An evaluation of moisture dynamics and productivity of *Sphagnum* and *Tomenthypnum* mosses in western boreal peatlands, Canada

by

Jonathan Daniel Goetz

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Western boreal peatlands have diverse ground covers of *Sphagnum* and brown mosses that have important hydrological controls on peatland-atmosphere interactions. Since peatland mosses are non-vascular, their shoot structural morphologies and community growth forms affect the storage and fluxes of water that are critical for maintaining productivity and evaporative functions. While many of the mechanisms of capillary rise are fairly well understood for *Sphagnum* mosses, there is less information on the water dynamics in communities of *Tomenthypnum nitens*, a dominant brown moss species in northern rich fens. This study investigated how the different hydrophysical characteristics of moss and peat profiles of *T. nitens* from a rich fen and intermixed *Sphagnum angustifolium* and *Sphagnum magellanicum,* from a poor fen affect capillary flow and water retention to support evaporation and productivity; and how different groundwater and atmospheric sources of water affected these processes.

Laboratory investigations indicated volumetric water content and gross ecosystem productivity decrease with water table depth for both mosses without the advent of precipitation, with *Sphagnum* capitula retaining 10-20% more water than *T. nitens* due to its moss structure and pore connectivity with the water table. Consequently, *Sphagnum* capillary rise was sufficient to sustain both high pore-water pressures for evaporation and high water content for productivity at all water table depths due to a gradual shift in average water-retaining pore sizes with depth. The structure of *T. nitens* moss turfs, consisting of live shoots and a basal layer of old, partially decomposed shoots sometimes overlying well-decomposed peat makes capillary rise more difficult, requiring extremely low matric pressures at the surface, sometimes causing desiccation of the uppermost portions of moss shoots, and hence reduced productivity. Additional nocturnal sources of atmospheric water from dew, distillation, and vapour fluxes provide small, but potentially critical sources of water to rewet desiccated moss shoots for early morning productivity for both *T. nitens* and *Sphagnum* mosses.

Investigations in the field, however, indicated that with frequent precipitation to rewet the moss and the turf base to refill large pores, evaporative demands at the *T. nitens* moss canopy could drive capillary flow from the water table to maintain adequate θ for productivity. *T. nitens* mosses also can grow in turfs disconnected from the underlying

peat, so that the basal layer temporarily retains water from precipitation for capillary rise. Thus, while capillary connection of the *T. nitens* moss turf with the underlying peat and water table is not critical to maintain productivity, it grows in a relatively large range of elevations from the water table, compared to *Sphagnum* and feather mosses. Rewetting of the capitula and the raising of the water table by precipitation provided higher water matric pressures within the moss matrix, and along with high evaporative demands, provided the mechanisms for sufficient capillary flow for productivity. Thus, *Sphagnum* could grow in habitats far from the water table like feather mosses, although the latter did not require capillary rise for productivity.

Furthermore, disequilibrium between water vapour and liquid in the pores of *T. nitens* in the near-surface suggested pressures calculated with the Kelvin equation may not provide an accurate characterization of actual matric pressures in the moss. However, as the disequilibrium is caused 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 *T. nitens* and other mosses. These results illustrate hydrological mechanisms that explain how moss growth form and habitat are linked. As such, the *Sphagnum* and *T. nitens* mosses are well adapted to maintain capillary in their poorly drained habitats in western boreal peatlands.

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Note: Sections 2.0 and 3.0 within this thesis are written as independent manuscripts for submission for publication. As such some of the content within the manuscripts repeats previously stated information.

1.0 Introduction

The western boreal region of Canada is a highly diverse landscape consisting of coniferous and mixed-wood forests and a variety of wetlands (Vitt et al., 2003). Approximately 31 percent of the landscape is covered by organic soils of at least 30-40 cm deep as peat (Vitt et al., 2000; Vitt et al., 2003), thus peatlands comprise a large portion of the landscape. These peatlands persist primarily in areas of poor drainage supported by enhanced groundwater flow from glacial deposits in addition to direct precipitation water sources (Devito & Mendoza, 2007). The sub-humid climate of the region suggests these peatlands experience high moisture variability due variable year-to-year precipitation and high potential evapotranspiration rates (Devito et al., 2005; Johnson & Miyanishi, 2008). While these peatlands are a major store of carbon, the state of knowledge about hydrological and ecological processes of the mosses that govern peat accumulation and evaporation is relatively incomplete due to the wide diversity of peatlands in the region. Therefore, there is an increasing need to understand the ecohydrological functions of these ecosystems as increased industrial development in the western boreal region disturbs large areas of these peatlands.

While ombrotrophic, *Sphagnum*-dominated bog peatlands are numerous within the western boreal region, fens can constitute up to 63 percent of the peatland area (Vitt et al., 2000). Fens are peatlands that receive water from both atmospheric (ombrogenous) and groundwater and/or surface (minerogenous) water sources. The contribution of minerogenous water input elevates their trophic status. Thus, fens range from (relatively ombrotrophic) poor fens dominated by a ground layer of mosses of the genus *Sphagnum*, to (mineratrophic) rich fens, typically dominated by a ground layer of brown mosses such as *Drepanocladus aduncus* (Hedw.) C.F.W., *Scorpidium scorpioides* (Hedw.) Limpr, *Aulacomium palustre* (Hedw.) Schagr., and *Tomenthypnum nitens* (Hedw.) Loeske (Vitt, 2000). As mosses dominate the ground layer of these boreal peatlands they can account for a significant fraction of both carbon (Gorham, 1991) and water exchange between peatlands and the atmosphere (Lafleur & Schreader, 1994; Williams & Flanagan, 1996). However, rates of peatland productivity and evaporation depend highly on the composition of moss ground cover (Bisbee, et al., 2001; Bubier et al., 2002; Heijmans et al., 2004a; Heijmans et al., 2004b; Humphreys et al., 2006; Brown et al., 2010; Petrone et

al., 2011). With the large diversity of peatlands within western boreal Canada, it is critical to recognize how the different peatland moss types, including *Sphagnum* and brown mosses, affect peatland-atmosphere processes. In doing so, there will be better understanding of hydrological and carbon dynamics for peatland restoration and reclamation of the disturbed peatlands in the western boreal region.

Peatland mosses are non-vascular so they lack active-water transport mechanisms to control water redistribution (Proctor et al., 2007). Instead, they rely on small capillary spaces in the moss structure (Dilks & Proctor, 1979; Proctor, 1982) for water transport from underlying soil, peats, litter or mats of old, partially decomposed moss below to meet productivity demands (Proctor, 1982; Elumeeva et al., 2011). These underlying substrates can act as reservoirs of water to which surplus water can drain and then be drawn up to maintain characteristic water contents until water pressures decrease sufficiently to break capillary contact (Dilks & Proctor, 1979; Proctor, 1982; Price & Whitehead, 2001; McCarter & Price, 2014; Ch. 2). The number and range of sizes of these pore spaces has important controls on water conduction and storage (McCarter & Price, 2012). Furthermore, studies have determined that precipitation events (Strack & Price, 2009) and small additions from dew (Csintalan et al., 2000), distillation (Carleton & Dunham, 2003), and vapour diffusion (Price et al., 2009) may provide sufficient moisture to increase water availability during relatively dry periods for physiological functions. Therefore, moss growth form is physiologically critical in relation to water storage and water losses (Proctor, 2000).

As *Sphagnum* and brown mosses thrive under different hydrological and biogeochemical conditions (Zoltai & Vitt, 1995), it is critical to understand how their water-relations affect water distribution and productivity within peatlands. For *Sphagnum* mosses, water is transported and stored within a wide range and number of pore spaces between overlapping pendant branches and leaves up to the photosynthesizing canopy of capitula (Hayward & Clymo, 1982; McCarter & Price, 2012). *Sphagnum* mosses also have cellular structures called hyaline cells that retain large amounts of water. Due to its strong capillary rise function, water table depth is the most important control on *Sphagnum* moss productivity (Hayward & Clymo, 1982; Schipperges & Rydin, 1998; Strack et al., 2006; Strack & Price, 2009). Much attention has been given to the water-

relations of *Sphagnum* mosses (c.f Hayward & Clymo, 1982; Price, 1991; Schipperges & Rydin, 1998; Strack et al., 2009; Strack & Price, 2009; Price & Whittington, 2010; McCarter & Price, 2012) due to their importance in carbon accumulation (Gorham, 1991) and peatland restoration (Quinty & Rochefort, 1997; Rochefort et al., 2003; Price & Whitehead, 2004; Strack et al., 2009). There has been some research on brown mosses like *T. nitens*, a robust and widely distributed species in boreal fen ecosystems (Busby et al., 1978; Busby & Whitfield, 1978) in terms of ecology (Vitt, 1990; Vitt & Chee, 1990; Vitt et al., 1995; Bond-Lamberty & Gower, 2007) and uses in peatland restoration (Graf & Rochefort, 2010; Pouliot et al., 2012). However, there is a lack of the quantification of the water stores and fluxes of water within the moss structure. *T. nitens* relies on water transport in capillary spaces formed in stem tomentum of rhizoids (felt-like covering of rhizoids on the stem) and overlapping leaves and branches (Busby et al., 1978). While Busby et al. (1978) noted that *T. nitens* growth is controlled by a balance between evaporation and capillary flow from the water table, the capacity of the water-conducting structures to transport capillary water to the moss canopy for photosynthesis is not well understood. While *T. nitens* can lose a considerable amount of water before desiccation (Busby & Whitfield, 1978), when capillary water is exhausted by evaporation moss pressures will drop rapidly and equilibrate with the vapour pressure of the surrounding air, thereby desiccating and ceasing all photosynthetic activity (Proctor, 2000). Therefore, there is a need to quantify the role of water table position, precipitation, and vapour sources of water on *T. nitens* water content to avoid desiccation. By contrasting the hydrophysical processes that govern moss water content in *Tomenthypnum* communities with those for *Sphagnum* communities it will improve understanding of the hydrological controls on water content and productivity of different moss types in natural peatlands and for restored and reclaimed peatlands. Therefore the specific objectives of this study are to:

1. Characterize the hydrophysical properties (bulk density, porosity, specific yield, water retention, saturated and unsaturated hydraulic conductivity, theoretical pore-size distribution) of *T. nitens* and *Sphagnum* moss and peat profiles to contrast the mechanisms that control water distribution and capillary rise;

2. Determine the relationship between water table position on *T. nitens* and *Sphagnum* moss water availability, productivity and evaporation with intact moss-peat monoliths in a controlled experiment;

3. Identify and contrast the ecohydrological controls on capillary rise of water within natural *T. nitens* profiles with *Sphagnum* profiles;

4. Determine the relative importance of water table connection and atmospheric water sources on productivity in *T. nitens*, *Sphagnum* and other boreal mosses in natural fens.

1.1 General Approach

The thesis is comprised of two distinct but related manuscripts. I was primarily responsible for implementing and carrying out the field work; designing, implementing and running the laboratory experiments; and the writing of the manuscripts. The first manuscript (Contrasting hydrophysical properties and capillary rise mechanisms for productivity of *Sphagnum* and *Tomenthypnum* moss monoliths) details how different hydrophysical characteristics (bulk density, porosity, specific yield, water retention, saturated and unsaturated hydraulic conductivity, and pore size distribution) of *T. nitens* and *Sphagnum* moss architecture affect the connectivity of water-conducting pores with the underlying peat. Using a controlled water-table experiment on peat monoliths in the laboratory, the effects of the connectivity on capillary flow to support evaporation and productivity processes were determined. This manuscript also tested the applicability of determining *T. nitens* moss pressure by the vapour pressure of the surrounding air within the moss structures. The second manuscript (Ecohydrological controls on moss water content and productivity of fen moss communities in western boreal peatlands, Canada) investigates natural sources of, and distribution and variability of *T. nitens* water content compared to *Sphagnum* and other boreal mosses with changes in water table and precipitation; and how those sources affect capillary rise, water retention, evaporation, and productivity by manipulating water availability. This thesis is a comprehensive assessment on the hydrological function of the *T. nitens* moss structure that compares and contrasts the hydrological mechanisms controlling water distribution and moss growth, with that in *Sphagnum* and other fen mosses.

2.0 Manuscript 1: Contrasting hydrophysical properties and capillary rise mechanisms for productivity of *Sphagnum* and *Tomenthypnum* moss monoliths

2.1 Summary

Morphological structures of peatland mosses largely influence moss strategies of water retention and water loss to maintain the high water pressure critical for physiological functions. While many of these mechanisms are understood for *Sphagnum* mosses, there is less information on the ecohydrological processes of *Tomenthypnum nitens* moss, a dominant brown moss species in northern rich fens. This study investigates how different hydrophysical characteristics of *Tomenthypnum nitens* and intermixed *Sphagnum angustifolium* and *S. magellanicum* affect capillary flow to support evaporation and productivity and if *Tomenthypnum* moss pressure (ψ) could be determined by the vapour pressure (*e)* in the pores of the moss structure. Laboratory investigations indicate that volumetric water content (θ) and gross ecosystem productivity (*GEP*) decrease with water table depth for both mosses, with *Sphagnum* capitula retaining 10-20% more water (θ range of 0.18-0.32) than *Tomenthypnum* (0.07-0.16). A gradual shift in the fraction of pores the conduct water with depth in the *Sphagnum* structure provided the mechanism for capillary flow to sustain relatively high θ, *GEP* and evaporation (*ET*) at all water table depths. The large pores of the *Tomenthypnum* moss structure, consisting of live shoots and partially decomposed shoots below, drained with decreasing water table, thereby highly reducing capillary flow with the dense, underlying peat and causing low moss θ at 50 cm water table depth. Only when the water table was raised into the moss structure at 10 cm to sufficiently increase the matric pressure to increase θ, *GEP,* and *ET*. However, despite the significantly lower volumetric water content and different hydrophysical properties than *Sphagnum*, *Tomenthypnum* was able to maintain capillary flow throughout the experiment. Disequilibrium between *e* and ψ in the near-surface of *Tomenthypnum* suggests it does not provide accurate characterization of moss ψ. This study helps understand the mechanisms that control capillary rise in different peatland moss growth forms that can affect peat-atmosphere interactions.

2.2 Introduction

The composition of moss ground cover and water availability in boreal peatlands are key drivers of the variability of carbon accumulation (Bubier et al., 1998; Bisbee et al., 2001; Heijmans et al., 2004a; Petrone, et al., 2011) and evaporative losses within and between peatlands (Heijmans et al., 2004b; Williams & Flanagan, 1996; Brown et al., 2010). Boreal peatlands comprise a variety of different moss communities that each 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 & Clymo, 1982; Waddington et al., 2011; McCarter & Price, 2012). 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 (Gimingham & Birse, 1957; Dilks & Proctor, 1979; McCarter & Price, 2012; Voortman et al., 2013). Connectivity within moss and peat structures are a function of pore-size distribution, geometry and tortuosity, which affect both water content and unsaturated hydraulic conductivity (Price et al., 2008; McCarter & Price, 2014) that are characteristic of moss species and growth forms (Proctor, 1982). Moss capillary structures also tend to be in contact with the capillary spaces of underlying peats, litter, or mats of old, partially decomposed shoots (Proctor, 1982). These can act as reservoirs of water to which surplus water can drain and then be drawn up to maintain characteristic water contents until water pressures decrease sufficiently to break capillary contact (Dilks & Proctor, 1979; Proctor, 1982; Price & Whitehead, 2001; McCarter & Price, 2014). These upward capillary water movements are driven by water pressure gradients at the canopy surface and atmospheric demand (Proctor, 1982; Rice et al., 2001). However, when matric water pressure becomes too low for free capillary flow, capillary water is evaporated and the water pressure of the cells (osmotic pressure) drops rapidly and equilibrates with the surrounding air, thereby desiccating and ceasing all photosynthetic activity (Proctor, 2000). Therefore the capacity of peatland mosses to distribute water from underlying layers can be an important control on peatland-atmosphere processes. While several studies have noted that different moss ground covers affect carbon and evaporation

processes (Busby et al., 1978; Williams & Flanagan, 1996; Skre et al., 1983; Bisbee et al., 2001; Heijmans et al., 2004a; Brown et al., 2010; Petrone et al., 2011), more insight is required to understand the function of the different mosses and their growth form on water distribution at the surface under a range of hydrological conditions.

Sphagnum and brown mosses have fundamentally different water strategies due to their different shoot morphology and community growth forms. *Sphagnum* mosses have a dual porosity matrix consisting of water in pore spaces between overlapping pendant branches and leaves, and a number of dead-end pores within cellular structures called hyaline cells that retain large amounts of water (Hayward & Clymo, 1982; Hoag & Price, 1997). Approximately 10-20% of *Sphagnum* porosity comprises spaces within hyaline cells (van Breeman, 1995). The pore openings of these cells are between 1 and 20 μm (Clymo & Hayward, 1982) and only release water in dry conditions at threshold pressures between -100 and -600 mb (Hayward & Clymo, 1982, Lewis, 1988). Thus, hyaline cells and a large range of pore sizes in the external structure (McCarter & Price, 2012) provide a relatively high water retention capacity, compared to other mosses (Skre et al., 1983; Williams & Flanagan, 1996). Conversely, brown mosses 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). This is the case with *Tomenthypnum nitens* (Loeske) Hedw., a widely distributed brown moss species common in northern rich fens, that grows in dense turf growth forms (Gimingham & Birse, 1957) with numerous closely spaces stems and branch leaves (Busby et al., 1978) of live and partially decomposing moss litter on dense, well-decomposed rich fen peat (Vitt et al., 2009). While these mosses can dominate the groundcover of rich fen peatlands and can maintain 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 to the surface for evaporation and productivity processes.

