

Measurement and modelling of bryophyte evaporation in a boreal forest chronosequence

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ABSTRACT

The effects of changing climate and disturbance on forest water cycling are not well understood. In particular, bryophytes contribute significantly to forest evapotranspiration in poorly drained boreal forests, but few studies have directly measured this flux and how it changes with stand age and soil drainage. We measured bryophyte evaporation (E) in the field (in Canadian *Picea mariana* forests of varying ages and soil drainages) and under controlled laboratory conditions, and modelled daily E using site-specific meteorological data to drive a Penman–Monteith-based model. Field measurements of E averaged 0.37 mm day⁻¹ and ranged from 0.03 (*Pleurozium schreberii* in a 77-year-old dry stand) to 1.43 mm day⁻¹ (*Sphagnum riparium* in a 43-year-old bog). In the laboratory, moss canopy resistance (which ranged from ~ 0 to 1500 s m⁻¹) was constant until a moss water content of ~ 6 g g⁻¹ and then climbed sharply with further drying; unexpectedly, no difference was observed between the three moss groups (feather mosses, hollow mosses and hummock mosses) tested. Modelled annual E ranged from 0.4 mm day⁻¹, in the well-drained stands, to ~ 1 mm day⁻¹ in the 43-year-old bog. The Penman–Monteith modelling approach used was relatively insensitive to most parameters but only explained 35% of the variability in field measurements. Bryophyte E was greater in bogs than in upland stands, was driven by low-lying mosses and varied with stand age only in the poorly drained stands; this suggests that bryophytes may provide a buffering effect to fire-driven changes in tree transpiration. Copyright © 2010 John Wiley & Sons, Ltd.

KEY WORDS boreal forest; black spruce; evapotranspiration; modelling; moss; evaporation

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INTRODUCTION

Significant changes in disturbance regimes have occurred for decades in the global boreal forest (Flannigan and Van Wagner, 1991; Kasischke and Turetsky, 2006), and future changes in boreal climate, CO₂ and fire are likely to be large (Flannigan *et al.*, 2005). In central Canada, 20th-century increases in fire-converted large areas of mature evergreen needleleaf conifers to stands dominated by young deciduous broadleaves, with significant consequences for regional C, nutrient and water dynamics (Kurz and Apps, 1999; Amiro *et al.*, 2006b; Bond-Lamberty *et al.*, 2007b). Given the large area and high carbon storage of the global boreal forest (Apps *et al.*, 1993; Gower *et al.*, 2001), it is important to be able to understand and predict the forest's responses to these factors and other future changes. A crucial part of this response will depend on how fire disturbance and the hydrological cycle interact.

The effects of changing climate and disturbance on evapotranspiration (ET, the land-atmosphere water

flux) and forest water cycling are not well understood, however. Human influences are changing northern hemisphere ET (Fernandes *et al.*, 2007), while at a smaller scale fire clearly affects stand water cycling (Ewers *et al.*, 2005; Amiro *et al.*, 2006a), watershed-scale hydrology (Valeo *et al.*, 2003) and regional climate (Chambers and Chapin, 2002). ET is closely coupled with net primary production through plant stomatal controls on transpiration (Campbell and Norman, 1998; Tang *et al.*, 2006); if ET changes with disturbance, this will have important implications for local, regional and continental growth and climate dynamics. Low temperatures and nitrogen availability constrain ET in the boreal forest (Baldocchi *et al.*, 2000; Ewers *et al.*, 2001), and boreal water vapour fluxes at the stand level vary with species composition (Linder and Troeng, 1980; Baldocchi *et al.*, 1997; Jarvis *et al.*, 1997), structural changes with stand age (Ewers *et al.*, 2005; Amiro *et al.*, 2006a,b), permafrost changes (Camill *et al.*, 2001a) and soil drainage (Lafleur *et al.*, 1997), among other factors.

Because much of the boreal forest is poorly drained, with high rates of primary production (Vitt *et al.*, 2001; Camill *et al.*, 2001b), slow decomposition rates and bryophyte-dominated successional pathways (O'Neill, 2000; Turetsky, 2003), mosses form a significant part of these ecosystems' carbon, nitrogen and water cycles

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(Skre and Oechel, 1981; Longton, 1992; Heijmans *et al.*, 2004b; Suzuki *et al.*, 2007). These areas sequester large amounts of C in peat, and their vulnerability to changes in climate, hydrology and fire will influence regional biogeochemical cycles (Camill *et al.*, 2001a). Bryophytes play important roles in the biogeochemical cycling of well-drained boreal forests as well (DeLuca *et al.*, 2002; O'Connell *et al.*, 2003) and influence vegetation–atmosphere exchange in many ecosystems (Lafleur and Rouse, 1988; Williams and Flanagan, 1996; Shimoyama *et al.*, 2004).

