Sphagnum under pressure: towards an ecohydrological approach to examining *Sphagnum* productivity

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ABSTRACT

The genus *Sphagnum* is the key peat-forming bryophyte in boreal ecosystems. Relying entirely on passive capillary action for water transport, soil moisture is often the limiting factor in *Sphagnum* production, and hence peat accumulation. While several hydrological models of peat physics and peatland water movement exist, these models do not readily interface with observations and models of peatland carbon accumulation. A conflict of approaches exists, where hydrological studies primarily utilize variables such as hydraulic head, while ecological models of *Sphagnum* growth adopt the coarse hydrological variables of water table (WT), volumetric water content (VWC) or gravimetric water content (WC). This review examines the potential of soil pressure head as a measurement to link the hydrological and ecological functioning of *Sphagnum* in peatlands. The non-vascular structure of *Sphagnum* mosses and the reliance on external capillary transport of water in the mosses make them an ideal candidate for this approach. The main advantage of pressure head is the ability to mechanistically link plot-scale hydrology to cellular-scale water requirements and carbon exchange. Measurement of pressure head may improve photosynthetic process representation in the next generation of peatland models. Copyright © 2008 John Wiley & Sons, Ltd.

INTRODUCTION

Northern peatlands represent a large portion of the Earth's total terrestrial carbon stores, storing 455 Pg of C (Gorham, 1991), a pool equal to 60% of atmospheric carbon (Schimel, 1995). The moss genus *Sphagnum* is responsible for approximately half of the carbon accumulation in peatlands (Rydin and Jeglum, 2006). Clymo and Hayward (1982) suggest that there might be more carbon in *Sphagnum* in both live shoots and peat than any other terrestrial plant genus. Peatland soils are constantly aggrading and degrading as a result of biotic processes, and are especially sensitive to external forcings in the form of climate, hydrology, or human disturbance (e.g. Grosvenier *et al*., 1997; Bubier *et al*., 2003; McNeil and Waddington, 2003; Turetsky *et al*., 2002) leaving them vulnerable to net mass loss by only small reductions in plant production (Clymo, 1984). While a wide variety of environmental factors control the growth of *Sphagnum* mosses, such as N, P, and K availability (e.g. Aerts *et al*., 1992; Hoosbeek *et al*., 2002), trace metals, and UV radiation (Gehrke, 1998), the largest control on peat accumulation is soil moisture availability (Clymo and Hayward, 1982; Belyea and Baird, 2006).

Early ecological studies demonstrated that *Sphagnum* mosses possess excellent water retention capabilities compared to typical forest litter, allowing for high cellular water contents (WCs) at field conditions (Grout, 1908;

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Kummel, 1925). The reliance on passive water transport in *Sphagna* makes them particularly susceptible to variation in soil moisture, with 90% of *Sphagnum* WC held externally between branches and leaves (Hayward and Clymo, 1982). The remaining 10% of water is essential to the functioning of chloroplasts for photosynthesis (Proctor, 2000). In peatlands altered by human activities, such as cutover or harvested peatlands in boreal Sweden and Canada (e.g. McNeil and Waddington, 2003; Tuittila *et al*., 2004), and undisturbed peatlands vulnerable to moisture stress due to climate variations in sub-boreal Canada (Bubier *et al*., 2003), water is the controlling factor in *Sphagnum* growth, and hence, peat accumulation and peatland sustainability (Girard *et al*., 2002).

The knowledge base on peatland ecohydrology has advanced over the last 25 years to the point where models of saturated flow take into account changes in peat volume and associated changes in hydraulic conductivity (Kennedy and Price, 2004). Similarly, our understanding of *Sphagnum* ecology has established the moisture-induced biological limits of carbon fixation in *Sphagnum* at the cellular (e.g. Gerdol *et al*., 1996), shoot (Maseyk *et al*., 1999), and plot scale (Campeau and Rochefort, 1996). Despite the extensive research in ecology and hydrology of peatlands, the understanding of interactions between these disciplines is limited. Many ecological studies (e.g. Robert *et al*., 1999; Poulin *et al*., 2005) rely on water table (WT) as an indicator of surface moisture availability; however, WT measurements often become disconnected from surface processes (Price, 1997). The widely used bog growth model of Clymo (1984) contains

no explicit hydrological parameters and simply assumes a static WT. Models of peatland hydrology often utilize simplified approaches to model moss growth (e.g. Borren and Bleuten, 2006) or do not account for peat accumulation whatsoever (Kennedy and Price, 2004). One of the difficulties in coupling ecological and hydrological processes lies in the paucity of commonly measured physical variables that are applicable in both ecological and hydrological field studies and models. This need for a greater synthesis of hydrological and ecological processes has been highlighted by Blodau (2002), and in the context of peatland remediation by Holden (2005).

Pore-water pressure, or pressure head, in the vadose zone is a potentially useful crossover parameter between the ecology and hydrology in systems dominated by plants lacking active vascular water transport. The advantage in pore-water pressure over other measurements lies in that it describes WC and flow in both soil and plant tissue networks. Easily measured in the field, pressure head also holds quantitative meaning for ecological studies of bryophytes, where the lack of vascular tissues limits water transport to capillary forces that are governed by pressure in the soil matrix. Here we present an overview of pressure head, its fundamentals, and review the advantages over other parameters as an indicator of both peatland hydrology and ecology as it applies to CO_2 gas exchange in the moss genus *Sphagnum*. Secondly, through this review we hope to encourage an increased utilization of field measurements of pressure head in future studies of *Sphagnum* photosynthesis.