Most mosses are poikilohydric, meaning they withstand desiccation to equilibrium of 50-90% relative humidity (Proctor, 1982). Under these desiccating conditions they become physiologically dormant, but can recover their physiological processes upon re-wetting within hours, although rates of recovery vary greatly between

species (Proctor, 1982; Proctor & Tuba, 2002; McNeil & Waddington, 2003; Hájek & Beckett, 2008). *T. nitens* can lose considerable amounts of water before desiccation (Busby & Whitfield, 1978), but the hydrological mechanisms that cause *T. nitens* desiccation are not well understood. While also poikilohydric, frequent and prolonged desiccation in *Sphagnum* mosses can negatively affect long-term productivity (McNeil & Waddington, 2003) and potentially result in death (Sagot & Rochefort, 1996) due to damage to photosynthesizing cells and collapse of hyaline cells. Upon rewetting, a pulse of respiration occurs in *Sphagnum* mosses to repair damage but normal photosynthetic activity may not recover for weeks (McNeil & Waddington, 2003). Thus it is critical for *Sphagnum* mosses to maintain capillary rise. Although recent studies have improved understanding of the importance of the hydraulic properties of *Sphagnum* structure on capillary flow from the water table to avoid desiccation (Price & Whittington, 2010; McCarter & Price, 2012; McCarter & Price, 2014), there is no information on the hydraulic conductivity of *T. nitens* and the pore structure function for water retention and capillary rise from the water table. Considering *T. nitens* does not have the water retention capacity of hyaline cells like *Sphagnum*, the relative capillary strength of *T. nitens* is unknown. Consequently, the objectives of this study were to: (1) characterize the hydrophysical properties of growth forms of *T. nitens* from a rich fen and intermixed *S. angustifolium* and *S. magellanicum* from a poor fen to contrast the mechanisms that control water distribution; and (2) determine how water table position affects the water content of *T. nitens* and *Sphagnum* profiles and their effects on moss productivity and evaporation processes.

2.3   Methods

Sampling

Peat-moss monoliths of predominantly intermixed *Sphagnum angustifolium* (C. Jens ex Russ.) and *Sphagnum magellanicum* (Brid.) and *T. nitens* were collected from Pauciflora Fen, an open poor fen (56°22'30"N, 111°14'05"W) and Poplar Fen, a treed rich fen (56°56'18"N, 111°32'35"W), respectively, near Fort McMurray, Alberta 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, with ericaceous shrubs including bog Labrador tea (*Rhododendron groenlandicum* (Oeder)), leatherleaf (*Chamaedaphne calyculata* (L.) Moench), water sedges (*Carex aquatilis* (Wahlenb.), and 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.) Schägr moss groundcover mainly on microtopographical highs, with Bog birch (*Betula pumila* (L.)) shrubs, Three-leaf Solomon's-seal (*Smilacina trifolia* (L.) Desf.) forbs, water horsetail (*Equisetum fluviatile* (L.)), and a large cover of tamarack trees and some black spruce. *T. 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* species, respectively. Both *Sphagnum* species are considered to be lawn species and can be frequently intermixed (Vitt & Slack, 1984) despite belonging to different *Sphagnum* sections.

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-litre buckets and saturated with local fen water to prevent deformation during transportation to the Wetland Hydrology Lab at the University of Waterloo. The monoliths were then drained and frozen, and then shaved to fit snugly into 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 (Figure 2-1). The tension disks were constructed of 2.3 by 30.5 cm diameter Lexan disks with a barbed fitting for drainage. Each disk used 15 μm Nitex screen with an air-entry pressure of -25
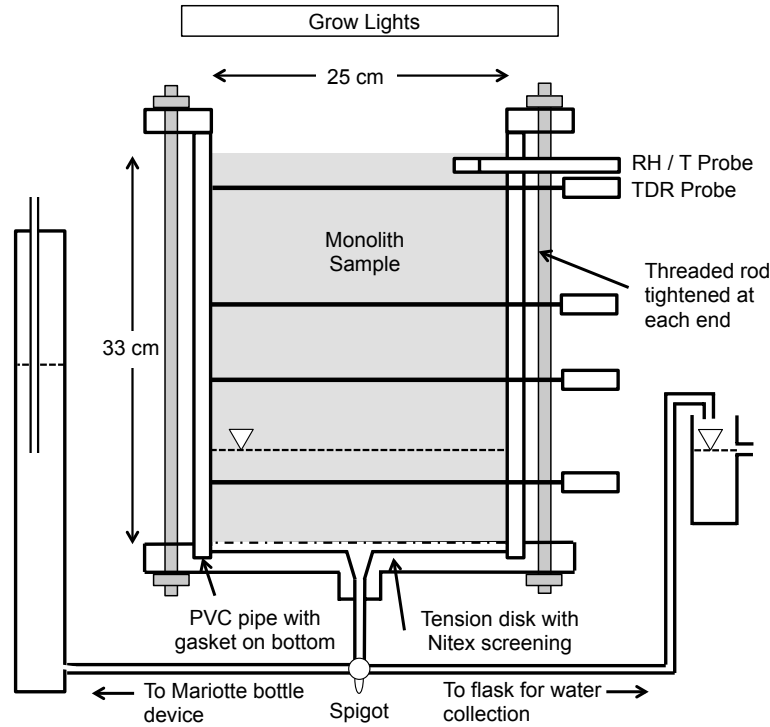
Figure 2-1 Monolith experiment design to monitor responses of θ (TDR), *RH* and *T* (only in *Tomenthypnum* 3 due to equipment availability), and CO_2 and ET_{in} fluxes (chamber and IRGA) at predetermined water table depths. A Mariotte bottle maintained constant head at each water table level. A tension disk with 15 μm pore-size Nitex screening was used to maintain tension at the bottom of the monolith with water tables below the bottom of the sample.

mb to fit atop a 0.3 cm by 22.7 cm diameter perforated surface that supported the screen. A 1.5 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 (Figure 2-1).

Tygon tubing attached to the barb of the disk was connected to a Marriotte device to provide constant pressure head for each pre-set water table depth (Figure 2-1). A spigot between the monolith and Marriotte device allowed for the collection of discharged water when the water table was lowered. Before the experiment the monoliths were saturated with low ionic strength water. 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.

The experiment was carried out in a partially climate-controlled room. Fluorescent bulbs provided photosynthetically active radiation (PAR) to the moss surface at ~150 μmol m^{-2} s^{-1} for 14 hours per day to provide the moss with sufficient light for photosynthesis (Busby & Whitfield, 1978). Relative humidity (*RH*) and temperature (*T*) were sustained at ~33% and ~27°C, respectively (vapour pressure deficit (VPD) of ~2.4 kPa); atmospheric conditions in which these mosses typically experience during growing seasons. 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, volumetric water content (*θ*) was measured with a Campbell Scientific TDR-100 system at 30-minute 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* structures and *Sphagnum* capitula. The 12.5 and 17.5 cm depths approximately correspond to layers above and below the visually determined interface (~15 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 ~15 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 gross ecosystem productivity (*GEP*; gCO$_2$ m^{-2} d^{-1}), from each monolith was determined by the difference between measured net ecosystem exchange (*NEE*) of CO$_2$ under full-light conditions and ecosystem respiration (R_{tot}) under blackout conditions (with an opaque shroud). *NEE* was measured using a clear Lexan chamber (11 by 25 cm diameter) connected to an infrared gas analyzer (IRGA; PP Systems EGM-4). CO$_2$ concentration change was measured by the IRGA every 15 seconds over a 105 second interval using

$$F = \frac{\Delta \cdot M}{N} \cdot \frac{V}{A} \cdot CF \qquad\qquad \textbf{Equation 2-1}$$

where F is the CO_2 gas flux (gCO_2 m^{-2} d^{-1}), Δ is the linear change of CO_2 concentration with time (μmol mol^{-1}), M is the molar mass of CO_2 (44.01 g mol^{-1}), N is the molar volume of a gas (0.224 m^3 mol^{-1}) at a standard temperature and pressure, V is the temperature corrected volume within the chamber (m^3), A is the area of the ground surface covered by the chamber (m^2), and CF is the conversion factor from ppm to mol (1 ppm = 10^{-6} mol). Inputs of CO_2 to the moss community are expressed as positive values. Every 5 seconds over a 35 second period, T and RH were measured with the IRGA to determine instantaneous evapotranspiration rates (ET_{in}; mm d^{-1}) 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) where

$$ET_{in} = 86.4 \frac{MVC}{A} \qquad\qquad \textbf{Equation 2-2}$$

and where M is the slope of the vapour pressure within the chamber over time (gH_2O m^3 s^{-1}), V is the temperature corrected volume within the chamber (m^3), C is the calibration factor (1.534) to account for vapour absorption within the chamber (dimensionless), A is the area of the ground surface covered by the chamber (m^2), and 86.4 is the conversion factor from gH_2O m^3 s^{-1} to mm day^{-1}. 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 quantify 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. RH and T were measured using a Vaisala HMT337 system (thermocouple for T and thin film polymer capacitive sensor for RH, with $\pm1\%$ RH accuracy and equilibrium response time less than 60 sec) in the air-filled pores at 30-minute intervals. Parallel instrumentation was not available for *Sphagnum*. For a given pore-water pressure, the vapour pressure of the air above capillary menisci are assumed to be in equilibrium.

As such, the ψ of a porous medium can be measured using the Kelvin equation (Stephens, 1996) where

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

Equation 2-3

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). Some studies (Alvenäs & Jansson, 1997; Kellner, 2001; Kettridge & Waddington, 2013) noted that the assumption that the pore-air vapour pressure is in equilibrium with the pore-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 the 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 calculated from Equation 2-3 can characterize the available water for *Tomenthypnum* moss communities in the near-surface, or whether equilibrium conditions are present.

Peat Parameterization

Following the monolith experiment, each monolith was frozen and cut into 5 cm high and 10 cm diameter cores, centered every 2.5 cm from the surface until 25 cm depth, and fitted into PVC rings of equivalent size (*Tomenthypnum* profile 2 did not have samples below 20 cm due to large roots). To determine water retention and unsaturated hydraulic conductivity of the sections, the following methods were used. The 5 cm subsections were saturated and placed on tension disks with 25 μm Nitex screening (air-entry pressure of less than -30 cm). Matric water pressures (ψ_m) of -3, -6, -12, -20, and

-30 mb (reversed to -12, -6, and -3 mb for hysteresis) 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}) was tested on each sample with methods used from McCarter & Price (2014) modified from Price et al. (2008). A tension disk (25 μm 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) out of the flask. After allowing Q to equilibrate for 60 minutes, a constant Q was measured over regular time intervals and used to determine K_{unsat} using Darcy's law.

Saturated hydraulic conductivity (K_{sat}) was measured using a Darcy permeameter. Due to the very fragile and porous nature of the moss samples, a modified wax method (Hoag & Price, 1997) was used to prevent preferential flow. As in McCarter & Price (2014), 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. A constant Q was measured over regular intervals to determine K_{sat} using Darcy's law.

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

$$\phi = 1 - \left(\frac{\rho_b}{\rho_p} \right)$$
<div align="right">**Equation 2-4**</div>

where ρ_p is particle density as determined using the liquid pycnometer method with kerosene for displacement (Blake & 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. 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 0.01. Analyses were performed with IBM® SPSS® Statistics 20.0.

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

$$r = \frac{2\gamma\cos\beta}{\rho g h},$$

Equation 2-5

and where γ is the surface tension of water, β is the contact angle (40° for moderately hydrophobic soils (Carey et al., 2007)), ρ is the density of water, and g is gravity acceleration. Total water-filled pore fraction (ϕ_{vw}) was determined by

$$\phi_{vw} = \frac{\theta_\psi}{\phi}$$

Equation 2-6

where θ_ψ is the volumetric soil water content for a given ψ and ϕ is the porosity. A sample with a higher fraction of water-filled pores for a given pore diameter compared to 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.

2.4   Results

Hydrophysical properties and hydraulic conductivity

Undecomposed *Tomenthypnum* moss (shoot lengths of 5-10 cm) overlaid denser, less porous peat. 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 and S_y ($p < 0.01$) compared to the *Sphagnum* capitula

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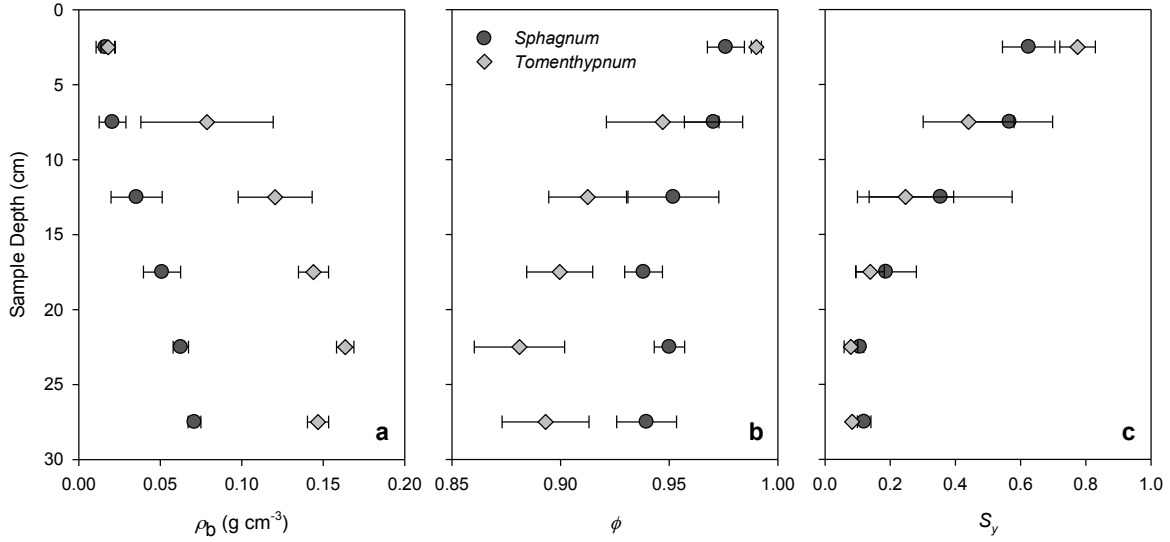
Figure 2-2 Mean (a) bulk density, (b) porosity, and (c) specific yield for *Tomenthypnum* and *Sphagnum* profiles, n of 5-8 and 2-6 in from 0-20 and 20-30 cm, respectively. Depths are the mid-depth of each 5 cm sample. Error bars represent one standard deviation.

canopy (Figure 2-2). ρ_b increased with depth in both moss types, although *Tomenthypnum* ρ_b was significantly higher (p < 0.01) with 0.147 ± 0.007 compared to 0.071 ± 0.004 g m^{-3} for *Sphagnum* (Figure 2-2). ϕ was significantly higher (*p* < 0.01) in the *Sphagnum* moss below 10 cm despite the reverse in the upper 5 cm (Figure 2-2). S_y declined with depth for both moss types, from 0.62 to 0.12 and 0.78 to 0.12 for *Sphagnum* and *Tomenthypnum*, respectively (Figure 2-2).

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 ± 0.05 compared to 0.51 ± 0.05 for *Sphagnum* mosses (Figure 2-3). At lower matric pressures, *Sphagnum* moss retained approximately 0.22 more water, on average, with each pressure drop (Figure 2-3). θ decreased an average of 0.25 ± 0.03 and 0.11 ± 0.03 for *Sphagnum* and *Tomenthypnum* mosses, respectively, for a pressure drop from -3 mb to -30 mb. Conversely, at greater depths, the *Tomenthypnum* sample generally retained more water than the *Sphagnum* at lower matric pressures (Figure 2-3). Samples from 22.5 cm depth experienced the highest water retention for both profile types with no systematic differences in retention curves at tested matric pressures (Figure 2-3). Hysteresis of θ

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occurred in each sample following similar, but lower θ, patterns to the drying curve (data not shown).

At the 2.5 cm depth (Figure 2-4) the theoretical pore-size distribution indicated that near-surface *Tomenthypnum* moss had a relatively low fraction of water-filled pores at any of the given theoretical pore sizes, compared to *Sphagnum*. In this upper layer, ~21% of the water in *Tomenthypnum* pore spaces occurred in pores < 661 μm, and about 14% of the water is in pores <99 μm. Thus, 79% of its void space is in pores > 661 μm, and 7% of its pore sizes were between 99 and 661 μm. In comparison, at this depth, ~45% of the water in *Sphagnum* pore spaces occurs in pores < 661 μm, and about 29% of the water is in pores < 99 μm and hyaline cells. Thus, in near-surface *Sphagnum*, about 55% of its void space was in pores > 661 μm, and 20% of its pore sizes are between 99 and 661 μm. With depth in the profiles, the proportions of pore sizes became less clear between profiles, both within and between moss types until 22.5 cm (due to high variability). But within each profile of each moss type, while the portion of pores less than 99 μm increased with depth until 17.5 cm, the proportion of pores greater than 99 μm and less than 661 μm remained relatively consistent. For *Sphagnum*, the proportion of pores between 99 and 662 μm ranged, on average per depth, between 0.18 and 0.23 of the total porosity. For *Tomenthypnum*, the same pore sizes ranged between 0.07 and 0.12 of the total porosity; approximately half that of *Sphagnum*. *Tomenthypnum* 3 exhibited denser and more decomposed organic material at 7.5 cm depth than the other *Tomenthypnum* monoliths. Additionally, in the 7.5 and 12.5 cm layers, a greater proportion of pore spaces <661 μm were water-filled in *Tomenthypnum* compared to *Sphagnum* (Figure 2-4), suggesting the partially decomposed *Tomenthypnum* moss was characterized by smaller pores, thus better water retention over a range of pressures, compared to *Sphagnum*.