Water loss in bryophytes is controlled by canopy structural properties (Proctor, 1980, 1982; Zotz *et al.*, 2000; Rice and Schneider, 2004), as opposed to vascular plants, in which leaf stomata regulate water fluxes. As a poikilohydric plant, a bryophyte—more specifically the water vapour partial pressure of the plant body—is always in equilibrium with ambient humidity (Green and Lange, 1994); this lack of active control over plant water status implies fundamentally different ecosystem-level dynamics as well (Longton, 1992; Turetsky, 2003). The morphology of the bryophyte canopy influences the development of a boundary layer adjacent to the plant surface (Campbell and Norman, 1998), which in turn greatly influences the plant water and carbon budgets (Zotz *et al.*, 2000; Rice *et al.*, 2001). Bryophyte water status is a function of factors spanning a wide range of scales: cell turgidity, osmotic potential, local hydrology, distance from the water table and thallus water content (Dilks and Proctor, 1979; Hayward and Clymo, 1982; Proctor, 1982, 2000a; Proctor and Tuba, 2002). Generally, the water dynamics of nonvascular plants are not as well understood or quantified as those of vascular plants and are rarely modelled (Bond-Lamberty *et al.*, 2007a; Sonnentag *et al.*, 2008).

The objectives of this study were to (i) measure *in situ* evaporation from bryophytes in boreal forest stands of varying ages and soil drainages; (ii) collect detailed data on moss evaporation rates under controlled laboratory conditions; and (iii) quantify the evaporative contribution of bryophytes contribution to stand-level ET across forest succession based on evaporation data and detailed field surveys of moss abundance. We used field chamber- and laboratory-based chamber measurements, and several modelling approaches, to estimate annual evaporative fluxes from bryophytes.

METHODS

Field measurements

The study was conducted in a well-drained black spruce (*Picea mariana* Mill. BSP)-dominated chronosequence west of Thompson, Manitoba, Canada, near the Boreal Ecosystem-Atmosphere Study (BOREAS) Northern Study Area (55°53'N, 98°20'W). The chronosequence consisted of four different-aged black spruce forests, all of which originated from stand-killing wildfire in mature forests. The oldest stand in the chronosequence

(~157 years in 2007) is the BOREAS NSA tower site (Dunn *et al.*, 2007). The carbon and water dynamics of these study sites have been extensively studied (Bond-Lamberty *et al.*, 2002, 2004; Ewers *et al.*, 2005). The stands were dominated by three tree species: trembling aspen (*Populus tremuloides* Michx.), black spruce and jack pine (*Pinus banksiana* Lamb.). Early successional deciduous tree species are replaced by black spruce in the older stands; the black spruce canopy closure, at 50–60 years, is associated with drastic thinning of the understory and growth of thick feather mosses. The dominant moss species are *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) Schimp. in the well-drained stands and *Aulacomnium palustre* (Hedw.) Schwaegr., *P. schreberi*, *Sphagnum warnstorffii* Russ., *S. riparium* Ångstr. and *S. fuscum* (Schimp.) Klinggr. in the poorly drained stands. The names and taxonomy given here follow the U.S. Department of Agriculture (USDA) plants database (<http://plants.usda.gov>).

All stands are within a 40-km² area. Regional mean annual temperature and precipitation were 0.8 °C and ~440 mm, respectively. Micrometeorological stations recorded local conditions at all burn sites (157, 77, 43 and 18 years). At each stand, above-canopy instruments were mounted in both the well-drained and the poorly drained stands. Net radiation (R_n) was measured using an NR-Lite net radiometer (Kipp & Zonen, Delft, The Netherlands), except at the oldest site where a Q7 net radiometer (REBS, Seattle, WA, USA) was used. Ground heat flux (G) was also measured at the 43- and 77-year-old sites using four HFT3 Heat Flux Transducers (Campbell Scientific, Logan, UT, USA), installed horizontally 2 cm below the active moss and litter layers. Other measurements included air temperature and relative humidity using HMP45C probes (Campbell Scientific) and a tipping-bucket type precipitation gauge (TE525M; Texas Electronics, Inc., Dallas, TX, USA). Incoming and outgoing photosynthetically active radiation (PAR) were measured above the canopy at each site using LI-190 PAR sensors (LI-COR Inc., Lincoln, NE, USA). Further details on the meteorological stations were given by Barker *et al.* (2009).

To estimate moss contribution to ET, four 5 m × 5 m plots were established in each stand. A surveyors' level was used to record relative elevation changes (to the nearest cm) for each 1 m² within the plot, and moss species recorded at each point; there were 36 points per plot. The correction factor (CF) that is necessary to account for the fact that a boreal bog, due to its surface morphology, occupies a greater surface than a horizontal plane (Vitt, 2007) was first estimated by calculating the mean surface area of each triangle composed of three adjacent sample points (i.e. each small triangle formed by the sample grid points) relative to the 0.5-m² area that its area would be in a horizontal plane. The CF was also independently calculated by recording the distance between plot corners, both by suspending a level tape measure above the plot and by laying the tape flat on the bog surface.

Direct measurement of moss ET fluxes was made from polyvinyl chloride (PVC) collars, interior diameter of 33 cm, set in the moss ground cover, with the top of the collar slightly (2 cm) protruding above the top of the moss; two collars were placed in the relatively homogeneous upland plots, while four collars (two on hummocks and two in hollows) were used in each poorly drained plot. A Licor-6400 (LI-COR Inc.) was connected to a custom Plexiglas chamber that exactly fit the PVC collars and was 15 cm high; the chamber interior was lined with a clear non-hygroscopic tape (Propafilm™), and a small interior fan ensured even mixing throughout the chamber. Because of the large volume (~13 000 cm³) of the measurement chamber, the system, with the leaf fan set to high, required several minutes to equilibrate before each measurement. Five measurements were then made and averaged to produce a single mean flux value (in mmol H₂O m⁻² s⁻¹, which was converted to mm H₂O day⁻¹); measurements were performed five to six times (in May, July and September) during the 2007 growing season. Fluxes were measured between 5 AM and 8 PM local time and thus did not include night-time values.

