

Role of morphological structure and layering of *Sphagnum* and *Tomenthypnum* mosses on moss productivity and evaporation rates

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Goetz, J. D. and Price, J. S. 2015. **Role of morphological structure and layering of *Sphagnum* and *Tomenthypnum* mosses on moss productivity and evaporation rates.** Can. J. Soil Sci. **95**: 109–124. Morphological structures of peatland mosses control moss water relations and the rate of water loss by drainage and evaporation, thus influencing their physiological functions. While many of these mechanisms are understood for *Sphagnum* mosses, there is a limited understanding of how these processes operate in *Tomenthypnum nitens*, a dominant brown moss species in northern rich fens. This study contrasts how different hydrophysical characteristics of *Tomenthypnum* and *Sphagnum* species affect capillary water flow that supports evaporation and productivity. Laboratory investigations indicate that volumetric water content (θ), gross ecosystem productivity, and evaporation decreased with water table depth for both mosses, with *Sphagnum capitula* retaining 10–20% more water (θ range of 0.18–0.32 cm³ cm⁻³) than *Tomenthypnum* (0.07–0.16 cm³ cm⁻³). Despite lower θ and a smaller fraction of pores between 66 and 661 μ m to retain water within the *Tomenthypnum* structure (10%) compared with *Sphagnum* (27%), both mosses had similar fractions of water conducting pore spaces and were able to maintain capillary rise throughout the experiment. While there was a larger difference in the bulk density and porosity of the *Tomenthypnum* moss compared with its underlying peat than there was in the *Sphagnum* profile, a layer of partially decomposed moss of intermediate properties was sufficient to provide a connection between the moss and peat under low water table conditions. In trying to characterize the soil-water pressure (ψ) in near-surface mosses of *Tomenthypnum* based on measurements of vapour pressure, we found disequilibrium conditions that severely underestimated ψ (i.e., very large negative pressures). It is this disequilibrium that drives evaporation and draws up capillary water to the moss surface for peatland-atmosphere carbon and water transfers.

Key words: Peatlands, bryophytes, water retention, hydraulic conductivity, theoretical pore-size distribution, water vapour

Goetz, J. D. et Price, J. S. 2015. **Influence de la morphologie et de la superposition des couches de mousses de type *Sphagnum* et *Tomenthypnum* sur la productivité de la plante et le taux d'évaporation.** Can. J. Soil Sci. **95**: 109–124. Dans les tourbières, la morphologie des mousses contrôle les relations entre l'eau et la plante, ainsi que la vitesse à laquelle l'eau disparaît par drainage et évaporation, ce qui exerce une influence sur les fonctions physiologiques de la mousse. Quoique beaucoup de ces mécanismes soient bien connus chez les mousses du genre *Sphagnum*, nos connaissances sont plus limitées sur ces processus chez *Tomenthypnum nitens*, une mousse brune qui domine dans les riches marais du nord. Cette étude illustre combien les caractéristiques hydrophysiques différentes des espèces des genres *Tomenthypnum* et *Sphagnum* modifient l'écoulement capillaire de l'eau, dont dépendent l'évaporation et la productivité. Les études en laboratoire indiquent que la masse volumique de l'eau (θ), la productivité brute de l'écosystème et l'évaporation diminuent avec la profondeur de la nappe phréatique pour les deux mousses, les capitules de *Sphagnum* retenant 10 à 20 % plus d'eau (θ de 0,18 à 0,32 cm³ par cm³) que ceux de *Tomenthypnum* (de 0,07 à 0,16 cm³ par cm³). Malgré une valeur θ plus faible et un plus petit nombre de pores de 66 à 661 μ m pour retenir l'eau chez *Tomenthypnum* (10 %), comparativement à *Sphagnum* (27 %), les deux mousses disposent d'un espace similaire au niveau des pores conducteurs et ont réussi à maintenir l'ascension capillaire durant l'expérience. Malgré la forte différence entre *Tomenthypnum* et la couche de tourbe sous-jacente pour ce qui est de la masse volumique apparente et de la porosité, comparativement à *Sphagnum*, une couche de mousse partiellement décomposée, aux propriétés intermédiaires, suffit à établir le lien entre la mousse et la tourbe, quand la nappe phréatique est très basse. Lorsqu'ils ont tenté de caractériser la pression de l'eau du sol (ψ) dans la mousse de *Tomenthypnum* près de la surface d'après la pression de vapeur, les chercheurs ont découvert un déséquilibre qui entraîne une sérieuse sous-estimation de ψ (à savoir, des pressions très négatives). C'est ce déséquilibre qui commande l'évaporation et attire l'eau par capillarité à la surface de la mousse, autorisant ainsi les transferts de carbone et d'eau entre la tourbière et l'atmosphère.

Mots clés: Tourbière, bryophytes, rétention de l'eau, conductivité hydraulique, répartition théorique des pores selon leur calibre, vapeur d'eau

Abbreviations: GEP, gross ecosystem productivity; ET_{in}, instantaneous evapotranspiration; IRGA, infrared gas analyzer; PAR, photosynthetically active radiation; RH, relative humidity; T, temperature; TDR, time-domain reflectometer; WUE, water use efficiency

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The composition of moss ground cover and water availability in boreal peatlands are key drivers of variability of carbon accumulation (Bubier et al. 1998; Petrone et al. 2011) and evaporative losses within and between peatlands (Williams and Flanagan 1996; Brown et al. 2010). Boreal peatlands comprise a variety of different moss communities that occupy different ecological and hydrological niches (Vitt 1990), such as *Sphagnum*-dominated bogs and poor fens and brown moss-dominated rich fens. The ability of these non-vascular plants to thrive within these wet environments depends partly on their ability to generate capillary rise and their water retention properties (Hayward and Clymo 1982; McCarter and Price 2014a). Their shoot morphological structures and community growth forms (general form adapted by colonies of moss shoots) affect the amount and connectivity of water-conducting pores for capillary rise (Voortman et al. 2013; McCarter and Price 2014a). Connectivity within moss and peat structures is a function of pore-size distribution, geometry, and tortuosity (Rezanezhad et al. 2010), which affect water content and ultimately unsaturated hydraulic conductivity (Price et al. 2008). The upward capillary water movement from underlying peat substrates is driven by soil-water pressure gradients within the moss structure caused by atmospheric demand at the canopy surface (Proctor 1982; Rice et al. 2001). However, when soil-water pressures become too low for free capillary rise, capillary water is evaporated and the water pressure of the moss cells drops rapidly and equilibrates with the surrounding air, thereby desiccating and ceasing all photosynthetic activity (Proctor 2000), and reducing evaporative losses to maintain saturated conditions in the peat profile below (Kettridge and Waddington 2014). Therefore, the capacity of peatland mosses to access water from underlying layers can be an important control on peatland-atmosphere processes.

Sphagnum and brown mosses have fundamentally different water strategies due to their different shoot morphology and community growth forms. *Sphagnum* mosses have a leaf and pendant branch system along their stems that supports the movement of water by capillary action to the apex of the plant, the capitulum, where most primary production occurs. When groups of *Sphagnum* grow together in hummocks, their capitula form a canopy that traps moisture, allowing the moss to create a microclimate to retain moisture (Strack and Price 2009). A dual porosity matrix exists within this *Sphagnum* structure; this includes well-connected pore spaces between overlapping branches and leaves that transmit water flow, and a typically smaller proportion of cellular spaces (hyaline cells) and dead-end pores that retain water (Hayward and Clymo 1982; Hoag and Price 1997). The pore openings of these cells are between 1 and 20 μm (Clymo and Hayward 1982) and only release water at threshold soil-water pressures between -100 and -600 mb (Hayward and Clymo 1982; Lewis 1988). Thus, hyaline cells and other small diameter pores in the external structure (McCarter and Price 2014a)

provide a relatively high water retention capacity. Conversely, brown mosses [such as *Tomenthypnum nitens* (Loeske) Hedw.] do not have hyaline cells and rely predominately on water transport in capillary spaces formed by paraphyllia (axillary hairs) and/or in stem tomentum of rhizoids [felt-like covering of rhizoids on the stem (Busby et al. 1978)]. *Tomenthypnum nitens* is a widely distributed brown moss species common in northern rich fens that grows in dense turf growth forms consisting of closely spaced stems with numerous overlapping branches and leaves (Busby et al. 1978) that form mats with a basal layer of partially decomposing moss litter over dense, well-decomposed rich fen peat (Vitt et al. 2009).

While these mosses can dominate the groundcover of rich fen peatlands while maintaining high productivity at high elevations from the water table (Vitt 1990), there is little information on the size and range of pores to retain and transmit capillary water from the underlying peat to the surface for evaporation and productivity processes.

Most mosses are poikilohydric, meaning when capillary water is not present water in moss cells rapidly equilibrate with the surrounding air pressure (Proctor 1982). Most mosses can withstand this desiccation to equilibrium of 50–90% relative humidity (Proctor 1982). Under these desiccating conditions they become physiologically dormant, but can recover their physiological processes within hours upon re-wetting, although rates of recovery vary greatly between species (Proctor 1982; McNeil and Waddington 2003; Hájek and Beckett 2008). Price et al. (2009) suggested that water vapour in *Sphagnum* profiles could provide potentially important sources of water for cell maintenance under dry conditions. However, the microclimate within moss growth forms and the relationship between vapour pressure of air surrounding mosses and the pressure of moss cells are not well understood, particularly for *T. nitens*. Some studies (Alvenäs and Jansson 1997; Kellner 2001; Kettridge and Waddington 2014) noted the assumption that pore-air vapour pressure is in equilibrium with soil-water pressure in the near-surface may not be valid where vapour is continuously transported to the atmosphere. In the case of *Tomenthypnum* moss, the top of the moss canopy is likely the actual evaporating surface, and thus is not in equilibrium. However, it may be possible that vapour pressure and pore water are at equilibrium just below the moss surface (2.5 cm depth). When the vapour pressure is at saturation it is highly likely that liquid water is present and moss pressures are at or near zero. When almost all of the accessible capillary water is exhausted and internal redistribution is minimal, vapour pressure decreases and moss cells rapidly equilibrate with the change in vapour pressure. Thus, this study tested whether ψ derived from the vapour pressure of the moss near-surface can characterize the available water for *Tomenthypnum* moss communities and if equilibrium conditions occur.