Figure 2-3 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.
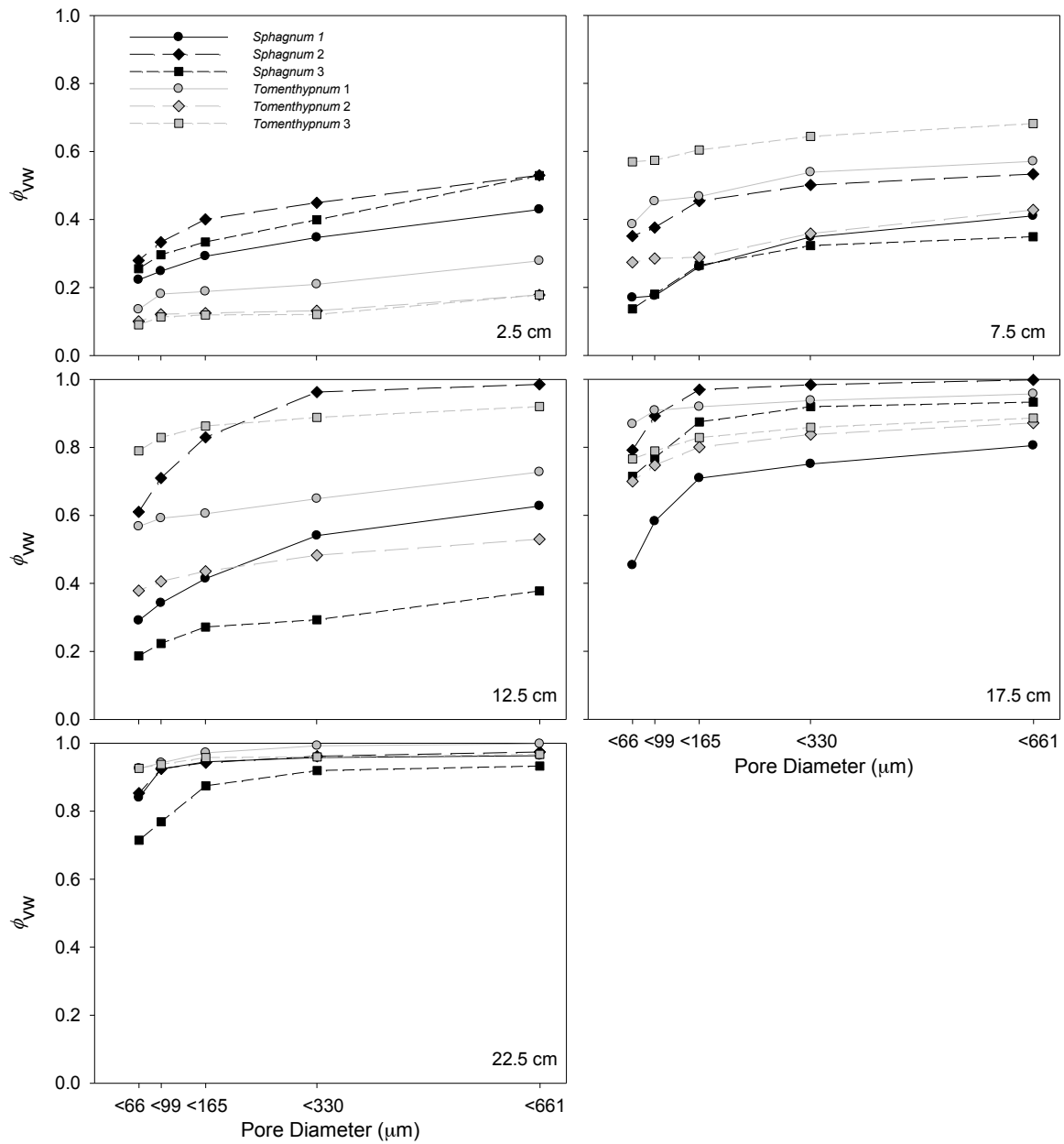
Figure 2-4 Relationships between theoretical pore-size distribution and the total fraction of water-filled pores for each *Tomenthypnum* and *Sphagnum* sampling depth. One sample profile (0-25 cm) was used per monolith; *Tomenthypnum* profile 2 did not have a 22.5 cm sample. Depths are the mid-depth of each 5 cm sample.

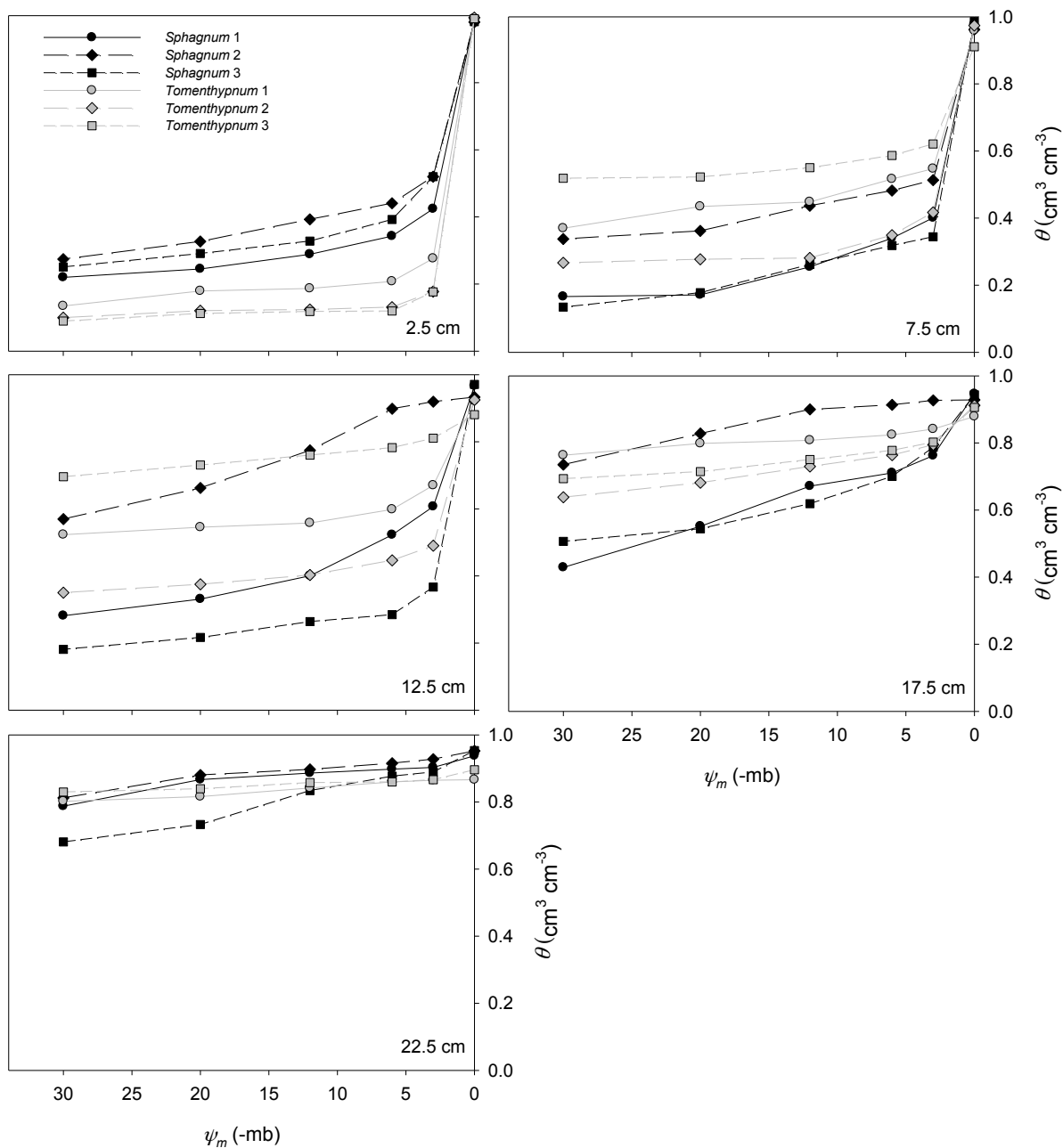**Figure 2-5** Hydraulic conductivity and pressure head relationships, $K(\psi_m)$, for each *Tomenthypnum* and *Sphagnum* sampling depth. One sample profile (0-25 cm) was used per monolith; *Tomenthypnum* profile 2 did not have a 22.5 cm sample. Depths are the mid-depth of each 5 cm sample.
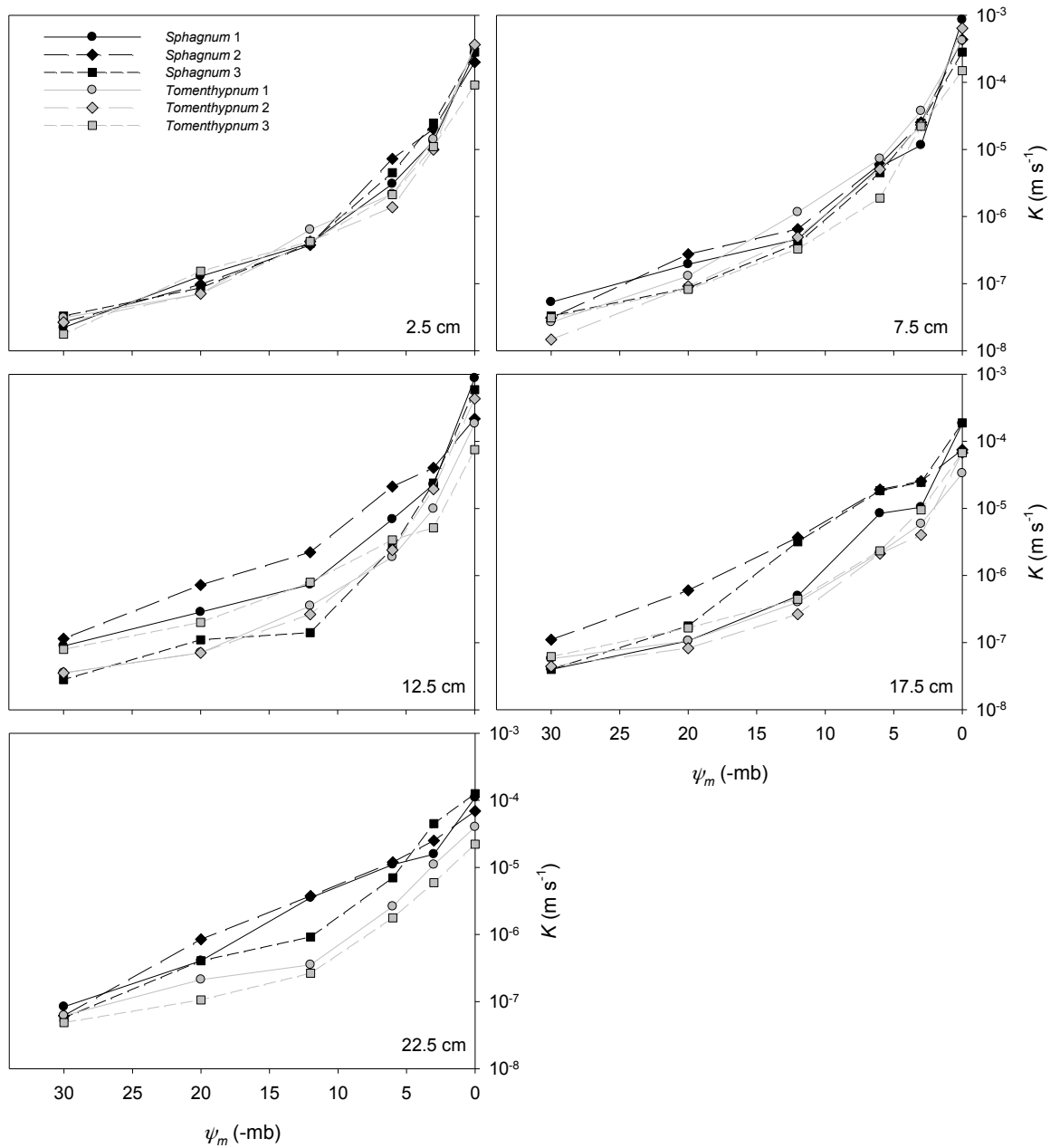
Monolith experiment

Measurements of θ within the monoliths (Figure 2-6b) displayed similar drying trends compared to the water retention curves (Figure 2-3) at all depths. The length of time for the equilibrium of θ at all depths was, on average, 9 days between water table depths when lowering the water table and, on average, 20 days with raising the water table. In the near-surface layer (2.5 cm), *Sphagnum* moss retained more water at all water table positions than *Tomenthypnum* moss (Figure 2-6b). At 50 cm water table depth, *Sphagnum* and *Tomenthypnum* θ at 2.5 cm depth decreased to 0.21 ± 0.01 and 0.07 ± 0.004, respectively. Upon visual inspection at this water table, the *Sphagnum* mosses were predominately green with only a small proportion of dried, white capitula. The *Tomenthypnum* mosses showed little change in colour, but were dry and crispy to the touch. However, 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 ± 0.01) and only when the water table position was raised to 10 cm was an increase observed (to 0.11 ± 0.01) (Figure 2-6b).

Sphagnum sustained sufficent and a larger range of moisture to maintain higher average ET_{in} fluxes throughout the experiment (ranging 4.1 to 7.8 mm d^{-1}) than *Tomenthypnum* (ranging 2.4 to 7.9 mm d^{-1}) (Figure 2-7a), despite greatly different θ. Note the higher values for *Sphagnum* profile 2, which was previously shown to have higher water retention (Figure 2-3). While *Tomenthypnum* exhibited a strong increase in ET_{in} with θ, *Sphagnum* ET_{in} was less responsive (Figure 2-7a). *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 (Figure 2-7a). Using θ across all monoliths there was a moderately strong and significant positive linear relationship with ET_{in} for *Sphagnum* ($R^2 = 0.55$, $p < 0.001$; Figure 2-7) and a strong and significant positive linear relationship with ET_{in} for *Tomenthypnum* ($R^2 = 0.88$, $p < 0.001$; Figure 2-7). Despite the higher average evaporative loss from the *Sphagnum* mosses, they sustained sufficient θ to support positive *GEP* (ranging from an average of 0.8 to 8.0 gCO$_2$ m^{-2} d^{-1}) across all water table positions (Figure 2-7b). θ and *GEP* relationships
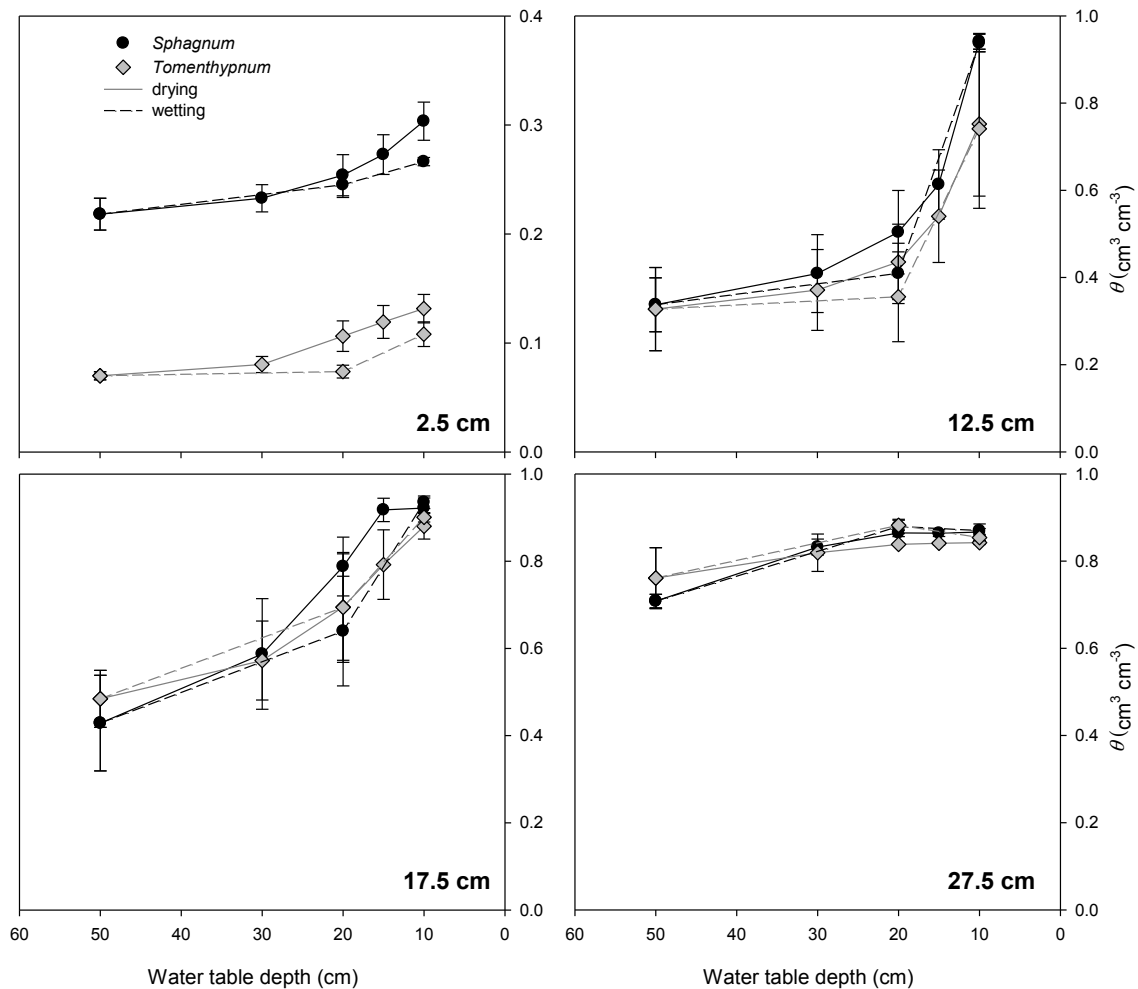
Figure 2-6 Changes in average θ at 2.5, 12.5, 17.5, and 27.5 cm depth (n=3 monoliths per moss and depth) of *Tomenthypnum* and *Sphagnum* with each subsequent water table change. Water table depths of 10, 15, 20, 30, and 50 cm and rewetting to 20 and 10 cm were used. Note the different scale used for θ at 2.5 cm than the other depths.