Laboratory experiment

We sampled and analysed the evaporation and drying characteristics of boreal mosses from three different microtopographic positions: hummock (*S. fuscum*), mesic (*P. schreberi*) and hollow (typically *S. warnstorffii* and/or *A. palustre*). Samples were taken in fall 2007 from the 77-year-old forest stand: the hummock and hollow samples from a bog, and the mesic samples from a well-drained area ~100 m away. Large samples ($N = 3$) of each type were excavated in one piece and put into translucent plastic tubs (53 cm × 38 cm × 13 cm, with exposed surface area of 2014 cm²). The moss samples completely filled the tubs (i.e. moss tops were level with or slightly higher than the tub walls). The tubs were transported to Madison, Wisconsin, USA, and stored in a dark 5 °C cold room for 1 month before the experiment began.

The experiment was run in a controlled environment room. Light was set to a 12 h/12 h light/dark cycle, with ~450 μmol m⁻² s⁻¹ photosynthetic photon flux density at the level of the moss samples during light hours; understory light levels in these forests typically range from 100 to 700 μmol m⁻² s⁻¹ (Heijmans *et al.*, 2004a), and this value is close to the mean growing season light level at these sites (B. Amiro, University of Manitoba, unpublished data). We recognize, however, that open-canopy photosynthetic photon flux density (PPFD) fluxes can be considerably higher, however (occasionally to 1500 μmol m⁻² s⁻¹ during our measurements). Relative humidity was held constant at 50%. The moss samples were randomly arranged in the room and sampled in a random order throughout the experiment. Drydown cycles of 25, 15 and 5 °C were run in that order. At the beginning of each cycle, the moss samples were allowed to equilibrate for 72 h before being watered with reverse osmosis water to field capacity: the plants and

accompanying organic material appeared saturated, but no (or minimal) water was collected at the bottom of the tub. After this point, no water was provided until the end of the drydown cycle; as the samples dried, their mass was recorded at regular intervals, to the nearest g using an Ohaus I-20 W balance. The total length of the drydown cycles was 168, 365 and 1010 h for the 25, 15 and 5 °C temperatures, respectively, with six to eight measurements made per temperature. Identical tubs filled with R/O water were used to measure the open-water evaporation rate during each drydown cycle.

At the end of the experiment, the moss in each tub was separated into surface (the top 2 cm for *Sphagnaceae* capitulum and 3–4 cm for *Pleurozium*), middle (fibric to hemic material) and lower (sapric material for *Pleurozium*) layers, with the middle and lower layers having roughly equal depth and mass. The final wet and dry masses for these layers were determined by drying at 70 °C to a constant mass. A subsample of the surface layer was weighed and its individual moss plants counted and used to compute (i) plant density, by the ratio of subsample to surface sample dry masses and (ii) leaf area, by the bryophyte-specific leaf area data of Bond-Lamberty and Gower (2007).

Data analysis and modelling

Two approaches were investigated for the use of the controlled environment experiment data to model bryophyte ET flux in the field. First, an empirical model was used to examine and quantify differences in water loss rates. This was a simple exponential decay model with both the initial value and the decay rate that allowed to vary with temperature and moss type:

$$E = (a + d_1T + d_2M)e^{-(b+d_3T)h} \quad (1)$$

where evaporation rate (E , mm day⁻¹) is a function of temperature (T , °C), moss type (M , considered here as a factor or treatment), and hours since saturation (h); d_1 , d_2 and d_3 were tested for significance to evaluate the effect of T and M . The use of h required one further assumption that 5 mm of precipitation was sufficient to saturate the moss. This was the minimum level necessary to change volumetric soil moisture at 30 cm (data not shown); 75–80% of annual rainfall comes in events above this 5 mm level (B. Amiro, University of Manitoba, unpublished data).

We also tested a model that used moss water content instead of time since saturation:

$$E = (a + d_1T + d_2M)e^{-(b+d_3T)w} \quad (2)$$

Here, the h term in Equation (1) has been replaced by w , the water content of the moss (g H₂O g⁻¹ dry mass) at time of measurement. Compared to Equation (1), Equation (2) is more physiologically appropriate but required continuous moss moisture level data for field application, whereas Equation (1) only required time since last significant rainfall, which was available from

our meteorological station (Barker *et al.*, 2009). The resulting models were used to model moss E flux over the course of the growing season.

The second approach used was based on the Penman–Monteith (Monteith, 1965; Campbell and Norman, 1998) equation:

$$E = \frac{s(R_n - G) + \rho_a c_p g_a D}{\rho_w \lambda [s + \gamma(1 + g_a/g_v)]} \quad (3)$$

Here, s is the rate of change of saturation vapour pressure with temperature ($\text{kPa } ^\circ\text{C}^{-1}$); R_n and G are net absorbed radiation and ground heat flux, respectively (both W m^{-2}); ρ_a and ρ_w are the densities of air and water, respectively (kg m^{-3}); c_p the air heat capacity ($\text{J kg}^{-1} ^\circ\text{C}^{-1}$); g_a and g_v are aerodynamic and canopy conductance, respectively (both m s^{-1}); D is vapour pressure deficit (kPa); λ is the latent heat of vapourization (J kg^{-1}); γ the psychrometric constant ($\text{kPa } ^\circ\text{C}^{-1}$); and E the canopy evaporation rate (m s^{-1}). Inverting this equation allowed us to solve for g_v based on data from the laboratory experiment.