Although studies have demonstrated *T. nitens* can lose considerable amounts of water before desiccation (Busby and Whitfield 1978), the water transport mechanisms required for *T. nitens* to avoid desiccation are also poorly understood. While there are numerous studies of the water retention and capillary rise properties of many peat types and *Sphagnum* mosses (Baird 1997; Carey et al. 2007; Quinton et al. 2008, 2009; Price and Whittington 2010; McCarter and Price 2014a, b), there is no similar information for *T. nitens* or the pore structure function for water retention from capillary rise from the underlying peat. It is hypothesized that while both *Sphagnum* and *T. nitens* utilize capillary rise to obtain water, *T. nitens* has lower residual water content than *Sphagnum* due to a lack of hyaline cells and as a result requires less water for productivity. Thus, the overall objective of this study was to compare the function of *Sphagnum* and *T. nitens* mosses and their growth forms on water distribution and moss production at the surface under a range of hydrological conditions. The specific objectives were: (1) to contrast the mechanisms that control water transport and retention between *T. nitens* from a rich fen and intermixed *Sphagnum angustifolium* and *Sphagnum magellanicum* from a poor fen, (2) to determine how water table position affects the water content, productivity, and evaporation processes in both *T. nitens* and *Sphagnum*, and (3) to determine if there is a relationship between moss soil-water pressure and vapour pressure in the near-surface of *T. nitens*.

MATERIALS AND METHODS

Study Sites and Monolith Sampling

Peat-moss monoliths were collected from Pauciflora Fen [consisting of *Sphagnum angustifolium* (C. Jens ex Russ.) and *Sphagnum magellanicum* (Brid.)], an open poor fen (lat. 56°22'30"N, long. 111°14'05"W) and Poplar Fen (consisting of *T. nitens*), a treed rich fen (lat. 56°56'18"N, long. 111°32'35"W) near Fort McMurray, AB, for laboratory experimentation and hydrophysical parameterization. Pauciflora Fen, pH ~4.5, is an 8-ha fen with groundwater flow-through. Vegetation of the poor fen consists mainly of *S. angustifolium* and *S. magellanicum* mosses and vascular plants consisting of bog Labrador tea [*Rhododendron groenlandicum* (Oeder)], leatherleaf [*Chamaedaphne calyculata* (L.) Moench], water sedges [*Carex aquatilis* (Wahlenb.)], stunted black spruce [*Picea mariana* (Mill.) BSP], and tamarack [*Larix laricina* (Du Roi) K. Koch] trees. Poplar Fen, pH ~6.6, is an 11-ha peatland system. Vegetation in this fen includes the dominant *T. nitens* and *Aulacomium palustre* (Hedw.) Schäger moss groundcover, with bog birch [*Betula pumila* (L.)], three-leaf Solomon's-seal [*Smilacina trifolia* (L.) Desf.], water horsetail [*Equisetum fluviatile* (L.)] and a large cover of tamarack trees and some black spruce. *Tomenthypnum nitens* as well as *S. angustifolium* and *S. magellanicum* communities (hereafter identified as *Tomenthypnum* and *Sphagnum*, in this study) were selected to represent

widely distributed peatland brown moss and *Sphagnum* lawn species, respectively.

The monolith samples (three from each fen, ~35 cm deep and 28 cm in diameter) were taken by pushing a cylindrical guide into the moss, facilitated with the use of a serrated knife to cut around the guide. When the guide was flush with the moss surface, peat blocks were cut adjacent to the monolith samples to allow for clean sample extraction. The monoliths were placed in 19-L buckets and saturated with local water to prevent deformation during transportation to the Wetland Hydrology Laboratory at the University of Waterloo. The monoliths were then drained and frozen, and then shaved to facilitate a tight fit in 25-cm (inner diameter) polyvinyl chloride (PVC) conduit. Final monolith heights for analysis were 33 cm.

Monolith Experiment

Each 25-cm-diameter monolith was placed atop a tension disk, modified and enlarged from those described by Price et al. (2008) to provide tension to the bottom of the peat representative of water tables below the monolith samples (Fig. 1). The tension disks were constructed of 2.3-cm by 30.5-cm-diameter Lexan disks with a barbed fitting for drainage. Each disk used 15- μ m Nitex[®] screen with an air-entry pressure of -25 mb to fit atop a 0.3-cm by 22.7-cm-diameter perforated surface

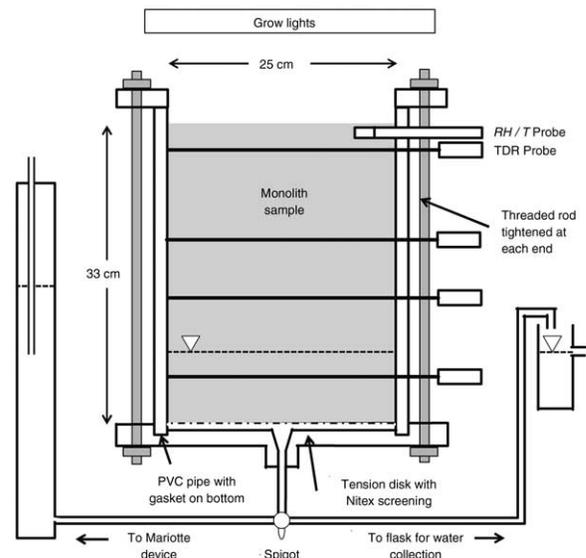


Fig. 1. Monolith experiment design to monitor responses of θ (time-domain reflectometer), relative humidity (RH) and temperature (T) (only in *Tomenthypnum* monolith due to equipment availability), and CO_2 and instantaneous evapotranspiration fluxes (chamber and IRGA) at predetermined water table depths. A Mariotte device maintained constant head at each water table level. A tension disk with 15- μ m pore-size Nitex screening was used to maintain tension at the bottom of the monolith with water tables below the sample.

that supported the screen. A 1.5-cm by 0.9-cm-deep and 1.5-cm-wide groove around the tension disk surface allowed seating of the monolith pipe. A rubber compression gasket prevented leakage between the tension disk and monolith pipe, with pressure exerted to maintain the seal via a clamp ring, threaded steel dowelling and wing nuts (Fig. 1).

Tygon tubing attached to the barb of the disk was connected to a Mariotte device to provide constant pressure head for each pre-set water table depth (Fig. 1). A spigot between the monolith and the Mariotte device allowed for the collection of discharged water when the water table was lowered. The monoliths were saturated with reverse osmosis water prior to water table manipulation. Water table (zero pressure head) was first set to 10 cm below the moss surface, then subsequently lowered to 15, 20, 30, and 50 cm and then raised to 20 and 10 cm. These intervals were chosen to replicate water table variation observed at the poor and rich fens under high and low water availability conditions. Each water table depth was determined to be at equilibrium when volumetric water content (θ ; $\text{cm}^3 \text{cm}^{-3}$) changes (see below) in each monolith exhibited negligible changes over 2 or more days.

The experiment was carried out in a partially climate-controlled room. Relative humidity (RH) and temperature (T) were sustained at $\sim 33\%$ and $\sim 27^\circ\text{C}$, respectively (vapour pressure deficit of $\sim 2.4 \text{ kPa}$), atmospheric conditions which these mosses experience during growing seasons. Fluorescent light bulbs provided photosynthetically active radiation (PAR) to the moss surface at $\sim 150 \mu\text{mol m}^{-2} \text{s}^{-1}$ for 14 h per day. While we note the low rates of PAR, the amount of light was likely not the controlling factor for changes in productivity rates for both moss types. Busby and Whitfield (1978) demonstrated that maximum gross ecosystem productivity (GEP) for *Tomenthypnum* occurs above $\sim 50 \mu\text{mol m}^{-2} \text{s}^{-1}$. Furthermore, the *Tomenthypnum* monoliths were collected from a treed fen in which the understory was shaded. Although light levels were spotty under the canopy, shaded areas experienced low light levels throughout the day, generally with PAR levels peaking in the range of $200\text{--}400 \mu\text{mol m}^{-2} \text{s}^{-1}$. Thus, laboratory PAR rates were only slightly below field levels in shady areas of the understory. As for the *Sphagnum* mosses, there have been several studies that demonstrate light levels in this study were not unreasonable. The light levels are comparable with half the maximum GEP as per Riutta et al. (2007), and McNeil and Waddington (2003) demonstrated that maximum GEP for the *Sphagnum* in their study was $\sim 300 \mu\text{mol m}^{-2} \text{s}^{-1}$. While the low light levels may limit some response of GEP to moisture, the moss communities seemed healthy throughout the experiment and patterns are representative of those observed in the field. Fans in the room (directed away from the samples) ensured air circulation. All above-ground vascular plant structures were clipped to limit water fluxes and productivity to the mosses.

To quantify changes in the moisture regime with water table, θ was measured with a Campbell Scientific TDR-100 system at 30-min intervals with CS605 time-domain reflectometer (TDR) probes at four depths within each monolith: 2.5, 12.5, 17.5, and 27.5 cm. The 2.5-cm depth corresponds to near-surface *Tomenthypnum* shoots and *Sphagnum capitula*. The 12.5- and 17.5-cm depths approximately correspond to layers above and below the visually determined interface ($\sim 15\text{-cm}$ depth) between partially decomposed moss litter (part of the moss turf with live moss shoots above) and the more dense well-decomposed peat substrate in the *Tomenthypnum* monoliths. The 27.5-cm depth corresponds to deeper, well-decomposed peat well below the interface. The *Sphagnum* profiles also showed changes in structure at $\sim 15 \text{ cm}$ so TDR depths were matched with the *Tomenthypnum* monoliths. Medium-specific TDR calibrations were derived using methods described by Topp et al. (1980).

