

Ecohydrology of *Sphagnum* moss hummocks: mechanisms of capitula water supply and simulated effects of evaporation

Colin P. R. McCarter* and Jonathan S. Price

Department of Geography and Environmental Management, University of Waterloo, 200 University Avenue West, Waterloo, ON, Canada, N2L 3G1

ABSTRACT

Maintaining sufficiently high surface (capitula) soil-water pressures to avoid the draining of hyaline cells (desiccation) is paramount to hummock-forming *Sphagnum* species' survival; however, the mechanisms of capitula water supply are poorly understood. This study investigates how the hydraulic characteristics of different *Sphagnum* species (*Sphagnum fuscum*, *Sphagnum rubellum* and *Sphagnum magellanicum*) contribute to desiccation avoidance, on the basis of numerical simulations parameterized with measured soil hydraulic characteristics for each species. Although having similar unsaturated hydraulic conductivity values, the upper 5 cm of *S. magellanicum* retains ~20% less moisture under tension than *S. fuscum* and *S. rubellum*; in fact, *S. rubellum* on average retained slightly more water than *S. fuscum*. Hydrus-1D was used to simulate daytime and nighttime conditions over a 7-day period, where daily potential evaporation was 4 mm, to explore the governing mechanisms controlling water supply to the capitula. The simulations showed that *S. fuscum* and *S. rubellum* were able to retain sufficiently high moisture content under the prevailing simulated water demand to sustain surface soil-water pressure heads (greater than -100 cm), whereas *S. magellanicum* could not prevent depressurization and the concomitant desiccation of its surface layer. A similar number of the same size pores were observed in all species; however, there was lower pore connectivity in *S. magellanicum* leading to the desiccation of the capitula. Contrary to previous studies, the results of this study indicate that it is not only soil-water retention but also pore connectivity that allows hummock species to thrive above the water table. Copyright © 2012 John Wiley & Sons, Ltd.

KEY WORDS *Sphagnum fuscum*; *Sphagnum rubellum*; *Sphagnum magellanicum*; evaporation; RET-C; Hydrus-1D; capitula; water retention; unsaturated hydraulic conductivity

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INTRODUCTION

Sphagnum moss has three distinct growth forms, hummock, lawn and hollow (Clymo, 1973; Rydin, 1993), each occupying a different ecological niche expressed through height of growth above water table, in the order hummock > hollow > lawn (Hayward and Clymo, 1982; Rydin, 1993). Bog peatlands are generally dominated by hummock species with small areas occupied by lawn and hollow species resulting in highly diverse microform topography (Rydin, 1993). *Sphagnum fuscum* is considered to be the dominant hummock-forming species in North America because it typically grows higher above the water table than other hummock species (e.g. *S. fuscum* > *Sphagnum rubellum* > *Sphagnum magellanicum*) and thus outcompetes them (Robroek *et al.*, 2007a). The ability of these non-vascular plants to thrive above the water table is considered to be due to the water retention and capillary rise (Hayward and Clymo, 1982; Waddington *et al.*, 2011) generated by their particular structure through its influence on pore-size distribution (Quinton *et al.*, 2008). Although water retention capacity of various *Sphagnum* hummock species has been shown to be higher than hollow or

lawn species (Hayward and Clymo, 1982), we are not aware of literature reporting unsaturated hydraulic conductivity of various species. Hummock species have a lower net ecosystem exchange than hollow species, typically attributed to higher water contents in hollows because of closer proximity to the water table (Waddington and Roulet, 1996; Strack *et al.*, 2006). However, higher water retention characteristics of hummock species could result in higher net ecosystem exchange during times of limited water availability (i.e. low water table) (Strack and Price, 2009), assuming vegetation composition remains constant (Strack *et al.*, 2006). As water supply and moisture content at the surface controls physiological processes such as carbon exchange (McNeil and Waddington, 2003; Strack and Waddington, 2007; Strack and Price, 2009; Dimitrov *et al.*, 2011) and evaporation (Williams and Flanagan, 1996; Kellner, 2001; Brown *et al.*, 2010), more insight is required into the magnitude and variability of these hydraulic characteristics and their influence on water exchanges within and from various *Sphagnum* species.

