  ( $\theta_{-100}$ ) was significantly higher ( $p < 0.05$ ) for the natural site ( $31.5 \pm 4.2\%$ ) than for the restored site ( $15.5 \pm 1.7\%$ ). While the overall shape of the curves is similar, the restored site had a lower VWC at any given pressure when compared to the other two sites.

Moisture retention curves for the upper (0–4 cm) samples showed a similar pattern to the lower samples

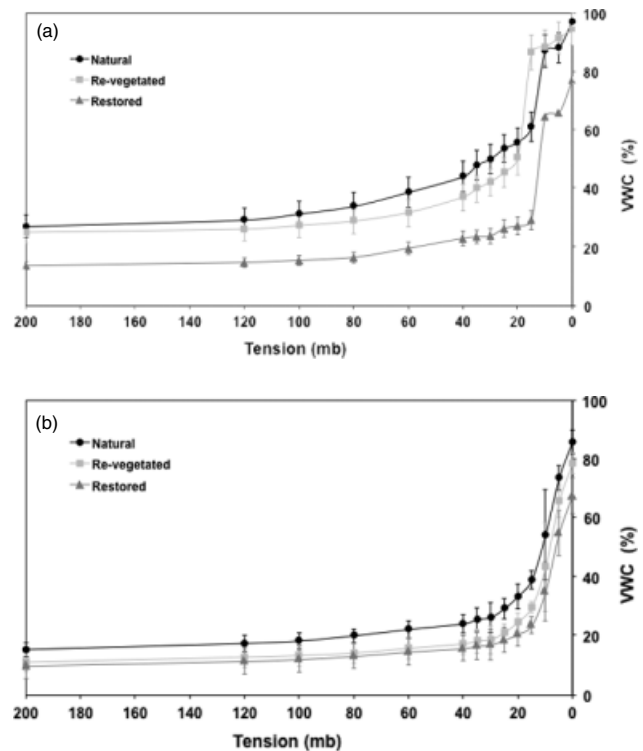


Figure 1. Soil moisture retention curves at the natural, re-vegetated and restored sites for (a) lower samples (8–12 cm) and (b) upper samples (0–4 cm).

Table II. Summary of moisture retention properties for the two surface peat layers at the three study sites (mean  $\pm$  standard deviation).

	$\theta_{-100 \text{ mb}}$	$\theta_r$
Upper (0–4 cm)		
Natural	$18.3 \pm 2.8$	$15.5 \pm 2.3$
Restored	$12.2 \pm 4.5$	$10.0 \pm 4.5$
Re-vegetated	$13.4 \pm 3.6$	$11.1 \pm 3.0$
Lower (8–12 cm)		
Natural	$31.5 \pm 4.2$	$27.2 \pm 3.9$
Restored	$15.5 \pm 1.7$	$13.7 \pm 1.3$
Re-vegetated	$27.2 \pm 3.9$	$24.9 \pm 3.5$

(Figure 1b). In general, at a given soil water pressure, VWC followed the trend: natural > re-vegetated > restored. Differences in VWC among the sites were much smaller than what was observed for the lower samples. The re-vegetated site had slightly higher values

at lower pressures than the restored site, but at higher tension VWC values were very similar for these two sites. Residual moisture content at a soil water pressure of  $-200$  mb for the re-vegetated and restored sites was  $11.1 \pm 3.0\%$  and  $10.0 \pm 4.5\%$ , respectively, and slightly higher retention was observed for the natural site at residual moisture content ( $15.5 \pm 2.3\%$ ); however, this difference was not significant. The same pattern was observed for VWC at  $-100$  mb, with differences among sites also not significant.

Differences between the upper and lower moisture retention properties were small for the restored site. Both residual moisture content ( $13.7 \pm 1.3\%$  for the lower samples and  $10.0 \pm 4.5\%$  for the upper samples) and moisture content at a soil water pressure of  $-100$  mb ( $15.5 \pm 1.7\%$  for lower and  $12.2 \pm 4.5\%$  for upper samples) for this site were not significantly different. This is not the case for the other two sites, which had lower residual moisture content and lower moisture content at a soil water pressure of  $-100$  mb for the upper samples in comparison to the lower samples ( $p < 0.001$  for re-generated site and  $p < 0.05$  for natural site for each of residual and  $-100$  mb moisture content).

Modelled moisture retention curves using the RETC code (van Genuchten, 1991) showed a good fit to the observed data (Figure 2). Modelled curves fit the observed data with an  $R^2$  value of 0.96 or better. Parameter values are reported in Table III.