The rate of community photosynthesis, or the GEP ($\text{g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$), from each monolith was determined by the difference between measured net ecosystem exchange of CO_2 under full-light conditions and ecosystem respiration under blackout conditions (with an opaque shroud). Net ecosystem exchange was measured using a clear Lexan chamber (11 cm by 25 cm diameter) connected to an infrared gas analyzer (IRGA; PP Systems EGM-4). Linear CO_2 concentration changes were measured by the IRGA every 15 s over a 105-s interval to determine the rate of CO_2 exchanges. Inputs of CO_2 into the moss community are expressed as positive values. Every 5 s over a 35-s period, T and RH were also measured with the IRGA to determine instantaneous evapotranspiration rates (ET_{in} ; mm d^{-1}) with methods as described by McLeod et al. (2004). ET_{in} was calculated by measuring the rate of vapour density increase over time, as described by Stannard (1988). A fan inside the chamber ensured well-mixed air during sampling. The chamber was aired out between measurements to ensure ambient conditions of CO_2 , T, and RH. Four sets of complete chamber measurements were completed on subsequent days for each monolith at each water table interval to monitor changes.

To monitor changes in the moss microclimate within the *Tomenthypnum* moss community, RH and T were measured using a Vaisala HMT337 system (thermocouple for T and thin film polymer capacitive sensor for RH, with $\pm 1\%$ RH accuracy and equilibrium response time less than 60 s) in the air-filled pores at 30-min intervals. To quantify soil-water pressures [ψ ; sum of both matric (ψ_{m}) and osmotic (ψ_{π}) pressures] within the *Tomenthypnum* moss structures at each water table depth, vapour pressure of the near-surface of one of the *Tomenthypnum* monoliths (at 2.5 cm depth) was monitored. While parallel instrumentation was not available for *Sphagnum*, the *Tomenthypnum* results were compared with a previous study by Price et al. (2009) where RH and T profiles were measured in *Sphagnum* monoliths. This study provides another example to help understand the vapour pressure

and soil-water pressure relationship. For a given soil-water pressure, the vapour pressure of the air above capillary menisci are assumed to be in equilibrium. As such, the ψ (mb) of a porous medium can be measured using the Kelvin equation (Stephens 1996) where

$$\psi = \frac{RT}{Mg} \ln\left(\frac{e}{e_s}\right) \quad (1)$$

and where R is the universal gas constant (8.314×10^{-6} MJ mol⁻¹ K⁻¹), M is the molar mass of water (0.018 kg mol⁻¹), g is the force of gravity (9.8 N kg⁻¹), and e/e_s is relative humidity expressed as a fraction of actual vapour pressure, e (MPa), to saturation vapour pressure, e_s (MPa), at T (K).

Peat Parameterization

Following the monolith experiment, each monolith was frozen and cut into 5-cm-high and 10-cm-diameter cores, centred every 2.5 cm from the surface to a depth of 25 cm, and fitted into PVC rings of equivalent size (*Tomenthypnum* profile 2 did not have samples below 20 cm due to large roots). The cutting process was completed with frozen samples to minimize effects on the hydrophysical structure from potential compaction from handling unfrozen samples. Furthermore, the source peat undergoes frequent freeze-thaw cycles and so freezing the samples should also have minimal impact on the hydrophysical structure. To determine water retention and unsaturated hydraulic conductivity of the sections, the following methods were used. The 5-cm subsections were saturated with reverse osmosis water and placed on tension disks with 25- μ m Nitex screening (air-entry pressure of less than -30 mb). Matric water pressures (ψ_m ; mb) of -3, -6, -12, -20, and -30 mb (reversed to -12, -6, and -3 mb to assess the hysteretic curve) were controlled via Erlenmeyer flasks positioned from the midpoint of each sample height, connected to the pressure plate. Samples were covered loosely with plastic wrap to minimize evaporative loss. Mass, height, and diameter of each sample were recorded once water loss had equilibrated at each ψ_m allowing for determination of θ . These matric pressures characterize the size range and relative number of pores retaining water, which are likely highly conducive for capillary flow in the active pore structure in peat and moss (Carey et al. 2007).

At each ψ_m step, unsaturated hydraulic conductivity (K_{unsat} ; m s⁻¹) was tested on each sample with methods used from McCarter and Price (2014b) modified from Price et al. (2008). A tension disk (25 μ m Nitex[®] screening) was placed on top of each sample (in addition to the one at the base) and was connected to a water reservoir providing a constant head. The Erlenmeyer flask was lowered by half the sample height and the reservoir height was set to a height equivalent to the ψ_m below the top of the sample. This provided an equally distributed pressure throughout the sample. Flow from

the constant head reservoir through the sample generated a discharge (Q ; cm³ s⁻¹) out of the flask. After allowing Q to equilibrate for 60 min, Q was measured over regular time intervals and Darcy's Law was used to determine an average K_{unsat} .

Saturated hydraulic conductivity (K_{sat} ; m s⁻¹) was measured using a Darcy permeameter. Due to the very fragile and porous nature of the moss samples, a modified wax method (Hoag and Price 1997) was used to prevent preferential flow. As in McCarter and Price (2014b), the outside edges of the samples were wrapped in two layers of plaster of Paris and coated and sealed in the permeameter with wax to ensure a watertight seal while leaving the top and bottom open for water flow. After allowing Q to equilibrate for 20 min, Q was measured over regular intervals to determine an average K_{sat} using Darcy's law.

Bulk density (ρ_b ; g cm⁻³), specific yield (S_y ; dimensionless), and porosity (ϕ ; dimensionless) were determined for all peat samples, including those not used for retention and hydraulic conductivity. S_y was determined using methods from (Price et al. 2008). ϕ and saturated θ were determined using

$$\phi = 1 - \left(\frac{\rho_b}{\rho_p}\right) \quad (2)$$

where ρ_p is particle density (g cm⁻³) as determined using the liquid pycnometer method with kerosene for medium displacement (Blake and Hartge 1986). Changes in ρ_b , S_y , and ϕ with each depth interval and between each moss type were compared using two-way analysis of variance (ANOVA) and Bonferroni post hoc tests using IBM[®] SPSS[®] Statistics 20.0. Low sample size at each depth limited tests for normality; however, it is assumed that the samples are from populations with normal distributions. Differences were deemed to be statistically significant if they met a significance level of 0.05.

The theoretical pore-size distributions of each sample was calculated by comparing the fraction of water filled voids with the diameter of the largest water-filled pore opening in the sample for a given pressure head (ψ_m or h) using methods from Danielson and Sutherland (1986) and the capillary rise equation (Bear 1972) for the theoretical pore opening radius (r ; μ m), where

$$r = \frac{2\gamma\cos\beta}{\rho gh}, \quad (3)$$

and where γ is the surface tension of water (N m⁻¹), β is the contact angle [40° for moderately hydrophobic soils (Carey et al. 2007)], ρ is the density of water (1.0 g cm⁻³), and g is gravitational acceleration (9.8 m s⁻²). A β of 40° was used in Eq. 3 because it is representative of both the range of contact angles of organic soils, ranging from close to zero for *Sphagnum* plants (Valat et al. 1991) to between 73 and 88° for peat (Waniek et al. 2000), and the range of β for moderately hydrophobic

soils under a range of θ conditions (Bachmann et al. 2002, 2003). Furthermore, changes in β have minimal effect on the pore size diameter compared with other parameters and therefore the choice of its value does not affect the conclusions of this study. Total water-filled pore fraction (ϕ_{vw} ; dimensionless) was determined by

$$\phi_{vw} = \frac{\theta_{\psi}}{\theta} \quad (4)$$

where θ_{ψ} is the volumetric soil water content for a given ψ ($\text{cm}^3 \text{cm}^{-3}$) and ϕ is the porosity. A sample with a higher fraction of water-filled pores for a given pore diameter compared with another has more pores less than or equal to that given diameter. The difference of ϕ_{vw} between two given pore diameters in a single sample indicates the fraction of pores being drained.

RESULTS

Hydrophysical Properties and Hydraulic Conductivity

Undecomposed *Tomenthypnum* moss (shoot lengths between 5 and 10 cm) overlaid peat with a higher bulk density. While there was no significant difference between ρ_b ($P=0.492$) and ϕ ($P=0.420$) of the live *Sphagnum* and *Tomenthypnum* mosses, the loose *Tomenthypnum* structure had significantly higher S_y ($P<0.01$) compared with the *Sphagnum* capitula surface (Fig. 2c). ρ_b increased with depth in both moss types, although *Tomenthypnum* ρ_b was significantly higher at 22.5 cm ($P<0.01$; Fig. 2a). ϕ was significantly higher ($P<0.01$) in the *Sphagnum* moss below 10 cm despite being lower in the upper 5 cm (Fig. 2b). S_y declined with depth for both moss types (Fig. 2c).

Water retention in the *Tomenthypnum* surface moss (2.5 cm depth) was low as the sample drained easily at ψ_m of -3 mb to an average θ of $0.21 \pm 0.05 \text{ cm}^3 \text{cm}^{-3}$ compared with $0.51 \pm 0.05 \text{ cm}^3 \text{cm}^{-3}$ for *Sphagnum* mosses (Fig. 3). At lower matric pressures, *Sphagnum* moss retained approximately $0.22 \text{ cm}^3 \text{cm}^{-3}$ more water, on average, with each pressure drop (Fig. 3). θ decreased an average of 0.25 ± 0.03 and $0.11 \pm 0.03 \text{ cm}^3 \text{cm}^{-3}$ for *Sphagnum* and *Tomenthypnum* mosses, respectively, for a pressure drop from -3 mb to -30 mb. However, at greater depths the *Tomenthypnum* samples generally retained more water than the *Sphagnum* at lower matric pressures (Fig. 3). The highest water retention was observed at a depth of 22.5 cm for both profile types. No systematic differences in retention curves were observed at the matric pressures tested (Fig. 3). Hysteresis of θ occurred in each sample of both moss types following similar, but lower θ , patterns to the drying curve (data not shown).

