Moisture controls on CO₂ exchange in a *Sphagnum*-dominated peatland: results from an extreme drought field experiment

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ABSTRACT

Peatlands store globally significant quantities of soil carbon, and *Sphagnum* moss is the main peat forming vegetation type in bogs. *Sphagnum* moss productivity is driven by the moisture content of its apical cluster of branches, the capitulum. Capitulum moisture content is dependent on the arrangement of leaves, branches and stems for a given species and also on hydrological conditions of the underlying peat. Despite this link, the response of CO_2 exchange in *Sphagnum*-dominated peatlands to extreme drought is still unclear, particularly under field conditions.

We used drainage to expose *Sphagnum rubellum* to extreme drought and monitored water table, volumetric water content (VWC), gross ecosystem photosynthesis (GEP), ecosystem respiration (ER) and net ecosystem exchange of CO₂ (NEE) at plots in a 25 m transect perpendicular to a deep drainage ditch and compared results to an undrained site. VWC in the upper 10 cm of peat was strongly related to water table at depths shallower than 55 cm. Below this depth, near surface VWC remained relatively constant between 25 and 28% and *Sphagnum* GEP was effectively shut down. This also resulted in decreased ER at these locations. The combined effect was a linear relationship between VWC and NEE with moist sites acting as net CO₂ sinks (up to $-5 \text{ g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$) whereas sites closest to the ditch were consistently small carbon sources. We suggest that understanding how climate change will alter peatland hydrology relative to the moisture thresholds of *Sphagnum* mosses is critical to determining the fate of their carbon sink function. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS carbon dioxide; climate change; ecosystem respiration; photosynthesis; volumetric water content; water table

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INTRODUCTION

Peatland ecosystems are an important component of the global carbon (C) cycle, storing approximately onethird the total soil C (Gorham, 1991), despite covering only 5% of the global land area (Matthews and Fung, 1987). They are net sinks of atmospheric carbon dioxide (CO₂) resulting in a long-term C accumulation rate in these ecosystems of ~29 g C m⁻² year⁻¹ (Gorham, 1991). Consequently, peatlands play a significant role in stabilizing atmospheric CO₂ concentrations (Frolking *et al.*, 2006).

Sphagnum moss is one of the most abundant plant types in peatlands, and is also the principal species involved in peat accumulation in bogs (Hayward and Clymo, 1982). Sphagnum is a non-vascular plant and having no control of its rate of water loss (Hayward and Clymo, 1982), requires a consistent supply of water to avoid desiccation (Sagot and Rochefort, 1996; Price, 1997). Sphagnum productivity is related to moisture content in the capitulum, the apical cluster of actively growing branches (Schipperges and Rydin, 1998). The similarity in gas exchange response of many Sphagnum species to changes in light and temperature suggests that performance is due primarily to different water relations, since different species occupy different levels above the water table (Schipperges and Rydin, 1998). As moisture is retained in the moss layer via capillarity, the growth form of the Sphagnum individual and moss colony is important for controlling water retention. For example, a species with a loose arrangement of branches and open colonies, Sphagnum fallax, may become desiccated (1.7 g fresh weight/g dry weight) with water tables only 10 cm below the surface, whereas S. nemoreum, which grows in denser colonies, maintains high capitulum moisture content (9.3 g fresh weight/g dry weight) even when water tables fall to 50 cm (Titus and Wagner, 1984).

Drainage decreases soil moisture content in peat, increasing the water tension therein, which can present very harsh conditions for *Sphagnum* growth and development (Price and Whitehead, 2004). As water table position becomes deeper, the pressure head in the near surface peat is reduced (i.e. becomes more negative; tension increases). As this pressure drops, narrower and narrower pores are drained until eventually the water-holding hyaline cells of *Sphagnum* mosses drain (Thompson and

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Waddington, 2008). Hayward and Clymo (1982) indicate that hyaline cell drainage occurs at pressure heads below –100 cm water. Studies relating pressure head and volumetric water content (VWC) for peat suggest that this threshold pressure is equivalent to a VWC of 40–50% (Price and Whitehead, 2004; Cagampan and Waddington, 2008). Beyond this threshold *Sphagnum* moss water content and hence productivity will likely be greatly reduced.