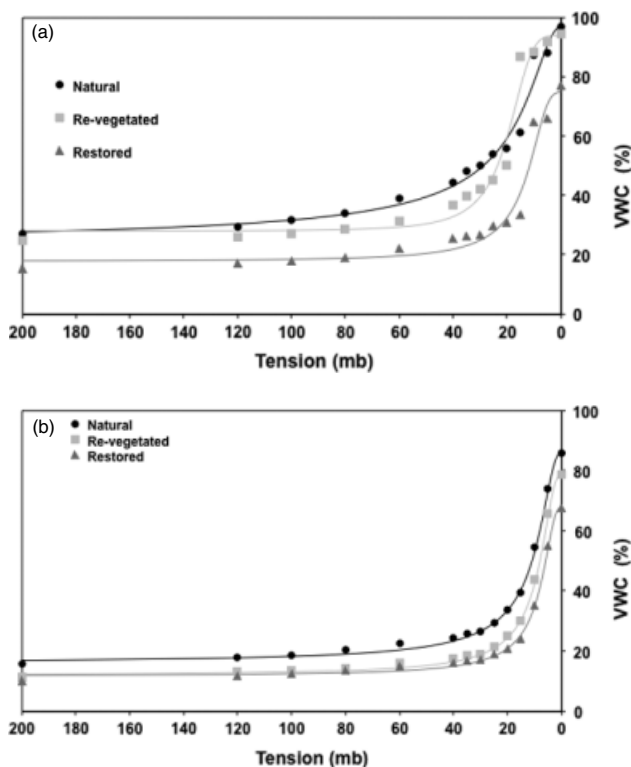


Figure 2. RETC model fit to observed moisture retention data for the (a) lower samples (8–12 cm) and (b) upper samples (0–4 cm). Observed experimental data are represented by points; modelled data are represented by lines.

Table III. RETC model curve fitting parameters ( $\alpha$ ,  $n$  and  $m$ ) for upper and lower moss samples from all three study sites.

	$\alpha$	$n$	$m$	$R^2$
Upper (0–4 cm)				
Natural	0.14	2.32	0.57	99.8
Restored	0.16	2.51	0.60	99.7
Re-vegetated	0.15	2.53	0.60	99.9
Lower (8–12 cm)				
Natural	0.09	2.01	0.50	97.8
Restored	0.09	2.96	0.66	95.9
Re-vegetated	0.06	4.18	0.76	97.3

## DISCUSSION

The return of a *Sphagnum* moss layer is essential for the rehabilitation of a degraded peatland ecosystem following disturbance. However, specific hydrological conditions are necessary for the re-establishment on degraded peat surfaces. For example, when soil water pressure drops below  $-100$  mb, the moss cannot generate capillary forces necessary to extract moisture from the cutover peat (Price, 1997).  $\psi$  is a better indicator of soil conditions and moisture availability than water table or volumetric moisture content as it is more sensitive and directly controls water supply to *Sphagnum* (Thompson and Waddington, 2008). However, spatially extensive measurements of  $\psi$  are not feasible, but relating distributed measurements of VWC to soil tension has its value.

While the studies were conducted in different years, the spatial and temporal variability of the surface VWC at the re-vegetated (Price and Whitehead, 2001) and restored sites (Lucchese, 2009) are quite similar. Mean restored site VWC was  $64.4 \pm 24.6\%$  and  $50.7 \pm 26.4\%$  for July and August, 2007, respectively, while re-vegetated site surface VWC in July and August in 1998 was  $55.4 \pm 11.5\%$  and  $49.3 \pm 14.8\%$ , respectively. At the re-vegetated site, Price and Whitehead (2001) demonstrated that  $\sim 80\%$  of *Sphagnum* that recolonized at this cutover site did so in locations where VWC  $> 50\%$ , which was coincident with  $\psi$  maintained above  $-100$  mb. Examination of Figure 1b indicates that for the laboratory peat 'pucks', the  $-100$  mb threshold did not occur until VWC reached a mean of  $< 14\%$  in the restored site samples. Comparison with the Lucchese (2009) field moisture survey reveals that  $\psi$  dropped below this  $-100$  mb threshold at only 1% and 3% of the site for July and August, respectively. This demonstrates that soil water pressure and moisture conditions in the upper living layer are ecohydrologically favourable for *S. rubellum* growth, even in a dry period. Furthermore, 71% of locations sampled in July 2007 had a VWC value  $> 50\%$ , while 44% of the locations sampled in August had a VWC value  $> 50\%$ , which demonstrates that not only is the site meeting the  $\psi > -100$  mb threshold but it is also maintaining a high moisture content on average at the site, even during a dry period. Maintaining high moisture content in the living moss layer is essential as water stored in the

unsaturated zone controls water availability to the surface (Price, 1997). It is no surprise that *Sphagnum* moss was found predominantly in wetter areas at Bois-des-Bel (Petroni *et al.*, 2004).