PRESSURE AND WATER MOVEMENT VIA CAPILLARY ACTION IN *SPHAGNUM*

For the purposes of this review the term pressure head is used, and is synonymous with pore-water pressure, tension, soil-water suction and matric potential; pressure head is represented by the symbol Ψ. The above terms are jointly defined as 'the energy per unit bulk volume of porous medium required to remove liquid from it isothermally against capillary forces holding it in place' (Case, 1994, 17). This pressure may be expressed as a negative pressure relative to the atmosphere expressed in Pa, or as a positive pressure head expressed in centimetres or metres of H_2O (10 cm $H_2O \approx 1$ kPa).

Theory of pressure and capillarity

The simplest use of pressure is to predict the behaviour of water in a cylindrical tube at negative pressure above the WT. This water is then available to plants not in contact with the saturated zone. The pressure exerted by capillary action against gravity in a small cylindrical tube can be described by the LaPlace equation of capillarity as:

$$\psi = \frac{2\sigma}{\rho \, gr} \tag{1}$$

where ψ is the tension across the interface (m H_2O), σ is the surface tension (J m^{-2}), ρ is the fluid density (kg

m^{-3}), g is the gravitational constant (9·81 m s^{-2}), and r is the radius of the tube (m). The above equation can be approximated for perfectly wetting surfaces as:

$$\psi = \frac{3}{D} \tag{2}$$

where ψ is pressure head in m H_2O and D is the diameter of a pore in μm (Lewis, 1988). This pressure can also be written as an equilibrium height of water (m) in a cylindrical tube:

$$h = \frac{2\sigma \, \cos \, \theta}{\rho \, gr} \tag{3}$$

where θ is the contact angle (in degrees).

For living *Sphagnum* plants, Valat *et al.* (1991) found the contact angle between tissues and water to be close to zero, therefore $\cos \theta = \cos 0 = 1$. Using Equation (3), the capillary height in living *Sphagnum* at equilibrium is approximated by:

$$h = \frac{1·4 \times 10^{-5}}{r} \tag{4}$$

where h is the height of the water column in m and r is the radius in m. Contact angles for peat lie between 73 and 88° (Waniek *et al.*, 2000). Therefore, the height of capillary rise in peat soils can be approximated by:

$$h = \frac{2·72 \times 10^{-6}}{r} \tag{5}$$

with the same units as Equation (4). Thus, there is a five-fold difference in capillary height between living mosses and peat because of contact angles. Other studies examining the contact angle of peat give values ranging between 15 and 60° for intact 'high bog' peat (Burghardt, 1985), and 110°, for hydrophobic, air-dried *Sphagnum* peat (Valat *et al.*, 1991).

Vapour pressure and capillarity

In addition to pressure as a product of geometry, essentially a substrate and cellular parameter, consideration must be given to the effect of humidity on the air–water interface. For a given pressure head, the air above the meniscus is assumed to be in equilibrium according to the equation:

$$\psi = \frac{R \times T}{M \times g} \ln(\frac{P_v}{P_o}) \tag{6}$$

where Ψ is the pressure head (m H_2O), R is the ideal gas constant (8·3 J mol K^{-1}), T is temperature in Kelvin, M is the molar mass of water (0·018 kg mol^{-1}), and g is the force of gravity (9·8 N kg^{-1}), P_v and P_o are vapour pressure and saturated vapour pressure, respectively (Stephens, 1996). If the vapour pressure is not in equilibrium, capillary water must be evaporated in order to re-establish it. Therefore, low humidities may induce an evaporative demand exceeding water transport, leading to a loss of capillary water and a lowering of

pressure heads. This relationship between vapour pressure and pressure head has been used to measure pressure head–volume relationships in *Sphagnum* and other bryophytes using a thermocouple psychrometer (Proctor *et al.*, 1998; Hájeck and Beckett, 2008). At pressures at and above −100 m H_2O, the equilibrium relative humidity (RH) is effectively saturated at 0·9931. RH values of 50%, common in the air above a cutover bog at midday in summer, are only in equilibrium with a meniscus at −10^4 m H_2O pressure. Such low pressures are not found in the vadose zone of intact or cutover peatlands, suggesting that sufficient evaporation occurs to maintain the vapour pressure of pore spaces near saturation. The conductance of water through *Sphagnum* to maintain vapour pressure saturation is substantial, as measurements of evaporation over a *Sphagnum* hummock can exceed those over adjacent open water (Nichols and Brown, 1980).

