

# Moisture controls on carbon dioxide dynamics of peat-*Sphagnum* monoliths

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## ABSTRACT

*Sphagnum* moss is the major peat-forming vegetation component in boreal peatlands. The relationship between *Sphagnum* productivity and moss moisture content has been documented; however, the link between moss moisture content and conditions in the underlying peat column is less clear. We conducted a pilot study in which we monitored volumetric moisture content with depth and gravimetric water content of *Sphagnum* capitula and CO<sub>2</sub> exchange for two peat monoliths with intact moss layer dominated by *Sphagnum fuscum* and *S. magellanicum*. Measurements were made under drying conditions and rewetting from below and following simulated precipitation events. Capitulum moisture content was related to water table position but varied between species. Both capitulum moisture content and water table position could be used to explain net CO<sub>2</sub> exchange and respiration during drying and rewetting from below, although hysteresis was apparent where respiration was lower on rewetting than drying for the same water table position. Precipitation complicated these relationships because small events (<5 mm) rewetted the upper few centimeters of moss resulting in a change in capitulum moisture content equivalent to a rise in water table position of ~20 cm. This change in capitulum moisture content resulted in substantial shifts in both photosynthesis and respiration rates without affecting water table position or subsurface volumetric water contents as shallow as 5 cm below the surface. While these small events will be difficult to measure in the field, this study suggests they are essential to effectively track or model *Sphagnum* productivity because they may contribute significantly to seasonal carbon balance. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS carbon storage; bryophyte; peatland; water table; precipitation; hydrology

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## INTRODUCTION

*Sphagnum* moss is the main peat-forming vegetation component in many boreal peatlands and its productivity is related to its moisture content (Schipperges and Rydin, 1998). In general, *Sphagnum* productivity follows a unimodal relationship with capitulum moisture content having highest rates of photosynthesis at moisture content between 4 and 25 g H<sub>2</sub>O (g dry wt)<sup>-1</sup> (McNeil and Waddington, 2003 and references therein). Above this optimum moisture content, the thickness of water films on *Sphagnum* leaves inhibits gas exchange and photosynthesis is reduced (Williams and Flanagan, 1998). Below optimum moisture content, physiological stress reduces the rate of photosynthesis (Gerdol *et al.*, 1996).

The rate of photosynthesis at particular water contents varies between species (Schipperges and Rydin, 1998). Species found on hummocks (dry locations), such as *S. fuscum*, generally have lower productivity at optimal moisture content than hollow or lawn species. However, hummock species are able to avoid desiccation better under field conditions than hollow species, even when growing at locations with deeper water tables (Titus and Wagner, 1984). Hummock species grow in tight colonies

compared with hollow species, thereby increasing capillary rise and maintaining higher moisture contents as water tables are drawn down (Hayward and Clymo, 1982; Titus and Wagner, 1984). Because *Sphagnum* mosses are non-vascular, they rely on capillary transport to move water up from the water table to the surface where photosynthesis occurs. Thus, when water is limiting, hummock species maintain higher moisture contents resulting in higher productivity than hollow species.

Although previous studies have enabled an improved understanding of *Sphagnum* species distribution across peatland microforms and general *Sphagnum* water relations (Hayward and Clymo, 1982), few studies have examined how moss moisture content is related to the underlying peat hydrology. As the upward capillary flow of water from the water table provides moisture to the photosynthesizing *Sphagnum* moss capitula, understanding this connection is critical for furthering our process-based understanding of peatland carbon dynamics. Furthermore, previous studies have generally investigated *Sphagnum* individuals separated from the underlying peat, undergoing rapid drying and rewetting cycles (McNeil and Waddington, 2003; Schipperges and Rydin, 1998), with limited consideration of the differential effects of moisture additions from below (groundwater) and above (precipitation) the capitulum (i.e. the upper

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growing and photosynthetic portion of a *Sphagnum* individual). Peatland water tables are generally drawn down slowly over the summer season and small additions of water via dewfall and light precipitation events may play an important role in *Sphagnum* moisture dynamics (Schipperges and Rydin, 1998).