For modelling E across the growing season, the onsite meteorological towers provided continuous data on R_n , G and D ; R_n was attenuated based on site-specific leaf area data (Bond-Lamberty *et al.*, 2002) using Beer's law with $k = -0.05$ (Landsberg and Gower, 1997) to provide ground-level radiation. We assumed that s was a simple function of temperature and saturated vapour pressure at that temperature (Campbell and Norman, 1998), $\rho_a = 1.20$, $\rho_w = 1000$, $c_p = 1.012$, $g_a = 0.017$, $\lambda = 2260000$ and $\gamma = 0.066$. The g_a value inverts a resistance of 60 s m^{-1} and is based on typical values for a short canopy as given in Bonan (2002). To quantify the error contribution of this and other parameters, a basic sensitivity analysis was performed by varying key

input parameters by $\pm 10\%$ and examining the resulting changes in model output.

Modelling resulting from both the simple empirical approach and the Penman–Monteith (P-M) approach were compared with the field data measured in 2007. Statistical analyses were conducted using the *lm* (linear model using least-squares regression), *nls* (nonlinear least squares), *slope.test* (from the *smatr* package) and other functions in R version 2.8.0 (R Development Core Team, 2008). Unless otherwise noted, all statistical analyses used the plot as experimental unit and a significance of $\alpha = 0.05$.

RESULTS

Field measurements

The well-drained study sites were dominated by *A. palustre* in the youngest stands, although more than half the ground area was moss-free in these stands, whereas the oldest stands had complete coverage by feather mosses (particularly, *P. schreberi*; Table I). The youngest poorly drained stands had low rates of bryophyte coverage, similar to their well-drained counterparts, but species mix in the mature bogs was much more diverse, with *Cladina* spp., *Sphagnum* spp. and feather mosses dominant.

The study sites exhibited small slopes of 0–4%; two plots in the poorly drained 18-year-old stand had slopes of 6% and 9%. Across the chronosequence, surface relief was considerably more varied in the poorly drained areas than in the upland stands (Figure 1). The CF necessary to account for this microtopography ranged from 1.00 to 1.02 when measured using the $1 \text{ m} \times 1 \text{ m}$ sampling grid. Values measured using a tape measure laid directly on the bog surface were considerably higher, from 1.06 at the youngest site to 1.11 at

Table I. Percentage cover of bryophytes by stand age (as of 2007) and drainage class; standard errors ($N = 4$ plots) are shown in parentheses.^a

Stand age	AUPA	CLSP	PLSC	POSP	SPSP	Other	None
<i>Well-drained stands</i>							
18	33 (15)	0 (0)	2 (1)	8 (10)	0 (0)	2 (1)	56 (10)
43	17 (15)	0 (0)	61 (15)	0 (0)	0 (0)	10 (8)	12 (7)
78	0 (0)	0 (0)	99 (1)	0 (0)	0 (0)	1 (1)	0 (0)
158	0 (0)	0 (0)	100 (0)	0 (0)	0 (0)	0 (0)	0 (0)
<i>Poorly drained stands</i>							
18	2 (4)	0 (0)	0 (0)	9 (6)	1 (1)	22 (16)	66 (24)
43	72 (22)	3 (5)	3 (5)	0 (0)	6 (9)	2 (4)	13 (13)
78	38 (5)	16 (4)	17 (9)	3 (4)	22 (12)	0 (0)	4 (2)
158	1 (2)	25 (22)	34 (26)	0 (0)	30 (24)	5 (3)	5 (4)

^a Categories include *Aulacomnium palustre* (AUPA), *Cladina* spp. (CLSP), *Pleurozium schreberi* and other feather mosses (PLSC), *Polytrichum* spp. (POSP), *Sphagnum* spp. (SPSP), other nonvascular plants, and none.

the oldest sites. These values imply that uncorrected flux measurements will underestimate the true flux by 5–10%. All flux numbers reported below include the appropriate site-specific topography correction.

Field measurements of bryophyte water fluxes averaged 0.37 mm day⁻¹ and ranged from 0.03 (*P. schreberii*, 77-year-old dry stand, September) to 1.43 mm day⁻¹ (*S. riparium*, 43-year-old bog, August). Measured field fluxes were correlated with both air temperature and relative humidity ($P < 0.001$ for both, combined relationship $F_{2,1269} = 55.68$, $P < 0.001$) but these only explained a small amount of the variance (adjusted $R^2 = 0.11$); fluxes were unrelated to PAR ($P = 0.583$).