During long periods of desiccation, when contact with the water table is lost, laboratory studies indicate that recovery of net photosynthesis can take place only if the water content of the capitula does not fall more than 10-20% below the water content at the compensation point (i.e. water content when net exchange of CO₂ is zero) which varied from 100 to 200% dry weight (Schipperges and Rydin, 1998). However, a low water position does not always result in low capitula water content as periodic rain events can alter the moisture level of the upper surface of the moss layer without altering water table position. Robroeck et al. (2009) suggest low capitula water content from a lack of rainfall, rather than a low water table position *per se*, is the main cause for a drop in moss photosynthetic capacity during dry conditions. Similarly, Strack and Price (2009) found that dew and small precipitation events could greatly alter photosynthesis and respiration rates. Nevertheless, little is known about the relationship between Sphagnum productivity and CO₂ emissions under extreme drought conditions (i.e. deep water table resulting from evapotranspiration » precipitation), particularly in field settings (McNeil and Waddington, 2003).

Although studies have determined that moisture controls Sphagnum growth and productivity, information concerning carbon dynamics under variable water table position is still scarce (Grosvernier et al., 1997). McNeil and Waddington (2003) examined net ecosystem CO₂ exchange and Sphagnum net primary production of an abandoned block-cut peatland. It was determined that the peatland was a source of CO_2 to the atmosphere during the dry summer months due to an increase in peat respiration and decrease in Sphagnum net primary productivity. Sphagnum photosynthesis was greatest at wet sites, and laboratory results indicated that drying and wetting cycles negatively affected Sphagnum net primary production and net CO2 exchange. The authors suggested that a better approach to examine seasonal variation in CO₂ exchange would be to obtain field measurements of Sphagnum moisture content, and this recommendation was incorporated as a significant part of this study. Tuittila et al. (2004) conducted a field experiment with the objective of quantifying the sensitivity of CO_2 exchange dynamics on the seasonal and spatial variation in water level on Sphagnum-dominated peat surfaces. A physiological-based model was constructed to examine the effect of water level variation on CO₂ balance in a cutover peatland with Sphagnum reintroduction in the first year of restoration. Although the model assessments were limited to conditions similar to that of the study by Tuittila et al. (2004), moisture conditions were the

most important factor controlling CO_2 exchange dynamics, since water level controls both the photosynthesis and respiration components of the C balance in peatlands.

The objective of this study was to improve our understanding of moisture controls on *Sphagnum* moss productivity (specifically productivity of *Sphagnum rubellum*) and peatland C exchange particularly under extreme drought. Moisture content was manipulated by severely lowering the water table via drainage by a ditch. CO₂ exchange in response to this manipulation was measured along a 'drought' gradient perpendicular to the ditch and compared to sites with natural hydrology.

STUDY SITE

This study was carried out at the Pointe-Lebel bog near Pointe-Lebel, Québec, Canada (49°14′N, 68°28′W). The 30-year climate normals (1971–2000) in the region for mean daily temperature are -14.4 °C and 12.6 °C for January and June, respectively, with annual precipitation of 1014.4 mm of which 641.1 mm falls as rain (Environment Canada, data available at http://www.climate. weatheroffice.ec.gc.ca/climate_normals/index_e.html). *Sphagnum rubellum* is the dominant moss species in the bog. Peat depth varies between 5 and 6 m.