Unlike vascular plants, *Sphagnum* moss lacks any root structure and relies on capillary rise to supply water to the capitula, which is the apical bud comprising the upper 2 cm of the plant (Clymo, 1973; Hayward and Clymo, 1982). Capitula density is positively correlated to soil-water retention in hummock species (Luken, 1985; Rydin, 1993) and grades *S. fuscum* > *S. rubellum* > *S. magellanicum*

*Correspondence to: Colin P. R. McCarter, Department of Geography and Environmental Management, University of Waterloo, 200 University Avenue West, Waterloo, ON, Canada N2L 3G1.
E-mail: cmccarte@uwaterloo.ca

(Rydin, 1985; Li *et al.*, 1992; Robroek *et al.*, 2007a; Thompson and Waddington, 2008). Sphagna also store water in hyaline cells for periods of water stress (Clymo, 1973). This water is withdrawn and enters capillary spaces when the soil-water pressure drops to a threshold value controlled by the diameter of the hyaline cell's pore opening (Lewis, 1988). If the water content drops further, the plant desiccates, limiting photosynthesis and evaporation while increasing soil respiration (Hayward and Clymo, 1982; Lewis, 1988; Schipperges and Rydin, 1998; McNeil and Waddington, 2003; Strack *et al.*, 2004; Strack *et al.*, 2006). Hayward and Clymo (1982) determined that the hyaline cells of *Sphagnum* drain at ~100–200 cm of pressure using the water retention curve; these values were corroborated and expanded by Lewis (1988) to include pressures up to ~600 cm. These values indicate the biological limit of *Sphagnum* to soil-water pressure. There has yet to be a systematic analysis of the biological limits of various *Sphagnum* species; however, species less suited to drought avoidance (i.e. *S. magellanicum*) will reach their biological limit (i.e. soil-water pressure) quicker than species better suited to drought avoidance (i.e. *S. fuscum*) (Hayward and Clymo, 1982; Rydin, 1985; Li *et al.*, 1992; Robroek *et al.*, 2007a; Thompson and Waddington, 2008). Although the physical structure of *Sphagnum* moss is well documented, the mechanisms that supply the capitula with water, thus avoiding water stress, are not (Price *et al.*, 2008; Thompson and Waddington, 2008; Price and Whittington, 2010).

The species type and community arrangement, along with degree of decomposition, impart a specific pore geometry and tortuosity that controls the water retention capacity and unsaturated hydraulic conductivity of *Sphagnum* moss (Price *et al.*, 2008; Rezanezhad *et al.*, 2009). These hydraulic properties govern the level of saturation that can be sustained at a given water table (soil-water pressure) and consequently the rate of water flow within peat and *Sphagnum*. Upward flow is driven by the atmospheric demand, but limited by the unsaturated hydraulic conductivity (K_{unsat}), which itself is a function of the volumetric water content (θ) (i.e. lower surface θ will decrease evaporation) and thus ultimately the pore-size distribution of the species of *Sphagnum*. Lower θ in a sample will result in a lower K for a given water table (Mualem, 1976; van Genuchten, 1980; Price *et al.*, 2008). Hummock species, having a higher water retention capacity, may experience greater net water loss by evaporation because of the more efficient capillary rise imparted by their structure, whereas hollow species are more dependent on a close proximity to the water table because of their lower water retention characteristics (Hayward and Clymo, 1982; Rydin, 1985; Robroek *et al.*, 2007b; Hajek and Beckett, 2008; Thompson and Waddington, 2008; Turetsky *et al.*, 2008). Recently, the hydraulic properties in living and dead but undecomposed *Sphagnum* mosses have been measured (Price *et al.*, 2008). Price and Whittington (2010) then successfully modelled evaporation and drainage from *Sphagnum* moss monolith experiments using Hydrus-1D and showed that the upper moss layer has relatively stable water contents. However, the hydraulic conductivity and water retention properties of different species of *Sphagnum*

mosses have not been adequately characterized, nor were their effect on capitula water content, which is key to productivity and survival during periods of limited water availability (Schouwenaars and Gosen, 2007; Price *et al.*, 2008; Price and Whittington, 2010). The objectives of this study, therefore, are to (1) compare and contrast the hydraulic properties (saturated and unsaturated hydraulic conductivity, water retention, bulk density and capitula density) of *S. fuscum*, *S. rubellum* and *S. magellanicum*; and (2) use Hydrus-1D with the fitted hydraulic parameters to examine the ability of each species to sustain high surface water pressures and evaporation under prescribed atmospheric water demands.

METHODS

Field sampling

The samples were taken from the St. Arsène peatland (*S. fuscum* and *S. rubellum*), ~10 km northeast of Rivière-du-Loup (47.93028°, –69.44833°), and the Saint-Charles-de-Bellechasse peatland (*S. magellanicum*) (47.25°, –71.63333°). At the St. Arsène peatland, *S. fuscum* and *S. rubellum* formed a hummock-hollow topography, whereas at the Saint-Charles-de-Bellechasse peatland, *S. magellanicum* grew in small low hummocks in visually wetter areas. Three profiles of each species were taken in 5-cm-depth increments by cutting, with scissors, and gently sliding a 5-cm-long section of 10-cm-diameter PVC pipe into the moss. The sample depths were centred at 2.5, 7.5, 12.5, 17.5, 22.5 and 27.5 cm. This was repeated until the top 30 cm of the hummock was sampled. When the 5-cm-long tube was flush with the exposed moss, the sample was cut along the bottom of the PVC pipe to withdraw an undisturbed 5-cm core section. In addition to the 30-cm profiles, 15 samples of the 0- to 5-cm layer (centred at 2.5 cm) of each species were taken to identify statistical differences in capitula density and bulk density within and between species. The samples were frozen before transport to the University of Waterloo's Wetland Hydrology Laboratory for analysis.