Laboratory experiment

In the laboratory, water evaporation rate from the moss surface depended on the water content of the moss and temperature (Figure 2). Peak evaporation rates (at moss saturation) were close to open-water E , although at the warmest temperature (25 °C) feather mosses did not approach this rate. Fitting the empirical equation (1) to these data revealed that there was no difference between the hummock and hollow *Sphagnum* species ($P = 0.462$), but feathermoss exhibited significantly ($P < 0.001$) different evaporative characteristics and

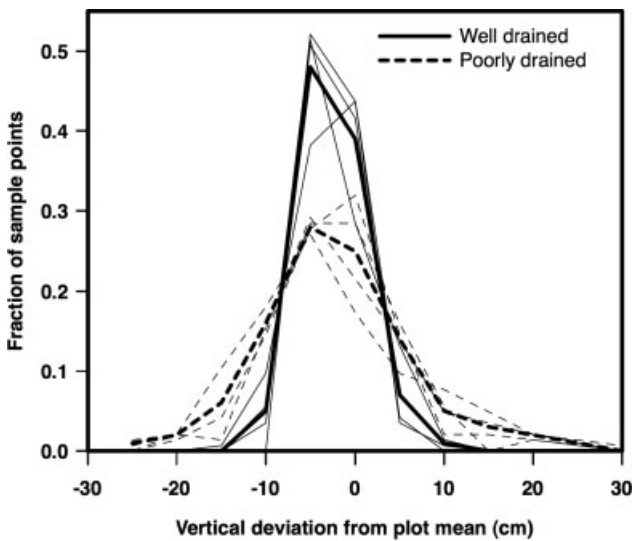


Figure 1. Microtopography of study sites showing fraction of detrended 1 m² sample points deviating from plot mean. Dark lines show mean of all sites, by soil drainage; for clarity lighter, site-specific lines are not individually labeled.

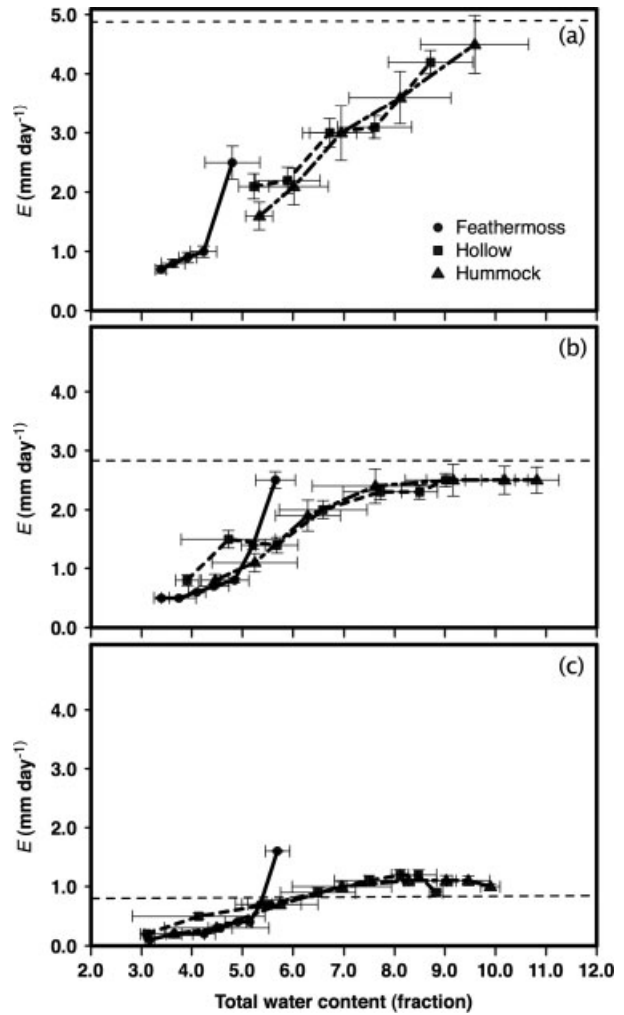


Figure 2. Evaporative water loss (E) as a function of water content, by moss type, for (a) 25 °C, (b) 15 °C and (c) 5 °C. Vertical error bars show standard deviation between samples ($N = 3$); horizontal error bars show range of water content (water mass divided by dry mass) over which measurement was made. Dashed lines show E for tubs of open water, under same conditions and with equal exposed area.

thus was analysed separately. Feathermoss evaporation rate increased by 0.06 mm °C⁻¹ (Table II). *Sphagnum* evaporation was more responsive to temperature (0.17 mm °C⁻¹), and the exponential decay rate was also temperature-dependent, unlike in feather mosses. Moss water content was unsurprisingly and inversely correlated with time since saturation, and thus the Equation (2) fit confirms that higher water contents meant higher

Table II. Fitted model parameters for Equations (1) and (2) based on the laboratory experiment, by moss type.^a

	a (mm)	b (h ⁻¹)	d_1 (mm °C ⁻¹)	d_3	N	AIC	RSE
<i>Equation (1)</i>							
Feathermoss	0.852	0.005	0.030		20	-2.55	0.294
<i>Sphagnum</i>	0.298		0.172	2.23e-04	40	-5.51	0.213
<i>Equation (2)</i>							
Feathermoss	0.005	-0.657	0.002		20	-30.99	0.099
<i>Sphagnum</i>	0.229	-0.115	0.024	-0.003	40	16.11	0.275

^a Observations (N), Akaike information criterion (AIC) and residual standard error (RSE) are also given. All parameters shown are highly significant ($P < 0.001$); note that parameter d_3 for *Sphagnum*, Equation (1), is shown in scientific notation.

