

Peat depth as a control on moss water availability during drought

Paul Moore¹, Benjamin Didemus¹, Alexander Furukawa¹, and James Waddington¹

¹McMaster University

December 7, 2020

Abstract

Peatlands are globally important long-term sinks of carbon, however there is concern that enhanced moss moisture stress due to climate change mediated drought will reduce moss productivity making these ecosystems vulnerable to carbon loss and associated long-term degradation. Peatlands are resilient to summer drought moss stress because of negative ecohydrological feedbacks that generally maintain a wet peat surface, but where feedbacks may be contingent on peat depth. We tested this ‘survival of the deepest’ hypothesis by examining water table position, near-surface moisture content, and soil water tension in peatlands that differ in size, peat depth, and catchment area during a summer drought. All shallow sites lost their WT (i.e. the groundwater well was dry) for considerable time during the drought period. Near-surface soil water tension increased dramatically at shallow sites following water table loss, increasing $\sim 5\text{--}7.5\times$ greater at shallow sites compared to deep sites. During a mid-summer drought intensive field survey we found that 60%–67% of plots at shallow sites exceeded a 100 mb tension threshold used to infer moss water stress. Unlike the shallow sites, tension typically did not exceed this 100 mb threshold at the deep sites. Using species dependent water content - chlorophyll fluorescence thresholds and relations between volumetric water content and water table depth, Monte Carlo simulations suggest that moss had nearly twice the likelihood of being stressed at shallow sites (0.38 ± 0.24) compared to deep sites (0.22 ± 0.18). This study provides evidence that mosses in shallow peatland may be particularly vulnerable to warmer and drier climates in the future, but where species composition may play an important role. We argue that a critical ‘threshold’ peat depth specific for different hydrogeological and hydroclimatic regions can be used to assess what peatlands are especially vulnerable to climate change mediated drought.

PEAT DEPTH AS A CONTROL ON MOSS WATER AVAILABILITY DURING DROUGHT

P.A. Moore*, B.D. Didemus, A.K. Furukawa, and J.M. Waddington

School of Earth, Environment and Society, McMaster University, Hamilton, ON, L8S 4K1

*Corresponding author: Paul Moore, paul.moore82@gmail.com

Key words: peatland, water table, tension, *Sphagnum* moss, peat, moisture stress

Short running title: Peat depth and moss water availability

ABSTRACT

Peatlands are globally important long-term sinks of carbon, however there is concern that enhanced moss moisture stress due to climate change mediated drought will reduce moss productivity making these ecosystems vulnerable to carbon loss and associated long-term degradation. Peatlands are resilient to summer drought moss stress because of negative ecohydrological feedbacks that generally maintain a wet peat surface, but where feedbacks may be contingent on peat depth. We tested this ‘*survival of the deepest*’ hypothesis by examining water table position, near-surface moisture content, and soil water tension in peatlands that differ in size, peat depth, and catchment area during a summer drought.

All shallow sites lost their WT (*i.e.* the groundwater well was dry) for considerable time during the drought period. Near-surface soil water tension increased dramatically at shallow sites following water table loss, increasing $\sim 5\text{--}7.5\times$ greater at shallow sites compared to deep sites. During a mid-summer drought intensive field survey we found that 60%–67% of plots at shallow sites exceeded a 100 mb tension threshold used to infer moss water stress. Unlike the shallow sites, tension typically did not exceed this 100 mb threshold at the deep sites. Using species dependent water content - chlorophyll fluorescence thresholds and relations between volumetric water content and water table depth, Monte Carlo simulations suggest that moss had nearly twice the likelihood of being stressed at shallow sites (0.38 ± 0.24) compared to deep sites (0.22 ± 0.18). This study provides evidence that mosses in shallow peatland may be particularly vulnerable to warmer and drier climates in the future, but where species composition may play an important role. We argue that a critical ‘threshold’ peat depth specific for different hydrogeological and hydroclimatic regions can be used to assess what peatlands are especially vulnerable to climate change mediated drought.

1. INTRODUCTION

Northern peatlands have acted as persistent sinks of atmospheric CO₂ throughout the Holocene (Loisel et al., 2014) and today represent a globally important soil carbon (C) reserve ($\sim 220\text{--}550$ Pg C) (Turunen, Tomppo, Tolonen, & Reinikainen, 2002; Yu, 2011). This long-term carbon sequestration is largely the result of *Sphagnum* moss productivity exceeding moss and peat decomposition and combustion rates (Rydin & Jeglum, 2013). There is a concern, however, that *Sphagnum* mosses and their associated peatland carbon stocks may be vulnerable to future climate change (Ise, Dunn, Wofsy, & Moorcroft, 2008; Dorrepaal et al., 2009), where evaporation rates are predicted to increase substantially within the next century (IPCC, 2013). While drier conditions may inhibit *Sphagnum* growth due to a greater frequency and severity of water stress (Moore & Waddington, 2015), these peatland mosses are generally considered resilient to drought owing to their water regulating traits and a number of negative ecohydrological feedbacks that act to maintain a wet near-surface (Waddington et al., 2015). Many of these key autogenic negative feedbacks are stronger where peat depths are greater (*e.g.* water table depth-peat deformation feedback) (Waddington et al., 2010). Indeed, most peatland and moss water availability research is biased to deep and large peatlands (*e.g.* Lindholm & Markkula, 1984; Price, 1997; Moore, Morris, & Waddington, 2015) where peatland ecohydrological resilience is higher (Morris & Waddington, 2011) and where the water table (WT) never falls below the peat layer. In contrast, the likelihood of drought-driven water table drawdown well below the moss layer is greater in shallow peat systems such as recently restored peatlands or natural locations undergoing primary peat formation (*i.e.* peat formed directly on mineral soil or rock). Dixon et al. (2017) used modelled water balance simulations to determine that peat deposits less than 0.5 m thick were least able to buffer prolonged periods of evaporation due to limited labile water storage and quickly experienced moss stress.

Mosses are non-vascular and must rely on water supplied to the growing surface via capillary rise from deeper in the profile and water storage in the capitula (apical bud) during rain-free periods (Thompson & Waddington, 2008). Both water storage and capillary transport in moss and the underlying peat is a nonlinear function of soil water tension (?) (*e.g.* McCarter & Price, 2014; Moore et al., 2015). As ? increases with a falling WT, capillary films become thinner and less connected, thus reducing the hydraulic conductivity of the peat matrix (Price & Whittington, 2010; Rezanezhad et al., 2010). Consequently, under dry conditions, steep hydraulic gradients in the near-surface are unable to counteract sharp declines in hydraulic conductivity, resulting in capillary transport being less than evaporative losses, and thus leading to near-surface desiccation (Schouwenaars & Gosen, 2007; McCarter & Price, 2014; Kettridge & Waddington, 2014). Under these conditions, *Sphagnum* chlorophyllous cells use water stored in large, adjacent, dead hyaline cells to maintain metabolic processes. However, hyaline cells are expected to drain when ? exceeds 100–600 mb (or hPa) (Hayward & Clymo, 1982; Lewis, 1988), leading to rapid desiccation of the chlorophyllous cells with continued evaporative losses. The nature of the relationship between water storage, hydraulic conductivity, and ? is dependent on the botanical origin and degree of decomposition of the peat (Rezanezhad et al., 2010; McCarter & Price, 2014; Taylor & Price, 2015). For example, in the near-surface and living moss layer, *Sphagnum* species with higher stem and branch packing densities (*e.g.* *Sphagnum* sections *Acutifolia* and *Sphagnum*) have generally been shown to possess both greater volumetric water content (VWC) and

hydraulic conductivity for a given ? (Titus & Wagner, 1984; Strack & Price, 2009; Hajek & Vicherova, 2014; McCarter & Price, 2014). Moreover, the greater ability of these *Sphagnum* species to retain and conduct water gives them the ability to maintain a hydrological connection with the WT at greater WT depths than species with weaker moisture retention and hydraulic conductivity (*e.g. Sphagnum* section *Cuspidata*), and thus they possess a greater ability to avoid desiccation in a given environment (Hayward & Clymo, 1982; Rydin, 1985). Water stress and the vulnerability to future drying, therefore, will likely be lower for peatlands where water table depth (WTD) and variability are minimized (Holden, Wallage, Lane, & McDonald, 2011; Moore & Waddington, 2015), and for moss species which possess stronger capillarity (Rydin, 1993). As such, to extend the modelling work of Dixon et al. (2017) to field conditions, we hypothesized that due to the link between WT depth, soil water tension, and moss water stress, mosses on shallower peat will experience greater frequency and severity of water stress due to greater WT variability and shorter hydroperiods (*i.e.* period of WT presence) compared to the same species growing on deeper peats. To test this 'survival of the deepest' hypothesis we measured near-surface tension, moisture content, and water table position in both *Sphagnum* dominated shallow peat wetlands and deeper peatlands on Canadian Shield rock barrens during a summer drought. By examining the effect of peat depth on the frequency and severity of water stress in moss during meteorological drought we aim to better identify factors which may make peatlands more vulnerable to longer term climate change mediated drought as a result of decreased moss productivity.

