

Ecohydrological controls on water distribution and productivity of moss communities in western boreal peatlands, Canada

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ABSTRACT

Different peatland mosses have varying strategies for water storage and capillary rise mechanisms depending on their particular hydrophysical properties and preferred water sources. To understand these strategies, the retention and redistribution of water from various sources in *Sphagnum*, feather and *Tomenthypnum* moss communities were addressed through investigation of the sensitivity of moss moisture dynamics to environmental variables, field surveys and a drought stress experiment. Feather mosses preferred habitats well above the water table, and their relatively low volumetric water content (θ) increased only with precipitation events. The relatively high residual θ (0.22) of *Sphagnum* capitula helped the moss type maintain conditions suitable for photosynthesis over a range of water table conditions. *Tomenthypnum* mosses occurred over a broader range of water table positions than *Sphagnum* or feather mosses because of their ability to use both capillary rise and atmospheric water for growth. While *Tomenthypnum* had relatively low near-surface θ (~0.10), evaporative losses were sustained by both small nocturnal additions by condensation of vapour and upward capillary rise. An intermediate layer of partially decomposed mosses supported contact with the underlying peat and helped transport sufficient water to the *Tomenthypnum* moss surface. However, *Tomenthypnum* θ and productivity changes were more sensitive to rainfall additions as the uppermost portion of moss shoots can easily desiccate under typical evaporative demand. As a result, nocturnal sources of atmospheric water from dew (~0.15 mm per night) and distillation (~0.10 mm per night) provided temporary relief from desiccation for potentially important early morning photosynthesis and helped drive evaporation and capillary rise. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS bryophytes; volumetric water content; vapour fluxes; photosynthesis; evaporation; water table; dewfall and distillation; fen peatlands

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INTRODUCTION

Mosses are the dominant peat-forming vegetation in northern peatlands (Kuhry and Vitt, 1996; Vitt *et al.*, 2009), storing ~220–550 Pg of carbon (Gorham, 1991; Turunen *et al.*, 2002; Yu, 2011) and accounting for a large fraction of water exchange between peatlands and the atmosphere (Williams and Flanagan, 1996). Mosses are non-vascular and poikilohydric plants that lack active-water transport mechanisms to control water loss (Proctor *et al.*, 2007); however, most mosses can withstand some desiccation through a variety of mechanisms (Proctor, 1982). Capillary spaces between leaf and branch structures provide a relatively constant and reliable source of external water (Hedenäs, 2001) from underlying peat substrates if

capillary contact is not restricted (Dilks and Proctor, 1979; McCarter and Price, 2014b). The structure of mosses and underlying substrates are typically organized to maintain capillary rise for characteristic water contents to avoid desiccation and for productivity rates that are characteristic for different species (Dilks and Proctor, 1979; Proctor *et al.*, 2007). As a result, variability of both carbon accumulation rates and water exchanges between and within peatlands are largely controlled by moss species composition (Heijmans *et al.*, 2004a, 2004b; Brown *et al.*, 2010; Petrone *et al.*, 2011).

While there are many studies on the differences of moss–water strategies (cf., Busby *et al.*, 1978; Dilks and Proctor, 1979; Skre *et al.*, 1983; Luken, 1985; Williams and Flanagan, 1996; Mulligan and Gignac, 2001; Rice *et al.*, 2001; Elumeeva *et al.*, 2011, to name a few), fewer studies describe the hydrophysical mechanisms for capillary rise in *Sphagnum* mosses (Hayward and Clymo, 1982; Thompson and Waddington, 2008; Price and Whittington, 2010; McCarter and Price, 2014a) and feather mosses

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(Williams and Flanagan, 1996; Carleton and Dunham, 2003). Even fewer studies detail the capillary rise mechanisms and sources of water in brown mosses (Busby *et al.*, 1978; Goetz and Price, 2015), which dominate many boreal rich fens. For *Sphagnum* mosses, capillary rise maintains higher soil water pressures, thus water contents, helping the capitula at the surface avoid desiccation (Hayward and Clymo, 1982; Price, 1997; McCarter and Price, 2014a). Elevated water contents are also sustained by water-retaining hyaline cells that only drain at low pressures (i.e. between -100 and -600 mb; Hayward and Clymo, 1982; Lewis, 1988). Comparatively, feather mosses, which typically grow in more well-drained forested environments and do not have the structural capacity to draw capillary water to the moss surface, rely predominantly on atmospheric sources for growth (Carleton and Dunham, 2003). Unlike *Sphagnum*, brown mosses do not have hyaline cells and thus predominately rely on external conduction and retention of water (Busby and Whitfield, 1978). *Tomenthypnum nitens* (Loeske) Hedw., a widely distributed brown moss species common in northern rich fens (Vitt, 1990), uses dense felts of rhizoid tomentum along the base of the stem (Busby *et al.*, 1978) to draw capillary water. It was determined by Goetz and Price (2015) that despite a highly porous structure, these mosses can sustain water transport to the canopy surface from underlying peat; however, low water tables can result in the desiccation of the uppermost portions of shoots. The relative importance of capillary rise compared with other atmospheric sources of water is not well understood.

Recent studies have shown that precipitation events can provide a critical source of water to maintain physiological processes (Robroek *et al.*, 2007; Strack and Price, 2009), as even small precipitation events (<1 mm) can temporarily increase *Sphagnum* water content equivalent to large increases of water table (Strack and Price, 2009). Other small additions from dew (Csintalan *et al.*, 2000), distillation (Carleton and Dunham, 2003) and vapour diffusion (Price *et al.*, 2009) may also provide sufficient moisture to maintain physiological functions under low-water-table conditions. Csintalan *et al.* (2000) demonstrated that moss water content and early morning productivity increased with nocturnal dewfall additions. Carleton and Dunham (2003) found that upward vapour fluxes from the underlying peat (distillation) could condense at the cooler surface and rewet feather mosses under certain microclimatic conditions. Price *et al.* (2009) suggested that upward vapour fluxes in *Sphagnum* profiles could provide potentially important sources of water for cell turgor maintenance under dry (low water content) conditions. Because of the low residual water content of *T. nitens* (Goetz and Price, 2015) and its ability to tolerate frequent desiccation (Busby *et al.*, 1978), it is hypothesized that

small precipitation events, dewfall, distillation and vapour fluxes will provide critical sources of water to maintain moss production under dry conditions. There is also an interest in the potential for brown mosses, including *T. nitens* to be used to re-establish fen vegetation on post-mined boreal landscapes (Price *et al.*, 2010). Therefore, there is a need to understand the relative importance of and quantify the roles of water table position, precipitation and vapour sources of water on the water content of *T. nitens* compared with other peatland mosses. The objectives of this study were to (1) characterize and contrast the distribution of water within *T. nitens* and *Sphagnum* communities; (2) identify how water table position and precipitation events affect water availability in *T. nitens*, *Sphagnum* and feather moss communities; and (3) compare the influence of those water sources on productivity and evapotranspiration from *T. nitens*, *Sphagnum* and feather moss communities.

STUDY AREA

The study was conducted in Poplar Fen, a brown moss-dominated, treed rich fen ($56^{\circ}56'18''\text{N}$, $111^{\circ}32'35''\text{W}$ and 325 m above sea level); its adjoining feather moss-dominated forested upland; and Pauciflora Fen, a *Sphagnum*-dominated open poor fen ($56^{\circ}22'30''\text{N}$, $111^{\circ}14'05''\text{W}$ and 740 m above sea level), located 65 km apart near Fort McMurray, Alberta, within the western Boreal Plain ecozone. The 30-year climate normals (1971–2000) in the region for annual temperature, precipitation and potential evapotranspiration are 1.7 C and 485 and 515 mm, respectively (Environment Canada, 2007), resulting in a sub-humid climate with potential evapotranspiration exceeding precipitation in most years.

Poplar Fen is an 11-ha rich fen peatland (pH ~ 6.6) with an average peat depth of 1 m within the study area. Groundcover moss vegetation within the study area of Poplar Fen includes the dominant *T. nitens* (Hedw.) Loeske and *Aulacomnium palustre* (Hedw.) mainly on microtopographical highs with *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) BSG, *Sphagnum capillifolium* (Ehrh.) Hedw., *Bryum pseudotriquetrum* (Hedw.) and *Drepanocladus aduncus* (Hedw.) Warnst. Vascular vegetation includes bog birch [*Betula pumila* (L.)], three-leaf Solomon's-seal [*Smilacina trifolia* forbs (L.)], water horsetail [*Equisetum fluviatile* (L.)] and a large cover of tamaracks [*Larix laricina* (Du Roi) K. Koch] and some black spruce [*Picea mariana* (Mill.) BSP]. Turfs of *T. nitens* and *A. palustre* (hereafter identified as *Tomenthypnum* mosses, as both have similar growth form and frequently grow intermixed; Johnson *et al.*, 1995) vary in thickness (4–15 cm) with partially decomposed litter basal layers and are found growing directly on dense,

decomposed peat and on ladders of tree and other vascular plant roots and stems for support. *P. schreberi* and *H. splendens* (hereafter identified as feather mosses) communities with Labrador tea [*Rhododendron groenlandicum* (Oeder) Kron and Judd] and large black spruce dominate the drier uplands on the fen boundaries.