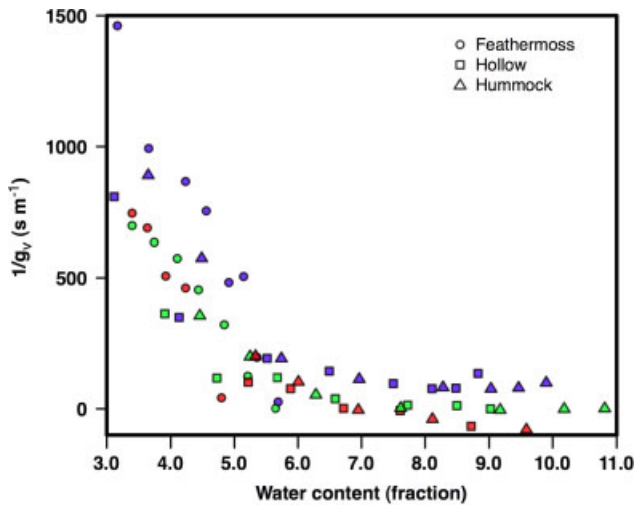


Figure 3. Moss canopy resistance (reciprocal of conductance g_v) versus water content, by moss type and temperature (red, 25 °C; green, 15 °C; blue, 5 °C).

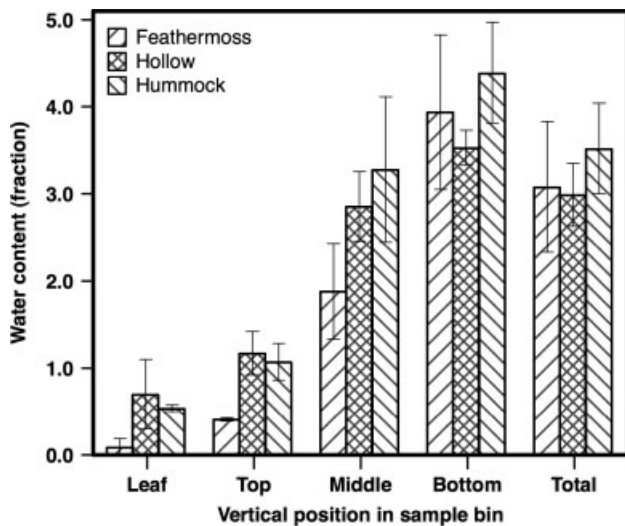


Figure 4. Vertical gradient in water content in laboratory experiment moss samples after the final (5 °C) drydown, by thirds (top, middle, bottom, each ~4 cm). Individual leaf and total bin water contents are also shown. Errors bars shown standard deviation between bins ($N = 3$).

evaporation rates; for feathermoss, this model explained a significantly higher amount of variability (Table II).

Using the inverted Penman–Monteith equation (3), canopy resistance ranged from ~ 0 (at 25 °C, some calculated values were < 0) to $\sim 1500\ s\ m^{-1}$ for dry, cold (5 °C) mosses (Figure 3). Resistance was constant until a moss water content of $\sim 6\ g\ g^{-1}$ and then climbed sharply with further drying; no difference was observed between the three moss groups (feather mosses, hollow mosses and hummock mosses) tested. Strong moisture gradients existed in the sample bins, with water contents $< 1.0\ g\ g^{-1}$ at the surface but $3\text{--}4\ g\ g^{-1}$ at a depth of 10 cm after the final drydown (Figure 4).

Growing season E flux from bryophytes

A comparison of observed field data (F_O) with modelled fluxes using the Penman–Monteith approach (F_M) from

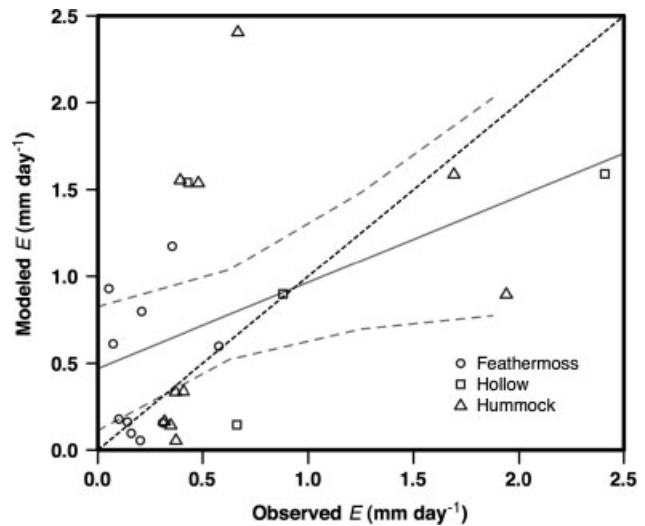


Figure 5. Observed versus modelled moss evaporation (E), by moss type, for the combined Penman–Monteith model. Dashed line shows 1 : 1 relationship; larger dash lines are 95% confidence intervals for the observed-modelled line.

the same days revealed a significant and positive correlation ($F_{1,22} = 11.68$, $P = 0.002$) but not a 1 : 1 relationship (Figure 5). The observed relationship was $F_M = 0.38 + 0.61 F_O$, with the intercept and slope significantly different from zero ($P = 0.023$) and one ($P = 0.038$; the 95% CI of the slope was from 0.239 to 0.977), respectively. The high degree of scatter in the observed data contributed to a modest adjusted R^2 of 0.35.