We chose to examine the response of Sphagnum rubellum to drought because this is a common bog species in Eastern Canada, growing predominately on lawns and low hummocks, and it was also the dominant Sphagnum species at our study site. To examine the effect of extreme drought on Sphagnum rubellum moisture dynamics and CO₂ exchange, two sites were compared: a drainage site (D) and a natural site (N). The natural site was chosen to characterize the undisturbed portion of the peatland, whereas the drainage site was selected to represent an area impacted by its proximity to a ditch and representing Sphagnum rubellum response to droughtinduced water table draw down. The drainage site was \sim 600 m from the natural site. The \sim 3 m deep drainage ditch was excavated during the 2003-2004 winter period. A transect was installed perpendicular to the drainage ditch to determine the extent and change of C fluxes with distance from the ditch due to varying levels of water table drawdown. Sampling locations were at 1.5, 3, 5, 10, 15 and 25 m away from the ditch and labelled D-1.5 to D-25. At the natural site, duplicate sampling locations (N1, N2) were installed for comparison. All sampling sites had less than 10% cover of vascular plants, with Sphagnum rubellum as the dominant vegetation type (100% ground cover).

METHODS

CO_2 exchange

Circular polyvinyl chloride (PVC) frames (20 cm in diameter), known as collars, were inserted into the peat to a depth of 20 cm at each sampling location.

Wooden platforms were constructed adjacent to each plot to reduce disturbance during measurements. CO₂ fluxes were measured 20-30 times at each plot between May 26 and August 14, 2005 using the static chamber technique as described by McNeil and Waddington (2003). Net ecosystem exchange (NEE) was measured by fitting a clear acrylic glass chamber, 20-cm diameter, 25-cm high, into a water-filled groove in the collar to create a gas seal. A fan inside the chamber ensured well-mixed air during the sampling period. The chamber was also connected to a pump that circulated cold water into a heat exchanger in the chamber, maintaining the air temperature inside the chamber within 2 °C of ambient air temperature. Changes in CO₂ concentration within the chamber were measured with a portable infrared gas analyser (EGM-2, PP-Systems, Massachusetts, PA, USA). Ecosystem respiration (ER) was measured by placing an opaque tarpaulin over the chamber. Gross ecosystem photosynthesis (GEP) was determined as the difference between NEE and ER. In this study we considered GEP and NEE under full-light conditions only (i.e. photosynthetic photon flux density greater than 1000 μ mol m⁻² s⁻¹). We have used the convention defined by Chapin et al. (2006) that positive values indicate a loss of C from the ecosystem to the atmosphere.

Environmental variables

The depth to the water table was measured at wells located beside each collar. The wells were constructed from PVC pipes (5 cm in diameter) that were perforated and inserted into the peat at depths of 1.0-1.5 m, depending on the site. Water tables expressed as positive values indicate the depth of the water level below the surface of the peat.

Soil temperature profiles to 20 cm depth were measured at depth intervals of 5 cm using a thermocouple probe inserted into the peat. Temperature profiles were measured at each collar during each CO_2 flux measurement.

VWC of the upper 10 cm of peat was measured using a HydroSense moisture probe (Campbell Scientific Canada, Edmonton, Alberta, Canada). The Hydrosense probe was calibrated for this peat soil by taking six peat cores from each of the six drained sampling locations at the D site on August 15, 2005 and returning them to the Ecohydrology Laboratory at McMaster University. Briefly, plastic film was attached to the bottom of the cores and water was added so that it was flush with peat surface. HydroSense VWC measurements as well as the weight of the samples were recorded throughout several days as the samples air dried to produce a calibration curve. For the natural site, removal of the peat within the plots was not possible, as they were needed for continued monitoring. Thus, VWC was determined using the relationship developed for the wettest site at the drainage site, D-25.

Moisture dynamics

Seasonal mean water table position was deepest adjacent to the ditch and was closer to the surface with distance from the ditch ranging from 130 cm at D-1.5 to 37 cm at D-25. The natural sites had a shallower water table of 14 and 16 cm. VWC in the upper 10 cm was generally related to the pattern of water table position. VWC was consistently higher at the natural site and D-25 than at sites closer to the ditch (i.e. D-1.5 to D-15). However, water table control on near surface VWC was not simple and an apparent break in the relationship between these variables occurred when the water table was below \sim 55 cm (Figure 1). Shallower water tables had a strong correlation with VWC (VWC = $-1.39 \times$ (water table) +102.6; $R^2 = 0.82$, p < 0.001). When water table was deeper than 55 cm there was no relationship with VWC and it remained relatively constant between 25 and 28% regardless of water table position (Figure 1).