Pauciflora Fen is an 8-ha poor fen (pH ~ 4.5) situated on a topographical high in the region, with an average peat depth of 2 m in the study area. The groundcover in the study area consists mainly of lawns of *Sphagnum angustifolium* (C. Jens ex Russ.) and *Sphagnum magellanicum* (Brid.) mosses, with Labrador tea, leather leaf [*Chamaedaphne calyculata* (L.)], water sedges [*Carex aquatilis* (Wahlenb.)] and sparse, stunted black spruce and tamarack trees. Communities of *S. angustifolium* and *S. magellanicum* in the poor fen, as well as *S. capillifolium* in the rich fen, are hereafter identified and generalized as *Sphagnum* mosses.

MATERIALS AND METHODS

Data were collected from 1 June to 3 August in 2011 and 2012, unless otherwise stated. Meteorological data were collected at each fen using Campbell Scientific Canada (Edmonton, Canada) data loggers logging every half hour at each study area. Precipitation (P) was measured automatically using a tipping bucket (HOBO RGB-M002; Onset Computer Corp.; Bourne, MA, USA) set 1.0 m above the ground surface with no tree canopy above. Manual rain gauges were used for P amounts between 3 and 23 June 2012 during malfunction of the automatic tipping-bucket gauge at both fens. Air temperature (T) and relative humidity (RH) measurements were located 3.0 m above the moss surface (HOBO Onset). Net radiation flux (R_n ; J day^{-1}) was measured (NR-lite2 net radiometer) at 3.0 m above the surface to obtain a representative measurement from moss and vascular vegetation. A soil heat flux plate (HFT-03) was installed 5 cm below the surface of a hummock to measure ground heat flux (G ; J day^{-1}). Soil heat flux plates can underestimate heat flux in organic soils due to poor contact and vapour flow disruption (Halliwell and Rouse, 1987; Petrone *et al.*, 2004), so the plates were installed into a piloted hole, ensuring good contact with the organic substrate. Potential error associated with the underestimation is assessed later in the Discussion section.

To better identify how water from different sources is both distributed and utilized for production by different peatland moss communities, three distinct experiments were performed: (1) a moss water dynamics study – recording *in situ* variables (temperature, relative humidity, volumetric moisture content and depth to water table) in moss–peat profiles (*Sphagnum* and *Tomenthypnum*) at both

fens; (2) a transect study – to quantify how volumetric water content of mosses varies with water table changes and precipitation events in *Tomenthypnum*, feather and *Sphagnum* moss communities at the rich fen site along three randomly chosen 25-m transects; and (3) a field drought experiment – examining the moss moisture dynamics and its effect on evapotranspiration and productivity of moss monoliths under imposed hydrological stresses.

Moss water dynamics study

Three *Tomenthypnum* turfs at the rich fen and one *Sphagnum* hummock at the poor fen were instrumented to monitor *in situ* volumetric water content (θ ; $\text{cm}^3 \text{cm}^{-3}$) and water table depth. The microclimate within the moss structure was also monitored in the *Tomenthypnum* turfs. The turfs were larger than 60 cm in diameter and 25 cm above adjacent hollows and relatively flat topped to ensure localized vertical water fluxes. The *Tomenthypnum* turfs, within approximately 25 m of each other, had predominantly *T. nitens* moss cover with some *A. palustre*. *L. laricina* trees surrounded the turfs. They were representative of the *Tomenthypnum* turfs measured in the transect study and the monoliths sampled for Goetz and Price (2015), with the exception of *Tomenthypnum* 2, which was disconnected from the underlying peat because of ladder support from *L. laricina* roots. The *Sphagnum* hummock had a mix of *S. angustifolium* and *S. magellanicum* mosses. Equipment limitations restricted the profile measurements to a single *Sphagnum* hummock. The representativeness of the *Sphagnum* hummock will be discussed further in the Discussion section. We compare results from the *Tomenthypnum* profiles with the *Sphagnum* profile that has distinctly different properties than the *Tomenthypnum* (Goetz and Price, 2015); the explanations of how their behaviour relates to their hydraulic properties are broadly applicable.

The water table beneath each moss hummock was monitored continuously using Odyssey™ capacitance water level loggers (Dataflow Systems Pty Ltd.; Christchurch, New Zealand) in immediately adjacent monitoring wells, with manual measurements for data verification. θ in *Tomenthypnum* 1 and the *Sphagnum* hummock were monitored non-destructively using Campbell Scientific CS650 water content reflectometers in the moss (2.5 and 7.5 cm depths), partially decomposed moss (12.5 cm) and underlying peat (22.5 cm depths) at 30-min intervals. A time-domain reflectometer (TDR)-100 system with CS605 probes measured θ in *Tomenthypnum* 2 and 3 at the same substrates and depths as *Tomenthypnum* 1, although *Tomenthypnum* 3 did not have a peat (22.5 cm) probe. All θ values were determined using medium-specific TDR calibrations from methods described by Topp *et al.* (1980).

To monitor the within-structure microclimate of the *Tomenthypnum*, near-surface *RH* and *T* were monitored at 2.5-cm depth in each *Tomenthypnum* turf using a Vaisala HMT337 system (Woburn, MA, USA) (thermocouple for *T* and thin-film polymer capacitive sensor for *RH*) in the air-filled pores at 30-min intervals. Parallel instrumentation was not available for *Sphagnum*. *RH* and *T* were also measured 25 cm above (HOBO) and 7.5 cm below the moss surface (copper–constantan thermocouples for *T* and assumed 100% *RH* based on preliminary measurements during a drydown period). These data were used to determine the significance of vapour fluxes and condensation in the near-surface (2.5 cm) layer. A simplified Penman–Monteith evaporation model for water vapour condensation was used to estimate potential nocturnal condensation (Garratt and Segal, 1988; Jacobs *et al.*, 2002; Moro *et al.*, 2007; Uclés *et al.*, 2014), where

$$\lambda E = \left(\frac{s}{s + \gamma} \right) (R_n - G) \quad (1)$$

and where λE is the latent heat exchange (J day^{-1}), s is the slope of the saturation vapour pressure–temperature curve (Pa K^{-1}), γ is the psychrometric constant ($0.0662 \text{ kPa K}^{-1}$ at 20°C), R_n is the net radiation flux (J day^{-1}) and G is the ground heat flux (J day^{-1}). This simplified model assumes that vapour condensation occurs at night when the air is typically near saturation and wind speed is low. As a result, the aerodynamic contributions of energy exchange in the Penman–Monteith model are minimal, and therefore, condensation is driven mainly by the radiative balance from the atmosphere and heat transfer through the moss medium (Garratt and Segal, 1988; Moro *et al.*, 2007). Furthermore, latent heat energy transfer in the moss can be partitioned into energy transferred from the condensation of dew (atmospheric) and distillation (from the underlying peat) (Garratt and Segal, 1988). Thus, total condensation rates (D_T) comprise of dewfall (D_f) and distillation (D_d), in $\text{kg m}^{-2} \text{ s}^{-1}$, where

$$D_f + D_d = \left(\frac{s}{s + \gamma} \right) \left(\frac{R_n - G}{L\rho} \right) \quad (2)$$

and where L is the latent heat of vaporization (J kg^{-1}) and ρ is the density of water (kg m^{-3}). D_T was estimated using the environmental variables in the *Tomenthypnum* at the rich fen and the *Sphagnum* in the poor fen in separate moss communities near the moss θ and *RH* instrumentation. To partition distillation fluxes in *Tomenthypnum*, subsurface vapour fluxes were determined using Fick’s first law, as per methods from Price *et al.* (2009), using moss and peat properties from Goetz and Price (2015) and

$$D_d = D_v^* \left(\frac{\varepsilon^{10/3}}{\phi^2} \right) \left(\frac{\partial C_v}{\partial z} \right) \quad (3)$$

where D_v^* is the diffusion coefficient of water vapour in air ($\text{cm}^2 \text{ s}^{-1}$), ε is the air-filled porosity, which accounts for changes in porosity due to θ fluctuations, ϕ is the soil porosity, $\partial C_v / \partial z$ is the change in vapour concentration (C_v ; kg m^{-3}) between 2.5- and 7.5-cm depths (z). Instrumentation for subsurface vapour fluxes was not available for *Sphagnum*. Assuming D_d constitutes a proportion of D_T (one measurement source nearby is applied to each *Tomenthypnum* turf for this analysis), the difference between the fluxes is the amount of condensation by D_f .

