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Peat depth as a control on Sphagnum moisture stress during seasonal drought

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Abstract

Peatlands are globally important long-term sinks of carbon, however there is concern that enhanced peat decomposition and 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 (WT) 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 (<40 cm depth) 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 WT loss, increasing ~5-7.5× greater at shallow sites compared to deep sites (≥40 cm depth). 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 WT 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.

KEYWORDS

moisture stress, peat, peatland, Sphagnum moss, tension, water table

INTRODUCTION 1

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 (~220-550 Pg C; Turunen et al., 2002; Yu, 2011). This long-term carbon sequestration is largely the result of Sphagnum moss productivity exceeding moss and peat decomposition and combustion rates (cf. Rydin et al., 2013). There is a

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concern, however, that *Sphagnum* mosses and their associated peatland carbon stocks may be vulnerable to future climate change due to enhanced peat decomposition and moss moisture stress (Dorrepaal et al., 2009; Ise et al., 2008), where summer water deficits are predicted to increase substantially within the next century (Granath et al., 2016; Helbig et al., 2020).

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., 2015). Indeed, most peatland and moss water availability research is biased to deep and large peatlands (e.g., Lindholm & Markkula, 1984; Moore et al., 2015; Price, 1997) where peatland ecohydrological resilience is higher (Morris & Waddington, 2011) and where the water table (WT) is typically shallow and rarely falls below the entire peat profile. In contrast, the likelihood of drought-driven WT drawdown well below the live 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 (ψ ; e.g., McCarter & Price, 2014; Moore et al., 2015). As ψ 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 (Kettridge & Waddington, 2014; McCarter & Price, 2014; Schouwenaars & Gosen, 2007). 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 ψ 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 ψ is dependent on the botanical origin and degree of decomposition of the peat (McCarter & Price, 2014; Rezanezhad et al., 2010; 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 ψ (Hájek & Vicherová, 2014; McCarter & Price, 2014; Strack & Price, 2009; Titus & Wagner, 1984). 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 et al., 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 peat. To test this 'survival of the deepest' hypothesis we measured near-surface tension, moisture content, and WT 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 ~20 km 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 (Figure S1). 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 WT. The wetland and peatland soil are mostly organic soil (peat) situated on a thin layer (0-5 cm) of mineral soil (Didemus, 2016). The surface cover of the ridges tends to consist of either small thin patches of mineral soil, moss cushions, lichen mats, or exposed bedrock (Hudson et al., 2020), 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 perched on the bedrock (hereafter referred to as sites) into two different classes based on average peat depth: (a) sites with average depths <40 cm hereafter referred to as shallow (S); and (b) sites with average depths ≥40 cm hereafter referred to as deep (D). The choice of a 40 cm threshold corresponds to the Canadian wetland classification for peatlands (National Wetlands Working Group, 1997), where depending on hydroclimatic setting, depths in excess of 40 cm will typically allow WT variation to remain within the peat profile. For each depth class, the catchment area of the site was categorized as being either large (L, >4000 m^2) or small (S, <4000 m²) providing a total of four depth/catchment categories. Three 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 with a large catchment area. An additional five sites from each category (for a total of 32 sites), were selected for an intensive field survey (hereafter referred to as IFS sites) conducted on DOY 221 during a period of increasing potential moisture deficit (Figure S2). All sites are located in a 2 km^2 area (Figure S1). 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.

The region has a cool-temperate and humid climate with 30-year daily average maximum and minimum air temperatures for May-October of 18.9 and 6.9°C, respectively (Dunchurch ~45 km NE from site; Government of Canada, 2019). In 2015, the average maximum and minimum daily air temperature from May through October was 20.6 and 10.8°C, respectively. The 30-year average cumulative rainfall from May until October is 563 mm (Government of Canada, 2019) and in 2015 the region received 498 mm in that period. The region exhibits seasonal variation in precipitation, where the 30-year precipitation normals for May-June is 167.9 mm, July-August is 166.7 mm, and September-October is 224.6 mm (Government of Canada, 2019).