In order to adequately include moss productivity in models of peatland carbon cycling, a better understanding is required of the peat-*Sphagnum*-atmosphere interactions that control moisture conditions in the capitula. Thus, we conducted a pilot study with the objectives to: (1) investigate the effect of relatively slow shifts in water table position and small precipitation events on *Sphagnum* moisture content and (2) determine the relationship between water table position/*Sphagnum* moisture content and *Sphagnum* productivity and net exchange of carbon dioxide from peat monoliths with an intact *Sphagnum* moss layer.

## METHODS

### Study site and monolith extraction

Peat-*Sphagnum* monoliths were collected from a bog near Puslinch, Ontario, Canada (43°24'31"N, 80°15'50"W). The study site is a 6-ha kettle-hole wetland with a low shrub-*Sphagnum* community dominating its central portion. Vegetation in this central zone consists of small shrubs including *Chamaedaphne calyculata*, *Betula pumila* and *Vaccinium oxycoccus*, stunted trees including *Picea mariana* and *Larix laricina* and herbs including *Eriophorum virginicum*, *Drosera rotundifolia*, *Sarracenia purpurea* and *Typha latifolia*. *Sphagnum* species present include *S. fuscum*, *S. magellanicum*, *S. capillifolium*, *S. papillosum* and *S. cuspidatum*. A complete site description can be found in Campbell *et al.* (1997) and Warner *et al.* (2007).

To collect the monoliths, a 30-l bucket (34 cm diameter, 35 cm deep) with the bottom removed was eased into the peat while the perimeter was hand-cut with a serrated knife. Once the top of the bucket was flush with the peat surface, a block of peat adjacent to the bucket was removed to allow us to cut underneath the bottom of the bucket, thus separating the monolith from the underlying peat. A plate was slid under the monolith and both sample and bucket were lifted out of the peat. The monolith was then slid into an intact bucket of equal size that had a 2-cm layer of gravel at the base to facilitate drainage or rewetting of the monolith from below. A nipple in the bottom of the intact bucket was fitted with a 0.75-cm internal diameter Tygon tube. This tube was used for draining and rewetting the monolith from below and was attached to a measuring tape on the side of the bucket to determine water table position. One monolith was collected from a hummock dominated by *S. fuscum* and a second from a lawn dominated by *S. magellanicum*. As only one sample for each *Sphagnum* type was used in the study, we consider this a pilot study

and results should be considered preliminary. All vascular vegetation was removed by clipping so that only moss productivity was considered. For ease of collection and to limit the effects of vascular vegetation removal, we collected the monoliths in areas where vascular vegetation cover was minimal (<10%); thus, decomposition of roots following clipping should have a limited effect on the resulting carbon exchange particularly given the relatively large volume of peat used.

### Experimental conditions

All experiments were carried out in a climate-controlled room. Relative humidity was maintained at 50% [vapour pressure deficit (VPD) = 1.24 kPa] until day 16 of the experiment at which time it was lowered to 40% (VPD = 1.49 kPa) to encourage evaporation. Both values of VPD are within the range of conditions termed moderate by Shurpali *et al.* (1995) when studying peatland micrometeorology. Temperature was maintained at  $21 \pm 1$  °C. Air was circulated in the room with a fan mounted ~60 cm above the monoliths. No natural light entered the room, so fluorescent lights provided photosynthetically active radiation at  $\sim 50 \mu\text{mol m}^{-2} \text{s}^{-1}$  at the *Sphagnum* surface between 7 am and 7 pm each day. This light level allowed maintenance of *Sphagnum* without excessive growth; however, it resulted in low rates of photosynthesis and often a positive net CO<sub>2</sub> exchange from the monolith (i.e. CO<sub>2</sub> was released from the monolith to the atmosphere). Despite the low light levels, both *Sphagnum* species appeared healthy throughout the experiment and growth form of the moss carpet was not altered.

Water table was initially raised to 5 cm below the surface in each monolith. At the start of the experiment, we allowed water table to fall in response to evaporation until it was lowered to 20 cm below the surface on day 39 of the experiment. It was then lowered by 5-cm increments at weekly intervals to 40 cm (day 56), maintained at this depth for 2 weeks (until day 70), and then raised at 5-cm intervals weekly until the water table was -25 cm in the *S. fuscum* bucket and -20 cm in the *S. magellanicum* bucket. Overall, the experiment lasted 100 days. According to a field study at the same wetland, average water table varied between 6 and 55 cm below the surface between May and October (Warner *et al.*, 2007) and thus the water table depths induced in this laboratory study are representative of potential field conditions.