Transect study

To compare water availability for different moss communities with changes in water table and after precipitation events, θ was measured in the top 5 cm of mosses every 1 m along three 25-m transects to determine water content variability on 8 days between 21 June and 8 August 2012. θ was measured non-destructively using a portable Campbell Scientific TDR-100 system with a CS605 TDR probe. Moss species’ presence was identified at each measurement point. The elevation of each θ measurement from the water table was determined using a level datum on each transect set 1.5 m from the water table at each end; all height measurements were recorded within a few hours to avoid the potential influence of water table fluctuations. Water table position distributions of different moss communities did not fit the normal distribution; thus, Kruskal–Wallis with Mann–Whitney *post hoc* *U*-tests were used to determine the statistical difference between the groups. To compare changes in θ distributions within each different moss community with changing water table and precipitation conditions, the non-parametric Wilcoxon signed-rank tests were used. Differences in water table position distributions between moss communities and θ distributions within moss communities were deemed to be statistically significant if they met a significance level of 0.05. Analyses were performed with IBM® SPSS® Statistics 20.0 (Armonk, NY, USA).

Field drought experiment

Twenty-one intact moss/peat monoliths (~35 cm deep and 28 cm in diameter) were sampled from the rich fen (nine *Tomenthypnum* and three feather moss) and the poor fen (nine *Sphagnum*) in triplicate for treatments. The monoliths were sampled 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 into buckets and returned to their sampling locations. As such, the monoliths were hydrologically disconnected from natural groundwater processes; thus, only precipitation and other atmospheric sources were

available to the monoliths. For each *Tomenthypnum* and *Sphagnum* sampling nest ($n=3$ for each moss type), three treatments were randomly applied to each of the monoliths. The first was a low water stress (LS) treatment in which the water table was maintained between 10 and 20 cm from the moss surface (Tuittila *et al.*, 2004, suggested the optimal water table depth for *S. angustifolium* productivity is ~12 cm). A small monitoring well was installed in each LS bucket to manually monitor and adjust the water level. The second treatment was drought stress (DS) to simulate hydrological disconnection from deep water table positions. Each DS monolith bucket had holes in the bottom and was set in another intact bucket to permit the drainage and collection of precipitation and gravitational water. The third was an extreme water stress (ES) treatment in which a mobile rain shelter excluded precipitation and the water table was initially set 25 cm below the moss surface. The inverted V-shaped rain shelters were constructed of two 50 × 50-cm wooden frames covered with clear polyethylene sheeting. Two of the sides were open to permit airflow to minimize the effects of the shelter on microclimate. The rain shelter decreased photosynthetically active radiation flux (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$) by only $18.7 \pm 1.2\%$ during the study period except during carbon and vapour gas exchange measurements when the shelters were removed. The feather moss monoliths did not include different treatments as they typically do not have the capacity to draw capillary water from the underlying peat (Carleton and Dunham, 2003) and growth is known to be severely limited by high water tables (Busby *et al.*, 1978; Bisbee *et al.*, 2001). These monoliths were categorized as DS treatment because of the absence of a water table, and precipitation water was removed through holes near the bottom of the buckets. All sampling locations had less than 10% cover of vascular plants (this was consistent throughout the experiment). Moss present in each moss group included *T. nitens* and some *A. palustre* in the *Tomenthypnum* monoliths, intermixed *S. angustifolium* and *S. magellanicum* in the *Sphagnum* monoliths and predominately *P. schreberi* in the feather moss monoliths. Elevated boardwalks were installed alongside the nests to minimize disturbance during measurement. Monoliths and treatments were installed on 28 and 29 June 2011 and were left for 2 weeks before beginning θ and gas exchange measurements, which occurred between 12 July and 12 August 2011. After each measurement, the buckets were randomly placed within each nest to reduce effects of potentially varying PAR and microclimates.

θ in the upper 5 cm of each monolith was measured horizontally using a HydroSense portable TDR (Campbell Scientific Canada; Edmonton, Canada) through holes in the sides of the buckets. The HydroSense probe was calibrated for each moss type. Moss cores of each type were taken to the Wetland Hydrology Lab at the University of Waterloo

where HydroSense θ measurements as well as the mass of the samples were recorded over several days while the moss samples dried from saturation to produce a calibration curve.

The rate of community photosynthesis, or the gross ecosystem production (*GEP*; $\text{gCO}_2 \text{m}^{-2} \text{day}^{-1}$), from each field monolith was determined by the difference between measured net ecosystem exchange (*NEE*) of CO_2 under full-light conditions only (i.e. $\text{PAR} > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and ecosystem respiration (R_{tot}) of CO_2 under blackout conditions. *NEE* was measured using a clear Plexiglas chamber (30 cm high by 30 cm diameter and permitting the transmission of ~87% of PAR) connected to a closed-system infrared gas analyser (IRGA; PP Systems EGM-4; Amesbury, MA, USA). R_{tot} was measured by placing an opaque shroud over the chamber. CO_2 concentration changes were measured by the IRGA every 15 s over a 105-s interval (for linear changes) to determine the rate of CO_2 exchanges. Inputs of CO_2 into the moss community are expressed as positive values. Over the same time interval, *T* and *RH* were also measured with the IRGA to determine instantaneous evapotranspiration rates (ET_{in} ; mm day^{-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). To create a gas seal, the chamber was fit into water-filled grooves created from 3-cm diameter Tygon tubing cut in half and attached to the outside of the buckets. 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*. Sampling times were irregular throughout the day to reduce confounding effects of different light and microclimate regimes. Because moss physiological processes are more sensitive to water availability changes than vascular components (Riutta *et al.*, 2007) and there were minimal changes in vascular plant composition and visual health over the measurement period, it is assumed that differences of gas fluxes between treatments are predominantly from the mosses.

As chamber and θ measurements provided only point measurements, all measurements were combined within treatments for statistical analyses of parameters to ensure a range of environmental conditions were captured. Data for θ were not normally distributed, so the non-parametric Wilcoxon signed-rank test was used. Data for ET_{in} and *GEP* were normally distributed within each treatment, so repeated-measures analyses of variance (ANOVA) and Bonferroni *post hoc* tests were used for comparison. The normal distribution, homogeneity and homosphericity of variances were tested using the Shapiro–Wilk, Levene’s and Mauchly’s statistical tests, respectively. Differences in θ , *GEP* and ET_{in} between the treatments were deemed to be statistically significant if they met a significance level of 0.05.

RESULTS

In June through August at the rich fen, the mean daily average T in 2011 and 2012 were 17.2 ± 7.2 and 15.5 ± 7.6 °C, and mean daily RH were $70.1 \pm 24.8\%$ and $74.4 \pm 23.2\%$, respectively. At the poor fen, the mean daily average T in 2011 and 2012 were 15.2 ± 5.1 and 16.8 ± 5.1 °C, and mean daily RH were $71.2 \pm 21.3\%$ and $67.9 \pm 21.9\%$, respectively. RH and T at both sites were similar to the 30-year average for the region (Environment Canada, 2007). The 30-year average total P for June to August is 229 mm (Environment Canada, 2007). Total P at the rich fen was 109 and 227 mm in 2011 and 2012, respectively, and in the poor fen was 300 and 359 mm in 2011 and 2012, respectively.

Moss water dynamics study

The turfs of *Tomenthypnum* moss in *Tomenthypnum* 1 and 3 were situated directly on the underlying, denser peat substrates. Moss shoots in both *Tomenthypnum* 1 and 3 were between 7 and 10 cm in length, sitting on ~5–10 cm of partially decomposed moss and vascular plant litter, which was above a peaty substrate at ~15–20 cm below the surface. *Tomenthypnum* 1 and 3 were, on average (2012 field season), 30.2 ± 8.9 and 35.2 ± 8.9 cm from the water table, respectively. The *Tomenthypnum* 2 turf consisted of moss shoots ~7.5 cm in length overlaying ~10 cm of very loose, partially decomposed moss and vascular plant litter. Within this lower layer, there were large open spaces and large tree roots supporting the turf structure above (i.e. poor direct contact with underlying peat). *Tomenthypnum* 2 was situated, on average, 39.7 cm above the water table in 2012. Average θ at 2.5 cm depth in each turf was 0.07 ± 0.01 , 0.12 ± 0.02 and 0.09 ± 0.01 for *Tomenthypnum* 1, 2 and 3, respectively, during the 2012 field season, and the highest water tables beneath turf surfaces were 22.6, 31.7 and 27.2 cm, respectively. The *Sphagnum* hummock in the poor fen, situated near the monolith sampling locations described by Goetz and Price (2015), consisted of moderately dense capitula at the surface and a gradual shift in peat decomposition with depth. The average water table depth below the *Sphagnum* moss surface was 44.9 ± 4.5 cm, with a minimum of 34.9 cm, and median near-surface θ of 0.22 over the 2012 field season (data not shown). Differences in *Tomenthypnum* and *Sphagnum* θ profiles with high and low water table events are reflected in Figure 1.