Shantz and Price (2006) demonstrated that in the initial 3 years post-restoration, before a significant moss layer had developed, runoff decreased, mean water table position increased and VWC in the upper 5 cm layer increased and spatially averaged  $\theta$  and  $\psi$  were maintained above 50% and  $-100$  mb, respectively. Spatial and temporal variations in these two parameters were reduced in comparison to the unrestored site. The authors also noted that these improvements occurred despite the increase in water table fluctuation in comparison to the non-restored portion of the peatland, which may be associated with the return of vascular vegetation at the site.

The ecohydrological properties of the new *S. rubellum* moss and peat layer in our restored site were found to differ from those of the adjacent natural peatland and of the naturally re-vegetated peatland, especially in the lower 8–12 cm layer. The lower bulk density of the lower layer at the restored site compared to the other two sites indicates that the degree of compaction and decay in this layer is lower than at the same depth in the other sites. This can be further substantiated by the lower Von Post degree of decomposition and higher porosity of the lower samples from the restored site in comparison to the natural and re-vegetated sites. This lower 8–12 cm layer represents new moss growth from earlier in the post-restoration period. This suggests that, while successful, the recolonization and growth of *S. rubellum* moss at the restored site requires time for the return of hydrophysical properties that resemble those of a natural site, as evidenced by similarities in the upper layers, which are growing later in the post-restoration period. It is likely that the time post-restoration has not yet been sufficient to allow for some important processes in peatland development such as decomposition and compaction to be restored to their normal functions. Alternatively, Schouwenaars and Gosen (2007) have shown through model simulations that recolonizing moss is most susceptible to water stress (from water table declines in the peat) when it reaches between 5 and 15 cm new growth, after which the ecohydrological properties of the moss enable sufficient water storage. It is possible that this period of increased vulnerability to water stress leads to lower bulk density and higher porosity. These changes would increase specific yield, a strategy that would retain more moisture within the new moss layer to combat periods of water table drawdown. It would also lead to lower moisture contents for a given  $\psi$ .

The specific yield values in this study are similar to values for the acrotelm layer in natural peatlands (e.g. 0.5–0.1; Price, 1992; Van Seters and Price, 2001).  $S_y$  was lowest for the lower depth samples from the natural site ( $0.22 \pm 0.01$ ) when compared to the restored site ( $0.36 \pm 0.06$ ) and re-vegetated site ( $0.33 \pm 0.08$ ), and also lower for the natural site than for the other two sites

for the upper samples. All sites had higher  $S_y$  for the upper layer in comparison to the lower layer. A high  $S_y$  in the upper layers of the acrotelm is essential to limit water table drawdown during dry periods and flooding during wet periods. This higher  $S_y$  value is expected and was observed for upper samples in relation to lower samples, as  $S_y$  depends on porosity and pore size, which are known to decrease with depth in the peat profile (Rizzutti *et al.*, 2004).

Capitula density at the surface of the new moss layer was lowest for the natural site, and highest for the restored site, a finding that agrees with Waddington *et al.* (2003). The authors hypothesized that the higher capitula density was a mechanism developed to cope with harsher hydrological conditions initially present at restored peatlands. This would allow *Sphagnum* lawns to maintain high moisture contents due to their tighter arrangement and thereby reduce the probability of desiccation and maintain a higher productivity (Waddington and Warner, 2001). However, this hypothesis is the opposite of that observed in our moisture retention laboratory experiment (Figure 1), where the peat at 8–12 cm depth at the restored site had lower moisture retention. Therefore, these data suggest that the moss that became the peat obtained from 8–12 cm depth at the restored site likely had a lower capitula density when it was alive than the moss presently at the surface (0–4 cm) at the same site. This is in line with the concept of maximizing  $S_y$  to combat water stress when the new moss layer is 5–15 cm thick by reducing bulk density and increasing porosity. That is, increased capitula density, while increasing moisture retention at lower  $\psi$ , imparts lower porosity and higher bulk density, which would result in a greater loss in water storage for a given lowering of the water table.