2. METHODS

2.1 Study area

This study was conducted at peatlands north of Parry Sound, Ontario, Canada within the Georgian Bay Biosphere Mnidoo Gamii, a UNESCO biosphere, situated within the Robinson-Huron Treaty of 1850 and the Williams Treaty of 1923, and located on Anishinabek territory. This eastern Georgian Bay region is on the Canadian Shield and is characterized by multiple west-east oriented granite bedrock ridges and valleys with numerous bedrock depressions of various depths and landscape positions along the ridges. The low bedrock permeability in these depressions support wetlands and peatlands with a perched water table. The wetland and peatland soil is mostly organic soil (peat) situated on a thin layer (0–5 cm) of mineral soil. The surface cover of the ridges tends to consist of either small thin patches of mineral soil, moss cushions, lichen mats, or exposed bedrock, while the intervening valleys more commonly consist of deeper mineral soil, ponds or deep and expansive peatlands.

To examine the effect of peat depth on moss water availability, we categorized peat-filled wetlands and peatlands perched on the bedrock (hereafter referred to as sites) into two different classes based on average peat depth: i) sites with depths < 40 cm hereafter referred to as shallow depth (S), and ii) sites > 40 cm in depth hereafter referred to as deep (D). In Canada, peatlands are defined as wetlands with peat depths greater than 40 cm (National Wetlands Working Group, 1997). For each depth class, the catchment area of the site was categorized as being either large (L, > 4,000 m²) or small (S, < 4,000 m²) providing a total of four depth/catchment categories. Three representative sites for each of these four categories (12 in total), were monitored (hereafter referred as the main sites) throughout the 2015 growing season and identified by a site depth and catchment area as well as three-digit site number. For example, site DL-234 describes site number 234, which is a deep site in a large catchment area. An additional five sites from each category (for a total of 32 sites), were selected for an intensive field survey conducted in mid-summer during a meteorological drought period (hereafter referred as IFS sites). The sites are dominated by *Sphagnum* moss, and vascular vegetation including leatherleaf (*Chamaedaphne calyculata*), sedges (*Carex spp.*), tamarack (*Larix laricina*), and jack pine (*Pinus banksiana*). Site and watershed characteristics of the main sites are summarized in Table 1.

2.2 Hydrological measurements

All hydrological measurements at the main sites were made over the 2015 growing season from day of year (DOY) 152 to DOY 325. Rainfall was recorded at 30-minute intervals at two tipping bucket rain gauges at

sites DS-808 and DL-415. Measurements from the tipping bucket rain gauges were validated with at least three manual rain gauges placed near each of the tipping buckets and at all sites. Water table position was measured at each of the main sites at 15-minute intervals using a water level sensor (Solinst Level Logger, Georgetown, ON) in a PVC groundwater well (5 cm inner diameter) installed to bedrock at the deepest position at the site.

Measurements of near-surface soil water tension and volumetric moisture content were made two times per week from June to September 2015 for the two most common *Sphagnum* species (*S. fallax* and *S. palustre*) at each of the main sites. Soil water tension was measured at 5 cm depth (5 cm) using tensiometers (2 cm outer diameter, Soil Measurement Systems, Tucson, Arizona, USA) and an UMS Infield tensicorder (Munich, Germany) accurate to ± 2 mb (or hPa). Integrated near-surface volumetric moisture content was measured manually over the 0–3 cm (VWC_{0–3 cm}) depth ranges using a ThetaProbe Soil Moisture Sensor ML3 (Delta-T Devices, Burwell, Cambridge, UK).

Near-surface tension and volumetric moisture content were also measured during a mid-summer meteorological drought for all 32 IFS sites on DOY 221 for a plot of *S. fallax* and *S. palustre* following the same methods for soil water tension and moisture content methods as described above. IFS tensiometers were installed on DOY 212 (July 31).

2.3 Modelling moss moisture stress

We modelled moss moisture stress by combining field data (see above) and the relationship between VWC and chlorophyll fluorescence for *S. fallax* and *S. palustre* derived from a controlled lab experiment.

Four replicate cylindrical samples of each species were taken from the field using a PVC collar (10 cm diameter, 5 cm depth). Samples were under-cut, carefully removed, and cheesecloth affixed to the PVC to support the sample from underneath. Vascular vegetation was clipped from the moss surface and the samples were saturated with water. Immediately prior to the start of the drying experiment, the samples were allowed to free drain for 24 h and then placed in a growth chamber to dry. The temperature and light levels of the growth chamber were kept constant at 25°C and 300 μ mol m⁻²s⁻¹ throughout the 14 days of the drying experiment. VWC was measured by weighing the samples daily, and subtracting the sample dry weight which was determined by oven drying at 60°C at the end of the drying experiment. Chlorophyll fluorescence was measured using a modulated chlorophyll fluorometer (Opti-Sciences, Inc. model OS30p+) for three capitula using clipped sub-samples that were dark adapted for 20 minutes. The optimal quantum yield of photosystem II as represented by F_v/F_m was measured, and reported F_v/F_m values represent the average of the three replicate capitula. Due to the destructive nature of chlorophyll fluorescence measurements, measurements were initially done every 2–3 days, and with greater frequency as the moss samples began to appear stressed.

An empirical relation between lab-measured VWC and F_v/F_m was used to define moss moisture stress. A rectangular hyperbola was used to represent the relation:

$$F_v/F_m = -\frac{1}{\alpha} \left(\beta \cdot VWC + \gamma - \sqrt{(\beta \cdot VWC + \gamma)^2 - 4 \cdot \alpha \cdot \beta \cdot \gamma \cdot VWC} \right) \quad (1)$$

where α is the curvature parameter, β is the initial slope, and γ is the maximum F_v/F_m . Because of the uncertainty of the onset of moss stress in relation to fluorescence parameters, we adopted a high and low VWC threshold corresponding to 75% and 25% of the fitted γ parameter (i.e. maximum F_v/F_m), respectively.

In order to estimate the proportion of the snow-free season (April to October 2015, inclusive) where moss was likely to be stressed, we used an empirical relation between VWC and WT to determine when modelled VWC was below the threshold defined by the lab-measured chlorophyll fluorescence. The relation between VWC and WT was modelled using a modified van Genuchten equation for *S. fallax* and *S. palustre* separately (Figure S1), where WT depth was used in place of tension. Based on lab samples (i.e. 5 cm deep surface

samples) porosity was taken to be 98% and residual water content was assumed to be 0% (*c.f.* McCarter and Price, 2014). The *fit* function in Matlab (MATLAB R2020a - The Mathworks Inc.) was used to estimate curve parameters, and *predint* used to generate prediction intervals for new observations. A simple Monte Carlo approach using 1000 iterations was used to generate modelled VWC using *predint* where new modelled observations were generated using normally distributed errors. For cases where the WT was lost, VWC was modelled based on the measured distribution of VWC in the field. A logarithmic distribution was used to represent measured VWC data.

2.4 Statistical analyses

All statistical analyses were done using Matlab. Unless otherwise stated, value pairs in parentheses represent the mean \pm std. A general linear model (*glmfit*) was used to test for the significance of site depth (*Depth* – shallow and deep), catchment area (*Catchment* – small and large), and species cover (*Species*– *S. fallax* and *S. palustre*) and their one-way interactions on $\theta_{5\text{ cm}}$, where the following model was evaluated: $Tension \sim 1 + Depth \times Catchment + Depth \times Species + Catchment \times Species$ (Wilkinson notation). Tension measurements consisted of random paired plots at all 32 IFS sites. A log-link function was used due to the right skew of the $\theta_{5\text{ cm}}$ data. Pairwise differences in the marginal means were assessed using Tukey’s post-hoc HSD.

3. RESULTS

3.1 Precipitation and water table depth

During the study period the region received a total of 350 mm rainfall with higher rainfall in early June, October, and early November than during the middle of the summer (Figure 1). Specifically, only about one-third of the study period rainfall (98 mm) occurred from DOY 174 (June 23) and DOY 271 (September 28) which was less than half of the long-term mean for this period (Environment Canada, 2015). We refer to this as the period of meteorological drought.

The WTD at all sites reached a springtime minimum in mid-June (DOY 164–166) (Figure 1). Following this period, the WT at deep sites experienced an overall decline until a maximum WTD occurred on DOY 272 (September 29) (Figure 1). The magnitude of deep site WT decline was unrelated to catchment size, with a range in WT decline of 48–65 cm.