across all *Sphagnum* monoliths resulted in a moderately strong and significant positive linear relationship ($R^2 = 0.71$, $p < 0.001$; Figure 2-7). Conversely, when the water table dropped below 20 cm, *Tomenthypnum* desiccated and there was insufficient water (low θ and ψ values) to maintain both evaporative demands and *GEP* (Figure 2-7b). *GEP* essentially ceased below θ of 0.10 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
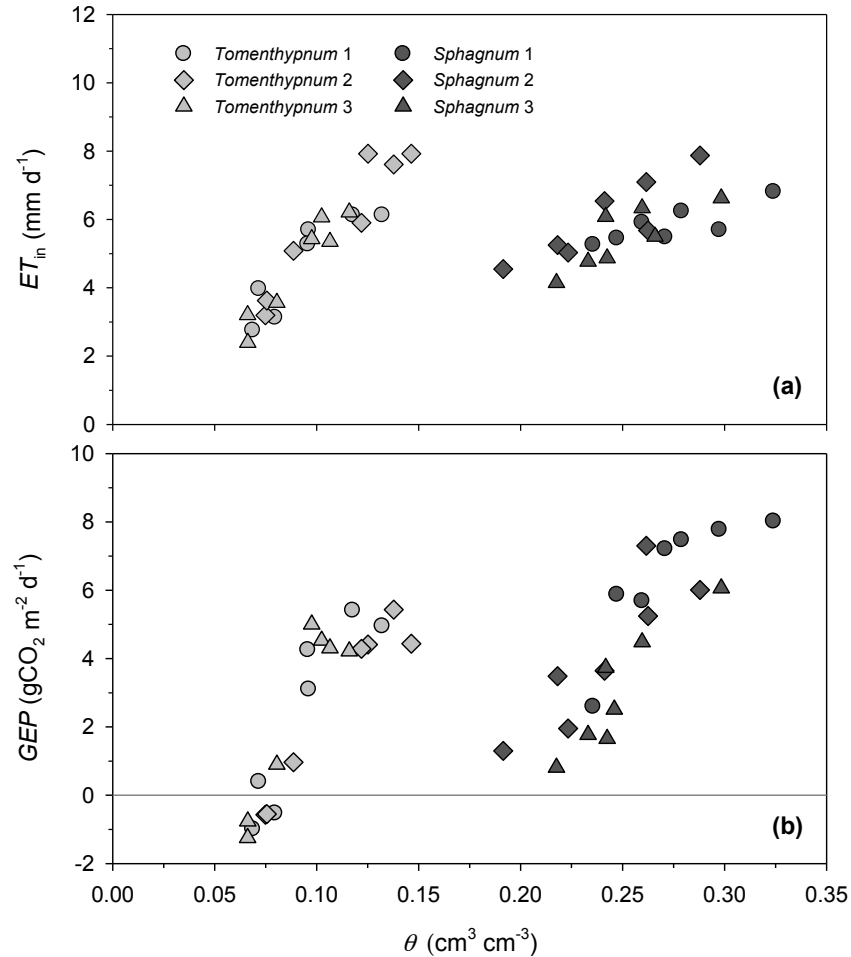
Figure 2-7 Relationships between *Tomenthypnum* and *Sphagnum* moss volumetric water content (θ) at 2.5 cm depth with (a) evaporation (ET_{in}) and (b) gross ecosystem productivity (*GEP*). Each symbol represents the average value of four measurements of each variable (θ, ET_{in}, and *GEP*) taken at each water table position.

water table, following a similar trend as θ. θ and *GEP* relationships across all *Tomenthypnum* monoliths resulted in a strong and significant quadratic relationship ($R^2 = 0.88$, $p < 0.001$; Figure 2-7).

RH and *T* within the monolith experiment room were relatively stable around 33% and between 27 and 28°C, respectively, over the measurement period (Figure 2-8a,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 (Figure 2-8a). *RH* increased to 58.7% and 99.0% with raising the water table to 20 and 10 cm (Figure 2-8a). 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
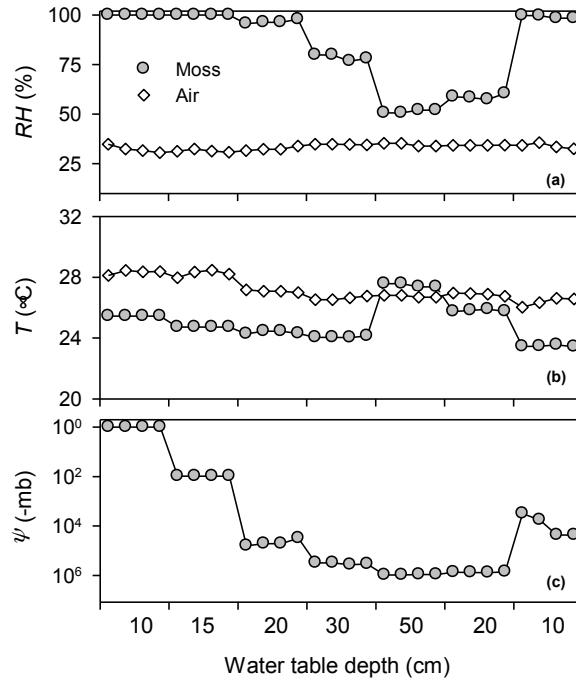
Figure 2-8 Changes in (a) daily mean relative humidity (*RH*) and (b) temperature (*T*) of *Tomenthypnum* 3 moss (2.5 cm depth) and the monolith room, and subsequent changes in (c) moss pressure (*ψ*), with each water table interval with lowering the water table depths of 10, 15, 20, 30, and 50 cm and rewetting to 20 and 10 cm. Mean daily values were from days that water content and gas flux measurements were completed.

cooler) (Figure 2-8b). 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 Equation 2-3, from 0 to -97 mb (Figure 2-8c). With the small decrease in moss *RH* from near saturation at 20 cm water table depth, *ψ* values fell considerably to -4.1×10^4 mb (Figure 2-8c). At 50 cm water table depth, *ψ* fell to -9.5×10^5 mb and only increased to -1.4×10^4 mb when *θ* at 2.5 cm increased at 10 cm water table depth (Figure 2-6).

2.5   Discussion

Mosses at the near-surface of both *Tomenthypnum* and *Sphagnum* profiles were characterized by low ρ_b, high *ϕ*, and high S_y, which are consistent with ranges observed in other studies for both live *Sphagnum* (Boelter, 1966; Hayward & Clymo, 1982; Price & Whittington, 2010; McCarter & Price, 2012) and brown mosses (Petrone et al., 2011; Voortman et al., 2013). Even though both *Sphagnum* and *Tomenthypnum* had high air-entry pressures between -3 and 0 mb matric pressure, approximately half the total

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Sphagnum porosity held water within capillary spaces and hyaline cells, compared to 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 μm). At the given pressures only external pore spaces greater than 66 μm were draining. Furthermore, as *Sphagnum* has approximately 20% more water held in small pores, including hyaline cells, than *Tomenthypnum*; it had the structure to maintain higher water retention with low 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 μm) that easily allows drainage of gravitational water; and the relatively low proportion of small pores (<99 μm; Figure 2-4), 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 80-90% of water held external when sufficiently wet (Busby & Whitfield, 1978).

Despite the low water retention, the relative proportion of water-conducting pores in *Tomenthypnum* may not be different than in *Sphagnum* (Figure 2-5). *Sphagnum* and *Tomenthypnum* $K(\psi_m)$ were comparable to similar studies of *Sphagnum* (Price & Whittington, 2010; McCarter & Price, 2012) and other brown mosses (Voortman et al., 2013). While the pore spaces in tomenta are approximately the same size as hyaline cell openings (~10 μm; Proctor, 1982), hyaline cells can have internal diameters upwards of 200 μm (Hayward & Clymo, 1982) and comprise of 10 to 20% of the pore space in *Sphagnum* (van Breeman, 1995). 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 peatland mosses. The relatively small differences in K_{sat} and K_{unsat} (Figure 2-5) 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 μm) with peat depth, indicating decreased peat particle size and increased compaction caused by decomposition (Boelter, 1966; Carey et al., 2007),

Sphagnum peat preserved relatively larger pore spaces (>99 μm) as the moss structure remained more intact (Johnson et al., 1990). This, corroborated by the physical properties (Figure 2-2), indicates that the *Sphagnum* peat was composed of lower ρ_b material with higher ϕ of primarily fibric peat (Boelter & Verry, 1977). The higher water retention capacity of *Sphagnum* 2 as likely due to variability in the sample location and was likely in an area of lower and more decomposed peat than the other monoliths, though still fibric in composition. 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 & Verry, 1977) characteristic of the fast decomposition rates of *Tomenthypnum* moss and vascular plants in rich fens (Szumigalski & Bayley, 1996; 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 (~50%) of pore spaces smaller than 99 μm 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 (Figure 2-5). 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 (McCarter & Price, 2014; Voortman et al., 2013). This was affected by the changes in the physical properties with depth, which is much greater in *Tomenthypnum* (Figure 2-2).

The relatively high *Sphagnum* capitula θ and the observed hysteresis when rewetting from 50 to 20 and 10 cm in the monolith experiment (Figure 2-6) suggests *Sphagnum* maintained upward capillary flow under moderate pressures. The gradual increase in the abundance of small pore sizes (≤99 μm) with depth indicates a transition from a structure characterized by numerous overlapping branches and leaves within

living *Sphagnum* (Turetsky et al., 2008) to a more dense, partially decomposed peat. However, as a large fraction of large pores (between 99 and 661 μm) remained in the *Sphagnum* structure compared to *Tomenthypnum* (Figure 2-4), for *Sphagnum* to have similar or greater θ (see 12.5 cm in Figure 2-6) would require higher pressures, on average (see 12.5 cm in Figure 2-3). 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 & Waddington, 2013), 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 capillary flow to decrease. The removal of the remainder of capillary water would require lower water tables (well below 50 cm) to lower pressures between -100 and -600 mb at the capitula to drain the hyaline cells after all external water has been exhausted (Hayward & Clymo, 1982; Lewis, 1988). When hyaline cell drainage occurs, the moss desiccates causing the *Sphagnum* to turn white, serious cell damage, hyaline cell collapse, and degradation of chlorophyll (Gerdol et al., 1996). When the water table was dropped to 50 cm, only a small proportion of capitula in each *Sphagnum* monolith exhibited this characteristic. 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 and smaller pore-size distribution in the capitula (Hájek & Beckett, 2008; McCarter & Price, 2012). The relationship between moss *GEP* and θ is in agreement with other studies for *Sphagnum* (McNeil & Waddington, 2003; Strack et al., 2009; Strack & Price, 2009) despite stressed environmental conditions (Shurpali et al., 1995). In the experiment, *Sphagnum* θ was not high enough to limit CO_2 diffusion into the *Sphagnum* moss, as was exhibited in other studies (Rydin & McDonald, 1985; Silvola & Aaltonen, 1984; Williams & Flanagan, 1996; Schipperges & 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 &

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 pore-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 and up through the tomenta of rhizoids and overlapping leaves to the moss canopy. As such, the moss maintained both positive *GEP* rates and relatively high ET_{in} rates. As the surface of the *Tomenthypnum* canopy is more porous than *Sphagnum*, the depth of turbulence penetration is likely greater (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, Figure 2-2). 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 matric pressure and high evaporative demand in the *Tomenthypnum* structure decreased θ at the near-surface (Figure 2-6). 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 (Figure 2-8b), and there was still positive *GEP* (Figure 2-7b). As such, only the smaller pores sizes could still maintain water conduction. At 50 cm water table depth as θ decreased further, capillary water lost to evaporation could not be replaced and the moss cell pressures at the top of the moss canopy likely rapidly equilibrated with the surrounding air, greatly reducing *GEP* rates (Figure 2-7) and increasing moss T. 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. However, vapour diffusion likely still occurred from the underlying peat layers as ET_{in} remained positive (see Figure 2-7; Cahill & Parlange, 1998; Price et al., 2009) and the peat remained sufficiently wet (17.5 cm depth; Figure 2-6).

Because *Tomenthypnum* can lose considerable amounts of water before desiccation (Busby & 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 & Whitfield (1978) and productivity ceased with low water tables (Figure 2-7), *Tomenthypnum* ψ may have dropped below -1×10^{5} mb where photosynthesis is known to cease in poikilohydric mosses (Busby & 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 matric 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 & Whitehead, 2001; Price & Ketcheson, 2009; Ketcheson & Price, 2013; McCarter & Price, 2014).

The results of this study provide further evidence that growth of *Tomenthypnum* is controlled by a balance between the evaporation rate and water transport to the canopy surface, as originally proposed by Busby et al. (1978) and tolerates frequent desiccation between wetting events. Moisture additions by precipitation, dew (Csintalan et al., 2000), and distillation (Carleton & Dunham, 2003) may provide small amounts of water to the moss surface when water tables are low. Considering *Tomenthypnum* mosses can grow in isolation from the water table or on large tree roots, as evident in the rich fen (see Ch. 3), the importance of precipitation, dew, distillation and vapour fluxes cannot be ignored (Ch. 3).

Vapour and moss pore water pressure

While there were clear trends in ψ with water table position and moss-peat connectivity, 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 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 pore-water 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 ~0.10 (Figure 2-8c) and calculated ψ was -4.1×10^4 mb (equilibrium RH of 98.5%). However, according to $\theta(\psi_m)$ relationships (Figure 2-3), θ of 0.10 occurred at approximately -30 mb: three orders of magnitude higher than the calculated ψ. Furthermore, in Price et al. (2009), 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 & Whitfield (1978) and Proctor (2000), providing a measure of the underestimation caused by assuming equilibrium conditions. To further add to the complexity, vapour fluxes (Figure 2-7a) 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.

2.6 Conclusion

Peatland moss composition can have a significant impact on the hydrophysical properties of the 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, the properties still both provided both moss types the necessary mechanisms for capillary rise. The gradual increase in the abundance of

smaller pores (pore sizes <99 μm) and maintenance of the proportion of larger pores between 99 and 661 μm with depth 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 than *Tomenthypnum*, a large fraction of the water was retained within hyaline cells. As this fraction of water is inactive under high pressure (greater than -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 structure of both *Sphagnum* and *Tomenthypnum* 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. However, when water tables were low, 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 that the basal layer of partially decomposed moss above the peat decreased the average pore size and provided greater connection with the denser peat, to support a small amount of capillary action with low water tables. Moreover, 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 variation. 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 capillary rise and 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 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.

3.0 Manuscript 2: Ecohydrological controls on moss water content and productivity of moss communities in western boreal peatlands, Canada

3.1 Summary

As different peatland moss communities have growth forms adapted to specific hydrological conditions, variability in moss composition can have strong influences on water storage and capillary rise mechanisms that are critical to sustain essential productivity and evaporation functions of peatlands. The controls of different water sources, and water redistribution, on the productivity of *Sphagnum*, feather, and *Tomenthypnum* mosses were addressed through several field investigations. Feather mosses preferred habitats well above the water table, and its relatively low water content increased only with precipitation events, suggesting it frequently tolerated desiccation. The *Sphagnum* mosses also occupied relatively high habitats above the water table, but high residual water content (0.22) of capitula and the gradual change to smaller pores near the water table facilitated relatively strong capillary rise that maintained conditions suitable for photosynthesis. *Tomenthypnum* occurred over a broader range of elevations above the water table than *Sphagnum* and feather mosses. Under all habitats, it had relatively low water content (~0.1) in the tomenta and overlapping leaves (near-surface), and water content and productivity was more affected by rainfall. A more decomposed peat maintained a zone of saturation relatively high in the moss profile, and consequently sustained a sufficiently high water content in contact with the overlying partially decomposed mosses that was generally available for transport to the tomenta as capillary rise, augmented by nocturnal sources of atmospheric water from dew (~0.15 mm/night), and distillation (~0.10 mm/night). Since there are few investigations on the importance of moss-substrate interactions in peatlands and the significance of atmospheric sources to help drive water relations, the results here provide valuable insights into the hydrological functions of underlying substrates for capillary rise.