Small precipitation events, 0.5, 1 and 5 mm, were administered with a spray bottle when water table was at -40 cm on days 56, 63 and 67, respectively, and during rewetting (5 mm on day 87; Figure 1).

### Moisture content determination

*Sphagnum* capitulum gravimetric moisture content was determined using 1 × 2 cm pieces of absorbent board made of milled peat, hereafter referred to as *tabs* (Johnson & Johnson, Inc., Guelph, Canada). These were

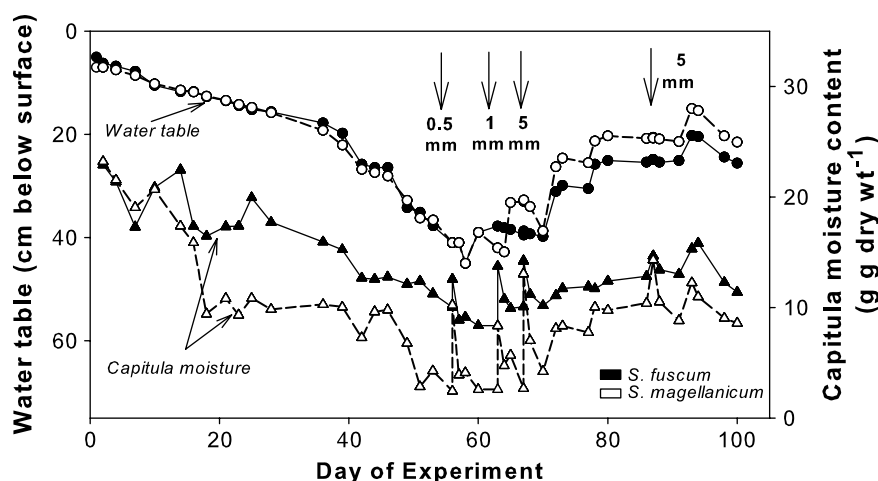


Figure 1. Water table position and *Sphagnum* capitula moisture content throughout the experiment. *Sphagnum fuscum* is shown as solid symbols and *S. magellanicum* as open symbols. Timing and magnitude of precipitation events are indicated by arrows and corresponding text.

inserted carefully just beneath the surface, between moss capitula, for 4 h. Tabs were calibrated according to gravimetrically determined moisture content in moss subsamples before the study. In order to calibrate the tabs, four samples each, 5-cm diameter, 5-cm high, of both *Sphagnum* species were collected in glass beakers with the same diameter as the samples. The samples were saturated and weighed. Two dry tabs were inserted into each sample and allowed to equilibrate for 4 h. After this time, the tabs were removed, weighed, dried for 24 h at 85 °C and reweighed. *Sphagnum* moss samples were also reweighed after the 4-h tab insertion and an average of initial and final moss weight was used. *Sphagnum* samples were allowed to dry for several days and then new dry tabs were inserted and the process was repeated. This entire process was repeated four times resulting in calibration over a range of *Sphagnum* gravimetric water contents of 1–27 g (g dry wt)<sup>-1</sup>. Following the final tab removal, *Sphagnum* samples were dried at 85 °C and this dry weight was used to determine the gravimetric moisture content of the samples for each measurement made throughout the calibration. Calibration functions were constructed by relating the gravimetric moisture content of the tab to the average gravimetric moisture content of the *Sphagnum* sample over the 4-h insertion period (i.e. average of initial and final *Sphagnum* gravimetric moisture content as determined by mass taken just before tab insertion and just after tab removal). A linear calibration function ( $R^2 = 0.89$ ,  $p < 0.001$ ) fit the data well and was simple to apply. There was no clear difference in the calibration function between the two species; thus, all data were grouped and one calibration curve was applied to both monoliths. For comparison with volumetric water content (VWC) measured in the underlying peat, we converted the gravimetric capitulum water content to VWC using the bulk density of the calibration subsamples of moss.

VWC in the underlying peat was determined with a Campbell Scientific TDR-100 system (Campbell Scientific Canada, Edmonton, Canada). CS605 time domain

reflectometry probe rods were inserted horizontally through drilled holes in the sidewall of the bucket at 5-cm depth intervals from 5 to 30 cm below the surface. After insertion, probe rods were sealed in place with silicon to maintain a watertight seal. VWC was determined hourly and logged with a Campbell Scientific CR10X data logger.