Compared with *Sphagnum* at the 2.5-cm depth (Fig. 4), the theoretical pore-size distributions indicated that near-surface *Tomenthypnum* moss had a relatively low fraction of water-filled pores at any of the given theoretical pore sizes. In this upper layer $\sim 21\%$ of the water in *Tomenthypnum* pore spaces occurred in pores $< 661 \mu\text{m}$, and about 14% of the water is in pores $< 99 \mu\text{m}$. Thus, 79% of its void space is in pores $> 661 \mu\text{m}$, and 7% of its pore sizes were between 99 and 661 μm . In comparison, at this depth $\sim 45\%$ of the water in *Sphagnum* pore spaces occurred in pores $< 661 \mu\text{m}$ and about 29% of the water is in pores with opening $< 99 \mu\text{m}$ (including hyaline cells). Thus, in near-surface *Sphagnum*, about 55% of its void space was in pores $> 661 \mu\text{m}$ and 20% of its pore sizes are between 99 and 661 μm . The proportions of pore sizes became less clear between profiles both within and

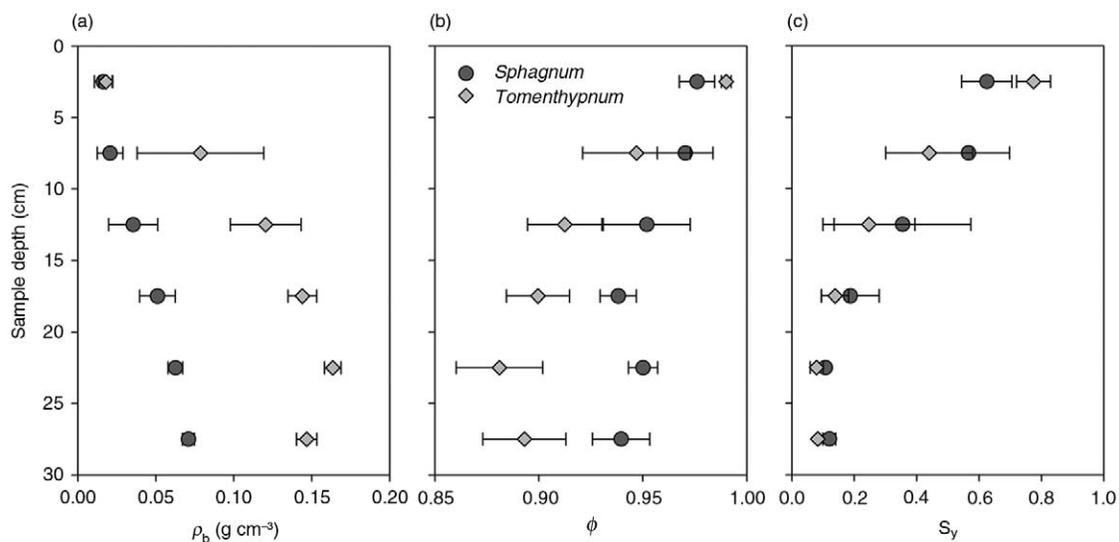


Fig. 2. Mean (± 1 standard deviation) (a) bulk density (ρ_b), (b) porosity (ϕ), and (c) specific yield (S_y) for *Tomenthypnum* and *Sphagnum* profiles, n of 5–8 and 2–6 in from 0–20 and 20–30 cm, respectively. Depths are the mid-depth of each 5-cm sample.

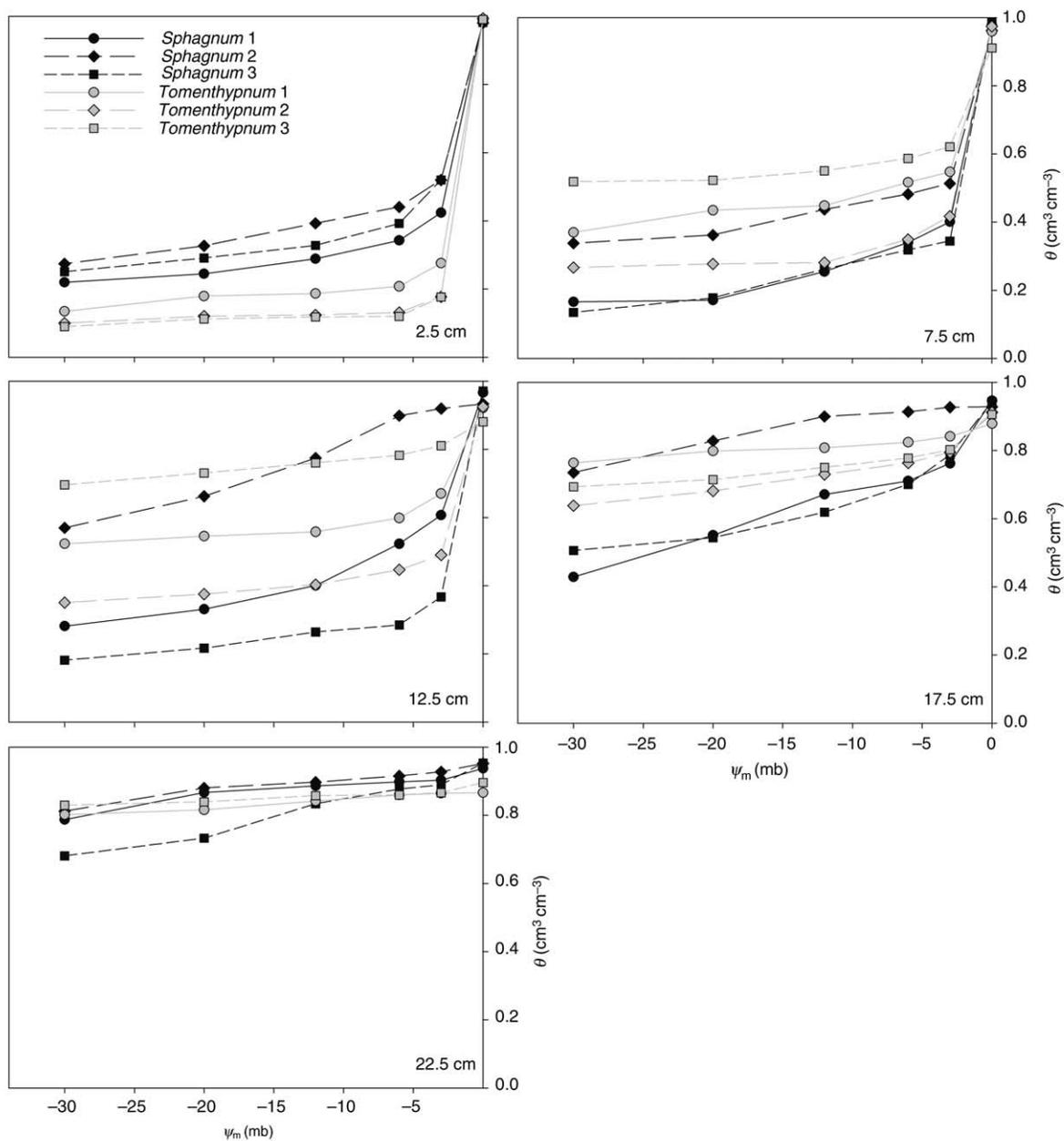


Fig. 3. Soil water retention curves, $\theta(\psi_m)$, for each *Tomenthypnum* and *Sphagnum* sampling depth. One sample profile (0–25 cm) was used per monolith; *Tomenthypnum* profile 2 did not have a 22.5-cm sample. Depths are the mid-depth of each 5-cm sample.

between moss types until 22.5 cm (due to high variability). But within each moss type, while the portion of pores $<99 \mu\text{m}$ increased with depth, the proportion of pores between 99 and 661 μm remained relatively consistent with depth. For *Sphagnum*, pores between 99 and 662 μm comprised between 18 and 23% of the total porosity. Approximately half the proportion of pores within the same range was observed in *Tomenthypnum*, accounting for between 7 and 12% of the total porosity. Two exceptions to the general trends discussed above

were *Sphagnum* 2 and *Tomenthypnum* 3, which exhibited denser and more decomposed organic material at shallower depths than the other respective moss type monoliths. Additionally, in the 7.5- and 12.5-cm layers, a greater proportion of pore spaces $<661 \mu\text{m}$ were water-filled in *Tomenthypnum* compared with *Sphagnum* (Fig. 4), suggesting the partially decomposed *Tomenthypnum* moss was characterized by smaller pores, thus better water retention over a range of pressures compared with *Sphagnum*.

