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, CO\(_2\) 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.
(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.) Schweegr, P. schreberi, Sphagnum warnstorfii 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 (Rn) 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.
BRYO PHYTE EVAPORATION IN BOREAL FOREST

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 drained 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 (~3,000 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. warnstorfii 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; under 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 RO 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:

\[ E = (a + d_1T + d_2M)e^{-(b+dt)h} \]  

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); d₁, d₂ and d₃ 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:

\[ E = (a + d_1T + d_2M)e^{-(b+dt)w} \]  

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:

$$E = \frac{s(R_n - G) + \rho_a c_p g_s D}{\rho_a [s + \gamma (1 + g_a/g_s)]}$$

(3)

Here, $s$ is the rate of change of saturation vapour pressure with temperature (kPa °C$^{-1}$); $R_n$ and $G$ are net absorbed radiation and ground heat flux, respectively (both W m$^{-2}$); $\rho_a$ and $\rho_w$ are the densities of air and water, respectively (kg m$^{-3}$); $c_p$ the air heat capacity (J kg$^{-1}$ °C$^{-1}$); $g_a$ and $g_s$ are aerodynamic and canopy conductance, respectively (both m s$^{-1}$); $D$ is vapour pressure deficit (kPa); $\lambda$ is the latent heat of vapourization (J kg$^{-1}$); $\gamma$ the psychometric constant (kPa °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), $\rho_a = 1.20$, $\rho_w = 1000$, $c_p = 1-012$, $g_a = 0-017$, $\lambda = 22.6 000$ and $\gamma = 0.066$.

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

Statistics 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 m × 1 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

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|c|c|c|c|c|}
\hline
Stand age & AUPA & CLSP & PLSC & POSP & SPSP & Other & None \\
\hline
Well-drained stands & & & & & & & \\
18 & 33 & 0 & 2 & 8 & 0 & 2 & 56 \\
(15) & (0) & (1) & (10) & (0) & (1) & (10) & \\
43 & 17 & 0 & 61 & 0 & 0 & 10 & 12 \\
(15) & (0) & (15) & (0) & (0) & (8) & (7) & \\
78 & 0 & 0 & 99 & 0 & 0 & 1 & 0 \\
(0) & (0) & (1) & (0) & (0) & (1) & (0) & \\
158 & 0 & 0 & 100 & 0 & 0 & 0 & 0 \\
(0) & (0) & (0) & (0) & (0) & (0) & (0) & \\
Poorly drained stands & & & & & & & \\
18 & 2 & 0 & 0 & 9 & 1 & 22 & 66 \\
(4) & (0) & (0) & (6) & (1) & (16) & (24) & \\
43 & 72 & 3 & 13 & 0 & 6 & 2 & 13 \\
(22) & (5) & (5) & (0) & (9) & (4) & (13) & \\
78 & 38 & 16 & 17 & 3 & 22 & 0 & 4 \\
(5) & (4) & (9) & (4) & (12) & (0) & (2) & \\
158 & 1 & 25 & 34 & 0 & 30 & 5 & 5 \\
(2) & (22) & (26) & (0) & (24) & (3) & (4) \\
\hline
\end{tabular}
\caption{Percentage cover of bryophytes by stand age (as of 2007) and drainage class; standard errors ($N = 4$ plots) are shown in parentheses.}
\end{table}

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.
Field measurements of bryophyte water fluxes averaged 0–37 mm day$^{-1}$ and ranged from 0–03 ($P. schreberi$, 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 ($25\,^\circ\text{C}$) 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 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>
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<th>Equation (1)</th>
<th>Feathermoss</th>
<th>0.852</th>
<th>0.005</th>
<th>0.030</th>
<th>20</th>
<th>−2.55</th>
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<td>−5.51</td>
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<table>
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<th>Feathermoss</th>
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<th>0.002</th>
<th>20</th>
<th>−30.99</th>
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<tr>
<td>Sphagnum</td>
<td>0.229</td>
<td>−0.115</td>
<td>0.024</td>
<td>−0.003</td>
<td>40</td>
<td>16.11</td>
<td>0.275</td>
</tr>
</tbody>
</table>

*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.

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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 ($N$D3).

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 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.

Modeled annual $E$ fluxes from bryophytes ranged from 0.4 mm day$^{-1}$ (146 mm year$^{-1}$), in the well-drained stands, to ~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 ~0.6 mm day$^{-1}$, while the Penman–Monteith equation results (which explicitly includes $R_n$ and its reduction under high leaf area) were ~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 $\rho_w$ and $\lambda$, the water density and latent heat of vapourization parameters; computed annual $E$ fluxes varied by ~10% with a ±10% variation in each parameter. The model was moderately sensitive to $g_a$ (aerodynamic conductance; varying $g_a$ ±10% resulting in ±2–7% annual fluxes in the well-drained stands and 1–4% in the poorly drained stands) and the minimum precipitation required to saturate the moss ($\mp$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 ($\rho_a$) (although there is no uncertainty in these inputs).
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 (Rochefort et al., 1990).

A number of previous studies have partitioned ET sources in boreal forests and bogs: Kellner (2001) reported that >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 cijnderii 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 ± 70 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% (~0.2 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 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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