Sample parameterization

Unsaturated hydraulic conductivity (K_{unsat}) was tested following the methods of Price *et al.* (2008), with soil-water pressures (ψ) of –4, –8, –16 and –24 cm. Two disks used for measuring the K_{unsat} of living mosses were used, one above and one below the sample. The upper disk was connected to an Erlenmeyer flask with a constant head overflow causing discharge (Q), whereas the bottom disk was connected to a water reservoir (beaker), also with a constant head. To control the soil-water pressure, we lowered the Erlenmeyer flask and beaker to the appropriate height to achieve the desired pressures (Price *et al.*, 2008). After the soil-water pressure was set, the samples were left to equilibrate for a minimum of 1 h before measuring the discharge. Only when the sample discharged at a constant rate was the K_{unsat} determined (using Darcy's law). After each pressure level, the samples were weighed, and the volumetric soil moisture content (θ) was determined.

The only deviation from the methods outlined by Price *et al.* (2008) was to have both the top and bottom screen mesh size of 25 µm as the tension on the screen was less than the air entry pressure of the mesh.

The saturated hydraulic conductivity (K_{sat}) was determined using a Darcy permeameter under steady-state flow conditions with a hydraulic gradient of 0.22 (Klute, 1986). K_{sat} values for *S. fuscum* and *S. rubellum* were potentially unreliable because of leakage around the core in the permeameter, so fitted values were used (see next section) without compromising the simulations, because K_{sat} in the range of pressures tested, was only a scaling factor. The pore opening radius (r) (theoretical pore-size distribution) was determined through the capillary rise equation (Bear, 1972) on the basis of a given pressure head (h)

$$r = \frac{2\gamma \cos\beta}{\rho gh} \quad (1)$$

where γ is the surface tension of water, β is the contact angle [40° for moderately hydrophobic soils (Carey *et al.*, 2007)], ρ is the density of water and g is gravitational acceleration. This value represents the maximum pore radius that is full of water due to capillarity forces for a given pressure head. The total fraction of water-filled pores (ϕ_{vw}) was determined by

$$\phi_{\text{vw}} = \frac{\theta_{\psi}}{\phi} \quad (2)$$

where ϕ is the porosity and θ_{ψ} is the volumetric soil moisture content for a given ψ . Higher fractions of water-filled pores indicate that the sample contains more water for a given pressure head, $\theta(\psi)$. The relationship between the pore diameter and fraction of water-filled pores illustrates both the pore-size distribution and the relative abundance of smaller pores. A sample with a higher fraction of water-filled pores less than or equal to a specified diameter must have more smaller pores than a sample with a lower fraction of water-filled pores at that diameter. Similar changes in the fraction of water drained (i.e. slope of the line) between a given set of pore diameters indicate pores of a similar size are draining. Steeper slopes indicated that more pores exist (and are being drained) between the given pore diameters.

Aside from sampling (see earlier discussions), bulk density (ρ_b), porosity ϕ and specific yield (S_y) were determined following the methods of Klute (1986). Capitula density was determined by counting the individual capitula in five 1-cm² squares on the surface of the sample and averaged for the sample. One-way ANOVA was performed on the 15 surface samples to determine the statistical difference between bulk density and capitula density within and between each species. Further, one-way ANOVA was performed to determine if the profile's surface sample's capitula and bulk densities are indicative of the larger surface sample set's values.

Parameter fitting

Hydrus-1D requires the use of a water retention function, $\theta(\psi)$, and a hydraulic conductivity function, $K(\psi)$, which here were based on the measured values (except as described earlier)

fitted with the van Genuchten/Mualem (van Genuchten, 1980) approach in the RET-C curve-fitting program (van Genuchten *et al.*, 1991). RET-C used measured saturated volumetric soil moisture content (θ_s) and measured K_{sat} (or fitted K_{sat} values for *S. fuscum* and *S. rubellum* on the basis of K_{unsat} values); and RET-C calculated (fitted) the values of residual volumetric moisture content (θ_r), the tortuosity parameter (l), alpha (α), n and $m = 1 - 1/n$ (curve-fitting parameters) (Table 1). To obtain the fitted K_{sat} values, the retention and K_{unsat} values were input into RET-C and allowed to fit K_{sat} . A new van Genchten/Mualem curve was then generated using the measured values in addition to the fitted K_{sat} value. As the mosses in the simulation were never saturated, fitted values of K_{sat} were not used to determine the outcome of the simulation. Although all the values are presented, geometric averages of K_{sat} , K_{unsat} and θ within species were used except *S. rubellum* profile 1, which was modelled separately because of differences in the $\theta(\psi)$ relation in the 2.5-cm sample. One-way ANOVA was run on the profile's average l parameter to determine any differences in pore connectivity and tortuosity.