Unlike *Tomenthypnum* 3, the moss at the surface of *Tomenthypnum* 1 was structurally connected with the underlying peat similar to the *Sphagnum* hummock, and its average water table elevation was close to the median in the transect study, as were changes in θ with P and water table (Figure 2). *Tomenthypnum* θ at 2.5- and 7.5-cm depths demonstrated little response to the relatively large variation in water table changes (Figure 1) and typically was controlled by the frequency and size of P events. On average,

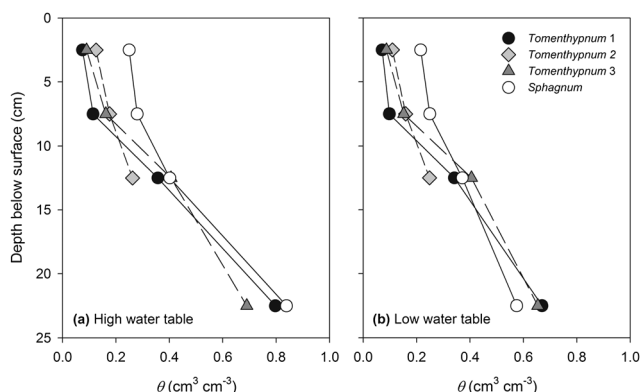


Figure 1. Vertical θ profiles (2.5-, 7.5-, 12.5- and 22.5-cm depths) of three *Tomenthypnum* turfs from the rich fen and one *Sphagnum* hummock from the poor fen under (a) high and (b) low water table conditions (~15-cm difference). High water table measurements were on days 202 and 208, and low water table measurements on days 212 and 180 for *Tomenthypnum* and *Sphagnum*, respectively, in 2012.

Tomenthypnum 1 θ increased by 0.03 during a P event (Figure 2), similar to *Tomenthypnum* 2 (0.03) and higher than *Tomenthypnum* 3 (0.01; data not shown). After wetting events, *Tomenthypnum* θ had prolonged recession limbs for several days until another P event occurred (Figure 2).

In situ Sphagnum θ at 2.5 cm retained 10–15% more water throughout the study period than did *Tomenthypnum* 1 (Figure 2). Like *Tomenthypnum*, there was little response in θ at 2.5-cm depth with the water table fluctuations, which ranged between 34.9 and 54.1 cm below the *Sphagnum* surface. *Sphagnum* θ at 2.5-cm depth only increased temporarily by 0.05–0.10 from a baseline of ~0.22 during P events and typically returned to pre-event levels quickly (Figure 2). *Sphagnum* θ at 7.5 and 12.5 cm exhibited similar trends except when water tables were high (around days 197 and 208) and θ was more responsive to water table position. The water table was consistently deeper in *Sphagnum* than in *Tomenthypnum* and less responsive to similar-sized precipitation events (Figure 2).

T within *Tomenthypnum* moss turfs 2.5 cm below the moss canopy ($n=7$) was 3.0 ± 0.4 °C cooler in the day and 1.4 ± 0.4 °C warmer at night than air 25 cm ($n=3$) above the moss surface (Figure 3b). The average daily maximum RH in the air above moss turfs was 95% at night and dropped to an average of 47% during the day (Figure 3c). RH of the air 25 cm above *Tomenthypnum* moss surface was never 100%, and the lowest RH was 22%. In contrast, RH of the air within the *Tomenthypnum* moss was saturated for 57%, 51% and 40% of the days for *Tomenthypnum* 1, 2 and 3, respectively. RH of 100% occurred mainly in the days immediately following precipitation events and also during the night (Figure 3c).

Nocturnal temperature inversions occurred at the rich fen to provide upward T (Figure 4a) and vapour density gradients (Figure 4b) that drive upward distillation fluxes

MOISTURE DYNAMICS AND PRODUCTIVITY OF BOREAL FEN MOSSES

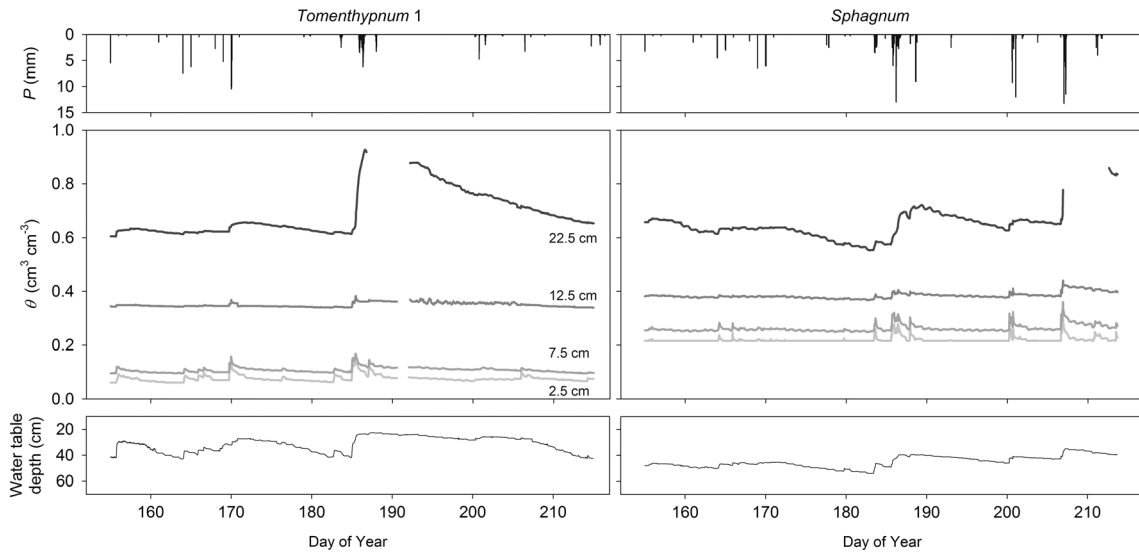


Figure 2. Time series θ changes of *in situ* measurements in *Tomenthypnum 1* in the rich fen and the *Sphagnum* hummock in the poor fen at 2.5-, 7.5-, 12.5- and 22.5-cm depths from 3 June to 2 August 2012. Precipitation events (P ; half-hourly) and water table fluctuations are also shown.

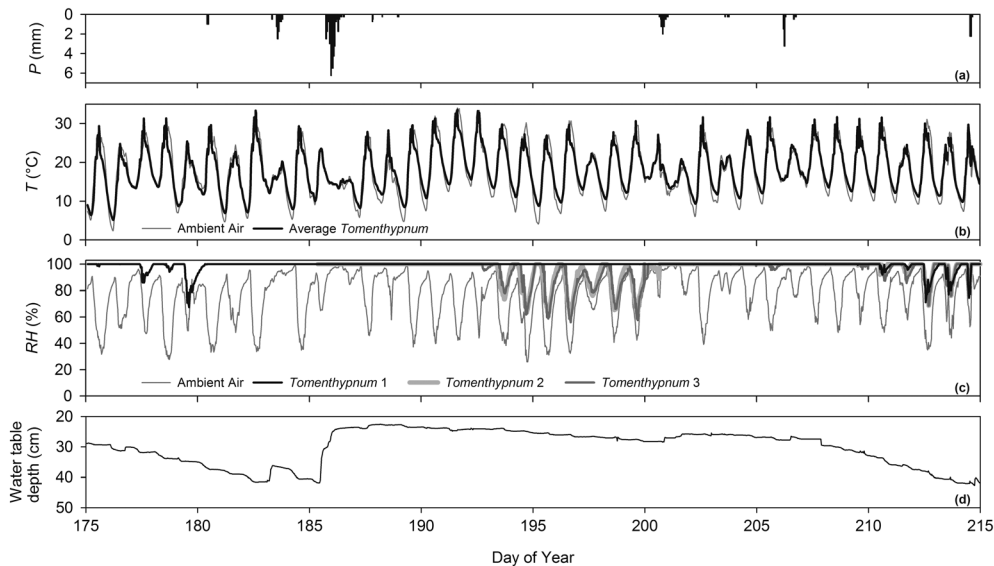


Figure 3. Time series of (a) P (half-hourly), (b) air and average *Tomenthypnum* (all three turfs) moss T and (c) RH (all three turfs) and (d) water table changes between 23 June and 3 August 2012. Air T and RH measurements were taken 25 cm above the moss surface, and moss T and RH measurements were located 2.5 cm from the moss surface. RH measurements in *Tomenthypnum 2* and 3 did not commence until day 185.