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. WT position was measured at each of the main sites at 15-min 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 measured position at the site. Depth measurements were made at 20–45 points per site using rebar inserted into the peat until it reached bedrock or mineral soil.

Measurements of near-surface soil water tension and volumetric moisture content were made two times per week from June to September 2015 at three locations (hereafter referred to as plots) within 5 m of the groundwater well for the two most common *Sphagnum* species (*S. fallax* and *S. palustre*) at each of the main sites. The relative elevation between the surface at the well and plot locations was surveyed using a SmartLevel (Smart Leveler, Smyrna TN) in order to adjust WT measurements. Soil water tension was measured at 5 cm depth (ψ_{5cm}) using tensiometers (2 cm outer diameter, Soil Measurement Systems, Tucson, Arizona) and a 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 for all 32 IFS sites for a plot of *S. fallax* and *S. palustre* following the same methods for soil water tension and moisture content methods as described above. All IFS measurements were completed between approximately 1000 and 1700 h by two teams, with order of site measurements pseudo-randomized according to site depth and catchment size. IFS tensiometers were installed on DOY 212 (July 31)

TABLE 1 Average peat depth, area, and catchment area characteristics of the magnetized statement.	nain sites
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Site class	Catchment area class	Site number	Peat depth (cm)	Site area (m ²)	Catchment area (m ²)	Catchment-site area ratio
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	4030	17.5
		405	31	590	4390	7.4
Deep	Small	301	83	1300	3700	2.8
		303	50	1100	3800	3.5
		808	62	1800	2630	1.5
	Large	234	75	2200	39 200	17.8
		408	137	11 000	76 000	6.9
		415	59	4800	23 800	5.0

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and there was no rainfall in the 5 days leading up to the measurements.

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 $\mu mol \; m^{-2} \; s^{-1}$ throughout the 14 days of the drying experiment following McNeil and Waddington (2003). 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. VWC estimates are based on the initial sample volume since no trend in volume was observed. 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 min. The optimal guantum 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 (lightening in colour of the Sphagnum capitula). Drying proceeded until all samples had low $F_{\rm v}/F_{\rm m}$ (i.e., <0.2 - cf. van Gaalen et al., 2007) for at least two consecutive days, after which samples were re-wetted and chlorophyll fluorescence measured for several days.

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

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

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 S3), 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% (cf. McCarter & Price, 2014). The *fit* function in MATLAB (MATLAB, 2020 – 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 *SD*. 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 (*Species* – *S. fallax* and *S. palustre*) and their one-way interactions on ψ_{5cm} , where the following model was evaluated: *Tension* ~ 1 + *Depth* × *Catchment* + *Depth* × *Species* + *Catchement* + *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 ψ_{5cm} 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, 2017). With lower than normal precipitation coinciding with high summer potential evaporative demand, there was an increasing moisture deficit during this period (Figure S2) and which we refer to as a period of meteorological drought.

The WTD at all sites were shallowest in mid-June (DOY 164– 166; Figure 1). Following this period, the WT at deep sites experienced an overall decline until the deepest 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 mid-June when the WT was shallowest



FIGURE 1 Rainfall and water table depth for deep (a) and shallow (b) main sites. Sites with large and small catchments are represented by grey and black lines, respectively. Grey- and white-filled circles indicate when the water table was lost and regained at the individual sites, respectively

(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 ψ to this WT loss. Both *S. fallax* and *S. palustre* experienced slight declines in VWC_{0-3 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 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 cm} (difference = 3.4%, F = -1.54, p = 0.126), and the WTD response being more subdued (WTD × 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, ψ_{5cm} 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 ψ_{5cm} at deep sites was on average 29 and 25 mb, respectively (Figure 3). Moreover, with the exception of one (potentially erroneous) measurement, ψ_{5cm} at deep sites did not exceed 40 mb (Figure 4c). While average tension during the

FIGURE 2 Time series of tension at 5 cm depth (thick solid lines) and VWC_{0-3 cm} (thin dashed lines), for *S. fallax* (black circles) and *S. palustre* (maroon triangles) 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 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 (thick solid lines) and VWC_{0-3 cm} (thin dashed lines) for *S. fallax* (black circles) and *S. palustre* (maroon triangles) 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 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. A presumed erroneous/outlier tension measurement (DOY 183) is included DL-408 but omitted from the connected data series

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. When WT is present, data is presented as black circles for *S. fallax* and maroon triangles for *S. palustre*. 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

drought period was much higher at the shallow sites, ψ_{5cm} generally followed a 1:1 relation with WTD when WT was present for both deep and shallow sites (Figure 4c,d).