Hydrus-1D modelling

Hydrus-1D version 4.18 (Šimůnek *et al.*, 2008) was used to numerically simulate the effect of 7 days of evaporation from a 30-cm moss profile of each species, with a water table depth of 40 cm. The results of the RET-C parameterization of the van Genuchten/Mualem equation of the measured values (van Genuchten, 1980) (Table 1) were input into Hydrus-1D to create profiles with six layers (0–5, 5–10, etc.). Each model had the same initial condition of a hypothetical equilibrium pressure profile above a water table ($\psi = 0$ cm) 40 cm below the surface. In Hydrus-1D, evaporation occurs at a specified potential rate as long as pressure in the surface node remains below a critical threshold pressure head (h_{CritA}). At lower pressures [i.e. below (more negative than) the critical threshold], the evaporation rate is determined by the pressure gradient between the top two nodes (≈ 0). Here, h_{CritA} was specified as -400 cm because it is a midpoint in the range of pressures suggested by Lewis (1988) under which hyaline cells will drain (and thus when water loss must be restricted). Although it is possible that evaporation is limited before this pressure limit, there have been no studies evaluating the relationships between surface soil-water pressure and evaporation in *Sphagnum*. A total of seven consecutive days with 12 h of potential evaporation and 12 h of no evaporation, totalling 0.4 cm day⁻¹ (which is a typical daily evaporation rate for Eastern Canadian bogs), was the only upper boundary condition. To simulate the diurnal cycle, potential evaporation starts at 0600 h (0.0026 cm h⁻¹) and increases linearly until 1500 h (0.058 cm h⁻¹), thereafter declining to 0.0 cm h⁻¹ by 1900 h. The bottom boundary was set to a constant flux of 0 cm h⁻¹ to ensure that only evaporation was affecting the profile. Because the capitula layer of these species are ~1 cm thick, the averages of the upper 0.9 cm (top four nodes) K_{unsat} for each profile was plotted and were used to infer the governing capitula K during evaporative and non-evaporative times.

Table I. The results of the RET-C parameterization and the inputs for each Hydrus-1D model.

Sample	Depth (cm)	θ_r	θ_s	α^a	n^a	K_s^a	l^a
<i>Sphagnum fuscum</i> ^b	2.5	0.01	0.92	0.43737	1.40542	1.75E+02	-2.314
	7.5	0.01	0.88	1.59467	1.33541	2.04E+02	-4.6288
	12.5	0.01	0.89	0.75671	1.37069	1.34E+02	-3.5225
	17.5	0.01	0.92	1	1.33612	1.73E+02	-3.8265
	22.5	0.01	0.90	0.41452	1.30266	7.32E+01	-4.2414
	27.5	0.01	0.91	0.06086	1.70654	1.03E+01	-0.4498
<i>Sphagnum rubellum</i> ^b	2.5	0.01	0.92	0.64882	1.31655	2.24E+02	-3.3701
	7.5	0.01	0.93	1.14077	1.27261	2.38E+02	-4.0672
	12.5	0.01	0.93	0.41644	1.31144	2.92E+01	-4.8435
	17.5	0.01	0.94	0.43482	1.21454	1.32E+02	-4.5596
	22.5	0.01	0.93	0.12883	1.27005	1.58E+01	-3.6091
	27.5	0.01	0.91	0.14679	1.2447	2.13E+01	-2.534
<i>Sphagnum magellanicum</i>	2.5	0.01	0.98	2.65563	1.43112	1.62E+02	-0.8822
	7.5	0.01	0.97	2.41735	1.39396	1.31E+02	-2.726
	12.5	0.01	0.96	2.11135	1.33735	2.68E+02	-1.0072
	17.5	0.01	0.96	0.88022	1.34139	2.02E+02	-1.1779
	22.5	0.01	0.95	0.25965	1.34413	2.09E+02	-2.3364
	27.5	0.01	0.94	0.07467	1.72628	1.30E+02	-0.3346
<i>Sphagnum rubellum</i> 1 ^b	2.5	0.01	0.90	0.81387	1.48032	4.44E+01	-3.3362
	7.5	0.01	0.92	2.75711	1.27847	1.14E+03	-4.7458
	12.5	0.01	0.92	1.80266	1.33706	7.82E+02	-5.216
	17.5	0.01	0.92	3.05632	1.26188	8.73E+02	-4.4547
	22.5	0.01	0.92	0.25114	1.17029	4.28E+02	1.05538
	27.5	0.01	0.91	0.29046	1.58	1.28E+01	-2.9912

^a Indicates which parameters were fitted in RET-C.

^b Indicates K_s was modelled on the basis of the K_{unsat} values.