Similar to the deep sites, each shallow site experienced an overall increase in WTD following the minimum in mid-June (Figure 1). All shallow sites lost their WT (*i.e.* the groundwater well was dry) for considerable time during the drought period. The first shallow site WT loss occurred between DOY 182 and DOY 196 and there was no WT at any shallow sites between DOY 202 and DOY 232 (July 21 and August 20), and with the exception of SS-407, no WT was present in any shallow site from DOY 202 to DOY 289 (July 21 to October 16) (Figure 1).

3.2 Moss water availability

Between DOY 176 (June 25) and DOY 211 (July 30) all shallow sites lost their WT providing an opportunity to evaluate the responsiveness of near-surface VWC and $\theta_{0-3\text{ cm}}$ to this WT loss. Both *S. fallax* and *S. palustre* experienced slight declines in $VWC_{0-3\text{ cm}}$ over the drought period, decreasing 6% and 12% on average for both deep and shallow sites, respectively (Figures 2 and 3). When WT was present, a general linear model (one-way interactions with WTD, species and depth category) showed that trends in $VWC_{0-3\text{ cm}}$ were significantly related to WTD (slope = -0.35, $F=-5.18$, $p=7.4E-07$), where shallow sites tended to have slightly lower $VWC_{0-3\text{ cm}}$ (difference = 3.4%, $F=-1.54$, $p=0.126$), and the WTD response being more subdued (WTD \times shallow slope = -0.19, $F=1.68$, $p=0.096$) (Figure 4a–b).

Near-surface tension, however, tended to be more responsive during the drought period. In particular, $\psi_{5\text{ cm}}$ increased dramatically at shallow sites following WT loss (Figure 2) increasing by 219 and 122 mb on average for *S. fallax* and *S. palustre*, respectively. By comparison, the maximum change in $\psi_{5\text{ cm}}$ at deep sites was on average 29 and 25 mb, respectively (Figure 3). Moreover, with the exception of one (potentially erroneous) measurement, $\psi_{5\text{ cm}}$ at deep sites did not exceed 40 mb (Figure 4c). While average tension during the drought period was much higher at the shallow sites, $\psi_{5\text{ cm}}$ generally followed a 1:1 relation with WTD when WT was present for both deep and shallow sites (Figure 4c-d).

3.3 Mid-summer drought intensive field survey

The mid-summer drought IFS allowed for a comparison of how near-surface VWC and ψ are both affected by WTD over a larger range of sites. On the day of the IFS (DOY 221) all 16 shallow sites did not have a WT present while, in contrast, all 16 deep sites had a WT present between depths of 34 and 70 cm.

$\text{VWC}_{0-3\text{ cm}}$ was low at shallow sites regardless of species or catchment size, having a median $\text{VWC}_{0-3\text{ cm}}$ of 1.1% at the time of the IFS. *S. fallax* $\text{VWC}_{0-3\text{ cm}}$ at the deep sites was similarly low to shallow sites, regardless of catchment area class. In contrast, the *S. palustre* $\text{VWC}_{0-3\text{ cm}}$ at the deep sites was comparatively higher during the IFS (5.8%).

$\psi_{5\text{ cm}}$ during the IFS varied significantly by site depth classification ($F=53.4$, $p<<0.001$), catchment size ($F=5.32$, $p=0.025$), and depth x size (Figure 5a; $F=3.43$, $p=0.070$), but not by species ($F=0.12$, $p=0.73$). In particular, shallow sites with a large catchment had the highest median ψ (153 mb). Median ψ measured at the shallow sites during the IFS was 105 and 130 mb, for *S. fallax* and *S. palustre*, respectively (Figure 5b). Using the 100 mb ψ threshold to infer water stress (Price and Whitehead, 2001), 60% of *S. fallax* plots and 67% of *S. palustre* plots in shallow sites exceeded this threshold during the IFS. The median $\psi_{5\text{ cm}}$ measured at deep sites during the IFS was much lower (41 and 35 mb) for both *S. palustre* and *S. fallax*, respectively. Unlike the shallow sites, ψ typically did not exceed the 100 mb threshold at the deep sites. At deep sites during the IFS, the 100 mb ψ threshold was only exceeded in *S. palustre* plots at a single site, and in *S. fallax* plots at 3 sites (~20% of sites).

3.4 Modelled moisture stress

Lab-measured chlorophyll fluorescence (F_v/F_m) for *S. fallax* and *S. palustre* capitula was positively related to sample VWC and well described by a hyperbolic fit (r^2_{adj} of 0.95 and 0.90, respectively). There was a relatively sharp transition from high to low F_v/F_m between VWC of 1–10% (Figure 6), which represents the onset of moisture stress in the capitula samples. Due to the rapid transition (relative to the measurement interval) in F_v/F_m , results are lacking over the ~3–6% VWC range and so we adopted a conservative approach of defining a high and low VWC threshold for the onset of moisture stress based on the VWC where F_v/F_m was 1/4 and 3/4 of the saturation value (see Eq. 1). Correspondingly, the high and low VWC thresholds were 5.4% and 1.8%, and 3.8% and 1.3% for *S. fallax* and *S. palustre*, respectively.

Although there were only slight differences in the estimated VWC threshold for the onset of moss stress, there was a greater differentiation in moisture retention by species where *S. palustre* tended to retain more water than *S. fallax* for WTD greater than ~10 cm (Figure S1). Using species dependent VWC- F_v/F_m thresholds and VWC-WTD relations, Monte Carlo simulations suggest that moss has nearly twice the likelihood of being stressed at shallow sites (0.38 +- 0.24) compared to deep sites (0.22 +- 0.18). The effect size of moss species on the likelihood of being stressed was greater than site depth category (Figure 7). Our model estimate of the likelihood of moss stress was three times greater for *S. fallax* (0.46 +- 0.17) compared to *S. palustre* (0.14 +- 0.13). Unsurprisingly, a high VWC-stress threshold resulted in a greater likelihood of moss stress (0.40 +- 0.23) compared to a low VWC-stress threshold (0.19 +- 0.16), having a similar effect size to site depth category.

4. DISCUSSION

4.1 Influence of site depth and species on moss water availability

Our findings are broadly similar to other studies which have shown that both WTD and species were critical factors affecting near-surface water availability for *Sphagnum* moss (Clymo, 1973; Luken, 1985; Rydin, 1985; Li, Glime, & Liao, 1992; Strack & Price, 2009). Our results show that during a meteorological drought period, $\psi_{5\text{ cm}}$ was greater in shallow sites versus deep sites, where species did not appear to have a significant effect (Figure 5). The Monte Carlo modelling exercise similarly predicted a greater likelihood of stress (magnitude cannot be directly inferred) for shallow sites, but where species was shown to be a significant factor.

The consistency in results with respect to site depth suggests that the loss of the WT at shallow sites has a strong influence on near-surface water availability, particularly with respect to ψ (e.g. Figure 4). While the WT was present, $\psi_{5\text{ cm}}$ was near a hydrostatic equilibrium tension relative to WTD (Figure 4c and d). It was only after a loss of the WT in the shallow sites that the $\psi_{5\text{ cm}}$ -WTD relation substantially differed between shallow and deep sites (e.g. Figures 2 and 3). A similar finding was shown by Price and Whitehead (2001) where a change in the relationship between ψ and WTD occurred when WTD was greater than ~ 70 cm. The shift in the relation between ψ and WTD, and a rapid increase in near surface ψ suggests that capillary transport is not sufficient to meet evaporative losses (see McCarter & Price, 2014; Waddington et al., 2015).

The seemingly inconsistent result with respect to species may have a number of contributing factors. First, the “likelihood of stress” metric is binary and so is insensitive to the magnitude of difference between species once the threshold is crossed (e.g. high versus extreme tensions are similarly classified as ‘likely to be stressed’). Second, we used a VWC relation rather than a gravimetric water content (GWC) relation for ease of comparison to our field data. GWC is a more physiologically relevant measure of moss water availability (e.g. Schipperges & Rydin, 1998; Nungesser, 2003; Van Gaalen, Flanagan, & Peddle, 2007; Hajek & Beckett, 2008) as it integrates differences in moss shoot (i.e. branch, stem, and capitula) and colony structure. Nevertheless, GWC was quantified for the lab experiment from which our VWC- F_v/F_m threshold was estimated. A comparison with GWC showed broadly similar results (Figure S2) where there was no major difference in the relationship between species, nor was GWC better correlated with F_v/F_m . Third, the Monte Carlo simulation incorporates all available WTD for the growing season while the ψ -WTD data spans the roughly one month meteorological drought period. Fourth, and finally, based on field data there was a fundamental difference between species in the VWC- ψ relationship where the two were more strongly correlated for *S. fallax* compared to *S. palustre* (Figure S3).