3.2 Introduction

Mosses are the dominant peat-forming vegetation in northern peatlands (Kuhry & 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 & Flanagan, 1996). Variability of both these carbon accumulation rates and water exchanges between and within peatlands are largely due to moss composition (Bisbee et al., 2001; Bubier et al., 2002; Heijmans et al., 2004a; Heijmans et al., 2004b; Brown et al., 2010; Petrone et al., 2011). In the western boreal region of Canada, gradients of atmospheric and ground water inputs can differ greatly in hydrological and chemical function that affect moss cover between peatlands (Zoltai & Vitt, 1995). For instance, ombrotrophic, acidic bogs and poor fens are dominated by ground covers of *Sphagnum* moss; and minerotrophic and alkaline rich fens are dominated by brown mosses, mainly of the bryophyte family *Amblystegiaceae* (Vitt, 1990). Feather mosses also occupy relatively dry habitats in peatlands and on upland forests surrounding peatlands (Heijmans et al., 2004a; Skre et al., 1983). Within these peatlands, moss composition is largely controlled by gradients of moisture availability within habitats of hummocks, lawns, and hollows (Vitt, 1990; Gignac et al., 1991; Hedenäs & Kooijman, 1996; Hájková & Hájek, 2004; Vitt et al., 2003; Mills & Macdonald, 2005). However, it is the ability of these non-vascular plants to thrive within these various habitats that depends partly on their ability to generate capillary rise and their water retention properties (Hayward & Clymo, 1982; Waddington et al., 2011; McCarter & Price, 2012; Ch. 2). Additionally, it is their ability to tolerate and recover from desiccation (Proctor, 1982; Proctor & Tuba, 2002; McNeil & Waddington, 2003; Hájek & Beckett, 2008). While there are many studies on the differences of moss growth form, habitat and water strategies (Gimingham & Birse, 1957; Busby et al., 1978; Dilks & Proctor, 1979; Schofield, 1981; Skre et al., 1983; Luken, 1985; Williams & Flanagan, 1996; Mulligan & Gignac, 2001; Rice et al., 2001; Elumeeva, et al., 2011;), and some have even described the hydrophysical mechanisms for capillary rise in *Sphagnum* (Hayward & Clymo, 1982; Price et al., 2008; Thompson & Waddington, 2008; Price & Whittington, 2010; McCarter & Price, 2012), and feather mosses (Williams & Flanagan, 1996; Price et al., 1997; Carleton & Dunham, 2003); there are only a few studies on the

capillary mechanisms in brown mosses associated with their distribution within rich fens (Busby et al., 1978; Ch. 2).

Peatland mosses are non-vascular and poikilohydric, so they lack active-water transport mechanisms and cannot control water loss (Proctor et al., 2007) and can withstand desiccation to equilibrium of 50-90% relative humidity (Proctor, 1982). Under these desiccating conditions they become physiologically dormant, but can recover their physiological processes upon re-wetting within hours, although rates of recovery vary greatly between species (Proctor, 1982; Proctor & Tuba, 2002; McNeil & Waddington, 2003; Hájek & Beckett, 2008). To obtain water, peatland mosses utilize capillary spaces between leaf and branch structures to provide a relatively constant and reliable source of external water (Hedenäs, 2001) from underlying substrates, such as peat, litter, or mats of partially decomposed moss that act as water reservoirs to draw up capillary water (Proctor, 1982; Elumeeva et al., 2011) as long as capillary contact is not restricted (Dilks & Proctor, 1979; Proctor, 1982; Price & Whitehead, 2001; McCarter & Price, 2014; Ch. 2). The structure of the mosses and the underlying substrates are typically organized to maintain capillary rise for characteristic water contents for productivity (Dilks & Proctor, 1979; Proctor et al., 2007). These relationships typically form a quadratic relationship with water content, as low water content limits water available for moss cells and photosynthesis and excess water can limit the diffusion of CO_2 into moss cells (Dilks & Proctor, 1979; Silvola & Aaltonen, 1984; Rydin & McDonald, 1985; Williams & Flanagan, 1996; Schipperges & Rydin, 1998). *Sphagnum* mosses conduct capillary rise through overlapping pendant branches and leaves from the water table to the capitula to maintain high water content to avoid desiccation (Hayward & Clymo, 1982; Price, 1997). *Sphagnum* mosses also utilize water-retaining hyaline cells that only drain at low pressures (i.e. between -100 and -600 mb) to increase desiccation avoidance (Hayward & Clymo, 1982; Lewis, 1988). Comparatively, feather mosses, which typically grow in drier, forested ecosystems, do not have the capacity to draw capillary water to the moss surface (Carleton & Dunham, 2003). Thus, they undergo frequent desiccation and rely on precipitation for rewetting (Busby et al, 1978), wetter microclimates, and small amounts of dew and distillation (Carleton & Dunham, 2003) for temporary desiccation relief and productivity.

Since brown mosses do not have hyaline cells, most rely on conduction and retention of water predominately externally (Busby & Whitfield, 1978). *Tomenthypnum nitens* (Loeske) Hedw., a widely distributed brown moss species common in northern rich fens (Vitt, 1990), conducts water through the pore spaces of numerous overlapping stems and branch leaves and through dense felts of rhizoid tomentum along the base of the stem (Busby et al., 1978). Rhizoids can also act to anchor the moss within underlying substrates (Glime, 2009). Its community growth form can be categorized as a turf (Gimingham & Birse, 1957). It was determined in Ch. 2 that despite a highly porous structure, these mosses could transport water to the canopy surface for photosynthesis from the peat and water table. However, with low water tables, the large pores of the moss and the underlying basal layer of partially decomposed moss and litter would drain and break capillary contact with the peat and evaporation would cause desiccation of the uppermost portions of moss shoots. McCarter & Price (2014) also suggested similar importance of basal layers to draw capillary water to new *Sphagnum* growth forms on cutover peatlands. As *T. nitens* can grow in habitats well above the water table (Vitt, 1990) and as Romose (1940) demonstrated that basal layers of partially decomposed litter may be important for water retention, the basal layers of partially decomposed moss in *T. nitens* turfs may have critical importance for the conductance of water to the moss canopy for photosynthesis.

While capillary rise is critical to maintain high productivity in peatland mosses, low water tables can restrict capillary rise and cause the desiccation of mosses (Schipperges & Rydin, 1998; Ch. 2). Therefore, mosses rely on other atmospheric sources of water to maintain physiological processes to avoid the effects of desiccation. Recent studies have shown that precipitation can be an important source of water to maintain physiological processes (Robroek et al, 2007; Strack & Price, 2009), as even small precipitation events (<1 mm) can temporarily increase *Sphagnum* water content equivalent to large increases of water table (Strack & Price, 2009). Other small additions from dew (Csintalan et al., 2000), distillation (Carleton & 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 productivity increased with nocturnal dewfall

amounts. Carleton & 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. Furthermore, Price et al. (2009) suggested that upward vapour fluxes in *Sphagnum* profiles could provide potentially important sources of water for cell maintenance under dry conditions. However, the importance of these sources of water on moss water content and productivity during water stressed conditions are not well understood, particularly for *T. nitens*. 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 to other peatland mosses. As *T. nitens* and *Sphagnum* mosses both utilize capillary flow for obtaining water, but *T. nitens* has more similar morphological structure to feather mosses, it is important to improve our understanding of the hydrological controls on *T. nitens* productivity by comparing those with the other moss types. Consequently, the objectives of this study were to (1) identify and contrast capillary and atmospheric water sources for *T. nitens* and *Sphagnum,* (2) characterize the distribution and variability of water in *T. nitens*, *Sphagnum* and feather mosses in relation to water table position and precipitation events, and (3) contrast the moisture controls of productivity of *T. nitens*, *Sphagnum*, and feather mosses by manipulating water table and atmospheric water availability. Approaching this study with these three objectives, that consist of three distinct but related experiments (see Methods section) provides a comprehensive investigation of the ecohydrological processes that govern capillary rise and productivity within dominant peatland moss types.

3.3   Study Sites

The study was conducted in Poplar Fen, a brown moss-dominated treed rich fen (56°56'18"N, 111°32'35"W and 325 masl), its adjoining feather moss-dominated forested upland, and Pauciflora Fen, a *Sphagnum*-dominated open poor fen (56°22'30"N, 111°14'05"W and 740 masl), 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, 485 and

37

515 mm, respectively (Environment Canada, 2014), 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 *Tomenthypnum nitens* (Hedw.) Loeske and *Aulacomnium palustre* (Hedw.) moss groundcover 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 in the rich fen includes bog birch (*Betula pumila* (L.)) shrubs, three-leaf Solomon's-seal (*Smilacena trofilia* forbs (L.)), water horsetail (*Equiseteum fluviatile* (L.)), and a large cover of tamaracks (*Larix laricina* (Du Roi) K. Koch) and some black spruces (*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 at feather mosses) communities with Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd) and large black spruces 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 and leather leaf (*Chamaedaphne calyculata* (L.)) ericaceous shrubs, water sedges (*Carex aquatilis* (Wahlenb.)), and sparse, stunted black spruce and tamarack trees. Colonies 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.

3.4 Methods

Data were generally collected from 1 June to 31 August 2011 and 2012, unless otherwise stated. Three experiments were performed: (1) a *moss turf water dynamics*

experiment – recording transient variables in moss profiles at both fens, including temperature, relative humidity, water content and water table to determine water and vapour fluxes to further explain capillary rise mechanisms from Ch. 2; (2) a *transect study* - measuring the spatial pattern of volumetric water content with water table changes and precipitation events to characterize their importance with moss-surface elevation from the water table in *Tomenthypnum*, feather, and *Sphagnum* mosses at the rich fen site along three randomly chosen 25 m transects; and (3) a *field drought experiment* - examining the moisture and CO_2 uptake of moss monoliths under imposed hydrological stresses.

Environmental Variables

Meteorological data were collected at each fen using Campbell Scientific Inc.™ data loggers logging every half hour. Precipitation (*P*) was measured automatically using a tipping bucket (HOBO Onset RGB-M002) set 1.0 m above the ground surface with no tree canopy above. Manual rain gauges were used for *P* amounts between days 155 and 175 of 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}) from the underlying peat through the moss. Soil heat flux plates can underestimate heat flux in organic soils due to poor contact and vapour flow disruption (Halliwell & Rouse, 1987; Petrone, et al., 2004) so the plates were installed into a piloted hole ensuring good contact with the organic substrate. Error associated with the underestimation is assessed later in the Discussion section.

Moss Turf Water Dynamics Experiment

Three *Tomenthypnum* turfs (separate from but near the transects) at the rich fen and one *Sphagnum* hummock at the poor fen were instrumented to monitor *in situ* volumetric water content (*θ*) 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 predominately *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 Ch. 2, with the exception of *Tomenthypnum* 2; which was disconnected from the underlying peat due to ladder support from *L. laricina* roots. The *Sphagnum* hummock had a mix of *S. angustifolium* and *S. magellanicum* mosses. Equipment limitations restricted somethe profile measurements to a single *Sphagnum* hummock, but this and other *Sphagnum* hummocks at the poor fen were well sampled to determine the hydraulic properties that control the variations in water content, as was the *Tomenthypnum* (see Ch. 2). The representativeness of the *Sphagnum* hummock will be discussed further in the Discussion section. Nevertheless, we acknowledge that the lack of replication limits the ability to make broad conclusions about *Sphagnum* in general. However, we compare our results from the *Tomenthypnum* profiles to a *Sphagnum* profile that has distinctly different properties than the *Tomenthypnum* (Ch. 2), and the explanations of how their behaviour relates to their hydraulic properties are broadly applicable.

The water table beneath each moss colony was monitored continuously using Odyssey™ capacitance water level loggers (Dataflow Systems PTY. Ltd.) in immediately adjacent monitoring wells, with manual measurements for verification. θ in *Tomenthypnum* 1 and the *Sphagnum* hummock were monitored non-destructively using Campbell Sci. 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-minute intervals; and using medium-specific TDR calibrations, from methods described by Topp et al. (1980). A 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.

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 (thermocouple for T and thin film polymer capacitive sensor for RH, with ±1% RH accuracy and equilibrium response time less than 60 sec) in the air-filled pores at 30-minute intervals. Parallel instrumentation was not available for *Sphagnum*. *RH* and T were also measured 25 cm above (HOBO Onset) and 7.5 cm below (copper-constantan thermocouples for T and assumed 100% RH based on preliminary tests during drydown) the moss surface. 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 (see Equation 3-2 below) was used to determine potential vapour condensation (Garratt & Segal, 1988; Jacobs et al., 2002; Moro et al., 2007; Uclés et al., 2014). The original Penman-Monteith model for the energy required to evaporate or condense water (latent heat (λE)), is

$$\lambda E = \left(\frac{s}{s+\gamma}\right)(R_n - G) + \rho_a C_p \left(\frac{e_s - e}{r_a}\right) \qquad \textbf{Equation 3-1}$$

where s is the slope of the saturation vapour pressure-temperature curve (Pa K^{-1}), γ is the psychrometric constant (0.0662 kPa K^{-1} at 20°C), ρ_a is the density of air (g m^{-3}), C_p is the specific heat capacity of air at constant pressure (J g^{-1} K^{-1}), e_s and e are the saturation and actual vapour pressure (MPa), respectively, and r_a is the surface resistance (Garratt & Segal, 1988). For vapour condensation to occur at night the air typically is near saturation (e_s-e = 0) or wind speed is low (r_a approaches infinity). As a result, condensation is driven mainly by the radiative balance from the atmosphere and heat transfer through the moss medium (Garratt & Segal, 1988; Moro et al., 2007), thus simplifying Equation 3-1 to

$$\lambda E = \left(\frac{s}{s+\gamma}\right)(R_n - G) \qquad \textbf{Equation 3-2}$$

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 & Segal, 1988). Total condensation rates (D_T) comprises dewfall (D_f) and distillation (D_d), in kg m^{-2} s^{-1}, where

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

Equation 3-3

,

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 colonies near the moss θ and *RH* instrumentation. To partition distillation fluxes in the *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 Ch. 2, and

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

Equation 3-4

where D_v^* is the diffusion coefficient of water vapour in air (cm^2 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

θ was measured in the top 5 cm of mosses every 1 m along three 25-m transects to determine water content variability on eight days between 21 June and 8 August, 2012. θ was measured non-destructively using a portable Campbell Sci. TDR-100 system with a CS605 time-domain reflectometer (TDR) probe. Moss presence was determined 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 elevation distributions of mosses were not normal, so nonparametric tests of Kruskal Wallis with Mann-Whitney post-hoc U-tests were used. θ distributions were also non-normal so Wilcoxon sign-rank tests were used to compare changes with antecedent water table and precipitation conditions.

Differences were deemed to be statistically significant if they met a significance level of 0.05. Analyses were performed with IBM[®] SPSS[®] Statistics 20.0.

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*, three feather moss) and the poor fen (nine *Sphagnum*) in triplicates 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; only precipitation and other atmospheric sources could be added naturally. 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 treatment (LS) 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 drilled in the bottom and was set in another 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 (PAR; μmol m^{-2} 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 & Dunham, 2003) and growth is

known to be severely limited by high water tables (Bisbee et al., 2001; Busby et al., 1978). These monoliths were categorized as DS treatment due to the absence of a water table. 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 presence 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 of June 2011 and were left for two 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 moisture probe (Campbell Scientific Canada) through holes drilled 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 productivity (*GEP*; gCO_2 m^{-2} d^{-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. PAR > 1000 μmol m^{-2} s^{-1}) and ecosystem respiration (R_{tot}) of CO_2 under blackout conditions. *NEE* was measured using a clear plexiglass chamber (30 cm high by 30 cm diameter and permitting the transmission of ~87% of PAR) connected to a closed-system infrared gas analyzer (IRGA; PP Systems EGM-4). R_{tot} was measured by placing an opaque shroud over the chamber. CO_2 concentration change was measured by the IRGA every 15 seconds over a 105 second interval and flux calculated using

$$F = \frac{\Delta \cdot M}{N} \cdot \frac{V}{A} \cdot CF \,,$$ **Equation 3-5**

where F is the CO_2 gas flux (gCO_2 m^{-2} d^{-1}), Δ is the linear change in CO_2 concentration with time (μmol mol^{-1}), M is the molar mass of CO_2 (44.01 g mol^{-1}), N is the molar volume of a gas (0.224 m^3 mol^{-1}) at a standard temperature and pressure, V is the temperature corrected volume within the chamber (m^3), A is the area of the ground surface covered by the chamber (m^2), and CF is the conversion factor from ppm to mol (1 ppm = 10^{-6} mol). Inputs of CO_2 to the moss community are expressed as positive values. Over the same time interval, T and RH were measured with the IRGA to determine instantaneous evapotranspiration rates (ET_{in}; mm d^{-1}) 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) where

$$ET_{in} = 86.4 \frac{MVC}{A}$$ **Equation 3-6**

and where M is the slope of the vapour pressure within the chamber over time (gH_2O m^3 s^{-1}), V is the temperature corrected volume within the chamber (m^3), C is the calibration factor to account for vapour absorption within the chamber (1.534; dimensionless), A is the area of the ground surface covered by the chamber (m^2), and 86.4 is the conversion factor from gH_2O m^2 s^{-1} to mm day^{-1}. To create a gas seal, the chamber 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. Since 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 measurement period, it is assumed that differences of gas fluxes between treatments are predominantly from the mosses.

For statistical analyses of parameters in this experiment, total seasonal mean and standard deviation were used to assess the variability within treatments with repeated

measures analyses. Data for θ were not normally distributed so the non-parametric Wilcoxon sign-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 Kolmogorov-Smirnov, Levene, and Maulchy's statistical tests. Differences were deemed to be statistically significant if they met a significance level of 0.05. Analyses were performed with IBM® SPSS® Statistics 20.0.