Modelled annual E fluxes from bryophytes ranged from $0.4\ mm\ day^{-1}$ ($146\ mm\ year^{-1}$), in the well-drained stands, to $\sim 1\ mm\ day^{-1}$ ($383\ mm\ year^{-1}$) in the 43-year-old bog (Table III). Results from the two modelling approaches were similar in the poorly drained stands, but the older well-drained stands' high leaf area meant that the two models diverged significantly at these sites: empirical model results were $\sim 0.6\ mm\ day^{-1}$, while the Penman–Monteith equation results (which explicitly includes R_n and its reduction under high leaf area) were $\sim 0.4\ mm\ day^{-1}$. There was no difference in annual flux between soil drainages because of the extremely low value ($0.08\ mm\ day^{-1}$) in the 18-year-old poorly drained stand; if this value was excluded, drainage was highly significant ($T_4 = -6.18$; $P = 0.003$) with bogs having a $0.44\ mm\ day^{-1}$ greater flux than upland stands. Stand age had no effect on annual E ($P = 0.769$).

The Penman–Monteith modelling approach used here was most sensitive to ρ_w and λ , the water density and latent heat of vapourization parameters; computed annual E fluxes varied by $\sim 10\%$ with a $\pm 10\%$ variation in each parameter. The model was moderately sensitive to g_a (aerodynamic conductance; varying $g_a \pm 10\%$ resulting in $\pm 2\text{--}7\%$ annual fluxes in the well-drained stands and $1\text{--}4\%$ in the poorly drained stands) and the minimum precipitation required to saturate the moss ($\pm 10\%$ resulted in annual flux changes of -7% to $+0\%$). In contrast, the model was insensitive to air heat capacity (c_p) and air density (ρ_a) (although there is no uncertainty in these inputs).

Table III. Modelled annual evapotranspiration (mm day^{-1}) from bryophytes, by soil drainage and stand age; these are stand-level values, taking into account both spatial area (Table I) and modelled flux (Table II).

	Well-drained stands				Poorly drained stands			
	18	43	78	158	18	43	78	158
<i>Empirical model</i>								
Feathermoss	0.06	0.36	0.57	0.58	0.05	0.04	0.21	0.34
Hollows	0.43	0.22	0.00	0.00	0.04	0.98	0.67	0.10
Hummocks	0.00	0.00	0.00	0.00	0.00	0.02	0.10	0.30
Total	0.49 (0.12)	0.58 (0.18)	0.57 (0.01)	0.58 (0.00)	0.09 (0.01)	1.04 (0.35)	0.98 (0.21)	0.75 (0.36)
<i>Penman–Monteith model</i>								
Feathermoss	0.05	0.29	0.37	0.40	0.04	0.03	0.16	0.30
Hollows	0.44	0.22	0.00	0.00	0.04	1.00	0.59	0.10
Hummocks	0.00	0.00	0.00	0.00	0.00	0.02	0.09	0.30
Total	0.49 (0.12)	0.51 (0.16)	0.37 (0.01)	0.40 (0.00)	0.08 (0.01)	1.05 (0.35)	0.83 (0.18)	0.69 (0.33)

^a Results are given both for the simple empirical model and the combined Penman–Monteith model. Numbers in parentheses are standard errors based on plot-to-plot ($N = 4$) variability in moss species abundance.

DISCUSSION

The changes in bryophyte dominance and species composition seen here are consistent with known patterns of post-fire moss regrowth in boreal forests (Bond-Lamberty and Gower, 2007; Fenton *et al.*, 2007; Benscoter and Vitt, 2008). In poorly drained areas, moss growth and differential growth rates create and reinforce the hummock-hollow microtopography characteristic of these areas (Yabe and Uemura, 2001; Benscoter *et al.*, 2005). Microtopography affects not only calculated fluxes—by 5–10% here, and sometimes much larger (30–40%) values (Vitt, 2007)—but also species distribution (Andrus *et al.*, 1983) and small-scale water balance and carbon fluxes, due to turbulence effects on the local environment (Rice and Schneider, 2004) and small-scale variations in the water table (Roy *et al.*, 1999). The correction values reported here are consistent with those previously measured in Ontario, Canada (Rocheffort *et al.*, 1990).

A number of previous studies have partitioned ET sources in boreal forests and bogs: Kellner (2001) reported that $\geq 50\%$ of ET originated from the moss surface in a Swedish *Sphagnum* bog; Admiral and Lafleur (2006) found that moss contributed 20–50% of total latent heat flux in the Mer Bleue bog, depending on moss moisture status; Suzuki *et al.* (2007) estimated that the mosses *Aulacomnium turgidum* and *Cetraria cucullata* (*sic*; presumably *Cetraria cucullata* ?) contributed 23% of ET in a leafless *Larix cjanderii* forest. Heijmans *et al.* (2004b) used lysimeters to measure moss evaporation rates of 0.3–1.5 mm day^{-1} in boreal black spruce forests in Alaska, USA, with low rates in dense well-drained forest and high rates in a *Sphagnum* bog. These values are largely consistent with our results, although the bog *E* values reported here are lower than some measured using lysimeter and eddy covariance methods (Heijmans *et al.*, 2004a; Humphreys *et al.*, 2006).