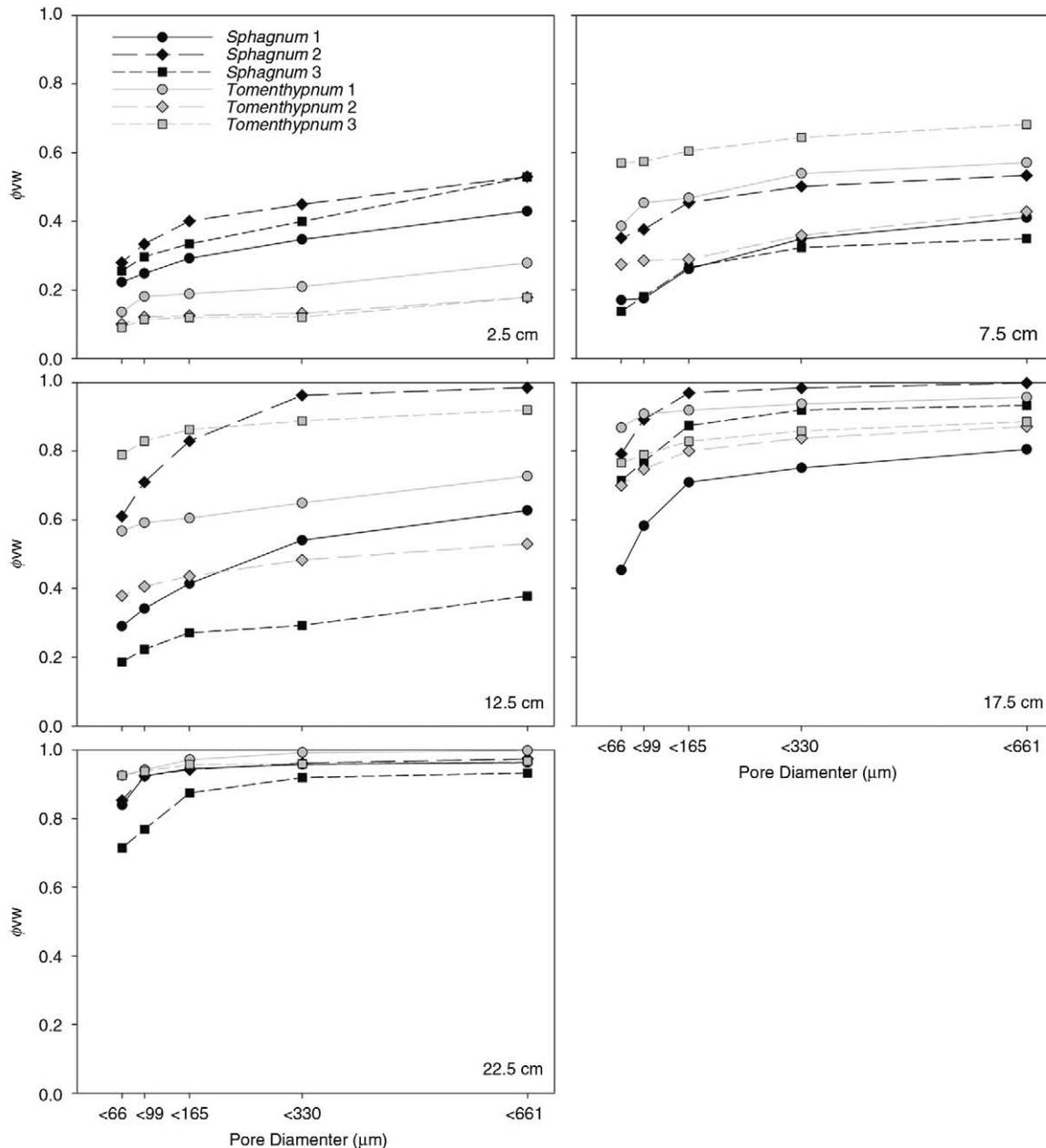


Fig. 4. Relationships between theoretical pore-size and the total fraction of water-filled pores (ϕ_{vw}) for each *Tomenthypnum* and *Sphagnum* sampling depth. One sample profile (0–25 cm) was used per monolith; *Tomenthypnum* profile 2 did not have a 22.5-cm sample. Depths are the mid-depth of each 5-cm sample.

Monolith Experiment

Measurements of θ within the monoliths (Fig. 6b) displayed similar drying trends compared with the water retention curves (Fig. 3) at all depths. Equilibrium of θ at all depths was established on average in 9 d during decreasing water table and on average in 20 d during increasing water table. In the near-surface layer (2.5 cm), *Sphagnum* moss retained more water at all water table

positions than *Tomenthypnum* moss (Fig. 6b). At the 50-cm water table depth, *Sphagnum* and *Tomenthypnum* θ at 2.5-cm depth decreased to 0.21 ± 0.01 and $0.07 \pm 0.004 \text{ cm}^3 \text{ cm}^{-3}$, respectively. Upon visual inspection at the lowest water table, a small proportion of the *Sphagnum* mosses were desiccated, while the majority of the *Sphagnum* remained above the threshold pressure. The *Tomenthypnum* mosses showed little change in

colour, but were dry and brittle to the touch. Unlike *Sphagnum*, the *Tomenthypnum* moss θ (2.5 cm depth) did not increase upon raising the water table from 50 to 20 cm (remained at $0.07 \pm 0.01 \text{ cm}^3 \text{ cm}^{-3}$) and only when the water table position was raised to 10 cm (above the relatively denser peat in both moss types) was an increase observed (to $0.11 \pm 0.01 \text{ cm}^3 \text{ cm}^{-3}$) (Fig. 6b).

Sphagnum sustained higher average θ ($0.26 \pm 0.03 \text{ cm}^3 \text{ cm}^{-3}$) throughout the experiment than *Tomenthypnum* ($0.10 \pm 0.02 \text{ cm}^3 \text{ cm}^{-3}$; Fig. 7a). While *Tomenthypnum* exhibited a strong linear increase in ET_{in} with θ ($b = 63.6$, $R^2 = 0.88$, $P < 0.001$; Fig. 7a), *Sphagnum* ET_{in} was less responsive to water content but maintained a strong and significant linear response ($b = 20.6$, $R^2 = 0.55$, $P < 0.001$; Fig. 7a). *Tomenthypnum* ET_{in} decreased with lower θ values, which coincided with a draining water table below 20 cm, but ET_{in} was relatively constant at θ above $0.10 \text{ cm}^3 \text{ cm}^{-3}$ averaging $4.5 \pm 0.7 \text{ mm d}^{-1}$ (Fig. 7a). Despite the higher average evaporative loss from the *Sphagnum* mosses, they sustained sufficient θ to support non-zero GEP (ranging from an average of 0.8 to $8.0 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$) across all water table positions (Fig. 7b). θ and GEP relationships across all *Sphagnum* monoliths resulted in a moderately strong and significant positive linear relationship ($R^2 = 0.71$, $P < 0.001$; Fig. 7b). Conversely, when the water table dropped below 20 cm, the upper most portions of *Tomenthypnum* moss shoots desiccated (crispy to the touch) and there was insufficient water (low and ψ values) to maintain both evaporative demands and GEP (Fig. 7b). GEP essentially ceased below θ of $0.10 \text{ cm}^3 \text{ cm}^{-3}$ as a result of the desiccation of the uppermost shoots. Upon raising the water table position from 50 cm, GEP did not increase until the 10-cm water table, following a similar trend as θ . θ and GEP relationships across all *Tomenthypnum* monoliths resulted in a strong and significant quadratic relationship ($R^2 = 0.88$, $P < 0.001$; Fig. 7b). The trade-off between moss production and water losses can describe the ability of *Tomenthypnum* and *Sphagnum* to store carbon while conserving water losses. Expressed as the instantaneous water use efficiency (WUE; $\mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$), this trade-off is estimated using the molar ratio of the amount of CO_2 fixed (GEP) per unit of water lost from the monolith surfaces (ET_{in}). On average, WUE was higher for *Sphagnum* ($0.31 \pm 0.15 \mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$) than for *Tomenthypnum* ($0.15 \pm 0.19 \mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$), and *Sphagnum* had an overall smaller decrease in WUE with decrease in θ ($b = 3.5$, $R^2 = 0.54$). For *Tomenthypnum*, there was little change in WUE when θ was $> 0.10 \text{ cm}^3 \text{ cm}^{-3}$ (averaging $0.30 \pm 0.05 \mu\text{mol CO}_2 \text{ mmol H}_2\text{O}^{-1}$, $b = -1.0$, $R^2 = 0.03$) but did exhibit a large decrease in WUE with decrease in θ below $0.10 \text{ cm}^3 \text{ cm}^{-3}$ ($b = 10.2$, $R^2 = 0.54$).

RH and T within the monolith experiment room were relatively stable around 33% and between 27 and 28°C, respectively, over the measurement period (Fig. 8a, b). RH at the *Tomenthypnum* 3 moss near-surface (2.5 cm depth) remained at or near 100% with 10 and 15 cm

water tables, then decreased with water table until 51.3% at the 50-cm water table depth (Fig. 8a). RH increased to 58.7 and 99.0% with raising the water table to 20 and 10 cm (Fig. 8a). Moss T was, on average, 2.9°C cooler than the air T with all water table depths except for 50 cm (0.7°C warmer) and 20 cm wetting (1.1°C cooler) (Fig. 8b). A slight decrease in RH from saturation at 15-cm water table depth from 10 cm resulted in a decrease in ψ , as calculated by Eq. 1, from 0 to -97 mb (Fig. 8c). With the small decrease in moss RH from near saturation at 20 cm water table depth, ψ values fell considerably to $-4.1 \times 10^4 \text{ mb}$ (Fig. 8c). At 50-cm water table depth, ψ fell to $-9.5 \times 10^5 \text{ mb}$ and only increased to $-1.4 \times 10^4 \text{ mb}$ when θ at 2.5 cm increased at 10-cm water table depth (Fig. 6).

DISCUSSION

Both *Tomenthypnum* and *Sphagnum* mosses (2.5 cm depth) were characterized by low bulk density, high porosity, and high specific yield, which are consistent with ranges observed in other studies for both live *Sphagnum* (Hayward and Clymo 1982; Price and Whittington 2010; McCarter and Price 2014a) and brown mosses (Petroni et al. 2011; Voortman et al. 2013). Although both *Sphagnum* and *Tomenthypnum* had high air-entry pressures, between -3 and 0 mb matric pressure, approximately half the total *Sphagnum* porosity held water within capillary spaces and hyaline cells, compared with only a fifth for *Tomenthypnum*. *Sphagnum* porosity consisted predominantly of two parts: the external pore spaces between overlapping pendant branches and leaves, and the hyaline cells (with pore openings $< 10 \mu\text{m}$). At the given pressures only external pore spaces greater than $66 \mu\text{m}$ were draining. Furthermore, as *Sphagnum* had approximately 20% more water held within pores with small openings (including hyaline cell) than *Tomenthypnum*, *Sphagnum* has the structure to retain more water with lower pressures. The poor water retention of the upper part of the *Tomenthypnum* profile was mainly attributed to two factors: the large proportion (approximately 79%) of the pore space (pores with openings $> 661 \mu\text{m}$) that easily allows drainage of gravitational water; and the relatively low proportion of small pores ($< 99 \mu\text{m}$; Fig. 4), approximately a tenth of the total porosity, to retain capillary water at low pressures. These small pore spaces were predominately external, occurring between overlapping leaves and branches and in the rhizoid tomentum, resulting in 80–90% of water held external when sufficiently wet (Busby and Whitfield 1978).