Using VWC data collected throughout the study period, the probability of exceeding given VWC values was determined for each plot (Figure 2). Using 40-50% VWC as a threshold, equivalent to when pressure heads fall below -100 cm water and hyaline cell drainage occurs (Price and Whitehead, 2004; Cagampan and Waddington, 2008), it is clear that all plots within 15 m of the ditch never exceeded this threshold. In contrast, the natural plots exceeded the threshold 100% of the time and D-25 exceeded the upper bound $\sim 70\%$ of the season. While this threshold is likely to be species dependent, Cagampan and Waddington (2008) also conducted their study at the Pointe-Lebel bog used in this study, also using *S. rubellum* and thus it should represent an appropriate threshold in this case.

CO_2 exchange

Seasonal average NEE under full-light conditions ranged from -6.9 and $-4.5~g~CO_2~m^{-2}~day^{-1}$ at the natural



Figure 1. Volumetric water content (VWC) in the surface 10 cm of peat versus water table position for all sites and all sampling dates. The line indicates the best-fit linear regression for data with water table shallower than 55 cm (VWC = $-1.39 \times$ water table + 102.6; n = 100, $R^2 = 0.82$, p < 0.001).



Figure 2. Exceedance probability for volumetric water content (VWC) in the surface 10 cm of peat for each study plot. Exceedance probability was calculated for each 5% interval of VWC and the plotted point indicates the percentage of measured values that exceeded the given VWC. The shaded box indicates the range of VWC determined by Price and Whitehead (2004) and Cagampan and Waddington (2008) corresponding to threshold soil pressure head of -100 cm water.

sites to 3.6 g CO₂ m⁻² day⁻¹ at D-1.5. All sites in the drainage transect had positive average NEE values (i.e. net CO₂ release) except D-25. Across all sites there was a significant positive relationship between seasonally averaged NEE and depth to water table ($R^2 = 0.77$, p =0.004); however, the relationship appears to be better represented with a hyperbolic curve in which CO₂ uptake is reduced as water table becomes deeper, with the site becoming a net source of CO_2 when water table is ~ 60 cm below the surface, and then plateaus when the water table is deeper (Figure 3a). There was also a significant negative correlation between seasonally averaged NEE and VWC ($R^2 = 0.93$, p < 0.001; Figure 3b). Seasonal average GEP was also greater at the natural plots (-11.5)and -13.3 g CO₂ m⁻² day⁻¹) than at any drainage plots. GEP was well explained by VWC with higher moisture content resulting in higher productivity ($R^2 = 0.97$, p <0.001; Figure 3b). The relationship with water table was

not as straightforward as all drainage sites within 15 m of the ditch had GEP close to zero.

ER was higher at the natural sites than any of the drained sites despite its shallower water table position. Overall, seasonal average ER decreased as the water table got deeper to a minimum value when water table was at 78 cm and then ER remained relatively constant as the water table fell deeper. Limited variability in VWC between drained sites makes it difficult to be certain of the VWC-ER relationship; however, the pattern of relatively constant ER when VWC is below ~60% with increasing ER as VWC increases is apparent (Figure 3b). An exponential growth equation fits the data well ($R^2 = 0.84$; p = 0.01), although other curves may also be appropriate.

Controls on seasonal variability in CO_2 were also investigated, but very few significant relationships were found between environmental variables and CO_2 exchange at any of the drained plots. ER was significantly related to peat temperature at 5 cm depth, but only at the natural plots and D-3 and D-10. At natural plots GEP had a unimodal relationship to VWC and water table with optimum productivity at 74% VWC and water table of 21 cm (Figure 4). At D-25 there was a weak linear relationship between VWC or water table and GEP with higher productivity when the site was wetter. GEP at other drained sites was not related to water table position or VWC (D-1.5 and D-3 are shown in Figure 4).