(D_d ; Figure 4c). During this period, there was a vapour density gradient (Figure 4b) from which the D_d was calculated [Equation (3)]. Based on Equation (2), condensation of vapour typically began at approximately 20:00 h and lasted until 06:00 h the following morning, averaging 10.6 h per night, while distillation occurred 10.5 h per night. Estimations of nightly average condensation and distillation rates in *Tomenthypnum*, using Equations (2) and (3), respectively, were 0.25 ± 0.04 and 0.15 ± 0.08 mm per night over the field season. Estimations of total condensation in *Sphagnum* were

0.35 ± 0.09 mm per night at the poor fen (distillation could not be determined as there was no requisite instrumentation). Nights where P events occurred were disregarded. While total nightly distillation fluxes were not significantly different between *Tomenthypnum* turfs (ANOVA; $p > 0.05$), upward vapour fluxes (and nocturnal distillation) were higher in moss turfs when the air-filled porosity was not saturated (Figure 5). For example, from days 195 to 198 in *Tomenthypnum 2* and 3 (Figure 3), the night-time vapour fluxes were 35% and 53% higher than rates in *Tomenthypnum 1* (Figure 5a), which was

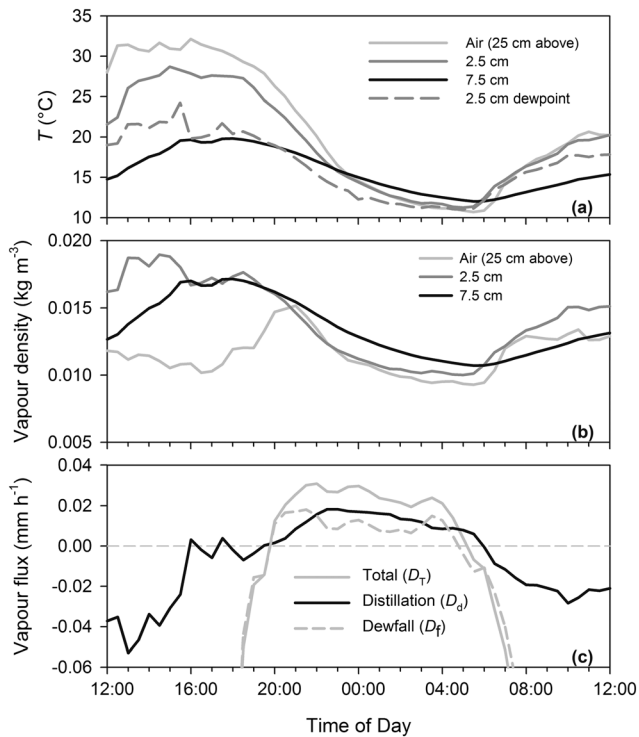


Figure 4. Diurnal variations in (a) T , (b) vapour density and (c) hourly vapour fluxes of dew and distillation above and within *Tomenthypnum* turfs for the night of day 196 of 2012. Air T and vapour density (solid light grey line) were measured 25 cm above the moss canopy, and moss T and vapour density were measured at 2.5 cm (solid medium grey line) and 7.5 cm (solid black line) below the moss canopy. The dew point temperature at 2.5 cm (dashed black line) was included. The difference between calculated total condensation flux (solid grey line) and calculated distillation flux (solid black line) is the dewfall flux (dashed grey line). Positive values indicate fluxes into the near-surface layer.

saturated. After the 13-mm rain event on day 200 when all moss turfs sustained vapour saturation, particularly at night (Figure 3), there were minimal differences in

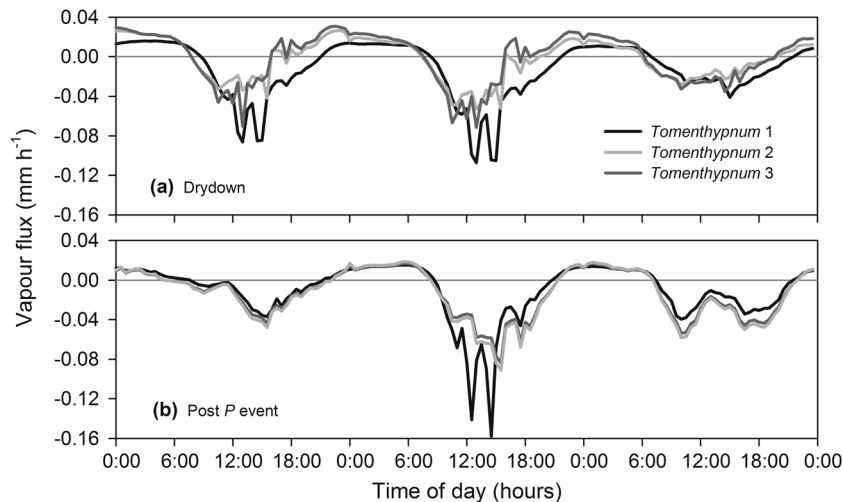


Figure 5. Time series vapour fluxes (mm h^{-1}) between the near surface (2.5-cm depth) and 7.5-cm depth in three *Tomenthypnum* turfs during (a) a drydown period (days 195–198; approximately 5 days since a rainfall event) and (b) after a wetting event on day 200 (days 202–205) in 2012. Positive values indicate fluxes into the near surface and negative values downward from the near surface.

distillation rates (Figure 5b). Assuming a total condensation of 0.25 ± 0.04 mm per night and average distillation of 0.15 ± 0.08 , the average condensation by dewfall per night, calculated as a residual, was 0.10 ± 0.09 mm; distillation therefore provided approximately 60% of water vapour for condensation in *Tomenthypnum* habitats. Over the 41 nights of measurement, the total amount of condensation that could occur at the moss surface was 12.0 and 7.8 mm in *Sphagnum* and *Tomenthypnum*, respectively.

Transect study

Over the three transects, there were generally more lawn-like moss structures than hummock and hollows as approximately 77% of moss elevations were between 17.5 and 40.0 cm above the mean 2011 and 2012 water table depths (Figure 6). This resulted in elevations 16% lower than 17.5 cm and only 7% higher than 40.0 cm (relatively steep portions of Figure 6). The five most frequent species present at each sampling point (by percent presence at the 75 points) along the three transects were *T. nitens* (80%), *P. schreberi* (47%), *A. palustre* (33%), *H. splendens* (27%) and *S. capillifolium* (11%). Grouped by their moss types, elevation distributions of *Tomenthypnum* ($n=40$, median of 34 cm), feather mosses ($n=21$; median of 34 cm) and *Sphagnum* mosses ($n=6$, median of 35 cm) from the water table were not significantly different (Figure 6; $p > 0.05$). However, the range of *Tomenthypnum* elevations (between 6 and 41 cm) extends much closer to the water table than that of feather (23–53 cm) and *Sphagnum* (19–41 cm) mosses (Figure 6). Only feather mosses occupied elevations above 41 cm above the water table. There were also other brown mosses, like *B. pseudotriquetrum*, associated with wetter

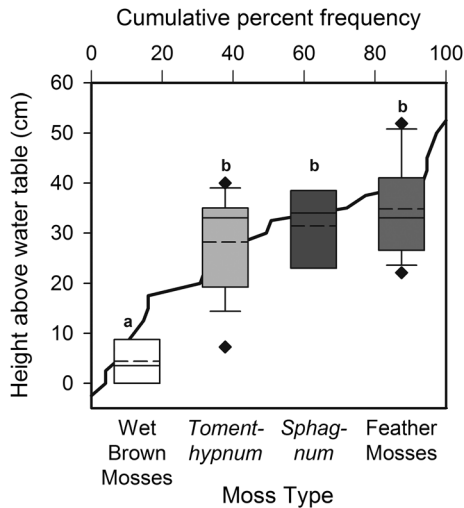


Figure 6. Boxplots of elevation distributions of *Tomenthypnum* ($n=40$), feather ($n=21$), *Sphagnum* ($n=6$) and wet brown mosses ($n=8$) from the water table in the rich fen and cumulative per cent frequency (black line) of all moss elevations above the water table. The water table depths were adjusted to the mean water table depth of the fen between 2011 and 2012 growing seasons. Boxes represent the first, second and third quartiles, and whiskers represent 10th and 90th percentiles. *Sphagnum* does not have 10th and 90th percentiles because of low counts. Plots with different letters indicate significant differences (Kruskal–Wallis; $\alpha=0.05$).

habitats (Figure 6) that were significantly different ($n=8$, median of 5 cm; $p<0.05$) but are not considered further in this analysis.