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.

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

The 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

Intensive field survey

3.3

 ψ_{5cm} 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

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* × *Catchment, and Depth* × *Species* are shown in (a) and (b), respectively



× 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 & Whitehead, 2001), 60% of *S. fallax* plots and 67% of *S. palustre* plots in shallow sites exceeded this threshold during the IFS. The median ψ_{5cm} 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 three 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_{adj}^2 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 Equation 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 S3). Using species dependent VWC- F_v/F_m thresholds and VWC-WTD relations, Monte Carlo simulations suggest that the 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



FIGURE 6 Lab-measured chlorophyll fluorescence stress metric for *Sphagnum fallax* (black circles) and *Sphagnum palustre* (maroon triangles) samples during a drying experiment (includes post-drying rewetting measurements). 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 (solid lines) hyperbola. High and low VWC stress thresholds (dashed lines) represent 25% and 75% of the maximum modelled F_v/F_m

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; Li et al., 1992; Luken, 1985; Rydin, 1985; Strack & Price, 2009). Our results show



FIGURE 7 Likelihood of moss stress for deep and shallow sites (*n* = 6 each) based on the proportion of the 2015 snow-free season where water availability is estimated to substantially reduce the efficiency of photosystem II. The likelihood is derived from continuous WT measurements and species dependent relations between WT-VWC (field – see Figure S3) and VWC- F_v/F_m (lab – see Figure 6) for both *S. fallax* and *S. palustre*. Uncertainty in the precise onset of water-induced stress is represented by a high and low moisture threshold (see Section 2)

that during a meteorological drought period, ψ_{5cm} 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 nearsurface water availability, particularly with respect to ψ (e.g., Figure 4). While the WT was present, ψ_{5cm} was near a hydrostatic equilibrium tension relative to WTD (Figure 4c,d). It was only after a loss of the WT in the shallow sites that the ψ_{5cm} -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. As the sites are underlain by granite bedrock with limited fracturing, 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., Hájek & Beckett, 2008; Nungesser, 2003; Schipperges & Rydin, 1998; Van Gaalen et al., 2007) 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 S4) 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 S5).

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 S3). 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 et al., 2008) and colony structure which affects evaporative losses (e.g., Elumeeva et al., 2011; Rice et al., 2001). Moreover, moss capitula water supply is mechanistically linked to the water transport ability (unsaturated hydraulic conductivity; Kunsat) of the underlying peat matrix. While we are unaware of any studies that have derived Kunsat relationships for S. fallax and S. palustre to date, species with a lower near-surface Kunsat have been shown to desiccate at shallower WT depths than species with higher K_{unsat} (McCarter & Price, 2014; Titus & Wagner, 1984).

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 S3 and S5). Therefore, despite similar VWC- F_v/F_m stress thresholds (Figure 6), S. fallax was predicted to become stressed at shallower WT depths. 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 et al., 2016). Wilkinson et al. (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 groundwatersurface water interactions have been shown to influence peatland water storage dynamics (Devito et al., 1996; Glaser et al., 1997). Given the study sites chosen, there was a moderately strong positive correlation between site area and peat depth (Figure S6). 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 ψ (e.g., correlation between WTD and ψ as shown in Figure 4c,d) we might expect to see an influence of catchment size on ψ 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 ψ compared to shallow sites in small catchments. Sphagnum species have a certain degree of phenotypic plasticity associated with environmental gradients. For example, the total hvaline cell volume can increase under drought conditions for certain Sphagnum species (Li et al., 1992) including S. palustre (Bu et al., 2013). Although conjectural, Sphagnum moss at shallow sites with small catchments could be adapted to drier conditions, and thus experience lower ψ during meteorological drought conditions. Unlike other peatlands studied on the Canadian Shield of southern Ontario (e.g., Devito et al., 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 | Implications for peatland development