DISCUSSION

Moisture controls on CO₂ exchange

As mentioned above, several studies have determined that water table position and moisture are important controls on *Sphagnum* productivity (e.g. McNeil and Waddington, 2003) and given that individual *Sphagnum* moss species occupy narrow niches as defined by the water table (Andrus *et al.*, 1983), this perhaps should not be a



Figure 3. Study plot specific seasonal average carbon dioxide exchange versus (a) water table position and (b) volumetric water content (VWC) in the surface 10 cm of peat. Error bars show standard error. Plotted curves are used to illustrate the general shape of the relationship and are all statistically significant (p < 0.01); however, alternative regressions may also be appropriate. See text for discussion of regression equations.



Figure 4. Controls on seasonal variation in carbon exchange at selected drained plots (left; D-1.5; D-3) and natural plots (right; N1, N2). Ecosystem respiration versus peat temperature at 5 cm depth (a); gross ecosystem photosynthesis (GEP) versus water table (b); and GEP versus volumetric water content in the surface 10 cm of peat (c) are shown for comparison.

surprise. In plots used for additional carbon exchange measurements in the natural portion of our study site (n = 12), plots with greater than 60% *Sphagnum rubellum* cover had average summer water tables 14–18 cm below the surface, but was observed to be present in plots with water tables 14–37 cm deep. Combining all data from our sites with shallow water tables (natural sites and D-25) resulted in a unimodal relationship between GEP and water table position with an optimum at water table of 18 cm, a value in agreement with observed distribution of the moss at this site. Previous field studies have found shallower water table optima of 12 cm for *Sphagnum angustifolium* (Tuittila *et al.*, 2004) and 8.5 cm for a

community including *Sphagnum papillosum*, *S. fallax* and *S. flexuosum* (Riutta *et al.*, 2007). In a laboratory experiment, Strack and Price (2009) observed optimum productivity at *Sphagnum* gravimetric capitulum moisture content of 19 and 22 g (g dry wt)⁻¹ corresponding to water tables of 11 and 6 cm for *S. fuscum* and *S. magellanicum*, respectively, based on their capitulum moisture–water table relationship. The optimum observed in this study is likely deeper as no sites with water table very close to the surface (above -10 cm) were investigated. Nevertheless, the optimum near surface VWC was 93%.

Our drainage experiment had a clear and persistent impact on water table position and VWC in the upper

10 cm of the peat profile. Although there was a clear relationship between water table position and VWC at relatively wet sites, this relationship broke down once the water table fell below 55 cm (Figure 1) suggesting that beyond this point surface moisture conditions are disconnected from the water table. When the water table was below 55 cm, VWC was relatively constant between 25 and 28%. Under these conditions, the maintenance of VWC is controlled by rewetting via dewfall and precipitation events and moisture retention by *Sphagnum* mosses and upper peat layers (Strack and Price, 2009). Under these conditions capillarity is no longer able to supply water to *Sphagnum* capitula.

Despite maintenance of VWC at ~27%, Sphagnum productivity was effectively shut down at all sites with an average water table below -55 cm (Figure 3). It has been shown elsewhere that the maintenance of moisture at low level for prolonged periods has a serious negative impact on Sphagnum health and productivity (Schipperges and Rydin, 1998). It is also likely that capitulum moisture content was often well below the 25-28% reported here as VWC was measured as an aggregate of the upper 10 cm of the peat profile. The low productivity at drained sites D-1.5 to D-15 is consistent with the fact that moisture content never exceeded the 40-50% VWC threshold suggested by soil water retention data reported elsewhere (Price and Whitehead, 2004; Cagampan and Waddington, 2008) at which soil pressure head would result in draining of hyaline cells (Figure 2).