CAPILLARITY AND PRESSURE WITHIN *SPHAGNUM*

Shoots of *Sphagnum* mosses are composed of a stem and clusters (fasicles) of 2–4 branches occurring along the length of the stem (Figure 1). Branches up to 1 cm long occur as the pendant type next to the stem, or spreading branches at a right angle to the stem. At the apical tip, a dense cluster of shorter branches forms the capitula. Concave leaves one cell thick consist of two types of cells: (i) dead, large (100 × 25 μm) hyaline cells function primarily for water storage and structural support; and (ii) smaller (8 μm) chloroplast-containing chlorophyllose cells arranged in a 1:1 pattern unique to the genus *Sphagnum*.
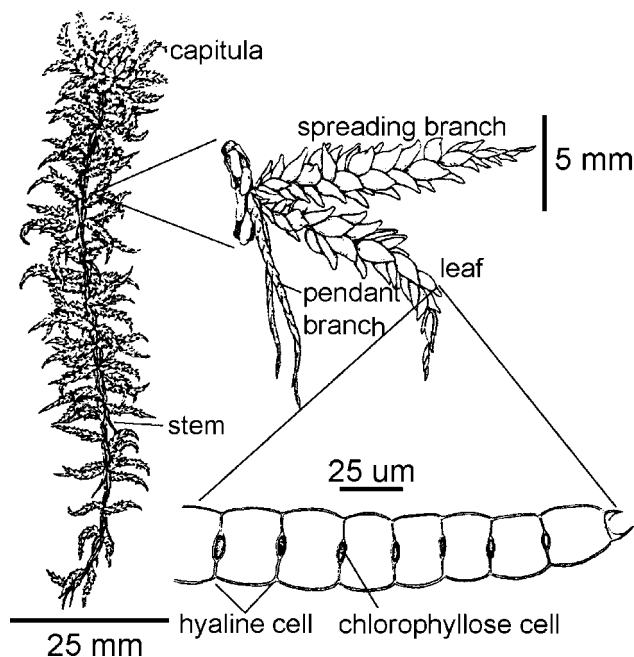

Figure 1. Morphology of a *Sphagnum magellanicum* shoot, with features typical to most ombotrophic *Sphagnum* species (modified from Crum and Anderson, 1981). Note the leaf closeup shown is in transverse cross-section, hyaline cells are typically 100 μm in length.

Unlike specialized internal tissues in vascular plants, mosses such as *Sphagnum* conduct water up from the substrate using only passive capillary action. In many bryophytes, thin-walled parenchyma cells join together in the interior of the stem to create elongated tubes analogous to xylem in vascular plants (Buck and Goffinet, 2000). In *Sphagnum,* poor connectivity of the parenchyma cells limits interior water conductance to 1% of total water transport; rather, 99% water is moved externally between branches and leaves and up the exterior of the stem (Proctor, 1982). In this manner, shoot density and contact between branches play an important role in the transmittance of water by regulating pore space distribution and connectivity. Tight networks of *Sphagnum* with abundant branches can distribute water evenly across a hummock or lawn, averaging out water stress. The distribution of water retention in *Sphagnum* shoots mirrors water conductance: only 10% of water is held internally within cells, the remainder is held between leaves and branches in larger (1 mm) pore spaces (Clymo and Hayward, 1982; Figure 2). Indeed, it is this external water that is responsible for the majority of water movement within and amongst *Sphagnum* shoots. For example, Price *et al.* (2008) observed a five orders of magnitude decline in hydraulic conductivity as pressure head fell below −25 cm H_2O (−2·5 kPa), corresponding to a loss of external water in the shoots.

Within leaves of *Sphagnum*, the hyaline cells play a vital role in maintaining water availability for the photochemical reactions in adjacent chlorophyllose cells (Proctor, 2000). The hyaline cells are empty, porous cells without organelles or cytoplasm that function solely for structural support and water transport (Lewis, 1988). Water transport in and out of hyaline cells is limited by movement across up to 15 pores in each hyaline cell (Malcolm, 1996). For pores at an air–water interface, maintenance of a meniscus and retention of water inside the cell is governed by capillary law (Hayward and Clymo, 1982; Lewis, 1988). At pressures exceeding the calculated value, the meniscus expands inwards towards the centre of the cell, eventually breaking and allowing the entry of air into the entire hyaline cell (Lewis, 1988). This 'air seeding' causes dewatering and cellular-scale damage to chlorophyll pigments and a large reduction in photosynthetic capacity (Gerdol *et al.*, 1996).