Sensitivity analysis

A sensitivity analysis was performed to determine the relative effect of $hCritA$, hydraulic conductivity, soil-water retention and θ_r on the simulations. Each test was carried out independently of each other, and all non-tested variables were the same as the original model. Both K_{sat} and θ_r were changed by an order of magnitude (both up and down) in Hydrus-1D, whereas $hCritA$ was set to four different values: -100, -300, -500 and -700 cm (note: Hydrus-1D expresses pressures as positive values). Soil-water retention (water content) values were raised or lowered by 0.03 and $0.1 \text{ cm}^3 \text{ cm}^{-3}$ (i.e. for the given water content). If the soil-water retention values were above $1.0 \text{ cm}^3 \text{ cm}^{-3}$, they were set to $0.99 \text{ cm}^3 \text{ cm}^{-3}$. The 'new' retention data were run in RET-C to determine the parameters needed for Hydrus-1D. As there was a stark difference (approx. -2) in l parameters between *S. magellanicum* and the other species, the l parameter was lowered by 2 in all the *S. magellanicum* materials to determine its effect on the outcome of the simulations. All variables besides soil-water retention were altered within Hydrus-1D.

RESULTS

Bulk density and capitula density

In the moss profiles, bulk density (Figure 1) generally increased with depth in all samples; however, this trend was most pronounced in *S. magellanicum*, which increased linearly with depth from $\sim 0.007 \text{ g cm}^{-3}$ at 2.5 cm to 0.14 g cm^{-3} at 27.5 cm. *S. fuscum* and *S. rubellum* increased from

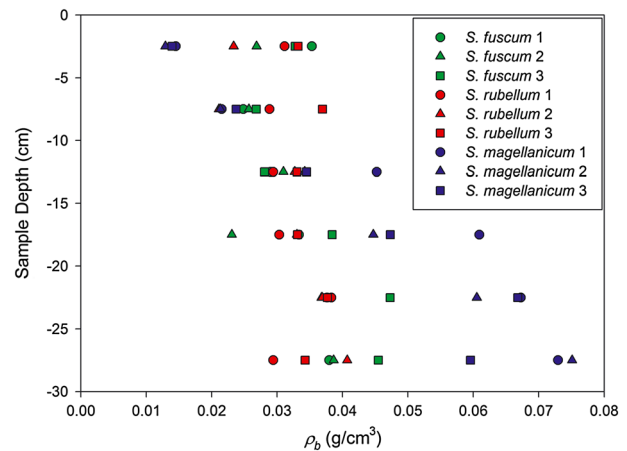


Figure 1. Measured bulk density by sample depth centred at the midpoint of each sample (every 2.5 cm).

~ 0.03 to 0.04 g cm^{-3} over the same depth range. For the additional 15 surface samples, each species average bulk density for *S. fuscum* was $0.03 \pm 0.005 \text{ g cm}^{-3}$, *S. rubellum* $0.022 \pm 0.0058 \text{ g cm}^{-3}$ and *S. magellanicum* $0.018 \pm 0.0054 \text{ g cm}^{-3}$. All profile samples fell within one standard deviation of the surface sample means. The results of the one-way ANOVA show no significant variance within the species but statistically different capitula densities at $p=0.001$ between each species. The bulk densities of the profiles and the surface samples are not statistically different at $p=0.05$.

Capitula densities for profiles 1, 2 and 3 from each species were as follows: *S. fuscum* 5.1, 5.8 and 4.9 cm^2 ; *S. rubellum* 3.2, 3.7 and 4.8 cm^2 ; and *S. magellanicum* 1.0,

1.1 and 1.0 cm², respectively; all species being statically different ($p=2.2 \times 10^{-16}$) from each other. For the additional surface samples, the average capitula density for *S. fuscum* was 5.6 ± 0.9 cm², *S. rubellum* 3.6 ± 0.7 cm² and *S. magellanicum* 1.0 ± 0.2 cm². All profile samples fall within one standard deviation surface sample means of their respective species' surface samples and are not statistically different at all levels ($p=2.14, 17.5$ and 5.9 , respectively). The results of the one-way ANOVA for surface sample's capitula density show no significant variance within the species but statistically different capitula densities at $p=0.001$ between each species.

Water retention and hydraulic conductivity

There was a general trend in water retention (for a given pressure) of *S. rubellum* > *S. fuscum* > *S. magellanicum*

(Figure 2); however, *S. rubellum* showed less consistency in the water relationships than *S. fuscum* and *S. magellanicum* (i.e. *S. rubellum* profile 1, which typically trended closer to *S. magellanicum*). For example, at 2.5 cm depth, *S. rubellum* (except profile 1) and *S. fuscum* retained ~ 0.2 cm³ cm⁻³ more water than the other samples at $\psi < 0$. Water retention for all samples (except *S. rubellum* profile 3) was lowest at 7.5 cm depth. The difference was marked for *S. fuscum* and *S. rubellum* and reflects the lower bulk density found at that depth (except *S. rubellum* profile 3) (Figure 1). Vertical shrinkage of the all samples was inconsequential in the *S. fuscum* and *S. rubellum* profiles, but *S. magellanicum* shrank vertically by an average of 1.4 and 0.8 cm in the 2.5- and 7.5-cm samples, respectively, over the course of the retention experiments. These changes in sample height were taken into account when determining the θ content of the