3.5 Results

For 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 ± 24.8 and 74.4 ± 23.2%, respectively. At the poor fen, the mean daily average T in 2011 and 2012 were 15.2 ± 5.1 and 16.8 ± 5.07 °C and mean daily RH were 71.2 ± 21.3 and 67.9 ± 21.9%, respectively. RH and T at both sites were similar to the 30-year average for the region (Environment Canada, 2014). The 30-year average total P for June to August is 229 mm (Environment Canada, 2014). 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. While the number of days with P events were similar in both years and locations (~40% of days) the rain events in 2011 were predominantly smaller; 81% and 54% of days with P were less than 5 mm at the rich and poor fen, respectively. Only the poor fen had three events exceed 20 mm with the largest being 77 mm. In 2012 there were three and eight days with P events greater than 20 mm for the rich fen and poor fen, respectively, with 63 and 33 mm events at the rich fen and 73 and 64 mm events at the poor fen.

Moss Turf 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 and 35.2 cm from the water table, respectively. Standard deviation of water table at the rich fen was 8.9 cm. 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 in Ch. 2, 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 maximum of 34.9 cm, and median near-surface θ of 0.22 over the 2012 field season (data not shown).

The changes in moss structure were reflected in the water content profiles during low and high water tables (Figure 3-1). Regardless of water table position, θ in the near surface (2.5 cm depth) in all *Tomenthypnum* moss turfs and the undecomposed moss (7.5 cm) were relatively low compared to the 12.5 and 22.5 cm depths. θ decreased in the top 15 cm of all turfs, on average, only 0.01 with a 15 cm decline in water table. However, the peat at 22.5 cm depth in *Tomenthypnum* 1 and 3 exhibited larger θ increases (0.08) with changes in the water table (Figure 3-1). The single *Sphagnum* hummock exhibited a more gradual increase in θ with depth. With a water table increase of ~12 cm at the poor fen (Figure 3-1) θ increased at all depths (0.03 at 2.5, 7.5, and 12.5 cm depth, and 0.27 at 22.5 cm depth).

Time series θ measurements in the *Sphagnum* hummock and *Tomenthypnum* 1 in response to precipitation and water table fluctuations are shown in Figure 3-2. *Tomenthypnum* 1 was compared with *Sphagnum* because it was structurally connected with the underlying peat, similar to *Tomenthypnum* 3 and *Sphagnum*, 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 3-2). *Tomenthypnum* θ at 2.5 and 7.5 cm depths
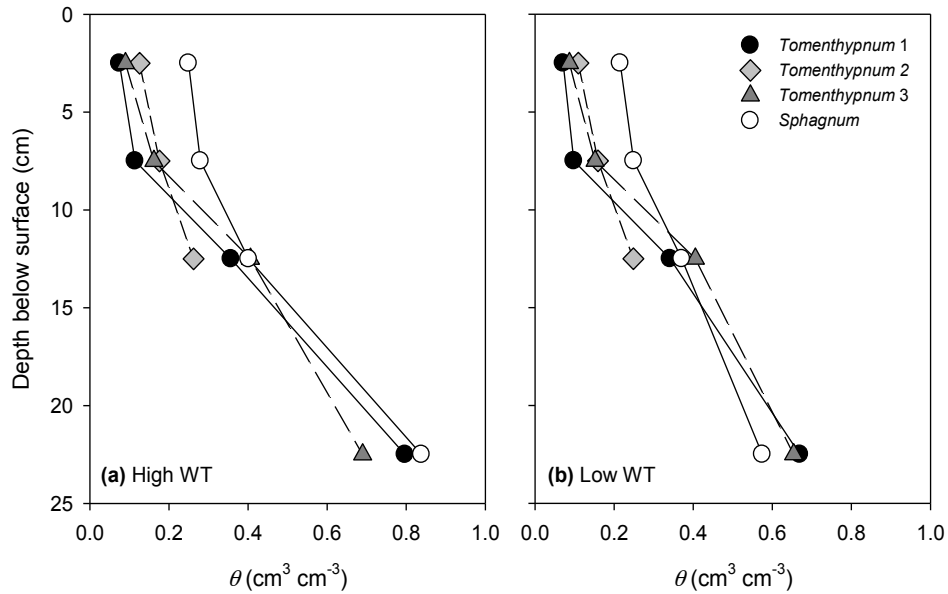
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Figure 3-1 Vertical volumetric water content (θ) profiles (2.5, 7.5, 12.5, 22.5 cm depths) of three *Tomenthypnum* turfs from the rich fen and one *Sphagnum* hummock from the poor fen under (a) high and (b) low water table conditions (~15 cm difference). 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. No 22.5 cm depth probe was available for *Tomenthypnum* 2.

demonstrated little response to the relatively large variation in water table changes (Figure 3-1). Wetting of the moss depended on the frequency and size of *P* events. *Tomenthypnum* 1 θ increased, on average, by 0.03 during a *P* event (Figure 3-2), similar to *Tomenthypnum* 2 (0.03) and higher than *Tomenthypnum* 3 (0.01; data not shown). After wetting events, *Tomenthypnum* θ had a prolonged recession for several days until another *P* event occurred (Figure 3-2). While θ in the peat at 22.5 cm depth retained more water than the surface, there was little θ variation when the water table was ≥ ~30 cm below the surface, but became essentially saturated when it rose to ~25 cm below the surface following a *P* event (71 mm) on days 185-186, then declined steadily until the end of the study period (Figure 3-2).

   In situ Sphagnum θ at 2.5 cm retained 10-15% more water throughout the study period than *Tomenthypnum* 1 (Figure 3-2). 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* capitula 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
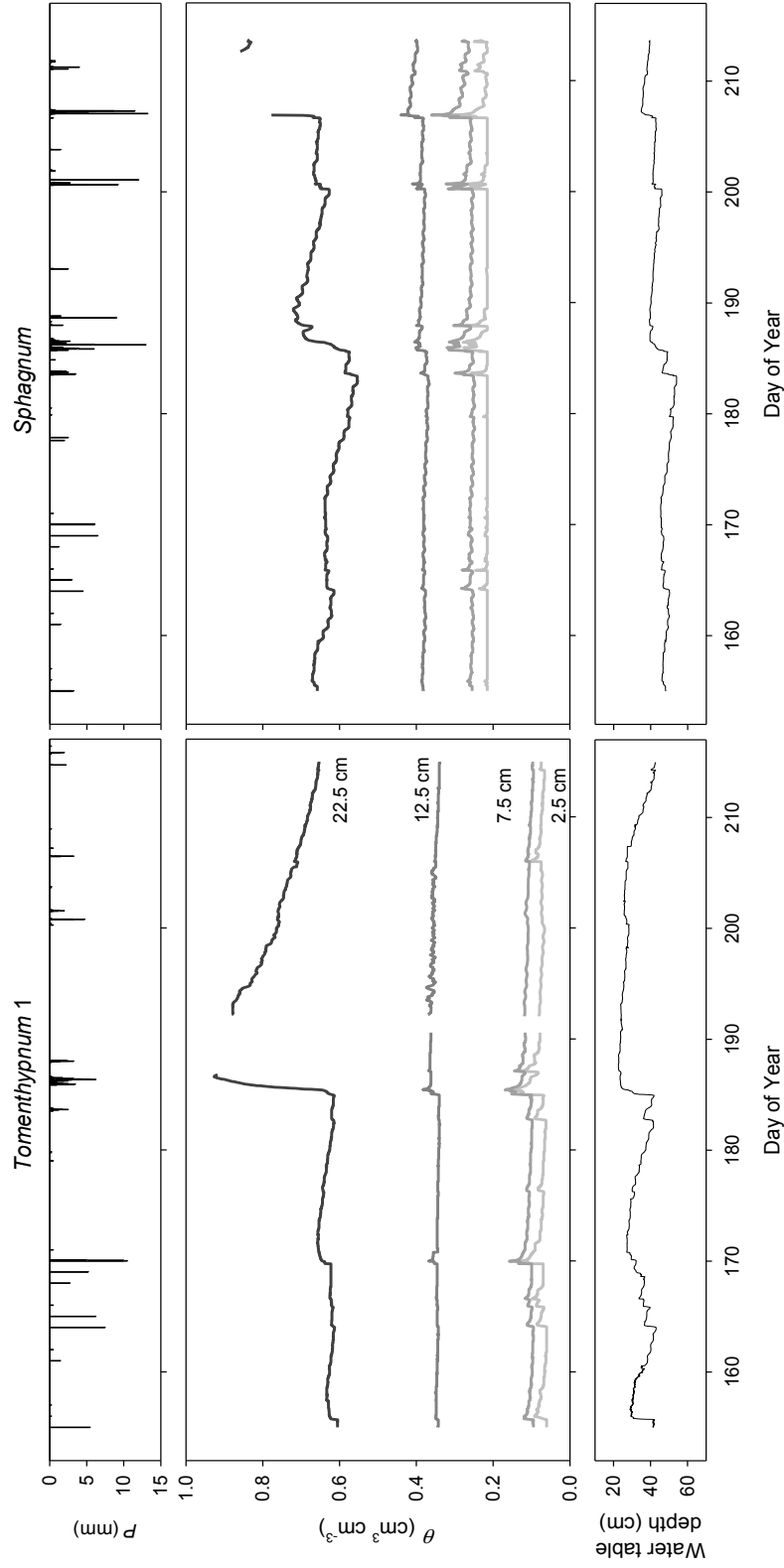
Figure 3-2 Time series volumetric water content (θ) changes of *in situ* measurements in *Tomenthypnum* 1 in the rich fen and the *Sphagnum* hummock in the poor fen at 2.5, 7.5, 12.5 and 22.5 cm depths from 3 June to 2 August 2012. Precipitation events (*P*, half-hourly) and water table fluctuations are also shown.

typically returned to pre-event levels within a day. *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 (it rose only 9 cm in response to 72 mm of rain on 185, compared to 17 cm for similar sized event at the rich fen. That event elicited a moderate increase in θ at 22.5 cm in *Sphagnum* (i.e., θ at 22.5 cm in *Sphagnum* increased much less in response to a larger rainfall), than did θ at 22.5 cm at the *Tomenthypnum* site to a comparatively smaller storm (Figure 3-2).

T within the *Tomenthypnum* moss turfs 2.5 cm below the moss canopy (n=7) were, on average 3.0 °C cooler in the day and 1.4 °C warmer at night than air 25 cm (n=3) above the moss surface (Figure 3-3b), with minimal variability between turfs (data not shown). 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 3-3c). RH of the air 25 cm above the moss surface was never 100% and the lowest RH was 22%. In contrast, RH of the air within the *Tomenthypnum* moss structure was saturated for 57, 51, and 40% of the days for *Tomenthypnum* 1, 2, and 3, respectively, throughout the study period; and when not saturated was 22% higher than the air above (Figure 3-3c). RH of 100% occurred mainly in the days immediately following moss wetting from rain events and also during the night (Figure 3-3c). *Tomenthypnum* 2 and 3 exhibited relatively similar RH patterns throughout the study period. *Tomenthypnum* 1 sustained vapour saturation during a period from 192-199 when the other turfs experienced daily drying. Water tables were relatively high during this period and *Tomenthypnum* 1 moss structure was only ~22 cm above the water table, compared to ~27 and ~32 for *Tomenthypnum* 2 and 3, respectively.

Nocturnal temperature inversions occurred at the rich fen to provide upward T (Figure 3-4a) and vapour density gradients (Figure 3-4b) to drive upward distillation fluxes (D_d; Figure 3-4c), the example given being for 14 July 2012. During this period there was a vapour density gradient (Figure 3-4b), from which the D_d was calculated (Equation 3-4). Dewfall (D_f) was then determined as a residual between D_d and total vapour condensation (D_T), the latter calculated from the energy budget with Equation 3-3 (Figure 3-4c). Condensation of vapour typically began at approximately 20:00h and lasted until 06:00h the following morning, averaging 10.6 hours per night. Distillation
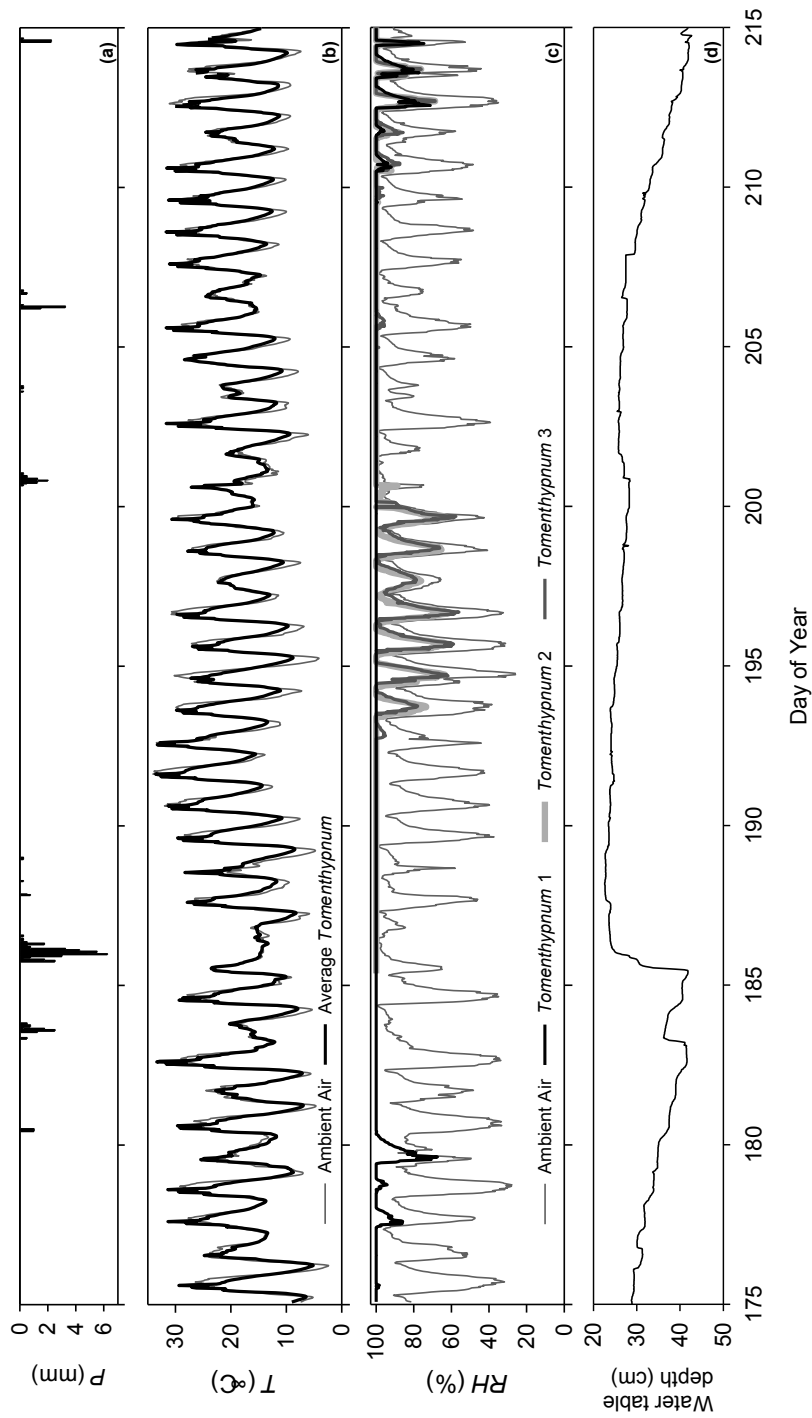
Figure 3-3 Time series of (a) precipitation (*P*; half-hourly), (b) air and average *Tomenthypnum* (all three turfs) moss temperature (*T*) and (c) relative humidity (*RH*; all three turfs), and (d) water table changes between 23 June and 3 August 2012. Air *T* and *RH* measurements were taken 25 cm 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.