Using capillarity law in the form of Equation (3) and the known radius of pores in hyaline cells, Clymo and Hayward (1982) calculated drainage of hyaline cells at pressures of approximately −200 to −300 cm H_2O, or −20 to −30 kPa (Figure 2). Direct measurements of hyaline cell drainage using an in-cell pressure transducer by Lewis (1988; Figure 3) reveal a close fit between predicted and observed air-seeding pressures.
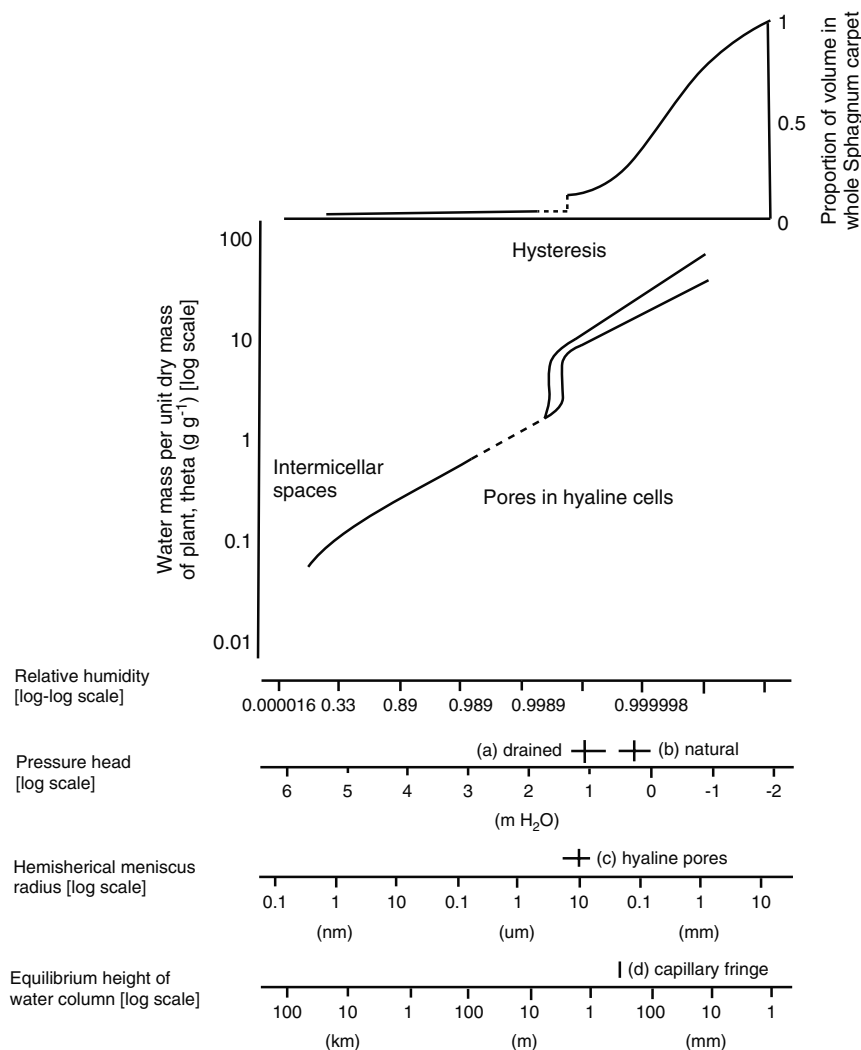
Figure 2. Relationship between water content in a *Sphagnum* hummock and pressure head, modified from Clymo and Hayward (1982). Equilibrium water column height, and meniscus radius are calculated on the basis of a perfectly wetting (i.e. $\theta = 0$) surface with a surface tension equal to pure water. Crosshairs (a) and (b) represent the 50th percentile of pressure head at 2·5 cm depth from Lindholm and Markkula (1984); the horizontal endpoints of the crosshairs represent the 5th and 95th percentiles.
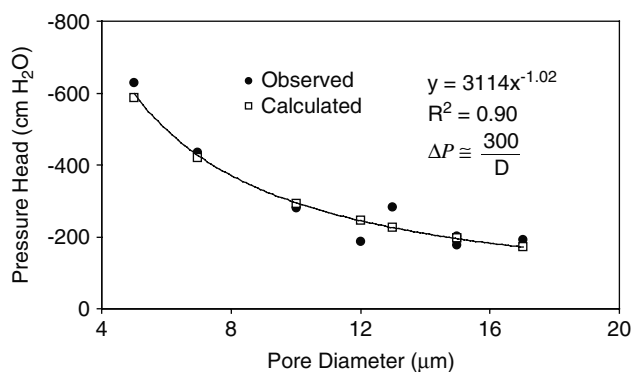

Figure 3. Relationship between pressure within a hyaline cell at drainage and pore diameter, modified from Lewis (1988).

OBSERVATIONS OF PRESSURE IN PEATL'S

In peatlands harvested for horticultural peat, any *Sphagnum* mosses able to re-colonize the cutover peat surface often grow under water-stressed conditions. In the harvesting process, the porous younger surface peat is removed, exposing the dense and older deep (catotelm) peat at the surface. Overlaying the cutover peat is *Sphagnum* and other vegetation grown since harvesting, often in the form of 'cushions' or hummocks (Robert *et al.*, 1999; Girard *et al.*, 2002). Although the peat stratigraphy is heavily altered by anthropogenic activity, cutover peatlands provide an interesting case study in the interaction of stresses, peatland ecology, carbon exchange, and hydrology (McNeil and Waddington, 2003; Tuittila *et al.*, 2004).

Price and Whitehead (2001) monitored pressure head within trenches at a cutover peatland both with and without a *Sphagnum* cover. Soil pressure heads below all *Sphagnum* hummocks and wet bare peat areas did not exceed -100 cm H_2O (-10 kPa) during the summer; whereas dry areas of bare peat routinely reached pressures over -150 cm H_2O. It is difficult to discern the ontology of higher pressures underneath *Sphagnum* hummocks in this situation. While the hydrological constraint for living *Sphagnum* of pressure heads lower than -100 cm H_2O is apparent from the work of Price and Whitehead (2001),
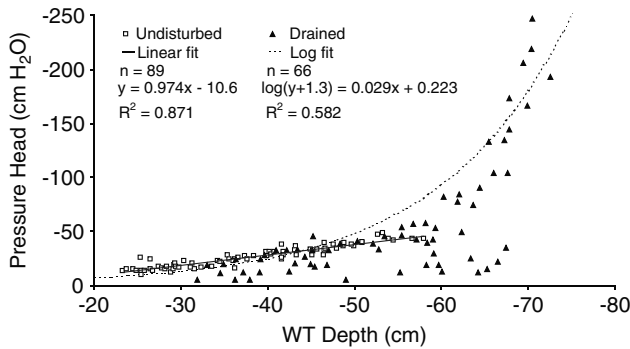
Figure 4. Water table—pressure head relationships in a natural and drained bog in Finland (modified from Lindholm and Markkula, 1984). The fitted curves and coefficients of determination are from Lindholm and Markkula, 1984. The following year, pressure head in the drained hummock changed to a linear relationship with water table.