During drought periods near-surface moisture is predominantly accessed through upward capillary transport (as opposed to direct wetting from rainfall) (McCarter & Price, 2014) and we found that *S. palustre* was able to maintain higher near-surface moisture at considerably deeper WT depths than *S. fallax* (Figure S1). The ability of *S. palustre* to maintain a higher water content for a given WTD is likely a combination of the species dependent structural characteristics of individual shoots which can enhance capillarity (Hayward & Clymo, 1982; Rice, Aclander, & Hanson, 2008) and colony structure which affects evaporative losses (e.g. Rice, Collins, & Anderson, 2001; Elumeeva, Soudzilovskaia, During, & Cornelissen, 2011). Moreover, moss capitula water supply is mechanically linked to the water transport ability (unsaturated hydraulic conductivity; K_{unsat}) of the underlying peat matrix. While we are unaware of any studies that have derived K_{unsat} relationships for *S. fallax* and *S. palustre* to date, species with a lower near-surface K_{unsat} have been shown to desiccate at shallower WT depths than species with higher K_{unsat} (Titus & Wagner, 1984; McCarter & Price, 2014).

However, it is important to note that if a moss species ordinarily desiccates at WT depths shallower than the depth of peat on which it grows, then the frequency with which it experiences water stress will not necessarily be intensified by the loss of the WT. Indeed we found that the loss of a WT had a larger overall influence on the likelihood of moss stress for the species with relatively high (*S. palustre*) versus low (*S.*

fallax) moisture retention (Figures S1 and S3). Therefore, despite similar $VWC-F_v/F_m$ stress thresholds (Figure 6), *S. fallax* was predicted to become stressed at shallower WT depths (Figure S1). Site depth may not only affect moss stress by influencing total saturated storage capacity, but may also influence near-surface moisture availability through differences in rates of WT decline as a result of basin area volume relationships (e.g. Brooks & Hayashi, 2002) or peat properties such as specific yield (e.g. Granath, Moore, Lukenbach, & Waddington, 2016). Wilkinson, Tekatch, Markle, Moore, & Waddington (2020) showed that shallow peat-filled depressions in the region tended to have a more rapid WT decline compared to deeper peatlands, which is supported by the lower average specific yield for shallow sites (Didemus, 2016) and more rapid WT decline during the meteorological drought period of this study (Figure 1).

4.2 Influence of catchment size on moss water availability

In addition to species-dependent moisture retention characteristics and site storage dynamics as mediated via peat properties, the likelihood of stress for moss species may also be affected by hydrological connectivity to the surrounding upland where groundwater-surface water interactions have been shown to influence peatland water storage dynamics (Devito, Hill, & Roulet, 1996; Glaser, Siegel, Romanowicz, & Shen, 1997). Given the study sites chosen, there was a moderately strong positive correlation between site area and peat depth (Figure S4). Meanwhile, a linear relationship between site and catchment area was not evident from our data. Since site area and depth are well correlated for the chosen study sites, it is likely that the storage capacity for water is proportional to site area. If storage capacity increases without a proportional increase in catchment area, one would not necessarily expect catchment size to have a strong control on site storage dynamics, all else being equal (particularly with respect to increases in storage during/following rainfall). Nevertheless, since storage dynamics were shown to be empirically linked to near-surface θ (e.g. correlation between WTD and θ as shown in Figure 4c–d) we might expect to see an influence of catchment size on θ if catchment size affects site water balance.

During the meteorological drought period, we found that catchment area had a significant effect on moss water availability for shallow sites, but not deep sites (Figure 5). Paradoxically, shallow sites in large catchments experienced higher median θ compared to shallow sites in small catchments. *Sphagnum* species have a certain degree of phenotypic plasticity associated with environmental gradients. For example, the total hyaline cell volume can increase under drought conditions for certain *Sphagnum* species (Li, Glime, & Liao, 1992) including *S. palustre* (Bu, Zheng, Rydin, Moore, & Ma, 2013). Although conjectural, *Sphagnum* moss at shallow sites with small catchments could be adapted to drier conditions, and thus experience lower θ during meteorological drought conditions. Unlike other peatlands studied on the Canadian Shield of southern Ontario (e.g. Devito, Hill, & Roulet, 1996), the catchments in this study do not have extensive mineral soils (shallow or otherwise) in the surrounding upland which could provide surface- or ground-water connections between rainfall events. Rather, hydrological connectivity with the surrounding landscape appears to be a function of fill and spill processes (e.g. Spence & Woo, 2006) where upland storage within the various study site catchments is largely in other similar small moss dominated wetlands. Consequently, catchment storage elements will become isolated during drought as their WT drops below the sill thus limiting hydrological connectivity.

4.3 Survival of the deepest

Given that site depth is linked to moss water availability during meteorological drought and the cumulative likelihood of stress throughout the growing season, our results suggest that shallow sites might have inherently lower moss productivity compared to deeper sites. Lab results show that the moss enters dormancy at low water content (i.e. near-zero F_v/F_m – Figures 6 and S2), where others have shown that recovery from desiccation is hysteretic and that the negative impact of repeated and/or prolonged drought can have a multiplicative type effect (Schipperges & Rydin, 1998; McNeil & Waddington, 2003). The greater WT drawdown rate and the regular absence of a WT in shallow sites during the growing season likely contributed to their overall higher $\theta_{5\text{ cm}}$ and lower $VWC_{0-3\text{ cm}}$ as compared to deep sites. The larger fraction of time that a given moss species experiences water stress in shallower sites should lead to increased periods of

dormancy and lower annual growth. As *Sphagnum* is considered a keystone species for peat formation (Van Breeman, 1995), there may exist a critical depth threshold that must be exceeded for many locations on the landscape for the production of *Sphagnum* peat to continue, despite seasonal drought. With drought expected to increase in length and severity under climate change, this could potentially lead to an ecological shift in peatlands from a *Sphagnum* dominated system to one dominated by forests (Dang & Leiffers, 1989; Kettridge et al., 2015) or more drought tolerant mosses, such as *Polytrichum* species (Laine, Vasander, & Sallantausta, 1995; Benschoter & Vitt, 2008). This then leads to two important ecohydrological questions: 1) what allows a shallow site to become deep?; and 2) what prevents a shallow site from becoming deep?

An answer to these questions could simply be time, where deep sites initiated earlier than shallow sites. Disturbance such as fire is one mechanism by which barrens landscapes in an otherwise forested biome are maintained (e.g. Asselin, Belleau, & Bergeron, 2006). Wildfire could maintain heterogeneity in site peat depth (and age if burned to bedrock) due to differences in smouldering vulnerability between deep and shallow peat-filled depressions (e.g. Wilkinson et al., 2020). Moreover, wildfire disturbance may readily remove surface vegetation cover thus promoting higher/rapid erosion of thin low density soils following fire (e.g. Markle, Wilkinson, & Waddington, 2020).

An alternative hypothesis, assuming basal dating shows similar or more random initiation periods with respect to site depth, would be that local bedrock morphometry imposes a strong control on peat accumulation in a rock barrens landscape, similar to the control of lake basin size on total sediment accumulation (e.g. Ferland, del Giorgio, Teodoru, & Prairie, 2012). For example, shallow sites may be located in small basins. Once a small bedrock depression is filled with peat, additional long term peat accumulation must be supported by a groundwater mound (Clymo, 1984). The process of groundwater mounding is scale dependent, where a greater absolute mound height (i.e. at the center of the accumulating peat deposit) and therefore greater potential peat depth is partly controlled by the lateral extent of the peat deposit (Ingram, 1982; Belyea & Baird, 2006). Thus for the infilling of a bedrock depression, depressions that are larger in area ought to be able to support deeper peat accumulation in the long-term (assuming otherwise favourable conditions and under steady state). However, greater long-term peat accumulation is possible if the peatlands are able to paludify the surrounding landscape, as has been shown for peatlands developing on mineral soils (e.g. Le Stum-Boivin, Magnan, Garneau, Fenton, Grondin, & Bergeron, 2019). To our knowledge, paludification of *Sphagnum* mosses onto bare rock has not been documented in the academic literature. In general, there is no surrounding mineral soil to paludify in the study catchments, therefore lateral expansion onto rock must be supported wholly by climatic conditions and water supply from the peatland itself. With no underlying soil water storage at the edge, expanding moss is likely to experience extreme/frequent desiccation. In fact, the small isolated patches of mineral soil outside of the peat-filled depressions tend to be dominated by more drought tolerant species such as *Polytrichum* moss and lichens (Markle, Sandler, Freeman, & Waddington, 2020).

Given that both the magnitude and frequency of drought are expected to increase due to climate change (IPCC, 2013) the differential response of shallow and deep peatlands are potentially far reaching. For example, while deep pristine peatlands will likely be resistant and resilient to drought, shallow peatlands such as younger and/or slow-accumulating peatlands (Vardy, Warner, Turunen, & Aravena, 2000), recently restored peatlands (Granath et al., 2016), and organic soils under moss and lichen mats on the upland rock barrens (Moore, Smolarz, Markle, & Waddington, 2019; Hudson, Markle, Harris, Moore, & Waddington, 2020) will be more vulnerable and conservation and potential adaptive management efforts may be necessary to maintain the carbon storage function of these sites. Given that peatland restoration has been emphasized as an important nature-based solution to mitigate climate change (Humpenoder et al., 2020), our research also highlights the vulnerability of peatland restoration efforts in situations where the peat and moss layer are shallow (Grand-Clement et al., 2015). We argue that shallow peat-filled depressions remain understudied within the peatland literature and that further research examining the role of hydrology and hydrogeological setting in controlling peat development, carbon cycling and disturbance history are critical to better understand how these systems might respond to future climate change.