Restored site peat retained less water at any given  $\psi$ , especially for the depth 8–12 cm. This was opposite to what we hypothesized prior to the study. Furthermore, this site showed no significant differences in moisture retention properties between upper and lower samples, whereas the other two sites did. Visual observation of lower restored samples revealed that peat fibres in restored samples were less compacted and more preserved relative to the re-vegetated and natural peats. We argue that this suggests that *S. rubellum* in a natural peatland is able to retain more moisture under decreasing  $\psi$  than the same species growing in a restored site, likely due to higher bulk density and the relatively more decomposed state of *Sphagnum* samples (see von Post in Table I). Moisture retention increases with higher bulk density (Boelter, 1968), which can help explain the differences observed between the moisture retention curves for the natural and restored sites, especially at the 8–12 cm depth. Soil water retention model using RETC provided a good fit to the moisture retention data obtained in the laboratory and was used to describe the observed moisture retention data. Until recently, RETC parameters were viewed as a useful way of easily and inexpensively

predicting hydraulic conductivity properties from moisture retention data (van Genuchten *et al.*, 1991), which could provide much needed insight into understanding water flux dynamics in the living moss layer (Price *et al.*, 2008). However, Price *et al.* (2008) tested this hypothesis and determined that hydraulic conductivity ( $K$ ) could not be accurately modelled based on moisture retention curves alone and suggested that theoretical pore-size distribution model (Mualem, 1976) does not well represent the structure of mosses. Nonetheless, observed moisture retention data in this study and modelled curves for the sites provide additional information that may not necessarily be as easily measured in the field with respect to the water storage properties of the *Sphagnum* moss layer.

An alternative explanation of our results points to the possibility that an adaptive strategy of *S. rubellum* is to allocate more of its sequestered CO<sub>2</sub> to vertical growth in the early stages of moss development. Turetsky *et al.* (2008) recently determined that different *Sphagnum* species allocate carbohydrates differently as an adaptive strategy for carbon accumulation in differing micro-environments. Given the broad range of moisture retention characteristics of *S. rubellum*, carbohydrate allocation of recently restored *Sphagnum* warrants further investigation. Nevertheless, we suggest there is a negative feedback to new moss growth in degraded peatlands whereby carbohydrate allocation exists in dynamic equilibrium with the soil water environment. If the surface of the degraded peatland remains wet, *S. rubellum* grows as in natural settings. At some thickness (5–15 cm), however, water table fluctuations are too great for the moisture requirements at the top of the moss layer, limiting and redirecting new growth (Schouwenaars and Gosen, 2007). This may translate into greater carbon stores directed to rapid vertical growth at the expense of lateral infilling (lower capitula density). Lower bulk density, higher porosity and higher specific yield would result in increasing moisture availability for those capitula. At some point (>15 cm in height), there exists enough water storage within the surface moss for new carbohydrates to be allocated to increased lateral density.

As previously observed in the Cacouna Bog, despite recolonization of *Sphagnum* in some areas as well as similar  $S_y$  and mean water table position at the regenerated portion of the block-cut bog and a nearby natural site, acrotelm thickness, water table fluctuations and maximum water table depth differed remarkably between the two sites (Price and Whitehead, 2001; Van Seters and Price, 2001). It is evident that the re-vegetated bog, even 30 years post-abandonment, had not yet developed an acrotelm able to stabilize water table fluctuations, which suggests that the presence of localized *Sphagnum* cushions (only about 10% of the site) with high  $S_y$  has a limited effect on water storage (Price and Whitehead, 2001). Rather, the development of a continuous moss lawn able to stabilize and contain water table fluctuations is required to restore the diplotelmic nature of degraded peatlands.