#### Carbon dioxide exchange

Net ecosystem CO<sub>2</sub> exchange (NEE) was measured in a clear cylindrical chamber (34-cm diameter, 33.5-cm high) placed over the monolith 2–3 times per week. Carbon dioxide exchange was measured for three consecutive days following simulated precipitation events. A piece of hose cut lengthwise and affixed to the outside of the bucket provided a channel that was filled with water when the chamber was in place to ensure a gas-tight seal during CO<sub>2</sub> flux measurements. A fan inside the chamber mixed the headspace. CO<sub>2</sub> concentration was measured with an infrared gas analyzer (EGM-2, PP Systems, Amesbury, USA) and NEE determined from the change in CO<sub>2</sub> concentration within the chamber over a 5-min sampling interval. Ecosystem respiration (ER) was determined by covering the chamber with an opaque shroud. On each measurement day, both NEE and ER were determined three times for each monolith. Gross ecosystem photosynthesis (GEP) was determined as NEE–ER. We have followed the convention outlined in Chapin *et al.* (2006) that positive values of NEE indicate a release of CO<sub>2</sub> from the monolith to the atmosphere.

## RESULTS

#### Moisture content and CO<sub>2</sub> exchange in relation to water table position

Water table fell on average 0.36 cm per day via evaporative water losses during the first 40 days of the experiment (Figure 1). The rate was not different between the two *Sphagnum* species (Student's *t*-test,  $p = 0.19$ ). After

this, water table was manually lowered and raised at 5-cm intervals each week (lowered down to -40 cm between day 42 and 56, raised beginning day 70). Following the reduction in relative humidity (day 16), capitulum moisture content fell for both species with *S. magellanicum* showing a more pronounced reduction (Figure 1).

To determine water table effects on capitulum moisture content, data for 2 days following a precipitation event were ignored. During the remaining periods, *Sphagnum* capitulum moisture content was significantly logarithmically related to water table position (*S. fuscum*,  $R^2 = 0.86$ ,  $p < 0.0001$ ; *S. magellanicum*,  $R^2 = 0.85$ ,  $p < 0.0001$ ; Figure 2). Hysteresis was not apparent, perhaps because spatial variability in moisture content of the capitula was larger than hysteresis effect (Figure 2). VWC at all depths (-5 cm and deeper) was also related to water table position. However, hysteresis was apparent in this underlying peat with VWC lower during rewetting than drying (not shown). Because of this hysteresis, the correlation between capitulum moisture content and VWC at any given depth was not as strong as the correlation between capitulum moisture content and water table. The VWC-water table relationship also varied between species. For a given water table, moisture content in the upper 15 cm of the peat column and in the moss capitula was up to 7% higher for *S. fuscum* than *S. magellanicum*, as has been reported in literature (Titus and Wagner, 1984).

Since there was a strong relationship between moisture content and water table, both were also correlated to CO<sub>2</sub> exchange. We discuss water table-CO<sub>2</sub> exchange relationships as water table is more commonly measured in the field and thus represents the data most likely to be available as model input. For given water table, GEP was similar for both species (Figure 3). Hysteresis was

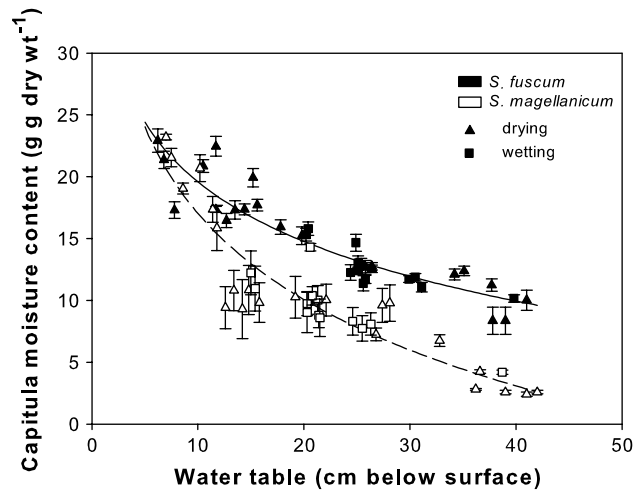


Figure 2. Relationship between capitula moisture content as determined by *tabs* and water table position for *Sphagnum fuscum* (solid symbols, solid line) and *S. magellanicum* (open, dashed). Error bars give standard deviation of five replicate tabs. Data points during drying (triangles) and rewetting (squares) are separated, but regression was fitted to the grouped data set for each species.