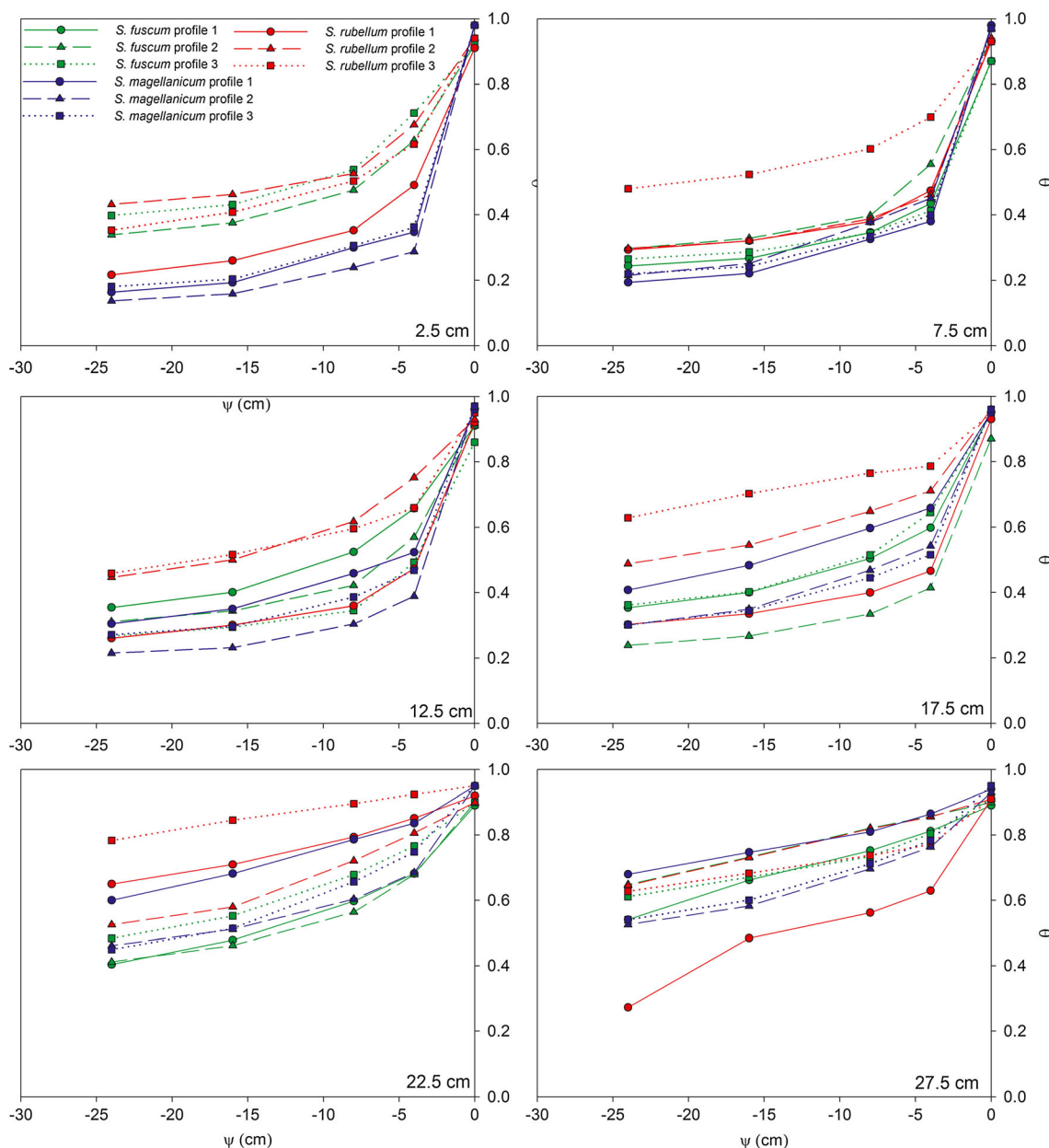


Figure 2. Measured soil-water retention curves, $\theta(\psi)$, for each sample plotted with equal sample depths. *Sphagnum fuscum* profile 1 2.5 cm was removed because of equipment malfunction.

S. magellanicum 2.5-cm samples. However, the change in θ due to change in sample height was only $\sim 0.04 \text{ cm}^3 \text{ cm}^{-3}$, and all other *S. magellanicum* sample depths showed minimal vertical shrinkage.