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## REFERENCES

- Boelter DH. 1968. Important physical properties of peat. In *Proceedings of the 3rd International Peat Congress*, Quebec City; 150–156.
- Chirino C, Campeau S, Rochefort L. 2006. *Sphagnum* establishment on bare peat: the importance of climatic variability and *Sphagnum* species richness. *Applied Vegetation Science* **9**(2): 285–294.
- Clymo RS. 1970. The growth of *Sphagnum*: methods of measurement. *Journal of Ecology* **58**: 13–49.
- Girard M. 2000. *La régénération naturelle d'écosystèmes fortement perturbés: le cas d'une tourbière exploitée du Bas-Saint-Laurent (Québec)*. MA thesis, Université Laval, Sainte-Foy, Québec, Canada.
- Gorham E. 1991. Northern peatlands: role in the carbon cycle and probable response to climatic warming. *Ecological Applications* **1**: 182–195.
- Greenwood MJ. 2005. *The effects of restoration on CO<sub>2</sub> exchange in a cutover peatland*. MSc thesis, McMaster University, Hamilton, Ontario, Canada.
- Hayward PM, Clymo RS. 1982. Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London, Series B* **215**: 299–325.
- Klute A. 1986. Water retention: laboratory methods. Pressure plate extractor. In *Methods of Soil Analysis Part 1—Physical and Mineralogical Methods*, 2nd edn, *Soil Science of America Book Series*, Klute A (ed.). SSSA: Madison, WI.
- Lavoie C, Grosvernier P, Girard M, Marcoux K. 2003. Spontaneous revegetation of mined peatlands: an useful restoration tool? *Wetlands Ecology and Management* **11**: 97–107.
- Lavoie C, Rochefort L. 1996. The natural revegetation of a harvested peatland in southern Québec: A spatial and dendroecological analysis. *Ecoscience* **3**: 101–111.
- Lavoie C, Zimmermann C, Pellerin S. 2001. Peatland restoration in southern Québec (Canada): a paleoecological perspective. *Ecoscience* **8**: 247–258.
- Lucchese M. 2009. *Peatland restoration: an ecohydrological assessment*. MSc thesis, McMaster University, Hamilton, Ontario, Canada.
- Mualem. 1976. A new model for predicting the hydraulic conductivity of unsaturated porous media. *Water Resources Research* **12**(3): 513–522.
- Petrone RM, Price JS, Carey SK, Waddington JM. 2004. Statistical characterization of the spatial variability of soil moisture in a cutover peatland. *Hydrological Processes* **18**: 41–52.
- Price JS. 1992. Blanket bog in Newfoundland: 2. Hydrological processes. *Journal of Hydrology* **135**: 103–119.
- Price JS. 1997. Soil moisture, water tension and water table relationships in a managed cutover bog. *Journal of Hydrology* **202**: 21–32.
- Price JS, Heathwaite AL, Baird A. 2003. Hydrological processes in abandoned and restored peatlands. *Wetlands and Ecological Management* **11**: 65–83.
- Price JS, Whitehead GS. 2001. Developing hydrological thresholds for *Sphagnum* recolonization on an abandoned cutover bog. *Wetlands* **21**(1): 32–40.
- Price JS, Whittington PN, Elrick DE, Strack M, Brunet N, Faux E. 2008. A method to determine unsaturated hydraulic conductivity in living and undecomposed *Sphagnum* moss. *Soil Science Society of America Journal* **71**: 487–491.
- Rizzutti AM, Cohen AD, Stack EM. 2004. Using hydraulic conductivity and micropetrography to assess water flow through peat-containing wetlands. *International Journal of Coal Geology* **60**(1): 1–16.
- Rochefort L, Quinty F, Campeau S, Johnson K, Malterer T. 2003. North American approach to the restoration of *Sphagnum* dominated peatlands. *Wetlands Ecology and Management* **11**: 3–20.
- 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**(2): 1–19.

- Shantz MA, Price JS. 2006. Hydrological changes following restoration of the Bois-des-Bel Peatland, Quebec, 1999–2002. *Journal of Hydrology* **331**: 543–553.
- Thompson DK, Waddington JM. 2008. *Sphagnum* under pressure: towards an ecohydrological approach to examining *Sphagnum* productivity. *Ecohydrology* **1**: 299–308. DOI: 10.1002/eco.31.
- Turetsky MR, Crow SE, Evans RJ, Vitt DH, Wieder RK. 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology* **96**(6): 1297–1305.
- van Genuchten M Th. 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Science Society of America Journal* **44**: 892–898.
- van Genuchten M Th, Leij FJ, Yates SR. 1991. *The RETC code for quantifying the hydraulic functions of unsaturated soils*. EPA/600/2–91/065. USEPA, Ada, OK.
- 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.
- Von Post L. 1922. Sveriges geologiska undersöknings torvinventering och några av dess hittills vunna resultat. *Sven. Mosskulturforen. Tidskr* **1**: 1–27.
- Waddington JM, Rochefort L, Campeau S. 2003. *Sphagnum* production and decomposition in a restored cutover peatland. *Wetlands Ecology and Management* **11**: 85–95.
- Waddington JM, Warner KD. 2001. Atmospheric CO<sub>2</sub> sequestration in restored mined peatlands. *Ecoscience* **8**(3): 359–368.
- Waddington JM, Warner KD, Kennedy G. 2002. Cutover peatlands: a persistent source of atmospheric CO<sub>2</sub>. *Global Biogeochemical Cycles*. DOI: 10.1029/2001 GB001398.