observed in CO<sub>2</sub> exchange, particularly ER and NEE. This hysteresis was also apparent when CO<sub>2</sub> exchange was related to capitulum moisture content. Quadratic relationships significantly fit ( $p < 0.01$ ) both GEP and ER data in relation to water table during drying for both *Sphagnum* species. This illustrates that an optimum water table/moisture content in the peat and moss exists at which either GEP or ER is maximized. Upon rewetting, the relationship between water table and CO<sub>2</sub> exchange was weaker. For ER, a linear relationship with water table was more appropriate than quadratic for both species. For *S. fuscum*, GEP was not significantly related to water table on rewetting; the drying and rewetting data were grouped and one quadratic relationship could be

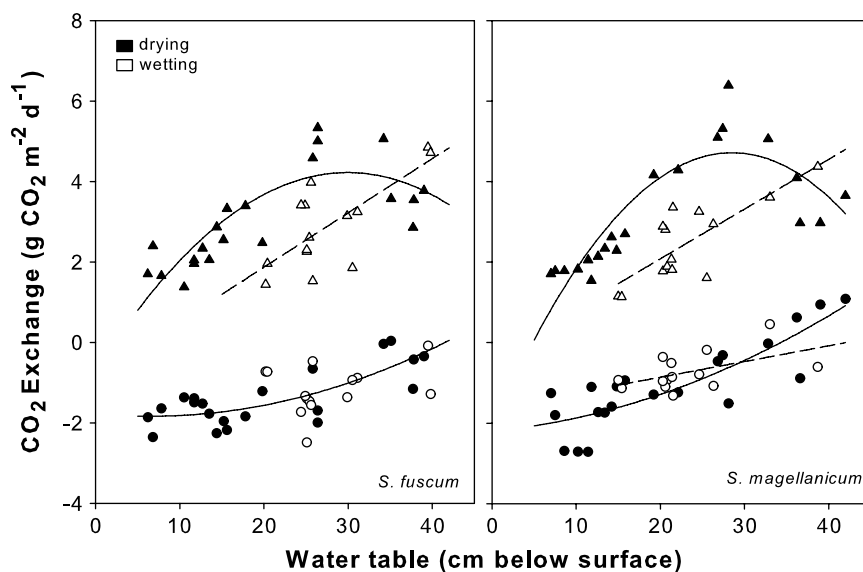


Figure 3. Gross ecosystem photosynthesis (circles, negative values) and ecosystem respiration (triangles, positive) under various water table positions for hummock species *Sphagnum fuscum* (left) and hollow species *S. magellanicum* (right). Values measured during drying are shown as solid symbols and solid line and rewetting as open symbols and dashed lines. Each data point represents the average of three replicate measurements made per sampling day. For clarity in the figure, standard deviation is not shown but was 0.1–1.8 and 0.1–1.1 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup> for GEP and ER, respectively. Data within 2 days following a precipitation event are not included.