Over the study period, the median (of top 5 cm) *Sphagnum* θ (0.15) was higher than *Tomenthypnum* (0.10) and feather (0.09) mosses, but distributions of *Sphagnum* θ did not vary significantly with water table position or P events (Figure 7). Water table position did not affect feather moss median θ differences, but median θ did increase significantly after P events (Figure 7).

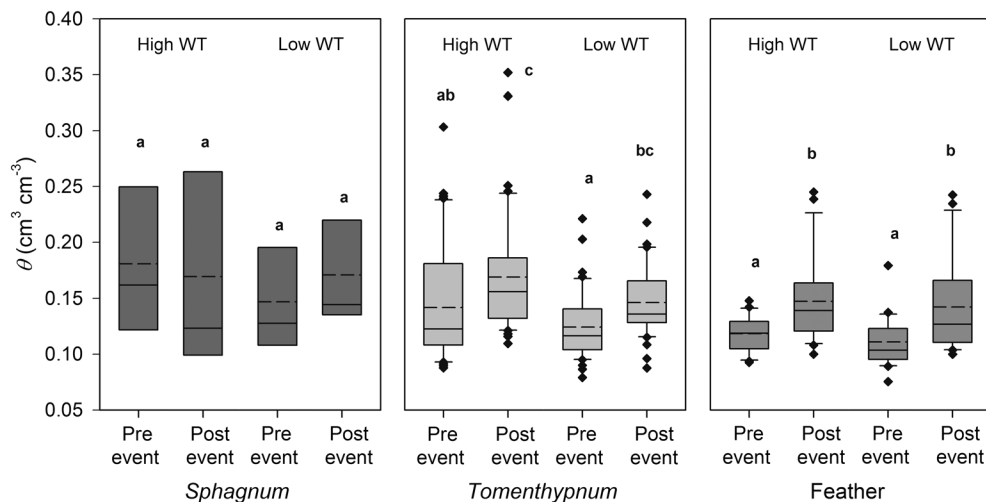


Figure 7. Boxplots of antecedent θ of near-surface (midpoint 2.5-cm depth) *Sphagnum* ($n=5$ measurement points), *Tomenthypnum* ($n=40$) and feather mosses ($n=21$) before and after P events under high and low water table conditions (~ 15 -cm difference) in 2012. θ measurements took place on days 198 (10 days since P) and 202 (after a 7-mm P event) for high water tables and 212 (4 days since P) and 217 (after a 5-mm P event) for low water tables. Plots with different letters indicate significant differences within each moss type (Wilcoxon signed-rank test; $\alpha=0.05$).

Tomenthypnum θ before and after P events was significantly different regardless of water table depth (Figure 7). Additionally, *Tomenthypnum* θ had a higher and larger range of θ values than feather mosses before and after P events regardless of water table position.

Field drought experiment

Water table depths in the LS treatments ranged between 10.5 and 21.0, and 11.0 and 22.0 cm in *Sphagnum* and *Tomenthypnum*, respectively. θ was higher in the LS treatments for both *Sphagnum* and *Tomenthypnum*, with averages of 0.26 ± 0.03 and 0.12 ± 0.02 and medians of 0.26 and 0.11, respectively, compared with the DS and extreme DS (ES) ($p<0.05$; Figure 8). Furthermore, θ was lower in ES than DS treatments for both *Sphagnum* and *Tomenthypnum* ($p<0.05$). *Sphagnum* θ was higher than *Tomenthypnum* θ under all treatments. θ in the *Tomenthypnum* treatments was within the range of the transect study surveys (generally between 0.05 and 0.20) (Figure 7). In the *Sphagnum* treatments, the capitula in LS treatments exhibited no desiccation (no appearance of whitening or bleaching from drying), while capitula in the DS exhibited some desiccation. All the capitula desiccated in the ES treatment by the end of the experiment. Similarly, *Tomenthypnum* shoots in the LS treatments were green and moist (no appearance of senescence), while there was a mix of green and brown (senescing) shoots in the DS treatment similar to many undisturbed *Tomenthypnum* turfs within the fen. Almost all shoots in the *Tomenthypnum* ES treatment were exhibiting senescence. Little or no changes in the vascular plant community structure or health occurred during the measurement period.

Tomenthypnum ET_{in} rates were higher in the LS than ES treatment ($p<0.05$) but not higher than in the DS

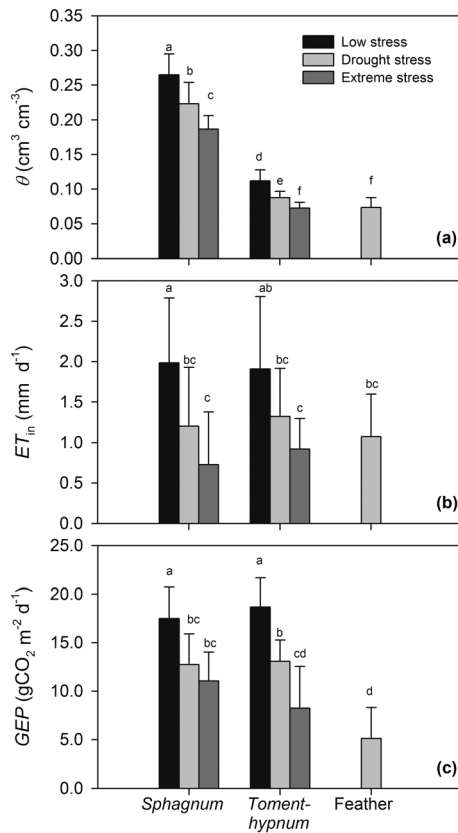


Figure 8. Total season treatment average of (a) θ (2.5-cm depth), (b) ET_{in} and (c) GEP for *Tomenthypnum* ($n=28$, including replicates and repeated measurements), *Sphagnum* ($n=33$) and feather moss ($n=24$) field monoliths in 2011. Error bars indicate one standard deviation. Letters indicate significant differences (Wilcoxon signed-rank tests for θ , repeated-measures analysis of variance and Bonferroni *post hoc* tests for ET_{in} and GEP ; $\alpha=0.05$).

treatment ($p=0.07$) (Figure 8b). There were no differences between ES and DS ($p=1.00$). ET_{in} rates of the *Sphagnum* LS treatment were higher than those of the other two treatments ($p<0.05$), which exhibited no differences ($p=1.00$) from each other. By using θ across all *Sphagnum* treatments, there was a weak, but significant, positive linear correlation with ET_{in} ($R^2=0.36$, $p=0.006$; Figure 9). Similarly, there was a weak positive linear correlation for ET_{in} and θ for *Tomenthypnum* ($R^2=0.41$, $p=0.003$; Figure 9). Feather moss ET_{in} was similar to DS and ES treatments of *Tomenthypnum* and *Sphagnum* ($p<0.05$; Figure 8) and showed no relationships with θ (Figure 9).

Tomenthypnum GEP rates were all significantly different ($p<0.05$) between treatments following trends in θ (Figure 8c). GEP in the *Sphagnum* LS treatment was higher than in the other two treatments ($p<0.05$), while there were no differences between DS and ES ($p=0.32$). By using θ across all *Sphagnum* treatments, there was a strong positive linear correlation with GEP ($R^2=0.90$,

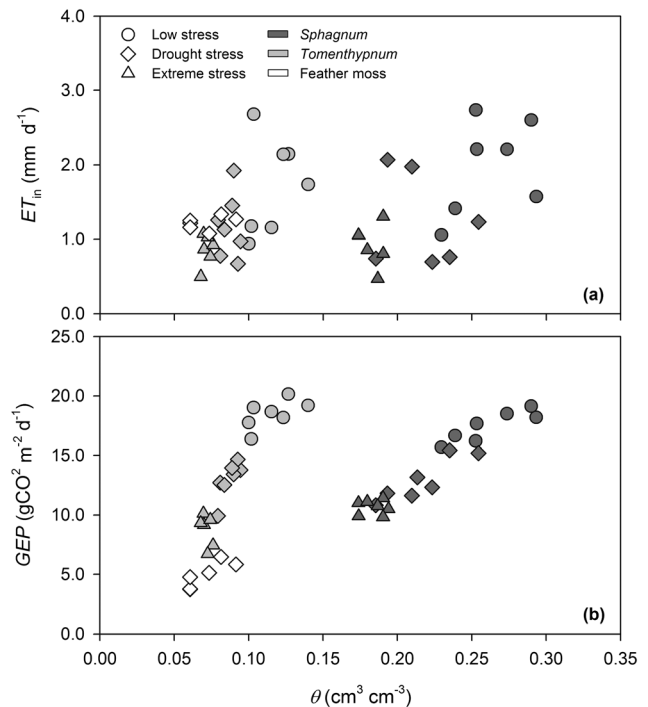


Figure 9. *Tomenthypnum*, *Sphagnum* and feather moss community ET_{in} and GEP trends with θ for all treatments (circle for low stress, diamond for drought stress and triangle for extreme drought stress) in 2011. Each symbol represents the average ET_{in} or GEP and θ for a moss type and treatment ($n=3$) taken on each day of measurements.