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Figure 3-4 Diurnal variations in (a) temperature (*T*), (b) vapour density, and (c) hourly vapour fluxes of dew and distillation above and within *Tomenthypnum* turfs for the night of day 196 (14 July) of 2012. Air *T* and vapour density (solid light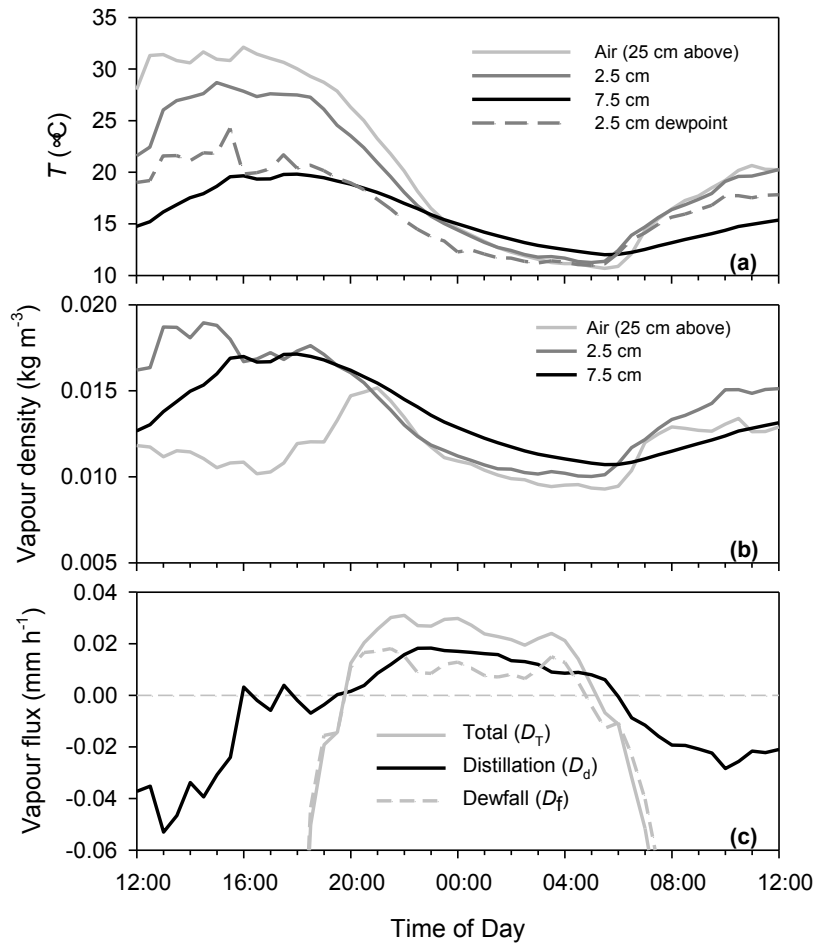 gray line) was measured 25 cm above the moss canopy and moss *T* and vapour density were measured at 2.5 (solid medium gray line), and 7.5 cm (solid black line) below the moss canopy. The dewpoint temperature at 2.5 cm (dashed black line) was included. The difference between calculated total condensation flux (solid gray line) calculated distillation flux (solid black line) is the dewfall flux (dashed gray line). Positive values indicate fluxes into the near-surface and negative values downward (D_d) or upward (D_f) from the near-surface.

occurred, on average, 10.5 hours per night. Estimations of nightly average condensation and distillation rates in *Tomenthypnum*, using Equations 3-4 and 3-5, 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*
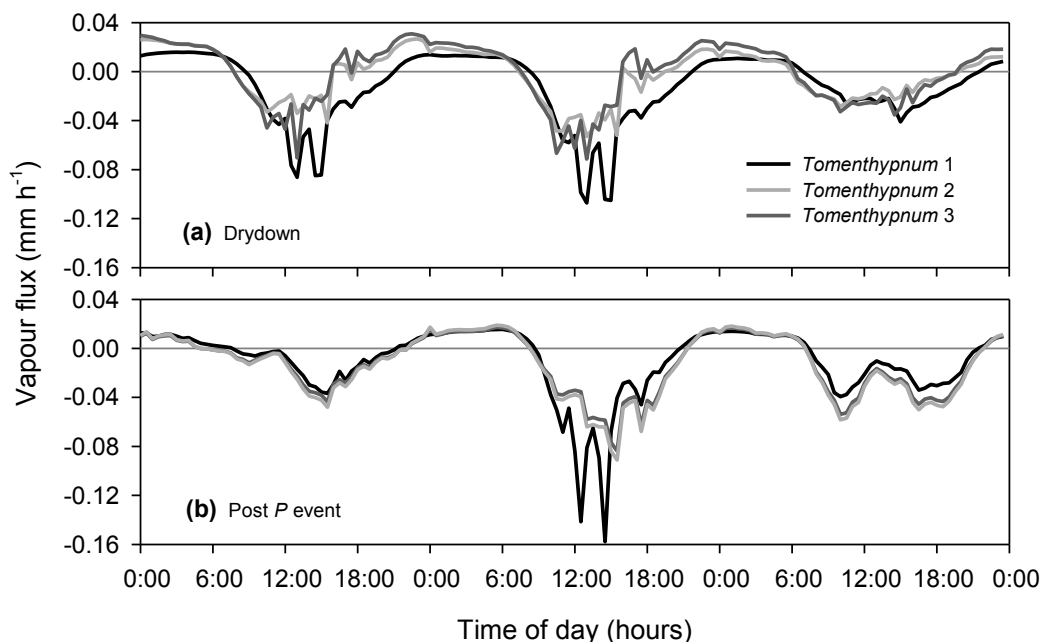
Figure 3-5 Time series vapour fluxes (mm per hour) between the near-surface (2.5 cm depth) and 7.5 cm depth in three *Tomenthypnum* turfs during (a) a dry-down period (days 195-198; approximately five days since a rainfall event) and (b) after a wetting event on day 200 (days 202-205) in 2012. Positive values indicate fluxes into the near-surface and negative values downward from the near-surface.

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 3-5). For example, from days 195-198 when the moss structure air was not saturated in *Tomenthypnum* 2 and 3 (Figure 3-3), night-time vapour fluxes were 35 and 53 percent higher than rates in *Tomenthypnum* 1 (Figure 3-5a). After the 13 mm rain event on day 200 when all moss turfs sustained vapour saturation, particularly at night (Figure 3-3), there were minimal differences in distillation rates (Figure 3-5b). Assuming the 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, is 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 was 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 depth (Figure 3-6). This resulted in 16% lower than 17.5 cm and only 7% higher than 40.0 cm elevations (relatively steep portions of Figure 3-6). 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. capilifolium* (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 3-6; $p > 0.05$). However, the range of *Tomenthypnum* elevations (between 6 and 41 cm) extend much closer to the water table than feather (23-53 cm) and *Sphagnum* (19-41 cm) mosses (Figure 3-6). Only feather mosses occupied elevations above 41 cm above the water table. There were also other brown mosses, like *B. pseudotriquetrum*, associated with wetter habitats (Figure 3-6) 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, 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 3-7). Water table position did not affect feather moss median θ differences, but median θ did increase significantly after *P* events (Figure 3-7). *Tomenthypnum* θ before and after *P* events were significantly different regardless of water table depth (Figure 3-7). 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.
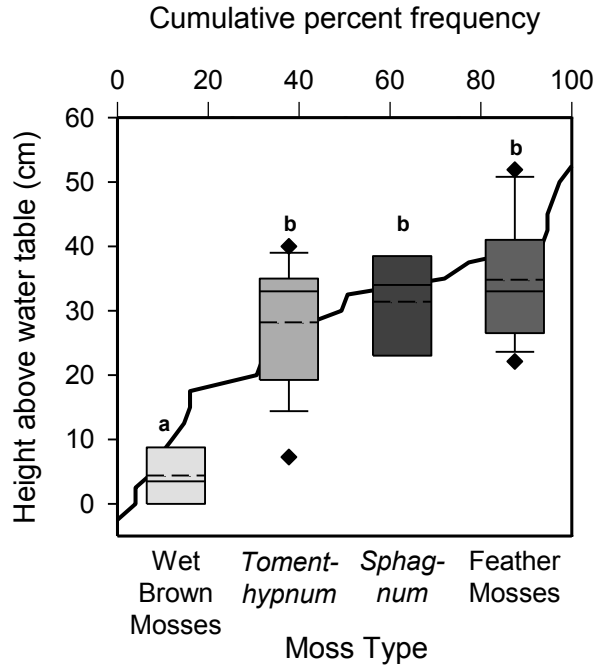
Figure 3-6 Boxplots (ends of boxes: 25th and 75th percentile; solid line at the median; dashed line at mean, error bars: 10th and 90th percentile) of elevation distributions of *Tomenthypnum* (n=40), feather (n=21), *Sphagnum* (n=6), and wet brown mosses (n=8) from the water table in the rich fen and cumulative percent 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. *Sphagnum* does not have 10th and 90th percentiles due to low counts. Plots with the different letters indicate significant differences (Kruskal Wallis; $\alpha = 0.05$).

Figure 3-7 Boxplots of antecedent volumetric water content (θ) of near-surface (midpoint 2.5 cm depth) *Tomenthypnum* (n=40), feather (n=21), and *Sphagnum* (n=5) mosses before and after precipitation events under high and low water table conditions (~15 cm differen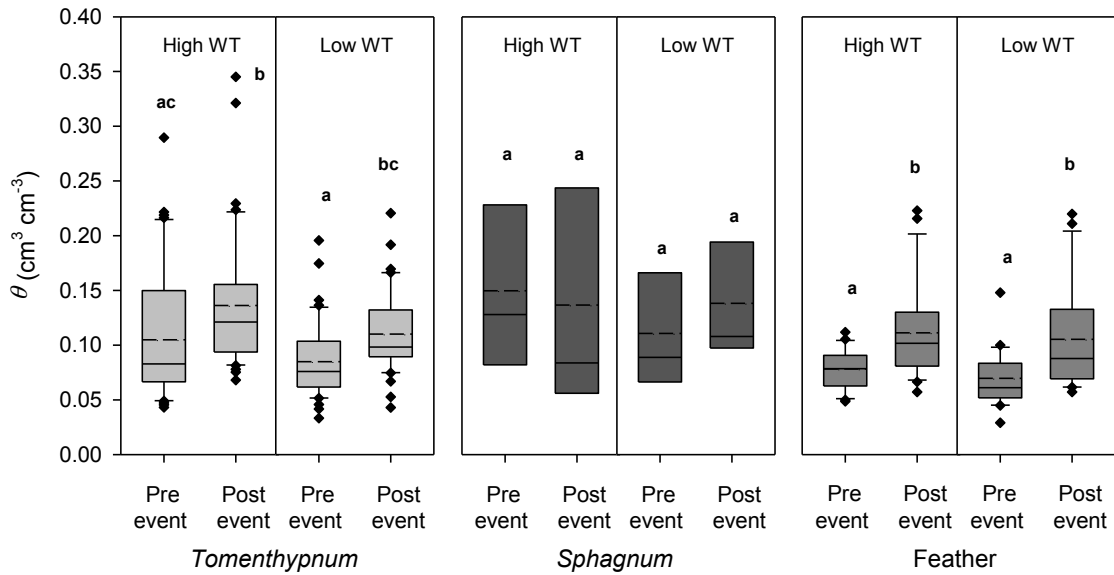ce) in 2012. θ measurements took place on days 198 (10 days since *P*) and 202 (after a 7 mm *P* event) for high water tables and 212 (4 days since *P*) and 217 (after a 5 mm *P* event) for low water tables. Plots with the different letters indicate significant differences within each moss type (Wilcoxon signed-rank test; $\alpha = 0.05$).

Field drought experiment

Figure 3-8 shows the differences (mean and standard deviation) in θ, ET_{in} and *GEP* under full-light conditions among the stress treatments for *Sphagnum* and *Tomenthypnum* in the poor and rich fens, respectively, in 2011. Water table depths in the low stress (LS) treatments ranged between 10.5 - 21.0 cm and 11.0 - 22.0 cm in *Sphagnum* and *Tomenthypnum*, respectively. There was significantly higher θ 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 to the drought stress (DS) and extreme drought stress (ES) ($p < 0.05$; Figure 3-8). Furthermore, θ was significantly 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 were within the range of the transect study surveys (generally between 0.05 and 0.20) from 2012 (Figure 3-7). In the *Sphagnum* treatments, the capitula

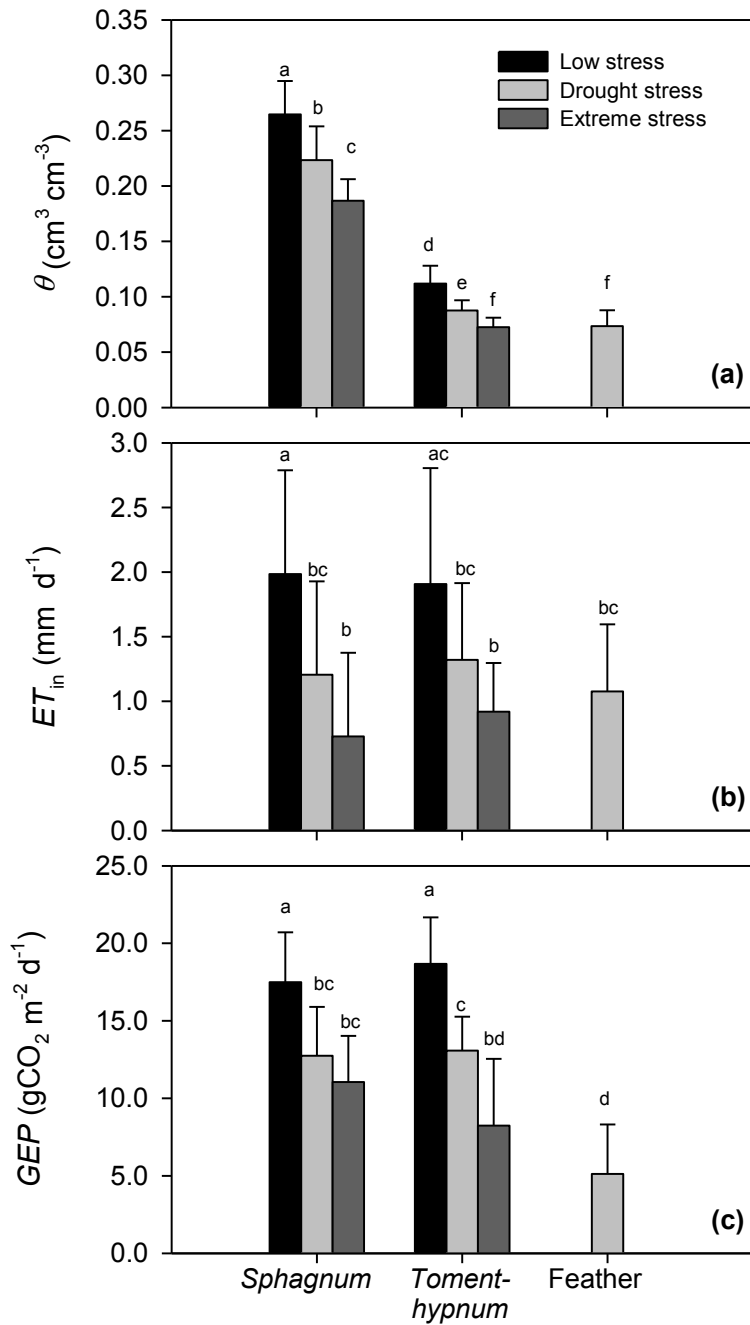**Figure 3-8** Treatment average of (a) volumetric water content (θ; 0-5 cm), (b) evapotranspiration (ET_{in}), and (c) productivity (*GEP*) for *Tomenthypnum*, *Sphagnum*, and feather moss field monoliths in 2011. Error bars indicate one standard deviation. Letters indicate significant differences (Wilcoxon sign-rank tests for θ, ANOVA and Bonferroni post hoc tests for ET_{in} and *GEP*; $\alpha = 0.05$).

in LS treatments were generally all visibly green and moist, compared to the capitula in the DS where they exhibited some whitening. All the capitula were white and desiccated in the ES treatment. Similarly, *Tomenthypnum* shoots in the LS treatments were green and moist, while there was a mix of green and brown (senescing) shoots in the DS treatment similar to many undisturbed *Tomenthypnum* turfs within the fen, and almost all shoots in the ES treatment were exhibiting senescence. Little or no changes in the vascular plant structure occurred during the measurement period.

Tomenthypnum ET_{in} rates were significantly higher in the LS than the ES treatment ($p < 0.05$) and not significantly higher than the DS treatment ($p = 0.07$) (Figure 3-8b). There were no significant differences between ES and DS ($p = 1.00$). ET_{in} rates of the *Sphagnum* LS treatment were significantly higher than the other two treatments ($p < 0.05$), which were not significantly different ($p = 1.00$) from each other. Using θ across all *Sphagnum* treatments there was a weak but significant positive linear relationship with ET_{in} ($R^2 = 0.36$, $p = 0.006$; Figure 3-9). Similarly, there was a weak but significantly positive correlation for ET_{in} and θ for *Tomenthypnum* ($R^2 = 0.41$, $p = 0.003$; Figure 3-9). Feather moss ET_{in} was similar to DS and ES treatments of *Tomenthypnum* and *Sphagnum* ($p < 0.05$; Figure 3-8) and showed no relationships with θ (Figure 3-9).