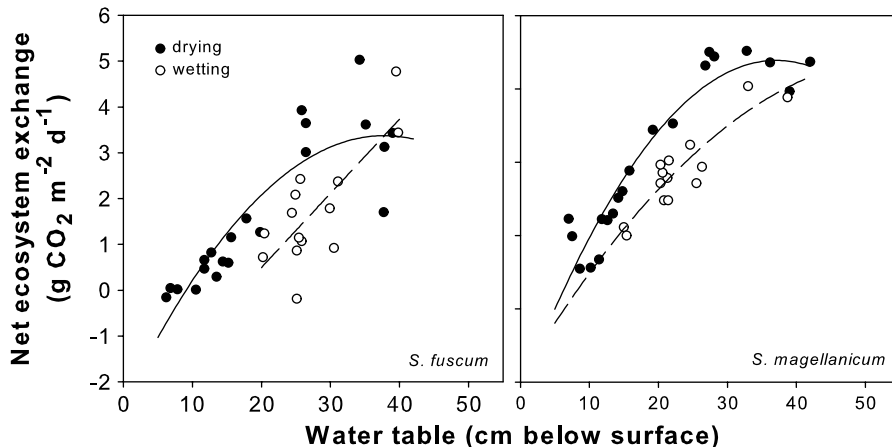


Figure 4. Net ecosystem CO<sub>2</sub> exchange related to water table position for *Sphagnum fuscum* (left) and *S. magellanicum* (right) during drying (solid symbols) and rewetting (open). Each data point represents the average of three replicate measurements made per sampling day. For clarity in the figure, standard deviation is not shown but was 0.1–1.8 g CO<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>. Data within 2 days of precipitation events are not included.

significantly fit to the grouped data. For *S. magellanicum*, only a linear relationship was significant between water table and GEP during rewetting.

While other studies have observed a pulse of *Sphagnum* respiration when mosses are rapidly rewetted (McNeil and Waddington, 2003), in this study, ER was lower upon slow rewetting. Little hysteresis was observed for GEP. The combination of these responses resulted in NEE hysteresis with monoliths of both species tending to release more CO<sub>2</sub> during drying than upon rewetting (Figure 4). In general, NEE was positive throughout the experiment (i.e. there was a net loss of CO<sub>2</sub> from the monoliths) because of the low light levels used in the study and the relative large volume of respiring peat.

#### Moisture content and CO<sub>2</sub> exchange in response to precipitation events

Small rainfall events of 0.5 or 1 mm increased the gravimetric moisture content of *S. magellanicum* capitula from 3 to 8–10 g (g dry wt)<sup>-1</sup> (i.e. a change in VWC of *Sphagnum* capitula from 0.04 to 0.08–0.09; Figure 5a), a moisture content change equivalent to raising the water table from 40 to 20 cm below the surface (according to Figure 2). Similar changes in capitulum moisture content were observed for *S. fuscum* with an increase from 9–10 to 14 g (g dry wt)<sup>-1</sup>. These small rainfall events had a limited effect on VWC measured 5 cm below the surface with TDR and because these small events are also difficult to measure in rain gauges, they may be missed in field studies.

Larger 5-mm precipitation events were applied when the water table was 39 and 25 cm below the surface for *S. fuscum* and 33 and 20 cm below the surface for *S. magellanicum*. When 5-mm precipitation was applied at low water table position (33 and 39 cm below the surface), increases in capitulum moisture content were larger than when the same size event was applied with water table closer to the surface. For example, *S. magellanicum* capitula moisture content increased from 3 to 13 g (g dry wt)<sup>-1</sup> and 10 to 14 g (g dry wt)<sup>-1</sup>

with water table at 33 and 20 cm below the surface, respectively.

Both GEP and ER were increased following rapid changes in capitulum moisture content caused by precipitation events (Figure 5b). These increases were generally short-lived (2–3 days). Because the increase in GEP and ER was generally similar, shifts in NEE in response to precipitation were not as clear. There was no clear relationship between the size of the precipitation event and the response of CO<sub>2</sub> exchange; however, sample size in this study was small and further investigation is needed to determine whether a relationship is present.

Because the water table was not sensitive to small precipitation events, GEP was better described by capitulum moisture content than water table position when all data were considered together (wetting and drying via water table changes and precipitation events). Relationships were similar for both species and optimization of the quadratic equation suggests optimal moisture content of 19 and 22 g (g dry wt)<sup>-1</sup> for *S. fuscum* and *S. magellanicum*, respectively. ER was still well described by an exponential relationship to water table even when precipitation events were included (*S. fuscum*:  $R^2 = 0.53$ ,  $p < 0.001$ ; *S. magellanicum*:  $R^2 = 0.54$ ,  $p < 0.001$ ).