$p<0.001$; Figure 9b). In contrast, there was a strong correlation quadratic relationship between GEP and θ for *Tomenthypnum* ($R^2=0.90$, $p=0.004$; Figure 9). Feather moss GEP was lower than *Tomenthypnum* and *Sphagnum* ($p<0.05$; Figure 8b) and exhibited a weak positive linear relationship with θ ($R^2=0.65$, $p=0.03$; Figure 9b).

DISCUSSION

While water storage near the surface for *Tomenthypnum* was approximately half that of *Sphagnum* (Figures 1 and 2), the θ profiles demonstrated that both *Sphagnum* and *Tomenthypnum* maintained hydrological connectivity with the underlying peat to distribute water. Limited water losses from both profiles resulted in relatively stable θ over the study period (Figure 2), indicating that between precipitation events, water losses by evaporation were replaced by capillary rise (Ketcheson and Price, 2013). Because daily evapotranspiration rates from boreal peatlands can be an order of magnitude greater (cf., Brown *et al.*, 2010) than the nocturnal condensation flux, which was 0.25 mm per night in *Tomenthypnum* and 0.35 mm per night in the *Sphagnum*, from each fen, capillary rise must have supplied the remaining water, or a larger decrease in θ would have been observed. Such small moisture additions

to the mosses can be undetectable to buried TDR probes (Strack and Price, 2009) but could be critical in sustaining moisture contents during sustained evaporation periods (McCarter and Price, 2014a). Furthermore, the increased evaporative flux caused by rewetting of the moss surfaces could help drive upward capillary fluxes throughout the day by decreasing the capitula surface resistance to evaporation (Kettridge and Waddington, 2014) and causing increased pressure gradients within the moss structure. However, the more uniform vertical distribution of water within the *Sphagnum* profile suggests greater upward fluxes than that of a more constrained profile (Ketcheson and Price, 2013), like *Tomenthypnum* (Figure 1). The differences in fluxes may be explained by the disparities in the hydrophysical properties of the two moss types. In the *Sphagnum* profile, a gradual shift from large pores near the surface to smaller, but more numerous, pores at depth provided a pore-water network that facilitated upward water distribution, even when the water table was relatively low (Figure 2; Goetz and Price, 2015). For *Tomenthypnum*, the large pores in the upper layer drained quickly when wetted by rain, but considerable water was retained in the 10- to 15-cm layer (Figure 2). The water in the partially decomposed layer was thus held high in the moss profile and became available for evaporation as it moved through the upper layer of moss shoots. In the upper layer, matric pressures can potentially drop to very low levels as pore vapour pressures associated with RH well below 100% (Figure 3) try to equilibrate with matric pressure (Kettridge and Waddington, 2014). Furthermore, given the flatter tails of the water retention curves for *Tomenthypnum* compared with those of *Sphagnum* (Goetz and Price, 2015), even small reductions of θ caused by evaporative water loss will result in large changes in matrix pressure and the imposition of strong hydraulic gradients. Because ET_{in} rates from *Tomenthypnum* communities were not significantly different from *Sphagnum* (Figure 8), large hydraulic gradients within the top 10 cm of the *Tomenthypnum* must have developed to overcome the capillary barrier effect (cf., McCarter and Price, 2014b; Ketcheson and Price, 2013). *Sphagnum* profiles from undisturbed peatlands with a gradual change in pore-size distribution, hence water retention characteristics, do not experience this capillary barrier effect (McCarter and Price, 2014b). They can also undergo a greater range of water content changes (Figure 9) without experiencing desiccating matric pressures. While resources were available to monitor only one *Sphagnum* hummock in the turf water dynamics study, its structure was similar to those sampled nearby as part of the same study (Goetz and Price, 2015). Nevertheless, because its hydrological response was not replicated, it is claimed only that the hydrological response is consistent with the processes as

governed by *Sphagnum* hummocks with properties like this one. We also acknowledge that the lack of replication limits the ability to make broad conclusions about *Sphagnum* in general. We note further that other studies have linked the hydrological processes with physical structure of *Sphagnum* mosses in a similar manner (Price *et al.*, 2008; Price and Whittington, 2010; McCarter and Price, 2014a, 2014b).

Because one of the profiles (*Tomenthypnum* 2) was not directly connected to the underlying peat (being lofted on the root structure of adjacent trees), capillary rise from the water table was not a requirement for maintaining a low but steady θ in *Tomenthypnum*. Although the poorly connected *Tomenthypnum* 2 did not have the benefit of access to deeper water to maintain θ at its 12.5 cm depth, it probably did limit percolation losses through a reverse capillary barrier effect (i.e. water under tension will not readily drain out of the matrix into the more open space below). Without the deeper connection, one would expect a greater variation in θ between P events, which was observed with the higher standard deviation of *Tomenthypnum* 2 over the study period.

Vapour fluxes, distillation and dewfall

Slow daytime warming of the peat and low heat loss at night caused by the low thermal conductivity of organic materials (Petroni *et al.*, 2004; O'Donnell *et al.*, 2009) resulted in nocturnal temperature gradients with higher temperatures below the surface than in the air 25 cm above. This provided the conditions for upward vapour fluxes to occur within the moss profile (Figure 4). Between days 175 and 215 in 2012, there was sufficient vapour flow for nocturnal distillation to provide a total water influx to the upper moss layer of 4.7 mm. Some moss turfs with saturated vapour near the surface (see *Tomenthypnum* 1 in Figure 5a) had lower nocturnal vapour fluxes than those that were not saturated because of reduced vapour gradients (*Tomenthypnum* 2 and 3).

Between days 175 and 215, total condensation (combined dewfall and distillation) was 7.8 mm in the rich fen (*Tomenthypnum*) and 12.0 mm in the poor fen (*Sphagnum*). The absolute value of these fluxes will vary depending on the properties of the moss, moisture gradients and the atmospheric and radiative conditions that vary both temporally and spatially. While the total fluxes are similar, differences could be explained by their respective geographic location; the poor fen elevation was ~420 m higher than that of the rich fen and had cooler nightly temperatures. The poor fen also had fewer trees to insulate against clear-air radiative cooling (Tuller and Chilton, 1973). In the rich fen, where we could discriminate between distillation and dewfall fluxes, each constituted about half of the vapour for flux (assuming that all upward vapour is retained in the near surface and

not lost to the atmosphere above). We note that for the example given (day 196), temperatures in the air 25 cm above the surface, and the air within the moss, did not reach the dew point temperature (Figure 4a). This implies that the actual moss surface temperatures were up to 5 °C colder than the ambient air because of radiative cooling, as was found by Brewer and Smith (1997), thereby lowering the condensing surface temperature below the dew point. Several studies have also demonstrated nocturnal moisture increases at soil surfaces despite temperatures above the dew point, as a result of vapour adsorption (Graf *et al.*, 2004; Agam and Berliner, 2006). While these vapour condensation estimates are small (7.8–12.0 mm over the season and only 0.24 mm per night) compared with potential evapotranspiration losses, which can range between 0.2 and 0.4 mm h⁻¹ in similar western boreal peatlands (Brown *et al.*, 2010), they may provide critical amounts for physiological processes, especially in the early morning before evaporation removes the water (Csintalan *et al.*, 2000).