Both moss moisture and radiation were important drivers of modelled evaporation rates (Figure 3, Table II). Increases in moss surface resistance under high-VPD

and low water table conditions can significantly affect stand-level fluxes in the field (Kim and Verma, 1996; Humphreys *et al.*, 2006); moss contribution to latent heat flux was strongly dependent on water table in the Mer Bleue bog (Admiral *et al.*, 2006). Kellner (2001) reported surface resistance (r_s) values of $160 \pm 70 \text{ s m}^{-1}$ for a Swedish *Sphagnum* bog, consistent with the results here (Figure 3). It is interesting that *S. fuscum* has a dense, tightly woven canopy to retard water loss (Rice and Schneider, 2004), but in the laboratory, this moss evaporated at the same rate as hollow and feather mosses. This result is surprising, as differential evaporative rates have been previously observed (e.g. Titus *et al.*, 1983). Moss water status is central to the regulation of biotic and abiotic processes of these plants (Dilks and Proctor, 1979; Proctor, 2000b), although moss moisture is largely decoupled from soil water levels (McFadden *et al.*, 2003; Raven, 2003) and difficult to measure in an automated manner in the field; it is for this reason we used, in the annual modelling, time since saturation to derive moss water content indirectly.

It is also useful to compare these results with those of other studies performed at these same sites. Barker *et al.* (2009) used eddy covariance to measure overall forest ET, from the energy balance residual (Amiro, 2009), at two (43 and 77 years) of these sites; they found (i) ET increased with stand age, from 1.4 to 2.3 mm day^{-1} in 2007; and (ii) ET rates were 10–20% ($\sim 0.2 \text{ mm day}^{-1}$) lower in poorly drained stands than in well-drained stands of the same age. This implies that bryophytes contributed 18–31% and 49–69% to the total ET flux at the well-drained and poorly drained stands, respectively, based on the data reported in Table III. These numbers are consistent with tree transpiration fluxes reported by Ewers *et al.* (2005) in these stands several years previously.

Boreal wildfires in central Canada effect species shifts over decadal periods, converting evergreen conifer (typically *P. mariana* or *P. banksiana*) stands to broadleaf deciduous ones (*P. tremuloides*), as well as changing the age structure of the forest (Kurz and Apps, 1999). The bryophyte *E* flux data reported here were relatively

invariant with stand age, suggesting that shifts in forest age will have little effect on this contribution to the overall ET flux: as well-drained stands age, increased moss coverage is balanced by a shift from *A. palustre* to feather mosses, while poorly drained stands exhibited no clear pattern once moss coverage was re-established. Young post-burn stands obviously have greatly reduced or absent moss cover and thus *E* from bryophytes, subject to a great degree of stochasticity (Fenton *et al.*, 2007), but ecosystem modelling suggests that increased solar radiation reaching the ground level, and thus increased soil evaporation, may largely compensate for this drop in biotic ET in post-burn stands (Kang *et al.*, 2006; Bond-Lamberty *et al.*, 2009).

A number of potential issues with this study's design and implementation should be noted. First, chronosequence designs are problematic for studying vegetation dynamics (Johnson and Miyanishi, 2008), although our ecosystem structure and flux data suggest that biogeochemical fluxes are more robust to this design choice (Bond-Lamberty and Gower, 2008). These chronosequence sites have been shown to be consistent with stands across northern Manitoba (Bond-Lamberty *et al.*, 2004), and Goulden *et al.* (2006) used Landsat data to conclude that this chronosequence comprised a valid space-for-time substitution. Second, the relatively limited field sampling and high errors seen in the field data mean that the ability of the laboratory-based models to predict daily fluxes is questionable (cf. Figure 5). High spatial variability, particularly in the bog sites, is difficult to capture with chamber measurements, but our use of a large measurements chamber may have resulted in large errors because of its large volume and long equilibration time. This may also explain why our results indicated that the bog bryophyte *E* flux were dominated by hollows, while other modelling results give the opposite result, with hummocks having the larger flux (Admiral and Lafleur, 2007). Third, we note that there was no wind in the chambers used to measure fluxes, either in the field or in the laboratory (except for the small fan used in the field measurements). Continental boreal forest wind speeds tend to be low, and measured values at these sites were generally $<2 \text{ m s}^{-1}$. Other assumptions made in the modelling component of this study had relatively small effects on computed annual fluxes.

In summary, the bryophyte contribution to ET (18–31% and 49–69% in well-drained and poorly drained stands, respectively) was significant in the forests studied here. Although our results were consistent with previously measured bryophyte *E* fluxes, it is not clear if the Penman–Monteith approach attempted here can capture these fluxes well enough for generalizable modelling. If the bryophyte evaporative flux will change to only a limited degree with increased landscape-level fire, this may provide a buffering effect to changes in tree transpiration resulting from fire-driven species shifts (Ewers *et al.*, 2005; Bond-Lamberty *et al.*, 2007b). However, the hydrological function of vascular plants remains better understood and quantified than that of nonvascular

bryophytes; given the importance of the hydrological cycle in these carbon-rich, fire-driven ecosystems, their dynamics need to be fully captured in ecophysiological models.

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