ACKNOWLEDGMENTS

This research was funded by a Seed Research Grant from the McMaster Centre for Climate Change. We thank Cam McCann and Alanna Smolarz for assistance in the field and to Madeleine Hayes and Justin Kruse for assistance with the analysis. We thank Dr. Sophie Wilkinson for comments on an earlier draft of this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Paul Moore <https://orcid.org/0000-0003-1924-1528>

Alexander Furukawa <https://orcid.org/0000-0001-6437-3314>

J. Michael Waddington <https://orcid.org/0000-0002-0317-7894>

REFERENCES

- Asselin, H., Belleau, A., & Bergeron, Y. (2006). Factors responsible for the co-occurrence of forested and unforested rock outcrops in the boreal forest. *Landscape Ecology* , 21(2), 271-280.<https://doi.org/10.1007/s10980-005-1393-1>
- Belyea, L. R., & Baird, A. J. (2006). Beyond “the limits to peat bog growth”: Cross-scale feedback in peatland development. *Ecological Monographs* , 76(3), 299-322.[https://doi.org/10.1890/0012-9615\(2006\)076\[0299:BTLTPB\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0299:BTLTPB]2.0.CO;2)
- Benscoter, B. W., & Vitt, D. H. (2008). Spatial patterns and temporal trajectories of the bog ground layer along a post-fire chronosequence. *Ecosystems* , 11 (7), 1054-1064.<https://doi.org/10.1007/s10021-008-9178-4>
- Brooks, R. T., & Hayashi, M. (2002). Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. *Wetlands* , 22(2), 247-255.[https://doi.org/10.1672/0277-5212\(2002\)022\[0247:DAVAHR\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2002)022[0247:DAVAHR]2.0.CO;2)
- Bu, Z-J., Zheng, X-X., Rydin, H., Moore, T., & Ma, J. (2013). Facilitation vs. competition: Does interspecific interaction affect drought responses in Sphagnum? *Basic and Applied Ecology* ,14(7) , 574-584.<https://doi.org/10.1016/j.baae.2013.08.002>
- Clymo, R. S. (1973). The growth of *Sphagnum* : some effects of environment. *The Journal of Ecology* , 61 (3), 849-869.<https://doi.org/10.2307/2258654>
- Clymo, R. S. (1984). The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 303(1117), 605-654.<https://doi.org/10.1098/rstb.1984.0002>
- Dang, Q. L., & Lieffers, V. J. (1989). Assessment of patterns of response of tree ring growth of black spruce following peatland drainage. *Canadian Journal of Forest Research* , 19 (7), 924-929.<https://doi.org/10.1139/x89-140>
- Devito, K. J., Hill, A. R., & Roulet, N. 1996. Groundwater-surface water interactions in headwater forested wetlands of the Canadian Shield., *Journal of Hydrology* , 181(1-4), 127-147.[https://doi.org/10.1016/0022-1694\(95\)02912-5](https://doi.org/10.1016/0022-1694(95)02912-5)

Didemus B. (2016). *Water storage dynamics in peat-filled depressions of the canadian shield rock barrens: implications for primary peat formation* . [M.Sc. Thesis McMaster University, Hamilton, Ontario]. Mac-Sphere.

Dixon, S. J., Kettridge, N., Moore, P. A., Devito, K. J., Tilak, A. S., Petrone, R. M., ... & Waddington, J. M. (2017). Peat depth as a control on moss water availability under evaporative stress. *Hydrological Processes* , 31 (23), 4107-4121.<https://doi.org/10.1002/hyp.11307>

Dorrepaal, E., Toet, S., van Logtestijn, R. S., Swart, E., van de Weg, M. J., Callaghan, T. V., & Aerts, R. (2009). Carbon respiration from subsurface peat accelerated by climate warming in the subarctic. *Nature* , 460 (7255), 616-619.<https://doi.org/10.1038/nature08216>

Elumeeva, T. G., Soudzilovskaia, N. A., During, H. J., & Cornelissen, J. H. (2011). The importance of colony structure versus shoot morphology for the water balance of 22 subarctic bryophyte species. *Journal of Vegetation Science* , 22(1), 152-164.<https://doi.org/10.1111/j.1654-1103.2010.01237.x>

Environment Canada. (2017). Canadian Climate Normals 1981-2010. [Data file]. Retrieved from https://climate.weather.gc.ca/climate_normals/index_e.html

Ferland, M. E., del Giorgio, P. A., Teodoru, C. R., & Prairie, Y. T. (2012). Long-term C accumulation and total C stocks in boreal lakes in northern Quebec. *Global Biogeochemical Cycles*, 26(4).<https://doi.org/10.1029/2011GB004241>

Glaser, P. H., Siegel, D. I., Romanowicz, E. A., & Shen, Y. P. (1997). Regional linkages between raised bogs and the climate, groundwater, and landscape of north-western Minnesota. *Journal of Ecology*, 3-16.<https://doi.org/10.2307/2960623>

Granath, G., Moore, P. A., Lukenbach, M. C., & Waddington, J. M. (2016). Mitigating wild-fire carbon loss in managed northern peatlands through restoration. *Scientific Reports*, 6(1), 28498.<https://doi.org/10.1038/srep28498>

Grand-Clement, E., Anderson, K., Smith, D., Angus, M., Luscombe, D. J., Gatis, N., ... & Brazier, R. E. (2015). New approaches to the restoration of shallow marginal peatlands. *Journal of Environmental Management* , 161, 417-430.<https://doi.org/10.1016/j.jenvman.2015.06.023>

Hajek, T., & Beckett, R. P. (2008). Effect of water content components on desiccation and recovery in Sphagnum mosses. *Annals of botany* , 101(1), 165-173.<https://doi.org/10.1093/aob/mcm287>

Hajek, T., & Vicherova, E. (2014). Desiccation tolerance of *Sphagnum* revisited: a puzzle resolved. *Plant Biology* , 16 (4), 765-773.<https://doi.org/10.1111/plb.12126>

Hayward, P. M., & Clymo, R. S. (1982). Profiles of water content and pore size in Sphagnum and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London. Series B. Biological Sciences* , 215 (1200), 299-325.<https://doi.org/10.1098/rspb.1982.0044>

Holden, J., Wallage, Z. E., Lane, S. N., & McDonald, A. T. (2011). Water table dynamics in undisturbed, drained and restored blanket peat. *Journal of Hydrology* , 402 (1-2), 103-114.<https://doi.org/10.1016/j.jhydrol.2011.03.010>

Hudson, D. T., Markle, C. E., Harris, L. I., Moore, P. A., & Waddington, J. M. (2020). Ecohydrological controls on lichen and moss CO2 exchange in rock barrens turtle nesting habitat. *Ecohydrology* , e2255.<https://doi.org/10.1002/eco.2255>

Humpenoder, F., Karstens, K., Lotze-Campen, H., Leifeld, J., Menichetti, L., Barthelmes, A., & Popp, A. (2020). Peatland protection and restoration are key for climate change mitigation. *Environmental Research Letters* , 15(10), 104093.<https://doi.org/10.1088/1748-9326/abae2a>