Tomenthypnum *GEP* rates were all significantly different ($p < 0.05$) between all treatments following trends in θ (Figure 3-8c). *GEP* in the *Sphagnum* LS treatment was significantly higher than the other two treatments ($p < 0.05$), while there were no significant differences between DS and ES ($p = 0.32$). Using θ across all *Sphagnum* treatments there was a strong and significant positive linear correlation with *GEP* ($R^2 = 0.90$, $p < 0.001$; Figure 3-9b). In contrast, there was a strong and significant quadratic relationship between *GEP* and θ for *Tomenthypnum* ($R^2 = 0.90$, $p = 0.004$; Figure 3-9). Feather moss *GEP* was significantly lower than *Tomenthypnum* and *Sphagnum* ($p < 0.05$; Figure 3-8b) and exhibited a moderately strong and weak positive linear correlation with θ ($R^2 = 0.65$, $p = 0.03$; Figure 3-9b).
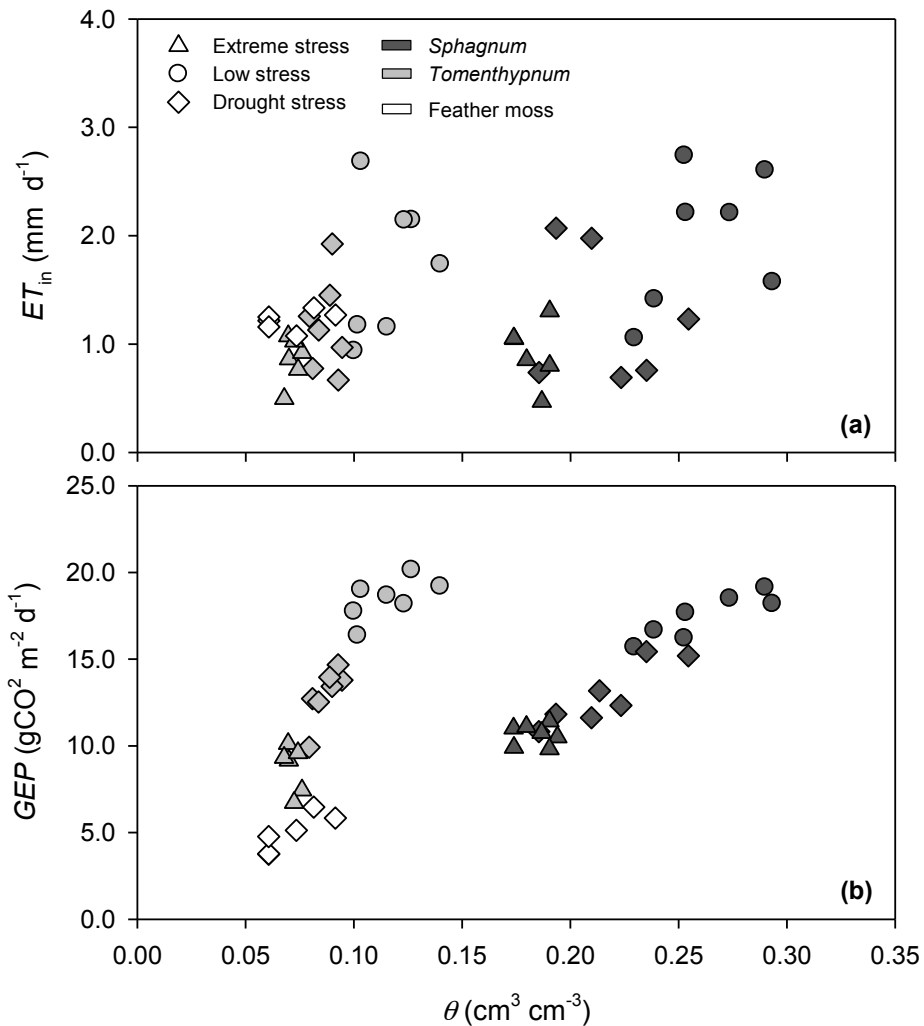
Figure 3-9 *Tomenthypnum, Sphagnum,* and feather moss community evapotranspiration (ET_{in}) and productivity (*GEP*) trends with volumetric water content (θ) for all treatments (circle for low stress, diamond for drought stress, and triangle for extreme drought stress) in 2011. Each symbol represents the average ET_{in} or *GEP* and θ for a moss type and treatment (n=3) taken on each day of measurements.

3.6 Discussion

Moss structure and capillary rise

Although Ch. 2 demonstrated that the different hydrophysical properties of *Sphagnum* and *Tomenthypnum* resulted in different capillary rise mechanisms and the reduced capacity of *Tomenthypnum* to maintain relatively high θ with low water tables, the *in situ* θ profiles demonstrated that *Tomenthypnum* turfs were just as capable of

maintaining capillary flow as *Sphagnum*. In Ch. 2, due to the relatively poor decomposition of the *Sphagnum* macrostructure (c.f. Johnson et al., 1990), there was a gradual increase with depth in the number of pores (albeit of smaller size) that contribute to flow. This shift provided a pore-water network that facilitated a capillary rise throughout the *Sphagnum* profile even when the water table was relatively low (Figure 3-2; and Ch. 2). This capillary rise occured between leaves and branches of the moss structure, with flow bypassing water held in the hyaline cells, which only drain at low pressures (-100 to -600 mb) (Hayward & Clymo, 1982; Lewis, 1988). With additions of precipitation to temporarily rewet *Sphagnum* capitula (Figure 3-2), and dew and distillation (~0.35 mm per night), capitula surface resistance to evaporation decreased (Kettridge & Waddington, 2013), which helped drive upward capillary fluxes throughout the day. Such small moisture additions to the capitula can be undetectable to buried TDR probes (Strack & Price, 2009). That the *Sphagnum* capitula θ in the *in situ* measurements avoided desiccation, is evidence that capillary flow was sufficient, despite it being constrained to the active and connected pores. Under extreme conditions, water migrates from hyaline cells and contributes to capillary water to prolong the period during which photosynthesis can occur. At some point, however, a θ and water table threshold will be reached, whereupon capillary rise becomes ineffective in sustaining upward flow (Hayward & Clymo, 1982), and eventually the moss becomes desiccated as in the ES treatment of the drought stress experiment. 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 (Ch. 2). Nevertheless, since 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 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 & Whittington, 2010; McCarter & Price, 2014).

Given that the net water loss (decrease in θ) from *Tomenthypnum* over the season was small (Figure 3-2), as was the case for *Sphagnum*, cumulative evaporative water demand must have been met by capillary rise from storage below, and supported by the condensation of vapour near the surface. Since daily evaporation was about an order of

magnitude greater than the condensation flux of 0.25 mm/night in *Tomenthypnum,* capillary rise must have been the dominant flux. The structure of the pore-network through which capillary rise must occur was different than in *Sphagnum* (Ch. 2), with relatively large pores near the surface (0-10 cm layer) that decreased abruptly in the 10-15 cm partially decomposed moss layer, than in peat layers (which at 22.5 cm were dominated by small pores equivalent to those in *Sphagnum*). The large pores in the upper layer of *Tomenthypnum* drained quickly when wetted by rain, but considerable water was retained in the 10-15 cm layer (Figure 3-2) in the active pores of the capillary network (i.e. similar θ to *Sphagnum* at this depth but without hyaline cells). With the smaller pores filled and few large pores to retain capillary water the layer was essentially at field capacity (Ch. 2) and any precipitation water essentially passed through to the peat below or was run off away from the *Tomenthypnum* turfs. The water in the partially decomposed layer was thus held high in the moss profile, and became available for evaporation as it moved into the upper layer. In the upper layer, matric pressures can potentially drop to very low levels as pore vapour pressures, associated with *RH* well below 100% (Figure 3-2), try to equilibrate with matric pressure (see Ch. 2). Furthermore, given the flatter tails of the water retention curves for *Tomenthypnum* than *Sphagnum* (Ch. 2), even small reductions of θ caused by evaporative water loss will result in very low pressures thus strong hydraulic gradients. The evaporation rates from *Tomenthypnum*, not being significantly different from *Sphagnum* (Figure 3-8), must be associated with hydraulic gradients strong enough to overcome the capillary barrier effect caused by the abrupt change in pore sizes below the 0-5 cm layer. *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 & Price, 2014). They can also undergo a greater range of water content changes (see Figure 3-9) without experiencing extreme (desiccating) matric pressures.

While capillary rise was evident as a water source for both *Tomenthypnum* and *Sphagnum*, capillary rise from the water table was not a requirement for maintaining a low but steady θ in *Tomenthypnum*, since one of the profiles (*Tomenthypnum* 2) was not directly connected to the underlying peat (being lofted on the root structure of adjacent trees). All three of the *Tomenthypnum* moss turfs had a layer at 10-15 cm that seemed to

provide water storage for upward water transfer (as indicated by a steady θ, Figure 3-4). 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. As evident in this study that capillary rise is occurring with a range of elevations from the water table (Figure 3-6), it is a critical mechanism to maintain water content for productivity.

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 (Petrone 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 3-4). The *Tomenthypnum* moss structure in the upper 5 cm has air-filled porosities between 80 and 90% (Ch. 2), and large pores through which vapour can flow. As such, 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 3-5a) had lower nocturnal vapour fluxes than those that were not saturated, due to 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, as well as with atmospheric and radiative conditions that vary 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 the rich fen, thus had slightly cooler temperatures. Furthermore, the poor fen had fewer trees to insulate against clear-air radiative cooling (Tuller & 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 3-4a). This implies that the actual moss surface temperatures were up to 5°C colder than the ambient air due to radiative cooling, as was found by Brewer & Smith (1997), thereby lowering the condensing surface temperature below the dew point. Furthermore, several studies have demonstrated nocturnal moisture increases at soil surfaces despite temperatures above the dew point, as a result of vapour adsorption (Agam & Berliner, 2006; Graf et al., 2004). Vapour adsorption could occur in the small pores spaces of the moss structure during relatively dry periods with actual vapour pressure remaining below saturation (Agam & Berliner, 2006). Finally, while these vapour condensation estimates are small (7.8-12.0 mm over the season and only 0.24 mm per night) compared to potential evaporation losses, which can be between 0.2 and 0.4 mm per hour (Brown et al., 2010), they may provide critical amounts for physiological processes, especially in the early morning before evaporation removes water (Csintalan et al., 2000).

Errors associate 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 & Lafleur, 2007) although the relative magnitude of the latent fluxes are likely representative. More intense investigations are needed characterize variability of nocturnal latent heat exchanges. Ground heat flux plates can underestimate total ground heat fluxes due to the interruption of vapour fluxes and do not respond to downward-directed vapour fluxes (see Figure 3-5) and therefore require corrections (Halliwell & Rouse, 1987). While some corrections have been applied to restored and cutover peatlands in Eastern Canada (Petrone et al., 2004; Ketcheson & Price, 2013), it is difficult to apply those 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 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.

Capillary rise strategies and 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 3-6) compared to the other mosses, and since θ responded solely to P events and not water table depths (Figure 3-7), 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 (c.f. Skre et al., 1983; Price et al., 1997; Mulligan & Gignac, 2001; Carleton & Dunham, 2003). These mosses do not have the capillary structure to draw water to the photosynthesizing canopy from the underlying water table or substrates (Carleton & Dunham, 2003) thus their water content did not respond to changes in water table depth (Figure 3-2). Since feather moss productivity slows at high water contents (Busby et al., 1978; Mulligan & Gignac, 2001), there is no need for a tightly woven structure that promotes capillary rise and water retention, thus their low θ and *GEP* rates (Figure 3-8 and 3-9). This supports the notion that feather mosses withstand prolonged periods of desiccation (Skre et al., 1983) and rely solely on precipitation (Figure 3-2; Busby et al., 1978) and dew and distillation formation (Carleton & Dunham, 2003) for sources of moisture to maintain physiological processes (Carleton & Dunham, 2003; Csintalan et al., 2000).

Sphagnum mosses also occupied positions well above the water table, albeit with a relatively small range (Figure 3-6), but θ changes with antecedent conditions and under both high and low water table conditions were small (Figure 3-7), indicating they drained

quickly when wetted by *P* but generated a relatively strong capillary rise that created a relatively stable θ (see also Figure 3-2), which is important to sustain physiological processes (Schipperges & Rydin, 1998; Strack et al., 2009). Thus, while *Sphagnum* had a high residual water content (Figure 3-2) on account of water storage in hyaline cells (Hayward & Clymo, 1982), precipitation water readily drained by transmitting water in the active pores (see Rezanezhad et al., 2012). We note the lower θ value of drained near-surface *Sphagnum* in the transect study compared to 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), thus less requirement for a tightly clustered community growth form (that causes better capillarity) for that species (see McCarter & Price, 2012). *Tomenthypnum* had a relatively wide range of elevations above the water table (Figure 3-6), similar to other studies (Vitt, 1990; Hedenäs & Kooijman, 1996), and larger θ fluctuations (Figure 3-7) suggesting it was more sensitive to direct *P* as a source of water compared to dependency 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 3-7).

While capillary rise was important for both *Sphagnum* and *Tomenthypnum* to maintain relatively high productivity (Figure 3-8), the drought experiment demonstrated the important controls of atmospheric water on *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 3-8) 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 3-4). 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* productivity is 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 3-6) the water table. In contrast, the *Sphagnum* moss monoliths experienced a much larger range of θ compared to *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). As both the *Sphagnum* and *Tomenthypnum* moss were desiccated in the ES treatments, *GEP* was likely due to vascular plant photosynthesis as they can comprise between 70 and 90% of the gross productivity (Riutta et al., 2007). However, as previously stated, the differences of gas fluxes between treatments are predominantly caused by the mosses as photosynthesis in vascular plants is less sensitive to moisture changes than in mosses (Riutta et al., 2007).

Combining data in the drought experiment for each moss type resulted in relationships indicative of their water strategies. ET_{in} increased generally with θ for both *Tomenthypnum* and *Sphagnum* (Figure 3-9) 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 3-9) suggest the importance of maintaining high θ, particularly for *Tomenthypnum* where small additions of water (i.e. steeper curve) by precipitation, for example, can greatly increase *GEP* rates. The quadratic relationships for feather and *Sphagnum* mosses fit strongly but were statistically weak (because the relationships were linear, not quadratic as expected) thus were linear in this study. The relationships may have been quadratic had θ been high enough to limit CO_2 diffusion and hence *GEP*, as seen in the results of Williams & Flanagan (1996).

While *Tomenthypnum* and feather moss shoots both tolerate frequent desiccation, it is their different response to moisture regimes that affect their hydrological niches. Busby & Whitfield (1978) and Williams & Flanagan (1996) showed feather mosses had decreased productivity with high water content, whereas *Tomenthypnum* mosses did not (Busby and Whitfield, 1978). Additionally, transplant studies have shown that placing feather mosses in wetter habitats are detrimental to their health (Busby et al., 1978;

Mulligan & Gignac, 2001). Since *Tomenthypnum* frequently exhibited higher water contents without detrimental effects on its productivity (Figure 3-8), the mosses clearly have different physiological tolerances to high water contents that are reflected in their positions closer to the water table.

3.7   Conclusion

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 to *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, despite the relatively low water tables, *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 and emergent moss shoots permitted the desiccation of the uppermost portions (few cm) of moss shoots. This desiccation 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 productivity, frequent wetting by precipitation as well as dew and distillation are likely more important for *Tomenthypnum* with its relatively low water content compared to *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. When hydrologically connected with the water table, *Tomenthypnum* acted similarly to *Sphagnum* mosses and utilized capillary flow from the water table. When hydrologically disconnected, the moss acted more like feather mosses that occur at relatively high elevations with respect to the water table, relying more on precipitation water when available. Notwithstanding the unreplicated *Sphagnum*

profile in the water dynamics experiment, the results were consistent with laboratory observations from the hummocks from the same fen as well for *Tomenthypnum*, as documented in Ch. 2. 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 behavior. Since there are few investigations on the importance of moss-substrate interactions in peatlands, particularly for mosses other than *Sphagnum*, the results here provide valuable insights into the hydrological functions of these layers.

4.0 Conclusion and Implications

Peatland moss composition can have a significant impact on the hydrophysical properties of the near surface moss and the underlying peat substrates. However, despite the differences in the properties and water retention capacity of intermixed *S. angustifolium* and *S. magellanicum* and *T. nitens* in this study, the properties still both provided both moss types the mechanisms for capillary rise. The responses of *T. nitens* and intermixed *S. angustifolium* and *S. magellanicum* water content with water table position demonstrates how the size and connectivity of capillary pore spaces within the moss structure and the underlying layers. This is a function of moss morphology and growth form, directly influence the hydrological connectivity with the underlying peat. As a result, the gradual shift in water-conducting pores with depth in the *Sphagnum* structure facilitated the upward transfer of water to the capitula to maintain high water contents and high pressures to avoid desiccation and sustain productivity. Precipitation water easily drained below the *Sphagnum* capitula to the water table for storage for capillary rise and had little impact on productivity alone. However, low water tables limited capillary rise along with water content and productivity. While *T. nitens* has limited storage capacity compared to *Sphagnum* mosses due to a lack of hyaline cells, it had similar abilities to conduct water within the active porosity within the rhizoid tomentum and between branches. An intermediate layer of partially decomposed moss shoots with greater water retention, being wetted by frequent precipitation or high water tables, acts to provide a supply of water for capillary rise from the layer itself (when hydrologically disconnected from the water table) or to connect with the underlying peat and draw capillary water from the water table. However, with an abundance of large pores compared to underlying dense, peat substrates, pores of the near-surface moss easily drain. Thus to generate capillary rise very low pressures are required, which is associated with the desiccation of moss shoots, and hence reduced productivity. The more frequent desiccation makes precipitation events, even small ones, particularly important for rewetting and re-establishing moss productivity.

Calculations of dew, distillation, and vapour fluxes within *T. nitens* profiles demonstrated that they also provide important sources of water that increase vapour pressure at the moss surface and moisture for photosynthesis, most likely important in

early morning. Furthermore, disequilibrium between vapour and *T. nitens* moss pressures in the near-surface suggest calculated pressures may not provide an accurate characterization of actual moss matric pressures. 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 *T. nitens* and other mosses. Greater quantification of atmospheric and vapour fluxes, relationships between *T. nitens* shoot density and water retention, relationships between moss pressure and vapour pressure under evaporation, and their effects on *T. nitens* productivity may elucidate the relative importance of different source waters and the ability of the brown moss to tolerate desiccation.

As the different water retention and water transport strategies of *Sphagnum* and *T. nitens* under a range of hydrological conditions have demonstrated, moss composition can have critical roles on water distribution within peatlands. While these mosses exist in different hydrological habitats both within and between fens, the ability of them to utilize capillary rise from the water table is the main driver of their productivity. However, the ability of *T. nitens* to not only tolerate, but also employ desiccation provides the mechanisms for *T. nitens* to become more drought tolerance and survive in a range of habitats. Therefore, these findings should provide insight into hydrological process than govern peatland ecosystem carbon and evaporation processes. This research is not only relevant to studies that are understanding ecohydrological processes within natural peatlands but provide insight into the hydrological conditions required for growth of different moss types in restored and reclaimed fen peatlands in the western boreal region and across Canada.

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