Because Sphagnum productivity was greatly reduced when near surface VWC was below 28%, its contribution to ER was also reduced at drained sites leading to a decrease in ER under the extreme drought treatment. Thus, despite the fact that many studies have observed that ER is higher under deeper water table, as water table fell from 15 cm at the natural sites to 80 cm at D-15, we observed a decline in average seasonal ER (Figure 3). When water table fell deeper than 80 cm ER increased, but remained below that of the natural sites. Reduced ER with deep water tables is likely linked to the fact that labile carbon has been used up in the early season and more recalcitrant substrates remain and that the water content near the surface is below optimal conditions for microbial respiration. In fact, in the Peatland Carbon Simulator (PCARS) numerical model of peatland carbon exchange decomposition is maximized when water table is 40 cm below the surface and declines when the water table moves either above or below this threshold (Frolking et al., 2002). Despite this reduction in ER at dry locations, all sites with a water table position deeper than 55 cm were on average net sources of CO_2 to the atmosphere under full-light conditions because Sphagnum uptake of CO₂ was virtually eliminated.

Establishing hydrological thresholds for Sphagnum stress

While the 55 cm water table threshold observed is specific to this study site and *Sphagnum rubellum*, through its dependence on peat hydrological properties

and Sphagnum species growth form, and their subsequent control on water supply from the water table to the photosynthetic moss layer and water retention within surface peat, this disconnect between surface moisture conditions and water table will occur at some depth in all peatlands. Although species of Sphagnum with more open growth forms, commonly found in hollows, are expected to be more adversely affected by drought, the threshold value observed here may be representative of many Sphagnum-dominated bogs. For example, in a 6year study of the C balance in a raised bog, Roulet et al. (2007) observed annual net loss of C from the peatland in 3 of the 6 years of the study and these years corresponded to 3 of 4 years in which water table fell below 60 cm during the growing season. Mechanistically, as the peatland dries Sphagnum productivity declines as water-holding hyaline cells are drained by decreasing soil pressure head (increasing tension). At soil pressures less than -100 cm, water held externally in pores formed between leaves and branches will be drained along with some hyaline cells (Hayward and Clymo, 1982), and this pressure has been observed to be a threshold for Sphagnum colonization in cutover peatlands (Price and Whitehead, 2001). Although measurement of pressure head in intact Sphagnum is difficult, it would allow for the process-based estimation of Sphagnum productivity under various environmental conditions regardless of differences in peat physical properties between sites (Thompson and Waddington, 2008).

Implications for climate change

The presence of a water table threshold for Sphagnum productivity suggests that any conditions persistently maintaining deeper water tables will reduce Sphagnum viability within the ecosystem and result in enhanced losses of soil C. Our drainage experiment had a persistent impact on VWC in the upper 10 cm of the peat profile, water table position and CO_2 exchange. However, the drainage experiment represented conditions likely only attainable through an extreme and prolonged multi-year drought. The natural Sphagnum lawn at the Pointe-Lebel peatland had a water table near 15 cm and if we assume a threshold for Sphagnum productivity of 55 cm, a change in water table position, $\Delta WT/\Delta t$, of 40 cm would be required. To determine under what conditions we would expect this threshold we applied a simple water balance approach:

$$\Delta S / \Delta t = P - \text{ET} \pm F \tag{1}$$

where $\Delta S/\Delta t$ is the change in water stored in the peatland over time, *P* the precipitation, ET the evapotranspiration and *F* the net lateral inflow and outflow of water, both surface and subsurface. Water table position $(\Delta WT/\Delta t)$ can be determined from $\Delta S/\Delta t$ (Roulet *et al.*, 1992) according to:

$$\Delta WT/\Delta t = (1/S_y)\Delta S/\Delta t - \beta(1/S_y)\Delta S/\Delta t \qquad (2)$$

where S_y is the specific yield of peat and β a buoyancy factor correcting for changes in peat surface position