There was no clear difference in the $K(\psi)$ between *S. fuscum* and *S. rubellum* in all samples at all depths (Figure 3), whereas *S. magellanicum* typically had higher K_{unsat} at the pressures tested (Figure 3). Although having lower soil-water retention characteristics, *S. rubellum* profile 1 had similar $K(\psi)$ to other *S. rubellum* samples. The 2.5-cm depth samples showed the largest decrease in K_{unsat} with soil-water pressure (~ 5 to 0.1 cm h^{-1}). However, there was only a limited increase in K_{unsat} between the 2.5-cm samples and the 27.5-cm samples at each pressure tested.

The 2.5 cm, and to a lesser extent the 7.5 cm, theoretical pore-size distributions for *S. magellanicum* (Figure 4) showed a smaller fraction of water-filled pores at the diameters

presented, compared with other species (although *S. rubellum* profile 1 plots closer to *S. magellanicum* at some depths). This suggests that there are more small pores (i.e. $< 82 \mu\text{m}$) in *S. fuscum* and *S. rubellum* than *S. magellanicum* (and sometimes *S. rubellum* profile 1), which retained water in the sample. The similar slopes of the lines between all species (Figure 4) indicate that a comparable amount of water has drained from the sample over the pore diameters tested. As the amount of water drained is similar, it stands to reason that a similar number of pores in this size range are being drained; thus, each sample has a similar number of pores within a given size range.

Modelling results

In response to the imposed potential evaporation rate of 0.4 mm day^{-1} , the pressure profiles at the end of the

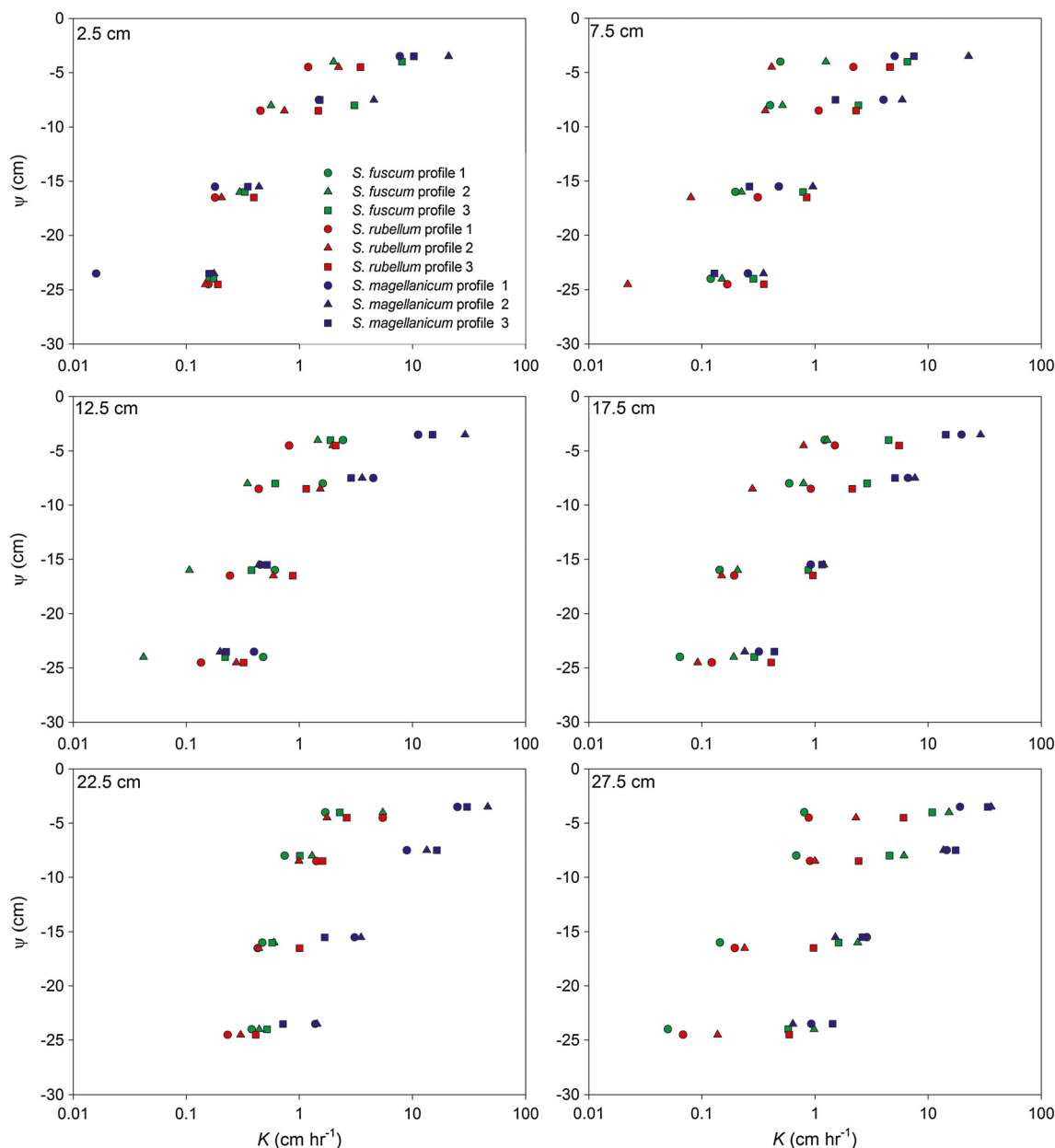


Figure 3. Measured hydraulic conductivity/pressure head, $K(\psi)$, for each sample plotted with equal sample depths. *Sphagnum fuscum* profile 1 2.5 cm was removed because of equipment malfunction.