- Ingram, H. A. P. (1982). Size and shape in raised mire ecosystems: a geophysical model. *Nature* , 297(5864), 300-303.<https://doi.org/10.1038/297300a0>
- Ise, T., Dunn, A. L., Wofsy, S. C., & Moorcroft, P. R. (2008). High sensitivity of peat decomposition to climate change through water-table feedback. *Nature Geoscience* , 1 (11), 763-766.<https://doi.org/10.1038/ngeo331>
- Kettridge, N., & Waddington, J. M. (2014). Towards quantifying the negative feedback regulation of peatland evaporation to drought.*Hydrological Processes* , 28 (11), 3728-3740.<https://doi.org/10.1002/hyp.9898>
- Kettridge, N., Turetsky, M. R., Sherwood, J. H., Thompson, D. K., Miller, C. A., Benscoter, B. W.,... & Waddington, J. M. (2015). Moderate drop in water table increases peatland vulnerability to post-fire regime shift. *Scientific Reports* , 5 , 8063.<https://doi.org/10.1038/srep08063>
- Laine, J., Vasander, H., & Sallantausta, T. (1995). Ecological effects of peatland drainage for forestry. *Environmental Reviews* , 3 (3-4), 286-303.<https://doi.org/10.1139/a95-015>
- Le Stum-Boivin, E., Magnan, G., Garneau, M., Fenton, N. J., Grondin, P., & Bergeron, Y. (2019). Spatiotemporal evolution of paludification associated with autogenic and allogenic factors in the black spruce–moss boreal forest of Quebec, Canada. *Quaternary Research*, 91(2), 650-664.<https://doi.org/10.1017/qua.2018.101>
- Lewis, A. M. (1988). A test of the air-seeding hypothesis using Sphagnum hyalocysts. *Plant Physiology* , 87 (3), 577-582.<https://doi.org/10.1104/pp.87.3.577>
- Li, Y., Glime, J. M., & Liao, C. (1992). Responses of two interacting Sphagnum species to water level. *Journal of Bryology* , 17 (1), 59-70.<https://doi.org/10.1179/jbr.1992.17.1.59>
- Lindholm, T., & Markkula, I. (1984). Moisture conditions in hummocks and hollows in virgin and drained sites on the raised bog Laaviosuo, southern Finland. In *Annales Botanici Fennici* (pp. 241-255). Finnish Botanical Publishing Board.
- Loisel, J., Yu, Z., Beilman, D. W., Camill, P., Alm, J., Amesbury, M. J., ... & Belyea, L. R. (2014). A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *The Holocene* , 24 (9), 1028-1042.<https://doi.org/10.1177/0959683614538073>
- Lucchese, M., Waddington, J. M., Poulin, M., Pouliot, R., Rochefort, L., & Strack, M. (2010). Organic matter accumulation in a restored peatland: evaluating restoration success. *Ecological Engineering* , 36 (4), 482-488.<https://doi.org/10.1016/j.ecoleng.2009.11.017>
- Luken, J. O. (1985). Zonation of Sphagnum mosses: interactions among shoot growth, growth form, and water balance. *Bryologist* , 374-379.<https://doi.org/10.2307/3242680>
- Markle, C. E., Wilkinson, S. L., & Waddington, J. M. (2020). Initial Effects of Wildfire on Freshwater Turtle Nesting Habitat. *The Journal of Wildlife Management* , 84(7), 1373-1383.<https://doi.org/10.1002/jwmg.21921>
- Markle, C.E., Sandler, N., Freeman, H., & Waddington, J.M. (2020). Multi-scale assessment of rock barrens turtle nesting habitat: Effects of moisture and temperature on hatching success. *Ichthyology & Herpetology*

- MATLAB. (2020). Version 9.8.0 (R2020a). Natick, Massachusetts: The MathWorks Inc.
- McCarter, C. P., & Price, J. S. (2014). Ecohydrology of Sphagnum moss hummocks: mechanisms of capitula water supply and simulated effects of evaporation. *Ecohydrology* , 7 (1), 33-44.<https://doi.org/10.1002/eco.1313>
- McNeil, P., & Waddington, J. M. (2003). Moisture controls on Sphagnum growth and CO₂exchange in a cutover bog. *Journal of Applied Ecology* , 40, 354-367.<https://doi.org/10.1046/j.1365-2664.2003.00790.x>
- Moore, P. A., Morris, P. J., & Waddington, J. M. (2015). Multi-decadal water table manipulation alters peatland hydraulic structure and moisture retention. *Hydrological Processes* , 29 (13), 2970-2982.<https://doi.org/10.1002/hyp.10416>
- Moore, P. A., & Waddington, J. M. (2015). Modelling Sphagnum moisture stress in response to projected 21st century climate change.*Hydrological Processes* , 29 (18), 3966-3982.<https://doi.org/10.1002/hyp.10484>
- Moore, P. A., Smolarz, A. G., Markle, C. E., & Waddington, J. M. (2019). Hydrological and thermal properties of moss and lichen species on rock barrens: Implications for turtle nesting habitat.*Ecohydrology*, 12: e2057,<https://doi.org/10.1002/eco.2057>
- Morris, P. J. & Waddington, J. M. (2011). Groundwater residence time distributions in peatlands: Implications for peat decomposition and accumulation. *Water Resources Research* , 47 (2).<https://doi.org/10.1029/2010WR009492>
- National Wetlands Working Group, 1997. The Canadian Wetland Classification System, 2nd ed. Wetlands Research Group, University of Waterloo, Waterloo, ON, Canada, 76 pp.
- Price, J. S. (1997). Soil moisture, water tension, and water table relationships in a managed cutover bog. *Journal of hydrology* ,202 (1), 21-32.[https://doi.org/10.1016/S0022-1694\(97\)00037-1](https://doi.org/10.1016/S0022-1694(97)00037-1)
- Price, J. S., & Whittington, P. N. (2010). Water flow in Sphagnum hummocks: Mesocosm measurements and modelling. *Journal of Hydrology* , 381 (3), 333-340.<https://doi.org/10.1016/j.jhydrol.2009.12.006>
- Rezanezhad, F., Quinton, W. L., Price, J. S., Elliot, T. R., Elrick, D., & Shook, K. R. (2010). Influence of pore size and geometry on peat unsaturated hydraulic conductivity computed from 3D computed tomography image analysis. *Hydrological processes*, 24(21), 2983-2994.<https://doi.org/10.1002/hyp.7709>
- Rice, S. K., Collins, D., & Anderson, A. M. (2001). Functional significance of variation in bryophyte canopy structure. *American Journal of Botany*, 88(9), 1568-76.<https://doi.org/10.2307/3558400>
- Rice, S. K., Aclander, L., & Hanson, D. T. (2008). Do bryophyte shoot systems function like vascular plant leaves or canopies? Functional trait relationships in Sphagnum mosses (Sphagnaceae). *American Journal of Botany*, 95(11), 1366-1374.<https://doi.org/10.3732/ajb.0800019>
- Rydin, H. (1985). Effect of water level on desiccation of Sphagnum in relation to surrounding Sphagna. *Oikos* , 45(3), 374-379.<https://doi.org/10.2307/3565573>
- Rydin, H. (1993). Interspecific competition between Sphagnum mosses on a raised bog. *Oikos* , 66(3), 413-423.<https://doi.org/10.2307/3544935>
- Rydin, H., & Jeglum, J. K., & Bennett, K. D. (2013). *The biology of peatlands, 2e* . Oxford University Press.

- Schipperges, B., & Rydin, H. (1998). Response of photosynthesis of Sphagnum species from contrasting microhabitats to tissue water content and repeated desiccation. *The New Phytologist* , 140(4), 677-684.<https://doi.org/10.1046/j.1469-8137.1998.00311.x>
- Schouwenaars, J. M., & Gosen, A. M. (2007). The sensitivity of Sphagnum to surface layer conditions in a re-wetted bog: a simulation study of water stress. *Mires and Peat* , 2 (2), 1-19.
- Spence, C., & Woo, M. (2006). Hydrology of subarctic Canadian Shield: heterogeneous headwater basins. *Journal of Hydrology* ,317 (1–2), 138–154.<https://doi.org/10.1016/J.JHYDROL.2005.05.014>
- Strack, M., & Price, J. S. (2009). Moisture controls on carbon dioxide dynamics of peat-*Sphagnum* monoliths. *Ecohydrology* ,2 (1), 34-41.<https://doi.org/10.1002/eco.36>
- Taylor, N., & Price, J. (2015). Soil water dynamics and hydrophysical properties of regenerating Sphagnum layers in a cutover peatland.*Hydrological Processes* , 29 (18), 3878-3892.<https://doi.org/10.1002/hyp.10561>
- Thompson, D. K., & Waddington, J. M. (2008). Sphagnum under pressure: towards an ecohydrological approach to examining Sphagnum productivity.*Ecohydrology* , 1 (4), 299-308.<https://doi.org/10.1002/eco.31>
- Titus, J. E., & Wagner, D. J. (1984). Carbon balance for two Sphagnum mosses: water balance resolves a physiological paradox. *Ecology* ,65 (6) 1765-1774.<https://doi.org/10.2307/1937772>
- Turunen, J., Tomppo, E., Tolonen, K., & Reinikainen, A. (2002). Estimating carbon accumulation rates of undrained mires in Finland—application to boreal and subarctic regions. *The Holocene* , 12 (1), 69-80.<https://doi.org/10.1191/0959683602hl522rp>
- Van Breemen, N. (1995). How *Sphagnum* bogs down other plants.*Trends in Ecology & Evolution* , 10 (7), 270-275.[https://doi.org/10.1016/0169-5347\(95\)90007-1](https://doi.org/10.1016/0169-5347(95)90007-1)
- Van Gaalen, K. E., Flanagan, L. B., & Peddle, D. R. (2007). Photosynthesis, chlorophyll fluorescence and spectral reflectance in Sphagnum moss at varying water contents. *Oecologia* , 153(1), 19–28.<https://doi.org/10.1007/s00442-007-0718-y>
- Vardy, S. R., Warner, B. G., Turunen, J. & Aravena, R. (2000). Carbon accumulation in permafrost peatlands in the Northwest Territories and Nunavut, Canada. *The Holocene* , 10 (2), 273-280.<https://doi.org/10.1191/095968300671749538>.
- Waddington, J. M., Morris, P. J., Kettridge, N., Granath, G., Thompson, D. K., & Moore, P. A. (2015). Hydrological feedbacks in northern peatlands. *Ecohydrology* , 8 (1), 113-127. DOI:<https://doi.org/10.1002/eco.1493>
- Wilkinson, S. L., Tekatch, A., Markle, C. E., Moore, P. A., & Waddington, J. M. (2020). Shallow peat is more vulnerable to high peat burn severity during wildfire. *Environmental Research Letters* , 15: 104032.<https://doi.org/10.1088/1748-9326/aba7e8>
- Yu, Z. (2011). Holocene carbon flux histories of the world’s peatlands: Global carbon-cycle implications. *The Holocene*, 21 (5), 761-774.<https://doi.org/10.1177/0959683610386982>

Table 1: Average peat depth, area and catchment area characteristics of the main sites.