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. As such, our 'survival of the deepest' concept has implications for examining primary peat formation and peatland development. Lab results show that the moss enters dormancy at low water content (i.e., near-zero F_v/F_m – Figure 6 and Figure S4), 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 (McNeil & Waddington, 2003; Schipperges & Rydin, 1998). 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 $\psi_{\rm 5cm}$ and lower $\rm VWC_{0\text{-}3cm}$ as compared to deep sites. Analogously, Lukenbach et al. (2016) showed that shallow areas at the peatland margin had greater WT depth and near-surface tension compared to deeper areas in the peatland interior during summer moisture deficit. 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 Breemen, 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 meteorological drought. With summer water deficits being expected to increase in many peatland dominated regions (e.g., Granath et al., 2016; Helbig et al., 2020) under climate change, this could potentially lead to an ecological shift in peatlands from a Sphagnum dominated system to one dominated by forests (Dang & Lieffers, 1989; Kettridge et al., 2015) or more drought tolerant mosses, such as Polytrichum species (Benscoter & Vitt, 2008; Laine et al., 1995). This then leads to two important ecohydrological questions: (a) what conditions allow a shallow site to develop into a deep site?: and (b) what processes prevent a shallow site from developing into a deep site?

An answer to these questions could simply be time, where deep sites initiated earlier than shallow sites. Alternately, the loss of accumulated peat due to wildfire may be affected by interacting processes related to peat depth, peat properties, and WT draw down. Organic soil depth has been linked to burn severity (e.g., depth of burn or carbon loss) for shallow organic soils (Shetler et al., 2008; Walker et al., 2020). Moreover, higher average depth of burn has been observed at peatland margins (Hokanson et al., 2016), where small, perched peatlands tend to have deeper WT at their edges (Hokanson et al., 2020) and the WT is more likely to drop below the peat profile. Wildfire could maintain heterogeneity in site peat depth (e.g., Benscoter et al., 2005) 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 et al., 2020) including the margin of peatlands.

An alternate hypothesis, assuming basal dating shows similar or more random initiation periods with respect to site depth, would be that local basin morphometry imposes a strong control on peat accumulation, similar to the control of lake basin size on total sediment accumulation (e.g., Ferland et al., 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 centre of the accumulating peat deposit) and therefore greater potential peat depth is partly controlled by the

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lateral extent of the peat deposit (Belyea & Baird, 2006; Ingram, 1982). Thus for the infilling of a bedrock depression, or for peatlands more generally once the peat surface rises above local/ regional groundwater flow, 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 et al., 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 lichen species (Markle et al., 2020).

Given that both the magnitude and frequency of meteorological drought are expected to increase for peatlands due to climate change (Helbig et al., 2020) 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 et al., 2000), recently restored peatlands (Granath et al., 2016), and organic soils under moss and lichen mats on the upland rock barrens (Hudson et al., 2020; Moore et al., 2019) 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 (Humpenöder 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).

In summary, our 'survival of the deepest' research demonstrates that peatland depth can act as a key indicator of the vulnerability of Sphagnum moss to moisture stress during meteorological drought, and can be used conceptually to identify the types of peatlands and peat deposits that are vulnerable to the increased summer water deficits predicted for the next century (Granath et al., 2016; Helbig et al., 2020). We suggest that the depth threshold (or range of depths) for peatland Sphagnum moss stress resistance to meteorological drought is likely to vary with hydrogeological and/or hydroclimatic setting due to their influence on the Sphagnum moss community, equilibrium peat and WT depth (e.g., Hilbert et al., 2000), and seasonal WT dynamics. As such, we suggest there is not only a critical need for advances in peat depth mapping techniques but also a need for a better understanding of the role of hydrology and hydrogeological setting in controlling peat development and carbon cycling in shallow peat-filled depressions in other landscapes and climates to better understand how these systems might respond to future climate change.

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DATA AVAILABILITY STATEMENT

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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