Despite the low water retention, the relative proportion of water-conducting pores in *Tomenthypnum* may not be different than in *Sphagnum* (Fig. 5). *Sphagnum* and *Tomenthypnum* $K(\psi_m)$ were comparable to similar studies of *Sphagnum* (Price and Whittington 2010; McCarter and Price 2014a) and other brown mosses (Voortman et al. 2013). While the pore spaces in tomenta are approximately the same size as hyaline cell openings ($\sim 10 \mu\text{m}$; Proctor 1982), hyaline cells can have internal diameters

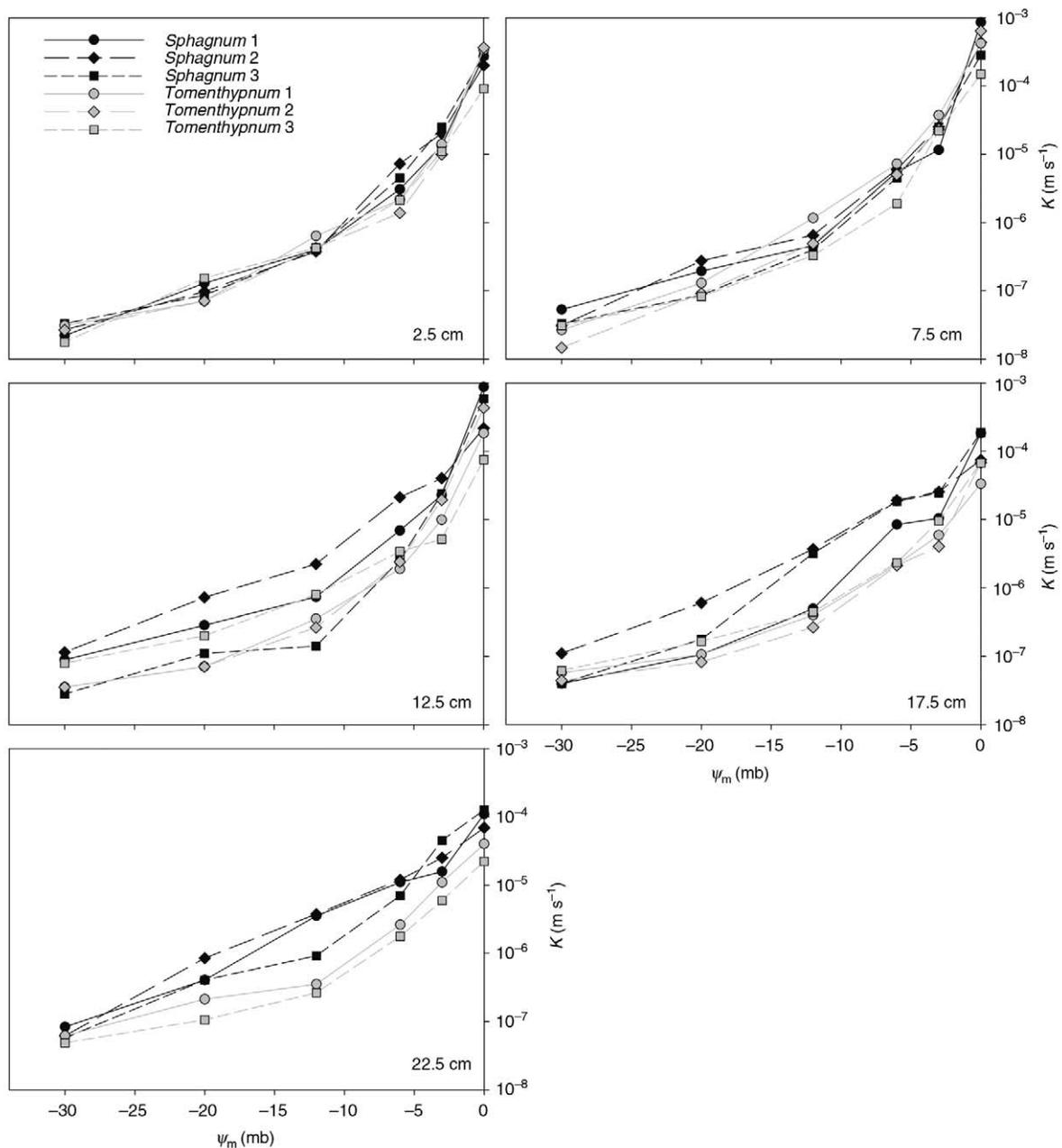


Fig. 5. Hydraulic conductivity and pressure head relationships, $K(\psi_m)$, for each *Tomenthypnum* and *Sphagnum* sampling depth. One sample profile (0–25 cm) was used per monolith; *Tomenthypnum* profile 2 did not have a 22.5-cm sample. Depths are the mid-depth of each 5-cm sample.

upwards of 200 μm and comprise of 10 to 20% of the pore space in *Sphagnum* (Hayward and Clymo 1982). Therefore, at the tested pressures, the relative amount of active pore spaces for water conductance were likely similar between mosses. This means pores less than 165 μm were likely the most available for water conductance in peat-land mosses. The relatively small differences in K_{sat} and K_{unsat} (Fig. 5) between *Sphagnum* and *Tomenthypnum*

mosses reflected the relatively small differences in water in active pore spaces, rather than total water in the sample.

While both peat types displayed an increase in the relative number of pores with small openings ($<99 \mu\text{m}$) with peat depth, indicating decreased peat particle size and increased compaction caused by decomposition (Carey et al. 2007), *Sphagnum* peat preserved relatively larger pore spaces ($>99 \mu\text{m}$) as the moss structure

remained more intact (Johnson et al. 1990). This, corroborated by the physical properties (Fig. 2), indicates that the *Sphagnum* peat was composed of lower ρ_b material with higher ϕ of primarily fibric peat (Boelter and Verry 1977). The higher water retention capacity of *Sphagnum* 2 and *Tomenthypnum* 3 is likely due to variability in the sample locations and was likely in an area of lower and relatively more decomposed peat than the other respective monoliths. Contrastingly, *Tomenthypnum* peat properties below the partially decomposed moss layer (12.5 cm and below for *Tomenthypnum* 3; and 17.5 and 22.5 for *Tomenthypnum* 1 and 2) indicated well-decomposed, hemic peat (Boelter and Verry 1977) characteristic of the fast decomposition rates of *Tomenthypnum* moss and vascular plants in rich fens (Vitt et al. 2009). While the partially decomposed layers of old *Tomenthypnum* shoots and vascular plant material (7.5 cm for *Tomenthypnum* 3 and 7.5 and 12.5 cm for *Tomenthypnum* 1 and 2) drained approximately 40% of its water from saturation to -3 mb, it still had a large proportion ($\sim 50\%$) of pore spaces smaller than $99 \mu\text{m}$ to retain water at low pressures. As a result, there was the potential for this layer to retain water for capillary rise for *Tomenthypnum* mosses. However, smaller peat particles and pore sizes with depth, the *Tomenthypnum* peat pore network may have had less connectivity as water concentrated in crevices and at small angles, thereby increasing the inactive porosity and tortuosity (Rezanezhad et al. 2010). This is evident in the $K(\psi_m)$ relationships with depth as *Tomenthypnum* K_{unsat} was approximately an order of magnitude lower at matric pressures between 0 and -30 mb at 22.5 cm depth (Fig. 5). Nonetheless, it was the connectivity of the pore-water networks between moss turf, consisting of both live moss and partially decomposed moss litter, and the underlying peat substrate that was critical for capillary flow for the mosses (Voortman et al. 2013; McCarter and Price 2014b). This was affected by the changes in the physical properties with depth, which was much greater in *Tomenthypnum* (Fig. 2).

The relatively high *Sphagnum* capitula θ and the observed increase in θ when rewetting from 50 to 20 and 10 cm in the monolith experiment (Fig. 6) suggests *Sphagnum* maintained upward capillary flow under moderate pressures. The gradual increase in the abundance of small pore sizes ($\leq 99 \mu\text{m}$) with depth reflects the progressive decomposition of the living *Sphagnum* pore structure (Turetsky et al. 2008) to a more dense, partially decomposed peat. However, due to a large range of pore sizes in the *Sphagnum* structure throughout the profile compared with *Tomenthypnum* (Fig. 4), *Sphagnum* exhibited greater changes in θ with ψ_m (Fig. 3). Thus, the *Sphagnum* structure provided relatively high matric pressure to fill those large pore spaces, providing the *Sphagnum* structure with a continuous capillary network from the water table to the capitula that favours capillary rise. At high water tables, the high water content of the *Sphagnum* capitula canopy provided little

surface resistance to diffusion (Kettridge and Waddington 2014), thereby creating conditions favouring high evaporation and sufficient water for photosynthesis. At lower water tables, the lowering of matric pressures in the *Sphagnum* structure reduced the capitula-atmosphere pressure gradients causing evaporation and thus capillary flow to decrease. When the water table was dropped to 50 cm, only a small proportion of capitula in each *Sphagnum* monolith exhibited desiccation, which typically occurs between -100 and -600 mb of pressure (Hayward and Clymo 1982; Lewis 1988). However, the smaller decrease in WUE with θ indicates that *Sphagnum* likely stores more carbon than *Tomenthypnum* as water losses become secondary to moss production across all θ in this study. The higher average WUE for *Sphagnum* than *Tomenthypnum* is a result of the greater average production and greater physiological resistance to water loss (Humphreys et al. 2006). The water retention characteristic of the species in this experiment, *S. angustifolium* and *S. magellanicum*, lawn species, are lower than hummock species like *S. fuscum* and *S. rubellum*, which have a greater capitula density (Hájek and Beckett 2008) and smaller pore-size distribution in the capitula (McCarter and Price 2014a). The relationship between moss GEP and θ is in agreement with other studies for *Sphagnum* (McNeil and Waddington 2003; Strack and Price 2009) despite stressed environmental conditions (Shurpali et al. 1995). In the experiment, *Sphagnum* θ was likely not high enough to create an aqueous diffusion barrier to limit CO_2 diffusion into the *Sphagnum* moss, as was exhibited in other studies (Rydin and McDonald 1985; Williams and Flanagan 1996; Schipperges and Rydin 1998). However, GEP peaked at θ values corresponding to a 15-cm water table, which is consistent with other investigations of *S. angustifolium* (Tuittila et al. 2004); the lesser desiccation tolerant of the *Sphagnum* species (Hájek and Beckett 2008) thus requires higher water tables. The relatively low θ for GEP may be due to greater water loss by the high evaporative demand. Nonetheless, the *Sphagnum* structure provided the necessary water conductance to maintain high soil-water pressures to retain water in hyaline cells and pore spaces in the capitula to avoid desiccation and maintain productivity at all water table positions.