## DISCUSSION

The differential response of *S. fuscum* and *S. magellanicum* capitulum moisture content to water table position is consistent with previous studies (Hayward and Clymo, 1982; Titus and Wagner, 1984). In addition, the sensitivity of *S. magellanicum* capitulum moisture content to a reduction in relative humidity suggests that despite increased evaporative demand, this species was unable to maintain sufficient capillary flow to equal evaporative losses and maintain capitulum moisture content. In contrast, *S. fuscum* was much less sensitive to the relative humidity reduction, likely because its tighter growth form enabled maintenance of good capillarity. Future

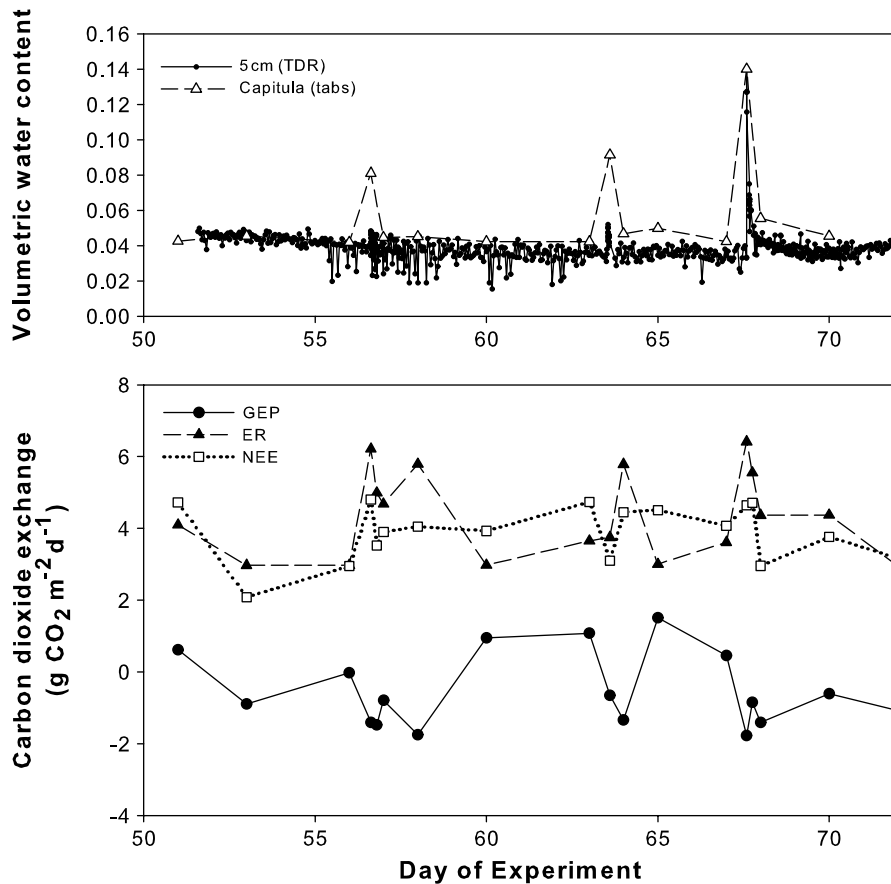


Figure 5. *Sphagnum magellanicum* capitulum moisture content and TDR 5-cm moisture content (top) and GEP, ER and NEE (bottom). All moisture contents are given as volumetric water content.

studies with replication are required to further investigate differential capitulum moisture maintenance strategies between species and how these relate to underlying peat hydrophysical properties.

When *Sphagnum* individuals have been dried separately, several studies have observed a unimodal relationship between moisture content and productivity (Williams and Flanagan, 1996; Schipperges and Rydin, 1998; McNeil and Waddington, 2003). In this study, reduction in GEP was observed at low moisture contents but not at high moisture contents. Because the highest water table position in the monoliths was  $-5$  cm, moisture content was not likely to be high enough to greatly limit diffusion. This is consistent with investigations of controls on photosynthetic rate in field studies that found optimum water level of  $-12$  cm for *S. angustifolium* (Tuittila *et al.*, 2004) and  $-8.5$  cm for a community including *S. papillosum*, *S. fallax* and *S. flexuosum* (Riutta *et al.*, 2007). Some of the limited response of GEP to moisture content observed in this study may also be related to the low light levels used; however, as the moss carpet remained healthy throughout the study and is often naturally shaded by shrubs in peatlands, the patterns observed should be representative of those observed in the field.

ER was higher at low water table position as has been observed in other laboratory studies with peat columns (Blodau and Moore, 2003). The relationship appeared to

be unimodal when the monoliths were dried, but this was not as clear on rewetting (Figure 3). When data from precipitation events were included, an exponential relationship between water table and ER gave the best fit. This suggests that although peatland ER may be reduced during drought as peat moisture content drops, in general, ER will increase with decreasing water table position in natural peatlands as small atmospheric moisture inputs help to maintain peat moisture content above some critical threshold for microbial activity.