Site class	Catchment area class	Site number	Peat depth (cm)	Site area (m ²)	Catchment area (m ²)	Catchment-s
Shallow	Small	223	28	160	280	1.8
		407	23	210	460	2.2
		502	26	290	600	2.1
	Large	217	37	680	52,680	77.5
		313	24	230	4,030	17.5
		405	31	590	4,390	7.4
Deep	Small	301	83	1,300	3,700	2.8
		303	50	1,100	3,800	3.5
		808	62	1,800	2,630	1.5
	Large	234	75	2,200	39,200	17.8
		408	137	11,000	76,000	6.9
		415	59	4,800	23,800	5.0

Figure captions:

Figure 1: Rainfall and water table depth for deep (a) and shallow (b) main sites. Sites with large and small catchments are represented by maroon and black lines, respectively. A flat line indicates when the water table was lost from the site.

Figure 2: Time series of tension at 5 cm depth (maroon lines) and $VWC_{0-3\text{ cm}}$ (black solid lines), for *S. fallax* (white-filled circles) and *S. palustre* (grey-filled squares) between DOY 176 (June 25th) and DOY 211 (July 30th) at the shallow sites (S). Large (L) catchment area sites are shown on the left, while small (S) catchment area sites are shown on the right. Water table depth (WTD - black dotted lines) is shown relative to the moss surface. Date of water table loss is indicated by a vertical dashed line.

Figure 3: Time series of tension at 5 cm depth (maroon lines) and $VWC_{0-3\text{ cm}}$ (black lines) for *S. fallax* (white-filled circles) and *S. palustre* (grey-filled squares) between DOY 176 (June 25th) and DOY 211 (July 30th) at the deep sites (D). Large (L) catchment area sites are shown on the left, while small (S) catchment area sites are shown on the right. Water table depth (WTD - black dotted lines) is shown relative to the moss surface.

Figure 4: Relation between water table depth and volumetric water content in the top 3 cm (a and b), and tension at 5 cm depth (c and d) for deep (a and c) and shallow (b and d) sites. Shallow sites lost their water table (denoted by 'no WT') with 'no WT' data shown as boxplots for *S. fallax* (black) and *S. palustre* (maroon). A 1:1 relation between tension and WTD is shown as a black solid line.

Figure 5: Box plot of tension measured at 5 cm depth during the mid-summer drought intensive field survey (DOY 221) for deep and shallow sites based on catchment size (a) and *Sphagnum* species (b). Letters denote significant pairwise differences, where the significance of one-way interactions Depth \times Catchment and Depth \times Species are shown in (a) and (b), respectively.

Figure 6: Lab-measured chlorophyll fluorescence stress metric for *Sphagnum fallax* (black) and *Sphagnum palustre* (maroon) samples during a drying experiment. The stress metric is the variable fluorescence over the maximum quantum yield (F_v/F_m) of dark-adapted samples. Empirical relations between F_v/F_m and volumetric water content (VWC) are shown using a rectangular (dashed lines) hyperbola. High and low VWC stress thresholds (dotted lines) represent the 25% and 75% of the maximum modelled F_v/F_m .