Figure 5. Exceedence probability of soil pressure head in (a) living *Sphagnum* hummocks. The 'abandoned' curves are unpublished data from J.S. Price at the Cacouna Bog, QC, Canada. 'Natural' and 'drained' are from Lindholm and Markkula (1984). Bare peat surface pressure head probabilities are shown in (b). Data from Price (1997).

the degree to which *Sphagnum* alter the hydrology of their surroundings by increasing peat capillarity and reducing evaporation to maintain favourable conditions is unclear.

In a natural peatland in Finland, Lindholm and Markkula (1984) found pressure heads in hummocks ranged between -5 and -50 cm H_2O, with a mean of -20 cm H_2O. At a nearby drained, though not cutover peatland, median pressure heads increased to -36 cm H_2O and maximum pressure head to -60 cm H_2O (Figure 4). Similar trends of higher pressures in drained and otherwise altered peatlands are seen in exceedence probability distributions of three bare peat surfaces of a drained peatland in the Lac St. Jean region of Quebec, Canada (Figure 5b). Sites covered by a straw mulch to reduce evaporation (Petrone *et al*., 2004b) and sites with blocked drainage ditches had a similar pressure head distribution as the drier abandoned cutover peatland shown in Figure 5a. Pressure heads in a drained cutover peatland and a peatland with blocked ditches and no other remediation is substantially lower than in the straw mulch or in a living *Sphagnum* hummock; the median pressure head in both cases is below the range of hyaline cell drainage (Hayward and Clymo, 1982; Lewis, 1988) and likely results in reductions of photosynthesis. The shift to more hospitable pressure heads for *Sphagnum* mosses that can be attributed to the straw mulch points to the importance of not just maintaining high WTs, but providing a resistance to evaporation to maintain low pressure heads in near surface peat.

MEASUREMENT TECHNIQUES OF WATER AVAILABILITY IN *SPHAGNUM* MOSSES

From the above, it is apparent that pressure head can be seen as a simple, physically based approach to quantifying water flow, retention, and vapour dynamics in porous media. In the case of *Sphagnum*, the mosses can be considered part of the vadose zone itself, and the same capillary laws can be applied to both the living mosses and the underlying peat. However, as mentioned previously, pressure head is not the dominant measurement
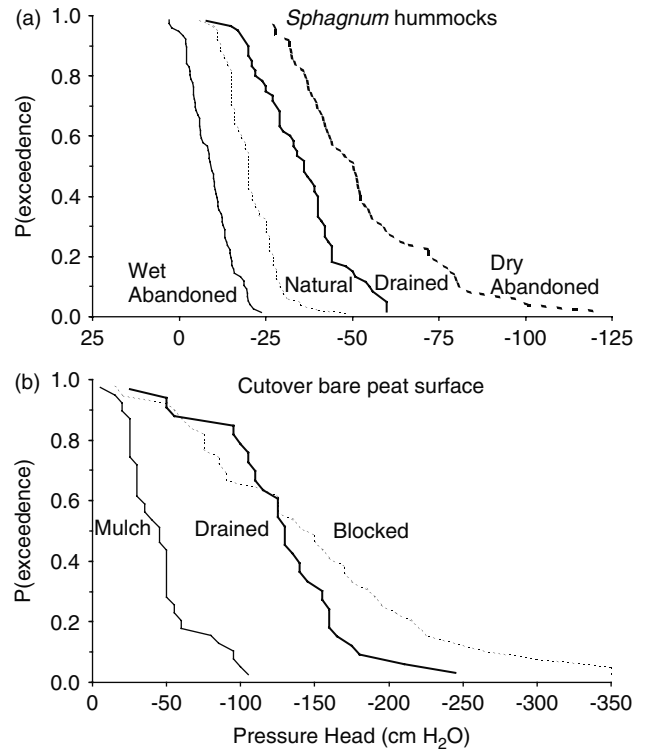
approach in hydrological studies of peatlands. In the following sections we review the traditional hydrological approaches for the study of *Sphagnum* production, and outline some of their drawbacks.

Water table position

WT is a widely used hydrological parameter because of its ease of measurement and straightforward significance in hydrology, as the top of the saturated zone where volumetric water content (VWC; m^3_{water} m^{-3}_{soil}) equals porosity, and $\Psi = 0$. In undisturbed peatlands a strong linear relationship ($r^2 > 0.9$) has been observed between soil pressure head and WT depth, although this relationship breaks down at the surface of hummocks alone ($r^2 < 0.5$; Lindholm and Markkula, 1984).

The assumption of a linear decrease in moisture availability has allowed WT to be used as a predictor of *Sphagnum* production (e.g. Hayward and Clymo, 1983; Rydin, 1985; Li *et al*., 1992; Silvola *et al*., 1996; Bubier *et al*., 2003), where it is assumed to be an indicator of the amount of water available to *Sphagnum* mosses at the peat–moss interface. However, all too often the relationship between WT depth and water availability for *Sphagnum* mosses is not explicitly stated or defined, and the limitations of this assumption are rarely explored.

Site-specific differences in peat properties such as porosity change the WT–VWC relationship, which results in a wide range of optimal WT depths for the

same *Sphagnum* species at different locations. For example, WT depths of optimal gross ecosystem productivity (GEP) for *Sphagnum fuscum* range from −5 to −25 cm on bare, cutover peat surfaces (Campeau and Rochefort, 1996), and range from −10 cm (Jauhianen *et al.*, 1997), to −40 cm (Silvola *et al.*, 1996) in natural, undisturbed peatlands.