with water table change ($\beta = 0$ for fixed surface and $0 < \beta < 1$ for non-fixed surface). While specific yield was not determined in this study, Price (1996) reports S_v of 0.55 in near surface Sphagnum peat and Petrone et al. (2008) give values of 0.59-0.63 for the upper 10 cm and 0.57-0.58 for 40-70 cm depth in two bogs in Alberta, Canada. Moreover, a few studies have also monitored Sphagnum bog surface level related to water table position. Surface level fell 2.5 cm for a 40-cm water table drawdown in a Quebec bog (Price, 2003), while Whittington and Price (2006) report a 5-cm drop in surface level at hummocks during a 20-cm experimental water table drawdown in a Sphagnum-dominated Québec poor fen. These scenarios result in β ranging from 0.06 to 0.25. Applying the reported range of values for S_v and β results in a required $\Delta S/\Delta t$ of 23–34 cm to decrease the water table position an additional 40 cm.

We applied the Penman-Monteith model for ET (Kellner, 2001) using 2005 May-August data for air temperature, relative humidity, and wind speed for this site (Environment Canada, Baie Comeau airport, 2 km from the research site), estimates of net radiation from a nearby peatland and assuming that ground head flux was 10% of net radiation (Roulet et al., 1992) to estimate ET under a warming scenario in which air temperatures increased by 5 °C and relative humidity remained constant. Estimates were taken from Kellner (2001) for surface roughness and bulk surface resistance for a shrubby, Sphagnum bog. Under this warming scenario ET losses increased by only \sim 70 mm between May and August. This suggests that it is unlikely that future climate warming will reduce water table position at this site below the threshold level that results in persistent reduction in Sphagnum productivity; if precipitation and net lateral water flows remain unchanged. However, this change would result in a lowering of the water table from 15 to 23 to 27 cm (depending on the actual values of S_v and β). On the basis of the relationships in Figures 1 and 3, this corresponds to a reduction in near surface VWC from 82% to 65-71% and average daily NEE under full-light from -5.3 to -3.7 to -3.0 g CO₂ m⁻² day⁻¹. While this estimated shift in NEE is based solely on the data collected in this study, clearly C storage could be further reduced as shifts in the peat thermal regime would likely result in warmer peat temperature leading to higher soil respiration (Waddington et al., 1998). We also acknowledge that this specific estimate of shifting C exchange is site and species specific and applies to short-lived drought (seasonal) situations and not persistent (multi-year) water table drawdown as the latter is known to result in ecological succession and less straightforward change in soil water retention, vegetation productivity and ecosystem carbon exchange. For example, Belyea and Clymo (2001) suggest that the relative proportion of hummock and hollow microforms will shift in response to shifts in acrotelm thickness (i.e. water table depth) resulting in altered productivity and hydrology over time. Thus, in the longer term peatland structure will evolve in response to shifts in climate, establishing a new equilibrium rate of carbon

sequestration. Despite the fact that this study is limited to short-term response, these results do indicate that, even without a dynamic change in vegetation, shifts in peatland carbon storage in a future climate where droughts, including severe droughts, become more common may not be as dramatic as has been demonstrated in the literature (e.g. Ise *et al.*, 2008).

CONCLUSION

Peatland ecosystems are contemporary and long-term net sinks for atmospheric CO2 (e.g. Gorham, 1991; Frolking et al., 2006); however, potential for persistent drought resulting from climate change (Roulet et al., 1992; Waddington et al. 1998) has raised concerns that peat soil C will be oxidized, shift these ecosystems to large sources of atmospheric CO_2 and act as a significant positive feedback to climate change. While lower water table position will increase peat aeration and likely ER and may reduce Sphagnum productivity, we have demonstrated here that climate warming is unlikely to result in water tables deep enough to substantially reduce Sphagnum photosynthesis. Therefore, this research suggests that release of soil C from Sphagnum-dominated peatlands may be less than previously suggested in response to warming temperatures.

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