Errors associated with the energy balance for dew and distillation must be considered. While estimates of total condensation assume the radiative fluxes to be characteristic of the mosses, as R_n was measured 3.0 m above the moss surface, the footprint of the net radiometer covered large heterogeneous areas of the fen, including the surface of vascular vegetation; thus, latent energy transfers from evaporative cooling and condensation on vascular plants could affect this rate (Admiral and Lafleur, 2007), although the relative magnitude of the latent fluxes is likely representative. More intense investigations are needed to characterize the variability of nocturnal latent heat exchanges. Ground heat flux plates can also underestimate total ground heat fluxes because of the interruption of vapour fluxes and do not respond to downward-directed vapour fluxes (Figure 5) and therefore require corrections (Halliwell and Rouse, 1987). While some corrections have been applied to restored and cutover peatlands in Eastern Canada (Petroni *et al.*, 2004; Ketcheson and Price, 2013), it is difficult to apply these to fens of different vapour and moisture regimes in the western boreal region. Nevertheless, night-time G fluxes accounted for less than 1% of R_n ; thus, any corrections would have minimal effect on the total energy transfer at night for dewfall. However, the characterization of the differences between actual and measured ground heat fluxes is critical to understand total energy exchanges in western boreal fens. This is the first instance of using radiative balance within peatlands to calculate condensation fluxes in mosses. However, there remains a need for future studies on latent heat fluxes from moss layers to focus on energy balances of evaporation and condensation solely from moss surfaces. With respect to the total condensation

flux determined from the energy terms, the relative magnitude of the fluxes is probably representative, if not the difference between them.

Water sources and moss productivity

The transect study demonstrated that differences between the habitats of the three main moss groups in the rich fen are related to differences in their water holding and transport properties. Feather mosses occupied a range of elevations that were well above the water table (Figure 6) compared with the other mosses, and because θ responded solely to P events and not water table depths (Figure 7), it is logical that these mosses thrive in conditions where water is more limiting and thereby do not require a structure that promotes capillary rise from underlying substrates (cf., Skre *et al.*, 1983; Price *et al.*, 1997; Mulligan and Gignac, 2001; Carleton and Dunham, 2003). Because feather moss productivity slows at high water contents (Busby *et al.*, 1978; Mulligan and Gignac, 2001), there is likely no need for a tightly woven structure that promotes capillary rise and water retention, thus their low θ and GEP rates (Figures 8 and 9). This supports the notion that feather mosses withstand prolonged periods of desiccation (Skre *et al.*, 1983) and rely solely on precipitation (Figure 2; Busby *et al.*, 1978) and dew and distillation formation (Carleton and Dunham, 2003) for sources of moisture to maintain physiological processes (Csintalan *et al.*, 2000).

Sphagnum mosses in the rich fen also occupied positions well above the water table, albeit with a relatively small range (Figure 6), but θ changes with antecedent conditions and under both high and low water table conditions were small (Figure 7). This indicates they drained quickly when wetted by P but relied on strong capillary rise to maintain a relatively stable θ (see also Figure 2). Schipperges and Rydin (1998) and Strack *et al.* (2009) both note that a stable θ is important to sustain physiological processes. Thus, while *Sphagnum* had a high residual water content (Figure 2) on account of water storage in hyaline cells (Hayward and Clymo, 1982), precipitation water readily drained by transmitting water in the active pores (Rezanezhad *et al.*, 2012). We note the lower θ value of drained near-surface *Sphagnum* in the transect study compared with that in the water dynamics study, which may be attributed to the forested location of the former (in the rich fen) where evaporative water demands from the mosses are lower (Brown *et al.*, 2010). This means a reduced requirement for a tightly clustered community growth form (that causes better capillarity) for that species (McCarter and Price, 2014a). *Tomenthypnum* had a relatively wide range of elevations above the water table (Figure 6), similar to other studies (Vitt, 1990; Hedenäs and Kooijman, 1996). Large θ fluctuations (Figure 7) suggest

Tomenthypnum was more sensitive to direct P as a source of water compared with dependence on the water table connectivity, which should produce a more stable θ . Nevertheless, capillary rise helped to stabilize θ near the surface under long periods of evaporative water loss and a range of water table positions (Figure 7).

While capillary rise was important for both *Sphagnum* and *Tomenthypnum* to maintain a relatively high GEP (Figure 8), the drought experiment demonstrated the importance of atmospheric water for *Tomenthypnum* moss physiological processes. When water tables were within 20 cm of the moss surface, capillary rise was likely not limiting (LS treatment) in either moss and provided high moisture availability, θ of ~ 0.26 for *Sphagnum* and ~ 0.12 for *Tomenthypnum*, for high and similar ET_{in} rates (Figure 8) despite the large differences in θ . When the water table was not present in the monoliths (DS treatments), θ dropped to ~ 0.22 in *Sphagnum* and ~ 0.08 in *Tomenthypnum*, similar to the *in situ* measurements (Figure 4). However, because atmospheric water was retained in the underlying layer of partially decomposed moss, *Tomenthypnum* was able to maintain sufficient capillary rise to sustain higher GEP and ET_{in} rates than it did without atmospheric water sources (ES treatment). It was under these conditions that *Tomenthypnum* GEP was highly sensitive to water additions by P , dewfall and distillation, which provide important sources of water to maintain long-term survival in turfs not directly connected (i.e. *Tomenthypnum* 2) or relatively far from (Figure 6) the water table. In contrast, the *Sphagnum* moss monoliths experienced a much larger range of θ compared with *Tomenthypnum*, because the *Sphagnum* moss monoliths experienced deeper drainage (lower parts of the profile drained more than it did in *Tomenthypnum* in the DS treatment). However, the lower θ in *Sphagnum* was sufficient to decrease GEP rates similar to those of the ES treatment with no atmospheric water sources, supporting the notion that water table disconnection, likely below 50 cm, can shut down productivity of the moss (Strack *et al.*, 2009). Just vascular plant photosynthesis is likely remaining at this point (Riutta *et al.*, 2007). As both the *Sphagnum* and *Tomenthypnum* mosses were desiccated in the ES treatments, positive GEP values are due to continuing photosynthesis from vascular plants, as they can comprise between 70% and 90% of the gross production within moss-vascular plant communities (Riutta *et al.*, 2007).

ET_{in} increased generally with θ for both *Tomenthypnum* and *Sphagnum* (Figure 9) as more water became available by capillary rise and could be replaced; the scatter is likely due to variation in the vapour pressure deficit during measurements (Brown *et al.*, 2010). The strong relationships between θ and GEP (Figure 9) suggest the importance of maintaining high θ for growth, particularly

for *Tomenthypnum* where small additions of water (i.e. steeper curve) by precipitation, for example, can greatly increase GEP rates. θ – GEP relationships for *Tomenthypnum* and feather mosses may have been quadratic had θ been high enough to limit CO_2 diffusion and hence GEP , as seen in the results of Williams and Flanagan (1996). While *Tomenthypnum* and feather moss shoots both tolerate frequent desiccation, it is their different responses to moisture regimes that affect their hydrological niches. Busby and Whitfield (1978) and Williams and Flanagan (1996) showed feather mosses had decreased production with high water content, whereas *Tomenthypnum* mosses did not (Busby and Whitfield, 1978). Because *Tomenthypnum* frequently exhibited higher water contents without detrimental effects on its GEP (Figure 8), the mosses clearly have different physiological tolerances to high water contents that are reflected in their positions closer to the water table.

CONCLUSIONS

The results of this study indicated that not only is capillary rise essential to maintain a water content suited to peatland moss species for photosynthesis but also that atmospheric inputs can provide small but critical amounts of water for physiological processes. Despite significantly lower water contents in *Tomenthypnum* compared with *Sphagnum* and limited response to water table changes in both moss types, each moss type was able to maintain capillary rise from the water table. In this study, *Sphagnum* generated capillary rise from the water table to maintain relatively constant water content within the photosynthesizing capitula. Comparatively, while *Tomenthypnum* was also able to maintain capillary rise from the water table to the upper 5 cm of moss turfs, the porous canopy permitted the desiccation of the uppermost portions (a few centimetres) of moss shoots. This desiccation likely decreases the soil-water pressure within the near surface, thereby increasing gradients to help drive capillary flow. Dewfall and distillation were shown to provide small amounts of water (< 0.5 mm per night) to both *Sphagnum* and *Tomenthypnum* mosses that could provide moisture for early morning photosynthesis. Given that relatively small increases in *Tomenthypnum* water content provided sharp increases in production, frequent wetting by precipitation as well as dew and distillation is likely more important for *Tomenthypnum* with its relatively low water content compared with *Sphagnum*. As a result, *Tomenthypnum* mosses were able to survive on atmospheric sources alone and provided the hydrological mechanisms for *Tomenthypnum* to grow in a range of elevations from the water table. Further monitoring of a greater number of moss profiles within these fens and other fens for water

content and energy fluxes could provide a greater characterization of the hydrological processes within different moss types. Furthermore, the corroboration of the different experiments describing water content changes with environmental conditions of different mosses lends confidence to generalizations about their behaviour. These findings provide insights into the complexity of moss–water relations, given the wide range of atmospheric water and capillary water sources for production of a variety of moss types.

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