Tuitilla *et al.* (2004) found a strong relationship between WT and photosynthesis in *Sphagnum* in a cutover peatland in southern Finland using a Gaussian response model (Figure 6). This model calculated an optimum water level of −10 cm and calculated a symmetrical response to WTs away from this optimum, leading to zero gross photosynthesis at −45 and +15 cm. In their study, the *Sphagnum* colonies observed were very young (1–3 years), and only thinly covered the peat (mean 50% capitulum coverage). The lack of an underlying porous layer of recent *Sphagnum* to buffer against evapotranspiration and moisture loss allowed a more variable moisture status at the site, more similar to the bare peat surfaces shown in Figure 5. Combined with the high WT at the site, short-term changes in evaporation were able to have a direct impact on WT and *Sphagnum* water availability.

At the surface of a drained *Sphagnum* hummock, Lindholm and Markkula (1984) found the WT to pressure head relationship switched from a logarithmic to a linear relationship between dry and wet years (Figure 4). Even this predicted curvilinear relationship may be interrupted by heterogeneities present in the peat profile giving rise to different peat properties such as porosity or pore size distribution, resulting in non-conformities in the WT-Ψ relationship. Lastly, events such as severe air-drying or fire induced hydrophobic behaviour in peat upon rewetting (Valat *et al.*, 1991), may cause temporal or depth-wise discontinuities of peat properties in a soil profile.
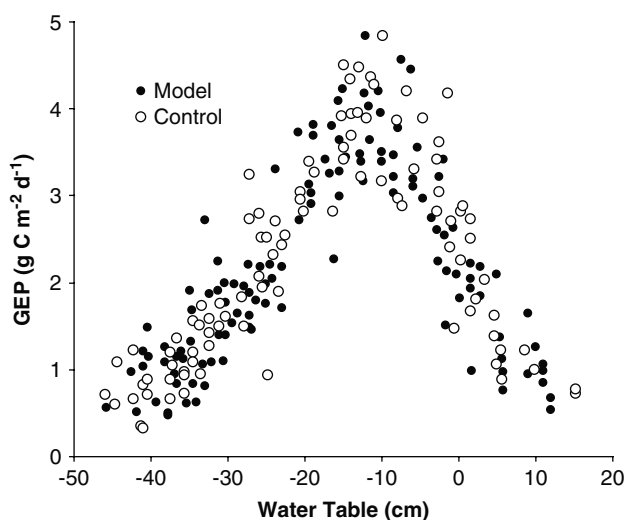
In summary, the WT is a simple hydrological variable and is effective as a predictor of *Sphagnum* moisture availability in certain conditions where the WT is shallow and responsive to atmospheric forcing. However, attempting to infer surface water availability with deep WT positions requires caution, particularly when the hydrology of the saturated zone disconnects from the surface.

Volumetric water content

With a number of time-domain reflectometry (TDR) and dielectric volumetric moisture probes suitable for both peat and moss available (Yoshikawa *et al.*, 2004), VWC is an inexpensive means of continually monitoring soil moisture. Instruments for VWC measurement have high temporal or spatial resolution when connected to a datalogger or via handheld devices (Petrone *et al.*, 2004a). However, VWC measurements are sensitive to porosity, so TDR and dielectric instruments must be calibrated for organic soil properties (Kellner and Lundin, 2001).

The flexible and fibrous nature of peat allows it to be remarkably elastic and plastic compared to mineral soils (Valat *et al.*, 1991). At a single point, porosity can vary with distance from the WT as peat shrinks or swells with decreasing or increasing moisture content (Kennedy and Price, 2005). Pore volume changes of up to 10% can occur in the shallow horizons of undisturbed peatlands and up to 15% in recently harvested peatlands (Price, 2003). Peat shows only a 0·5% expansion of volume during a 10–30 °C increase of temperature (DeLapp and LeBoeuf, 2004), suggesting the effect of thermal expansion on VWC is minimal. These processes alter porosity and must be considered before VWC can be used as an indicator of soil water availability. *In situ* measurements of VWC integrate both drainage and filling of pore spaces, as well as the expansion and contraction of peat, where no change in mass WC is accompanied by changes in volume.

McNeil and Waddington (2003; Figure 7) used VWC as the hydrological variable in a laboratory experiment to determine the response of *Sphagnum* GEP to wetting and drying cycles. GEP decreased after VWC dropped below 40%, and did not recover for 21 days after subsequent re-saturation. Although no specific VWC–pressure head curve is available for the site, Price (1997) found in a similarly cutover and drained peatland that 40% VWC corresponded roughly to the point at which pressure head dropped sharply against VWC, indicating the drainage of large pores at −50 to −100 cm H_2O.

Price (1997) found a curvilinear relationship between VWC and unsaturated zone pressure head in a managed cutover bog in southern Quebec. Even after incorporating the variance involved in this relationship, empirical VWC–Ψ relationships may be constructed for individual sites at shallow depths, such that Ψ could be continuously monitored. Caution must be exercised, as this relationship is seasonally variable, where identical VWC profiles in mid-summer and late spring can have pressures