With high water tables (> 30 cm drying and 10 cm rewetting) the *Tomenthypnum* structure provided sufficiently high θ and K_{unsat} to drive upward capillary water flow within the small pore spaces along rhizoids in the old moss shoots, through the tomenta of rhizoids, and overlapping leaves to the moss canopy. As such, the moss maintained both non-zero GEP rates and relatively high ET_{in} rates, which resulted in relatively high and consistent WUE. Little changes in WUE with θ above $0.10 \text{ cm}^3 \text{ cm}^{-3}$ likely indicate *Tomenthypnum* utilizes a defined amount of water for production and excess water is evaporated. As the surface of the *Tomenthypnum* canopy is more porous than *Sphagnum*, the depth of

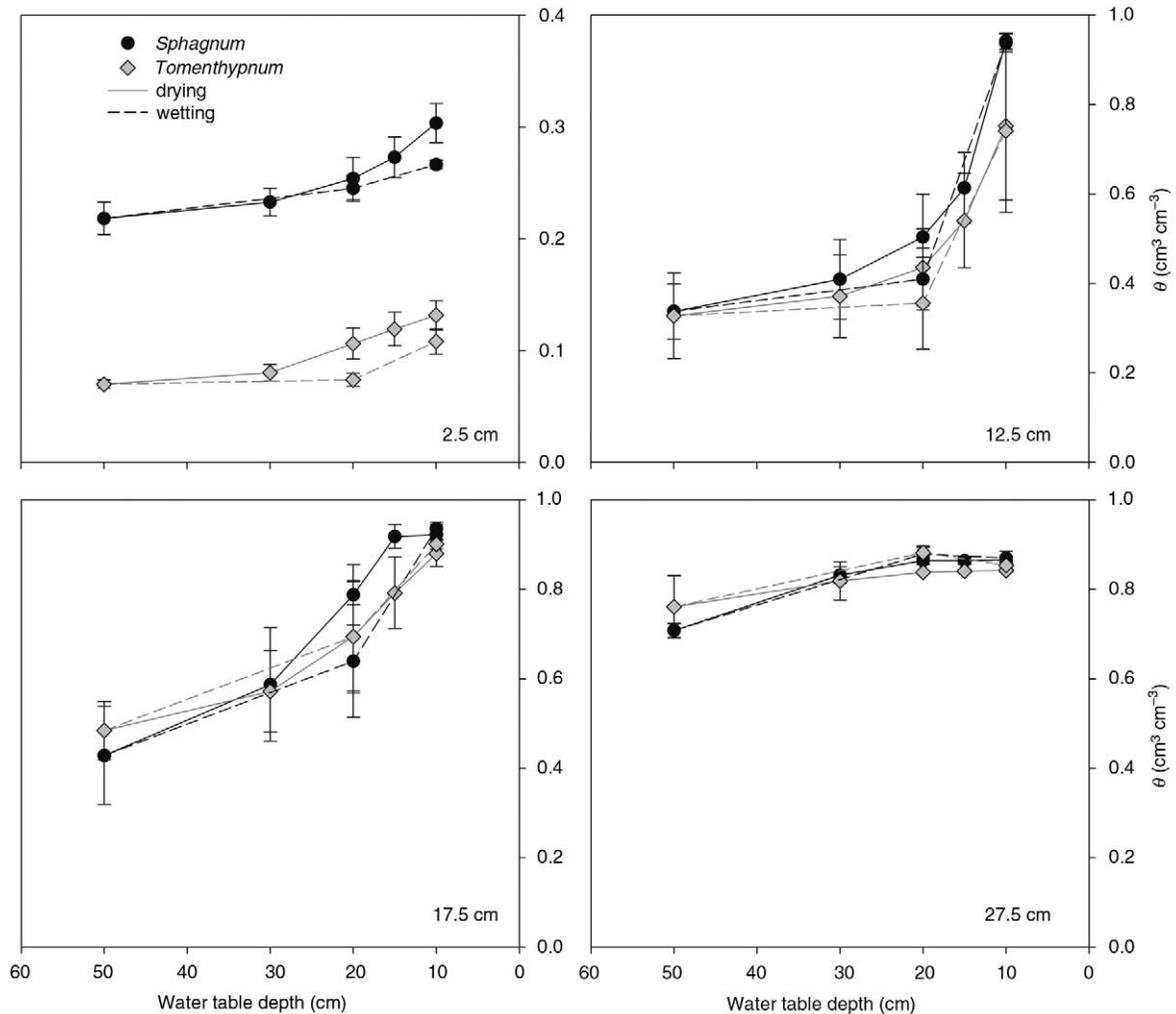


Fig. 6. Changes in mean (± 1 standard deviation) θ at 2.5, 12.5, 17.5, and 27.5 cm depth ($n = 3$ monoliths per moss and depth) of *Tomenthypnum* and *Sphagnum* with each subsequent water table change. Water table depths of 10, 15, 20, 30, and 50 cm (solid lines) and rewetting to 20 and 10 cm (dashed lines) were used. Note the different scale used for θ at 2.5 cm than the other depths.

turbulence penetration is likely greater (cf. Rice et al. 2001). Consequently, while capillary flow is required to sustain evaporation, it does not need to reach the surface of the tomenta, as vapour exchanges can occur slightly deeper in the moss shoots, and the aerial portions of the plant can desiccate. However, unlike *Sphagnum*, the *Tomenthypnum* structure could not sustain high capillary flow from the underlying peat with low water tables. The loose large-pore structure of the moss at the surface overlying denser, apparently well-decomposed peat resulted in a fairly abrupt change in the pore size and geometry (ranging between 10 and 15 cm in the *Tomenthypnum* monoliths, Fig. 2). As the water table position was lowered in *Tomenthypnum*, thereby decreasing matric pressures between the partially decomposed basal layer and the underlying peat, the large pores connecting the layers

drained and capillary flow within the moss layer decreased and likely disconnected many water conducting structures of the moss. At 30-cm water table depth, decreasing soil-water pressure and high evaporative demand in the *Tomenthypnum* structure decreased θ at the near-surface (Fig. 6). However, capillary water was still present, as evident by the evaporative cooling (Price et al. 2009) that kept the moss T lower than the air (Fig. 8b) and the non-zero GEP (Fig. 7b). As such, only smaller pores sizes within the tomenta could still maintain water conduction. As indicated by the decreased WUE below θ of $0.10 \text{ cm}^3 \text{ cm}^{-3}$, it is likely that production is reduced at these lower θ values to maintain water availability for evaporation to drive water conduction. At 50 cm water table depth the capillary water lost to evaporation could not be replaced and the moss

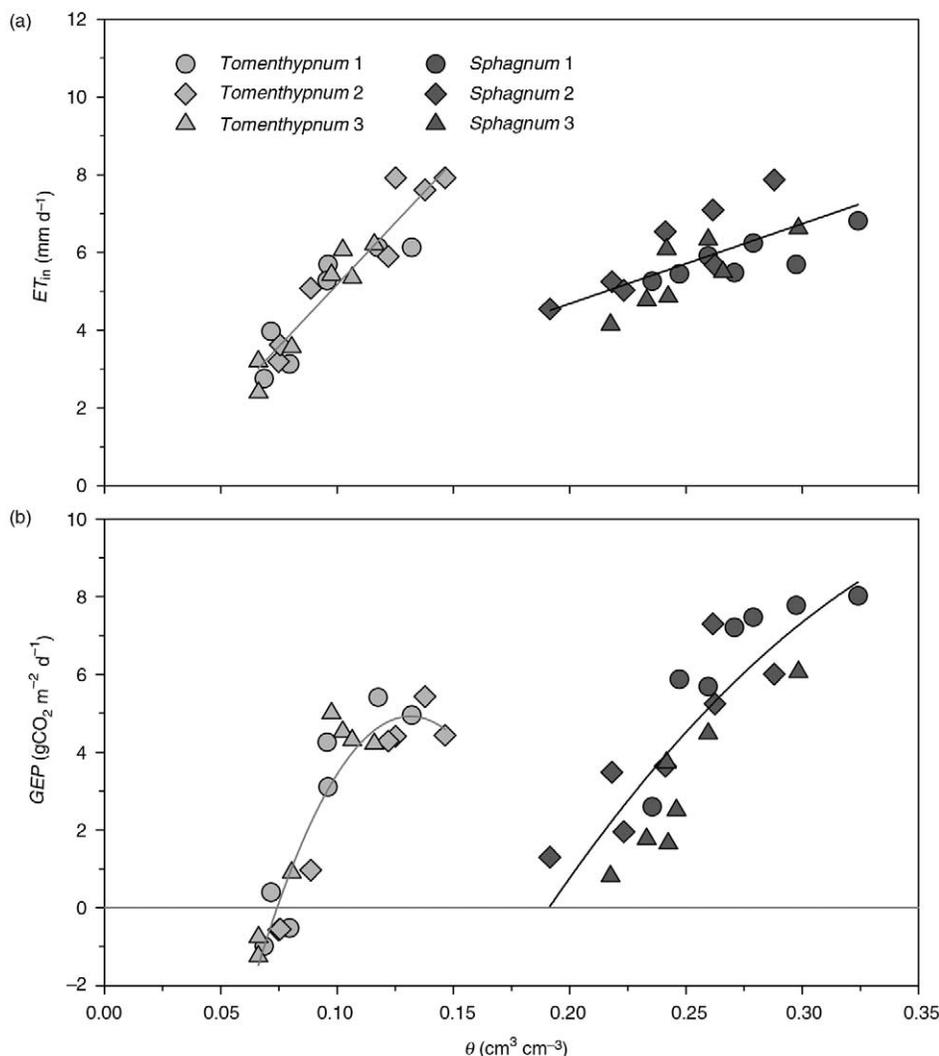


Fig. 7. Relationships between *Tomenthypnum* and *Sphagnum* moss θ at 2.5 cm depth with (a) instantaneous evapotranspiration (ET_{in}) and (b) gross ecosystem productivity (GEP). Each symbol represents the mean value of four measurements of each variable (θ , ET_{in} , and GEP) taken at each water table position.