Studies on *Sphagnum*  $\text{CO}_2$  exchange during drying and rewetting have observed a pulse of respiration following rewetting (McNeil and Waddington, 2003), yet this was not observed in this study. We slowly rewetted monoliths from below resulting in gradual increases in moisture content in *Sphagnum* capitula and this was likely to limit the sudden respiration response. When mosses were rapidly rewetted via precipitation events, a pulse of ER was observed (Figure 5). In contrast, slow rewetting resulted in hysteresis in ER in which ER was lower at the same water table upon rewetting than drying. This may be because labile carbon has been consumed or because hysteresis in the moisture content–water table relationship maintains moisture content below ideal conditions upon rewetting. The use of peat-*Sphagnum* monoliths in this study makes it impossible to separate *Sphagnum* respiration from soil respiration in the underlying peat; however, as the small precipitation events used in this study had

little effect on VWC below the capitula, the pulse of ER observed following precipitation must be dominated by *Sphagnum* autotrophic respiration. In the field, *Sphagnum* moss will be dried slowly as water table is drawn down during drought and rewetted quickly by precipitation. Research with more replicate samples and careful monitoring of the magnitude and spatial variability of *Sphagnum* capitula moisture content at fine resolution in the laboratory and field are needed to determine whether hysteresis in *Sphagnum* CO<sub>2</sub> exchange is important for determining NEE.

Small precipitation events of 0.5 and 1 mm were not readily discernible from peat VWC as measured with TDR, even at only 5 cm beneath the moss surface (Figure 5). These events are also difficult to measure in precipitation gauges and thus would often be missed in the field. However, their effect on GEP and ER was apparent, suggesting that they must be included when describing *Sphagnum* carbon exchange. Moreover, 0.5 mm is close to the volume of dewfall events reported in other ecosystems (Richards, 2004) and several studies have reported overnight rewetting for *Sphagnum* (Titus and Wagner, 1984; Kim and Verma, 1996). Observed rewetting of *Sphagnum* in the field may also result from distillation as has been observed in other mosses (Carleton and Dunham, 2003). Distillation occurs when water from deeper saturated layers is evaporated during warm daytime temperatures, remains as vapour within the moss canopy and re-condenses at the moss surface as the temperature drops overnight. If dewfall/distillation events occur frequently (several times a week), the *Sphagnum* surface would remain much moister, and presumably more productive, than would be predicted by a water table position driven by larger precipitation events and evapotranspiration estimates. This higher moisture content will also reduce tension in the upper peat layers, thereby enhancing hydraulic conductivity and water movement from the underlying peat to the moss layer.

More research is needed to quantify diurnal shifts in *Sphagnum* moisture in the field, determine sources of moisture gain (dewfall vs distillation), quantify controls on dewfall and determine the relationship between extent of rewetting and change in corresponding *Sphagnum* CO<sub>2</sub> exchange.

#### IMPLICATIONS AND DATA REQUIREMENTS

Because *Sphagnum* moss can play an important role in peatland net primary productivity, particularly during spring and fall when *Sphagnum* productivity is greatest due to near-optimal moisture content (Moore *et al.*, 2002) and when vascular plant productivity is limited by low temperatures in the rooting zone (Moore *et al.*, 2006), accurate models of peatland carbon cycling require models of *Sphagnum* productivity and thus capitulum moisture content. We need a better description of peat hydraulic properties and unsaturated zone processes to

accomplish this at the local scale. We also require knowledge regarding spatial variability in peat hydrophysical properties and moss response to moisture additions and dewfall.

At the ecosystem or regional scale, it is advantageous to model *Sphagnum* productivity with limited data requirements. Currently, the peatland carbon simulator (PCARS) estimates *Sphagnum* productivity with moisture and temperature functions (Frolking *et al.*, 2002). Moisture is currently driven only by water table position; however, this study reveals the potential importance of moisture additions via small rainfall events and/or dewfall (or distillation) that are not strongly coupled to water table position; this could be incorporated by considering relative humidity and ground surface temperature.

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