Figure 6. Gaussian relationship between water table and photosynthesis in a *Sphagnum* hummock (modified from Tuittila *et al.*, 2004). The relationship is computed using constrained non-linear regression standardized to Sphagnum area = 97%, PAR = 1 000 μmol m^{-2} s^{-1}. Black dots represent data points used to construct the model, and white dots are control observations.
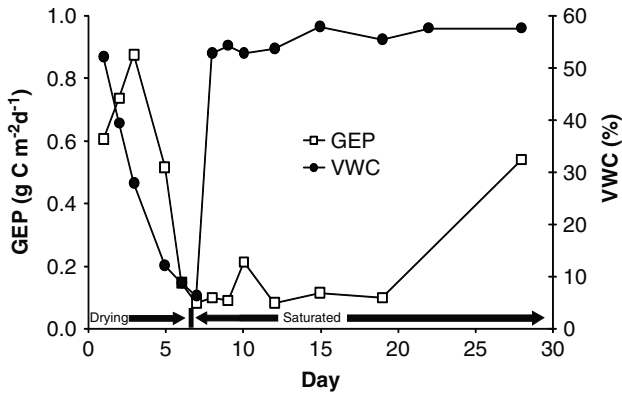
Figure 7. Carbon exchange in a *Sphagnum* colony as a result of a laboratory drying experiment, modified from McNeil and Waddington (2003). Closed circles denote volumetric water content (VWC).

15 cm H_2O lower in mid-summer, indicating high water retention as peat compression strengthens capillary action in the smaller pore-spaces (Kennedy and Price, 2004).

VWC is an accurate representation of water availability in *Sphagnum* as long as a strong and static relationship can be inferred between pore-water volumes and pressures. Once this relationship changes because of dewatering and compression, the relationship between volume and capillarity is lost. Strictly volumetric measurements of water do not reveal any information about pore size, and hence water availability for plants relying on capillary transport.

Sphagnum water content

WC (a unitless water mass : dry mass ratio or as an equivalent percentage $\times 100$) is a direct measurement of WC within living *Sphagnum* shoots and is the most common approach adopted from an ecological perspective. Hydrologically, WC is related to moisture availability in the uppermost peat horizons, often approximated as distance to the WT (Rydin, 1985; Jauhianen *et al.*, 1997; Figure 8). WC measurements of *Sphagnum* are stronger predictors of GEP in *Sphagnum* as compared to other more desiccation-tolerant mosses (Williams and Flanagan, 1996).
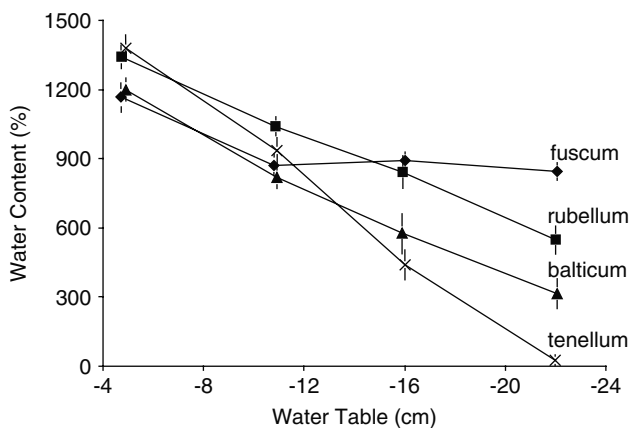

Figure 8. Capitula water content as a function of water table, modified from Rydin (1985). Error bars are ± 1 SE at $n = 15$.
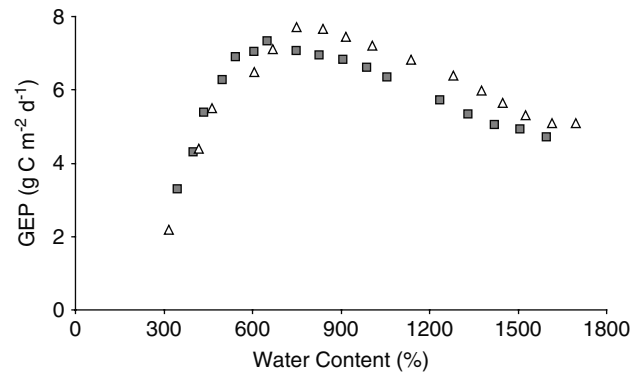

Figure 9. *Sphagnum* spp. (section Acutifolia) production as a function of whole shoot water content. Different symbols represent repetition of the experiment. Modified from Williams and Flanagan (1996).

Optimal GEP for individual shoots occurs at WCs between 500 and 1500% (Silvola and Aaltonen, 1984; Williams and Flanagan, 1996; Schipperges and Rydin, 1998; Maseyk *et al.*, 1999). GEP declines sharply as *Sphagnum* shoots dry below optimal WC, reflecting cellular damage to chlorophyll pigments as water is drained from chlorophyllose cells (Gerdol *et al.*, 1996). The decline in GEP at a WC of 600% in the study by Williams and Flanagan (1996; Figure 9) approximately corresponds to draining of hyaline cells in Figure 2 from Hayward and Clymo (1982). A more gradual decline in *Sphagnum* GEP is observed at a higher WC, where CO_2 diffusion into the chloroplasts is limited because of excess water in the chlorophyllose cells (Proctor, 2000). Relationships between GEP and WC are species and section specific, and are related to the morphology and geometry of the capitula, leaves, and branches (Silvola and Aaltonen, 1984; Li *et al.*, 1992; Rydin, 1993). Additionally, species-interaction effects are observed, where hollow species have a higher WC when surrounded by hummocks species (Rydin, 1985).