cell pressures at the top of the moss canopy likely rapidly equilibrated with the surrounding air, greatly reducing GEP rates (Fig. 7b) and increasing moss T (Fig. 8b). The negative GEP values are likely the result of a combination of low light levels, high peat soil respiration rates (from warm temperatures), and measurement uncertainty and error. The higher moss T than the air when the water table depth was at 50 cm is likely due to heat transfer from the grow lights. Note the high variability in T in Fig. 8b is caused by the drop in air T near the surface of the moss when the grow lights were turned off at night. Nevertheless, vapour diffusion likely still occurred from the underlying peat layers as ET_{in} remained positive (see Fig. 7a; Price et al. 2009) and the peat remained sufficiently wet (17.5 cm depth; Fig. 6). Note that it is

unlikely that water tables remain below 30 cm beneath the moss surface for extended periods in natural fens, so the low water contents experienced in the investigation may not be representative of natural θ variation.

While there were clear trends in ψ_m with water table position, the calculated ψ values in the near-surface *Tomenthypnum* monolith may substantially underestimate actual moss matric and osmotic pressures when capillary water is present (i.e., actual ψ may be less extreme, or closer to zero). Since gas exchange in the unsaturated pore network is much faster than unsaturated water flow (Price et al. 2009), it seems unlikely that capillary pressures will have dropped to the equilibrium levels calculated on the basis of RH. For instance, a drop in RH to 99.9% equates to a drop in soil–water

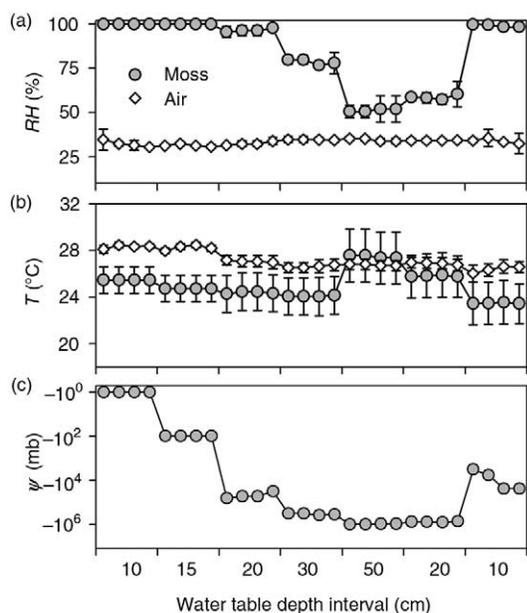


Fig. 8. Changes in (a) daily mean relative humidity (RH) and (b) temperature (T) of *Tomenthypnum* 3 moss (2.5 cm depth) and the monolith room, and subsequent changes in estimation of (c) moss pressure (ψ), with each water table interval with lowering the water table depths of 10, 15, 20, 30, and 50 cm and rewetting to 20 and 10 cm. Mean daily values and error bars (1 standard deviation) were from days that water content and gas flux measurements were completed.

pressure to -1.4×10^3 mb, which is very likely not the case. At 20-cm water table depth the average θ at the same depth (2.5 cm) was $\sim 0.10 \text{ cm}^3 \text{ cm}^{-3}$ (Fig. 8c) and calculated ψ was -4.1×10^4 mb (equilibrium RH of 98.5%). However, according to $\theta(\psi_m)$ relationships (Fig. 3), θ of $0.10 \text{ cm}^3 \text{ cm}^{-3}$ occurred at approximately -30 mb, three orders of magnitude higher than the calculated ψ . Furthermore, Price et al. (2009) observed that although RH values at 5-cm depth ranged between 92 and 95%, indicating calculated ψ between -1.5×10^5 and -7.4×10^4 mb, the *Sphagnum* samples were not desiccated, and capillary flow and evaporation were occurring. This suggests that actual *Sphagnum* moss pressures were near zero and the vapour pressure was not in equilibrium. In the monolith experiment we note that *Tomenthypnum* GEP ceased below a calculated ψ of almost -1×10^6 mb, which is an order of magnitude lower than the threshold identified by Busby and Whitfield (1978) and Proctor (2000), providing a measure of the underestimation caused by assuming equilibrium conditions. To further add to the complexity, vapour fluxes (Fig. 7a) are occurring within the moss structure and can cause changes in vapour pressure that may affect the viability of capillary water. Given these uncertainties, further study is needed to investigate the relationships between actual moss ψ and vapour pressure in non-equilibrium conditions. Nonetheless, the disequilibrium that occurs

(i.e., evaporation-driven vapour gradients) within the *Tomenthypnum* moss and peat and structures is likely an important mechanism to drive vapour and capillary water fluxes.

Because *Tomenthypnum* can lose considerable amounts of water before desiccation (Busby and Whitfield 1978) it is likely inherent in its physiological design to tolerate desiccation and photosynthesize at low water contents (Rice et al. 2001). However, since θ and GEP relationships were similar to Busby and Whitfield (1978) and productivity ceased with low water tables (Fig. 7b), *Tomenthypnum* ψ may have dropped below -1×10^5 mb where photosynthesis is known to cease in poikilohydric mosses (Busby and Whitfield 1978; Proctor 2000). Only upon raising the water table position to the bottom of live moss shoots and layers of partially decomposed moss at 10 cm depth were soil-water pressures high enough at that depth to refill the large pore spaces and re-establish capillary contact, thereby increasing θ and GEP. This capillary barrier effect has also been shown to occur in other studies on new, low-density *Sphagnum* growth on dense cutover peat (Price and Whitehead 2001; Ketcheson and Price 2013; McCarter and Price 2014b). As a result, moisture additions by precipitation, dew (Csintalan et al. 2000), and distillation (Carleton and Dunham 2003) may provide small amounts of water to the moss surface when water tables are low to provide relief from prolonged desiccation.

CONCLUSION

Peatland moss composition can have a significant impact on the hydrophysical properties of near-surface moss and the underlying peat substrates. However, despite the differences in the properties and water retention capacity of *Sphagnum* and *Tomenthypnum* in this study, both provided both moss types the necessary mechanisms for capillary rise. The gradual increase in the abundance of small pores ($< 99 \mu\text{m}$) with depth and a large range of pore sizes throughout the profile in *Sphagnum* facilitated a continuous network of connected pores from the water table to the capitula that favours capillary rise. Although the *Sphagnum* retained almost twice the amount of water in this experiment as *Tomenthypnum*, a large fraction of the water was retained within hyaline cells. As this fraction of water is inactive under low pressure (< -100 mb), it likely did not contribute to the active water-conducting structure of the *Sphagnum* growth forms. As a result, the active water-conducting structures of both *Sphagnum* and *Tomenthypnum*, mainly the external capillary water network between overlapping branches and leaves, were likely similar, as exhibited in the similar K_{unsat} in the near-surface. This provided the *Tomenthypnum* a suitable pore structure to maintain capillary flow from the underlying peat when water was not limited with high water tables. With adequate capillary contact between the underlying peat and the partially decomposed layer, the high water content and high hydraulic conductivity sustained capillary rise for photosynthesis.

When water tables were 30 cm or below, the draining of the high proportion of large pores in layers of live *Tomenthypnum* moss restricted hydraulic conductivity and capillary rise from the underlying peat, and the uppermost portions of the moss shoots desiccated. However, it is likely that the layer of partially decomposed moss above the peat provided greater connection with the denser peat, to support a small amount of capillary action with low water tables. Furthermore, *Tomenthypnum* may rely on precipitation in addition to dewfall, distillation, and vapour fluxes from the underlying wet peat to provide small amounts of water for temporary relief from desiccation. Greater quantification of atmospheric and vapour fluxes and their effects on *Tomenthypnum* productivity may elucidate the relative importance of different source waters on capillary rise and the ability of the brown moss to tolerate desiccation. These results illustrate the importance in understanding the hydrological mechanisms (water retention and pore geometry, distribution, and connectivity) of moss growth forms to better understand peatland hydrological and ecological processes.

The disequilibrium between vapour and moss pressure suggests calculated ψ can grossly underestimate actual moss pressure by several orders of magnitude and therefore does not provide an accurate characterization of moss pressure. However, as the disequilibrium is driven by vapour pressure gradients between the moss and the atmosphere, it is likely a driving factor that helps maintain vapour and capillary water fluxes to provide moisture for *Tomenthypnum*. Future studies are required to determine relationships between *Tomenthypnum* and *Sphagnum* moss pressure and vapour pressure in disequilibrium to fully comprehend the importance of evaporation.

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