Figure 1

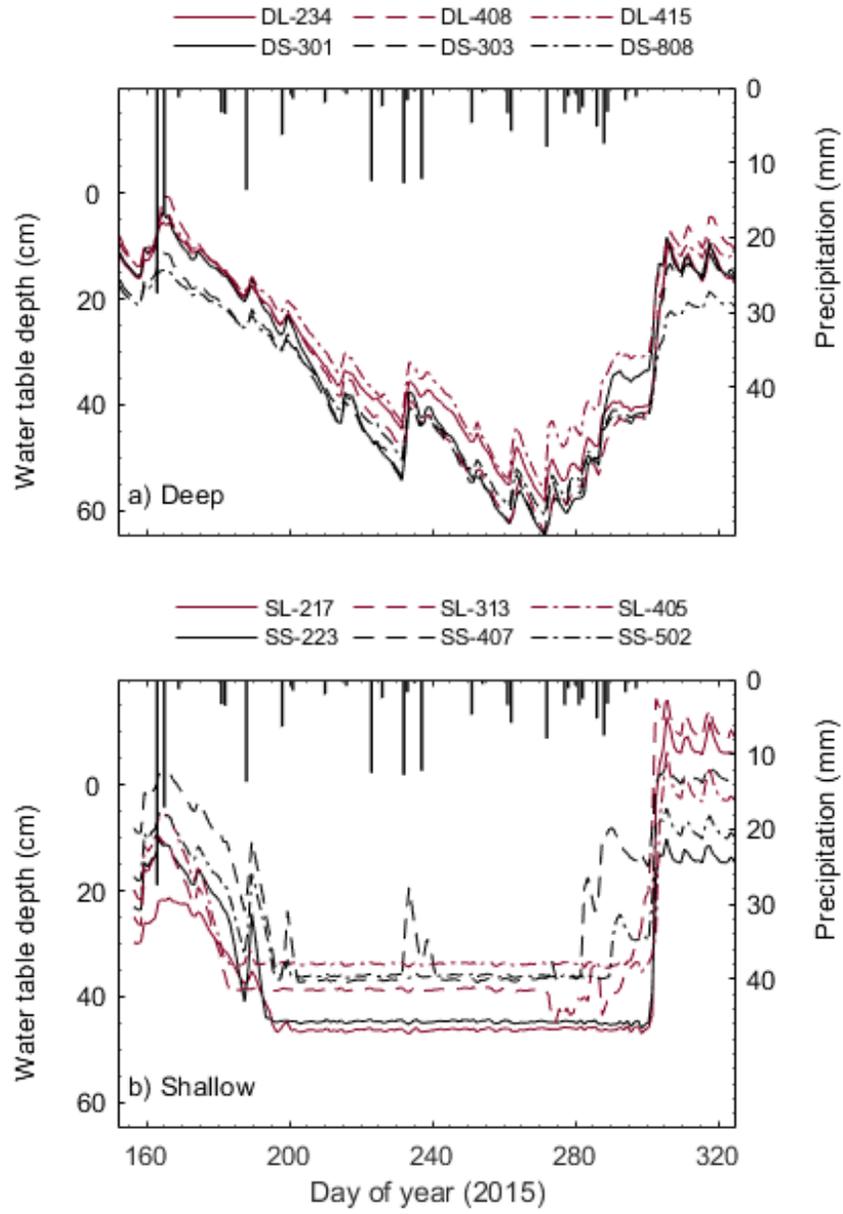


Figure 2

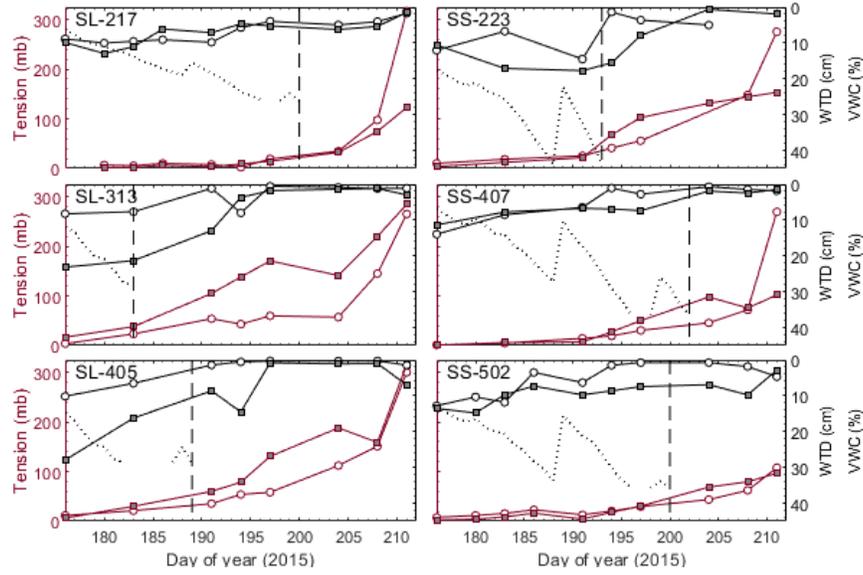


Figure 3

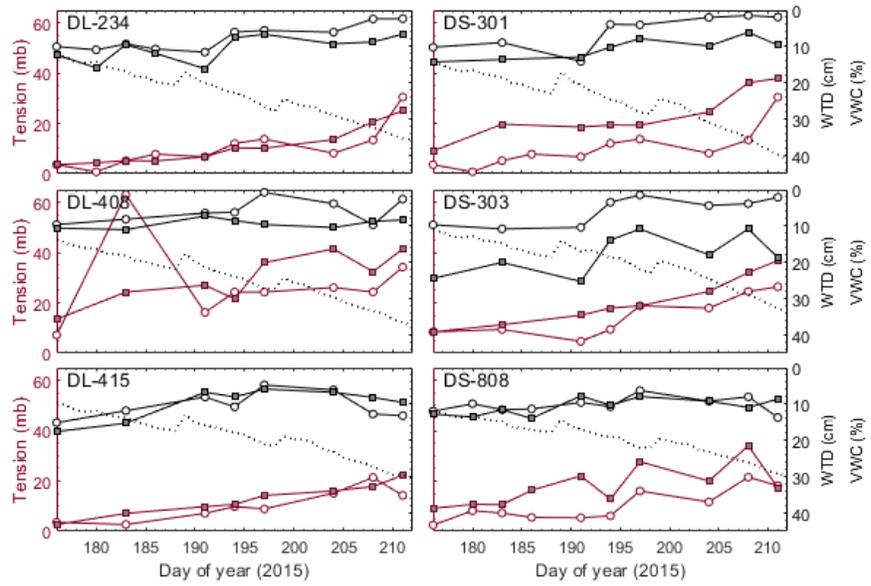


Figure 4

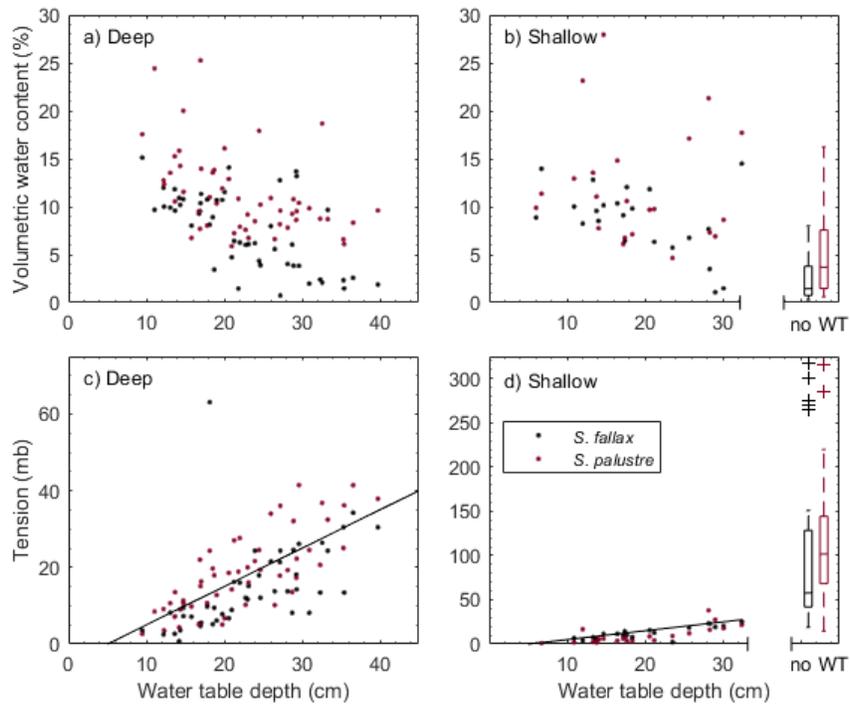


Figure 5

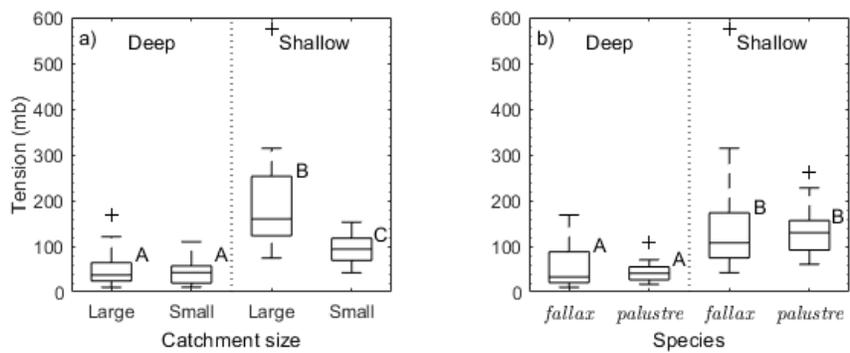


Figure 6

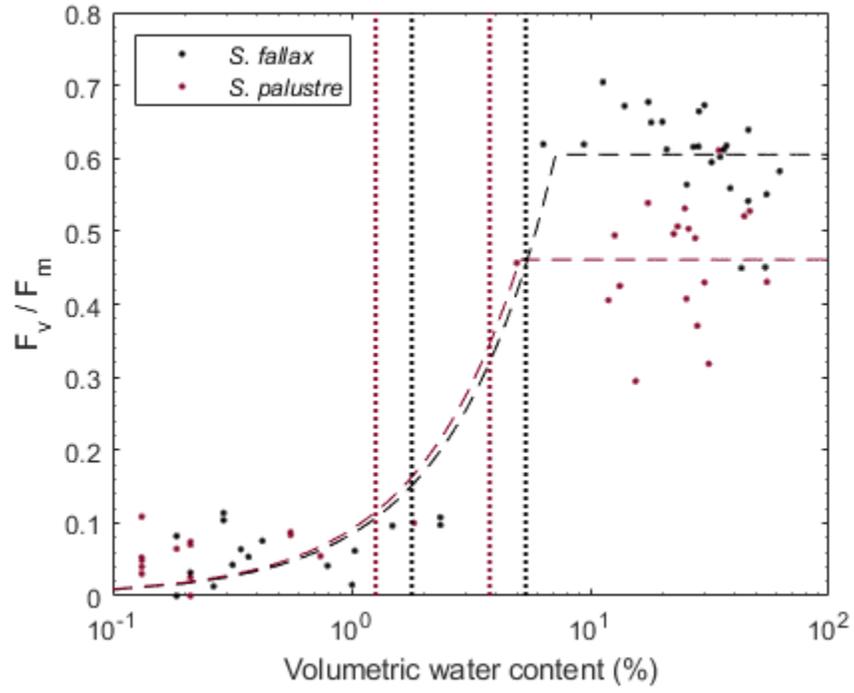
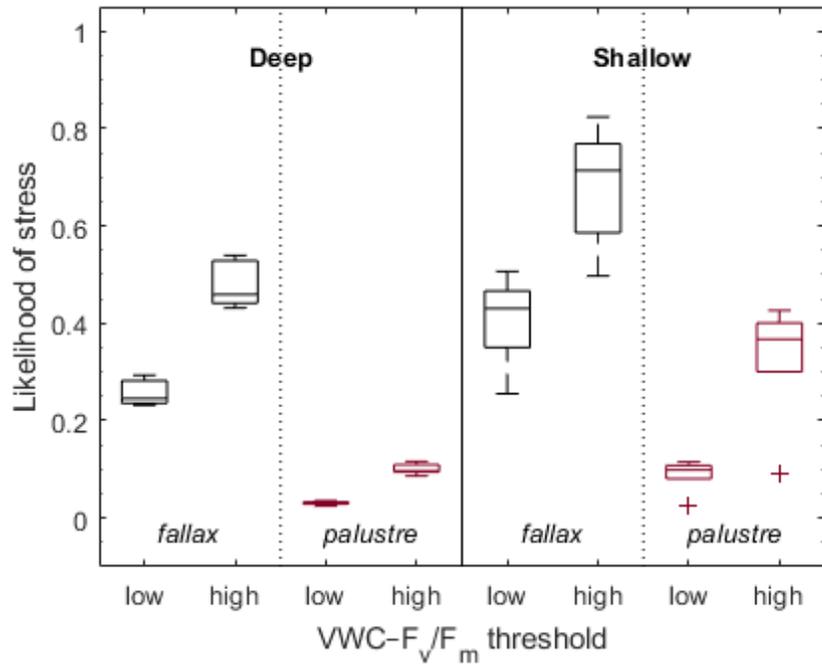


Figure 7



Hosted file

MooreP - HP_manuscript - Table01.pdf available at <https://authorea.com/users/8834/articles/497554-peat-depth-as-a-control-on-moss-water-availability-during-drought>