A recent study by Hájeck and Beckett (2008) utilized thermocouple psychrometry to control vapour pressure and induce an equivalent pressure head on shoots of six different *Sphagnum* species. Their technique did not utilize direct CO_2 exchange measurements, but instead used chlorophyll fluorescence techniques to gauge photosynthesis. A steep decline was observed in fluorescence parameters only at 100% WC in *S. fuscum*, dramatically lower than declines in photosynthetic fluorescence ratios seen at *ca* 1200% WC in others studies (Van Gaalen *et al.*, 2007). Using the vapour pressure–pressure head relationship given in Equation (6), pressure at the point where fluorescence parameters declined was equivalent to -300 m H_2O of pressure head, one-hundred times higher than any field observations of *in situ* soil pressure head in *Sphagnum* mosses. Unfortunately, the lack of direct CO_2 exchange measurement and the new technique utilized prevent a direct comparison between the study by Hájeck and Beckett (2008) and previous examinations of WC, productivity, and pressure head.

The primary disadvantage of WC measurements is the requisite destructive sampling and detachment from the

underlying peat. Although this may be desirable for process studies of cellular level functions of *Sphagnum* (e.g. Williams and Flanagan, 1996; Schipperges and Rydin, 1998), this method is less suited to long-term field studies, where repeated measurements on *Sphagnum* colonies are desirable but only pseudo-replicate destructive sampling of adjacent moss samples is possible (e.g. Silvola and Aaltonen, 1984; Murray *et al.*, 1989). Additionally, attention must be given to whether capitulum, stem, or whole shoot WC is measured, as each segment of a shoot can have different WCs (Jauhianen *et al.*, 1997). Clymo and Hayward (1982) showed a hysteric relationship between WC and soil pressure head in *Sphagnum* (Figure 2). When related to average pore radii in the corresponding *Sphagnum* structures, a distinct drop in WC is observed at 800–900% as hyaline cells embolize and drain at pressures of −200 to −300 cm H_2O.

FUTURE RESEARCH DIRECTIONS

Previous studies relating water retention abilities of different *Sphagnum* species have attributed differences to shoot geometry (Silvola and Aaltonen, 1984; Malcolm, 1996). The high capitulum density of *S. fuscum* is often cited as a factor in its advantages as a hummock species. However, previous studies of the spatial characteristics of *Sphagnum* have only considered at most bulk density with depth or shoot density; quantitative observations of pore spaces in living *Sphagnum* shoots has not progressed past the approximations of Hayward and Clymo (1982), from over 25 years ago. The geometry of water retaining cavities at the cellular, tissue, and inter-shoot scales is an unknown and likely an important factor in water retention, vapour transport and species differences in habitat. A further understanding of the *Sphagnum* canopy structure may yield clues to hydrological survival strategies for hummock species such as *S. fuscum, Sphagnum rubellum.*

Assuming *Sphagnum* shoot WC is a function of pressure head, we suggest that pressure head will likely show a species interaction similar to that studied by Silvola and Aaltonen (1984) and Li *et al.* (1992). In order to preserve the geometry of the *Sphagnum* colony, techniques to measure pressures within intact *Sphagnum* canopies would be a valuable addition to the study of *Sphagnum* dynamics. The laboratory transducer apparatus for measuring pressure inside a hyaline cell of Lewis (1988) could perhaps be modified for this purpose. Given the large impact that RH has on forcing vapour pressure above menisci out of equilibrium (Proctor, 1982), a coupled pressure transducer and RH with depth measurement system in conjunction with standard lab-scale hydrological monitoring (temperature, VWC, pressure head with depth) would provide invaluable data to assist in the process understanding of moisture transfer and sustainability in intact *Sphagnum* canopies. Such small-scale data can later be upscaled to the plot scale and applied to update existing *Sphagnum* production models (i.e. Tuittila *et al.*, 2004)

Lastly, analysis techniques for field data need to be improved to the point where individual variables can be isolated and contrasted between sites. The Gaussian response of *Sphagnum* productivity to WT in Tuittila *et al.* (2004) constructed using constrained non-linear regression is an example of the advanced analysis techniques suited towards this heterogeneous and complex system.

CONCLUSIONS

While measurements of pressure are in no means perfect, the drawbacks of more common hydrologic measurements highlight the necessity for a more robust methodological framework for measuring water availability as a control of *Sphagnum* productivity. Detachment of the WT from surface moisture dynamics, a problem with WT measurements, emphasizes the importance of monitoring atmospheric water fluxes and surface hydrological processes of *Sphagnum* mosses. Measurements of VWC stress the importance of monitoring peat pore structure and geometry over time. Species interaction effects in WC show the significance of neighbouring *Sphagnum* shoots and the relatively unexplored area of *Sphagnum* canopy topology. Monitoring of atmospheric water fluxes, peat expansion, and species interaction in addition to pressure head would allow for a more holistic view of water transport, the geometry of water holding pores, and photosynthesis.

The largest contribution a further understanding of *Sphagnum* growth dynamics can make is in the coupling of hydrological and ecological processes for the purpose of peatland models. In broad, low-resolution peatland models linked into land-use classifications such as the Canadian Land Surface Scheme (CLASS; Frolking *et al.*, 2002), soil pressure head has the advantage of being able to adjust to changes in vadose zone hydrology based on physics, and not relying on an empirical relationship.

Pressure head works as a direct framework for understanding *Sphagnum* production because of its first-principles approach to quantifying water retention and allocation within cellular cavities. Lacking the stasis and assumptions of other hydrologic measures of water availability, pressure uses the same robust framework as the classical physical hydrologic measurement of hydraulic head in providing a variable that is applicable and comparable across both space and time in both pristine and anthropogenically altered peatland ecosystems.

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