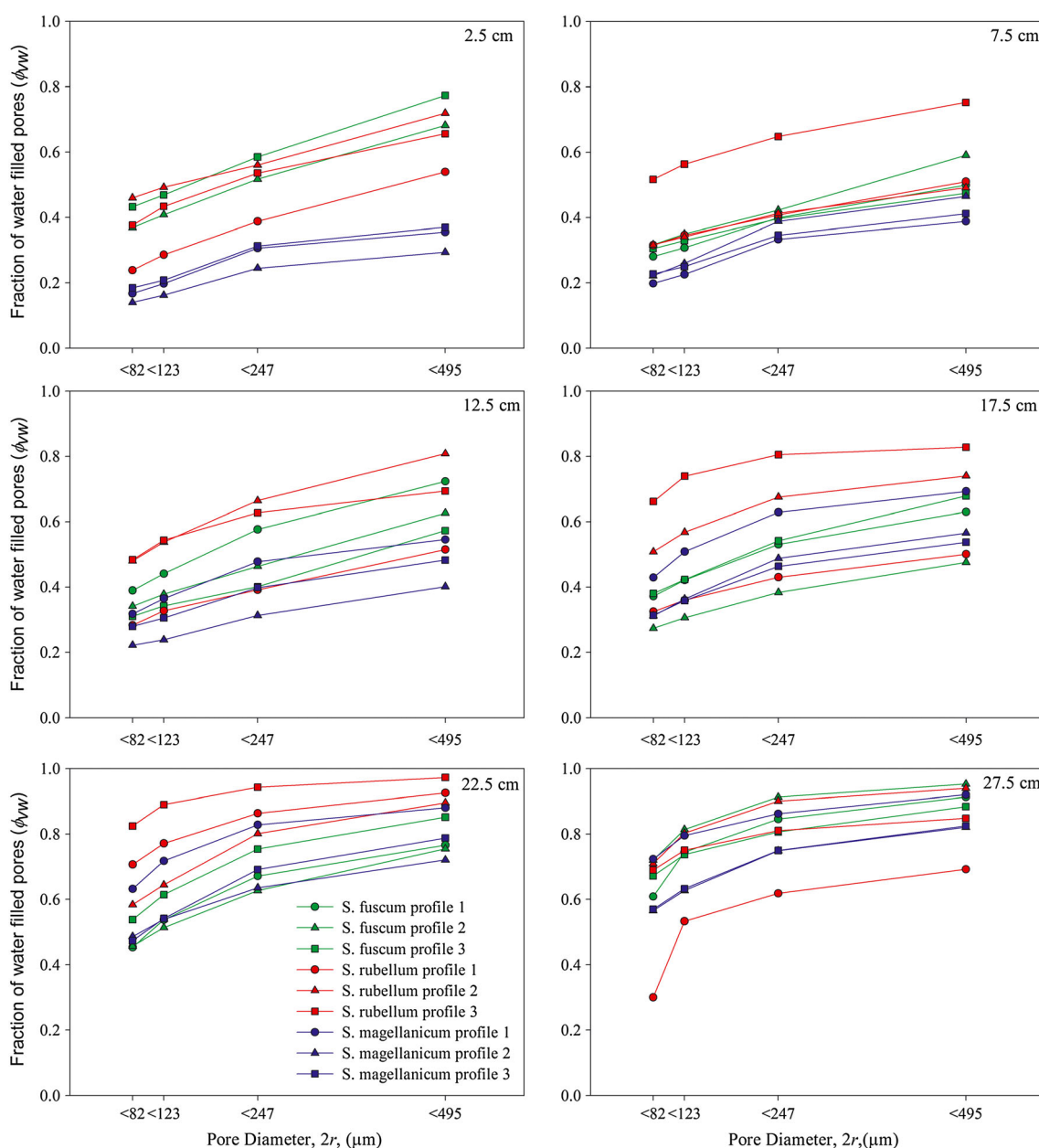


Figure 4. Fraction of water-filled pores plotted with theoretical pore-size distributions. The theoretical pore sizes represent every pore less than or equal to the given value. Higher fractions of water-filled pores indicate there are more smaller pores in a sample than lower plotted values. Shallower slopes of the lines designate a more even pore-size distribution at the pressures tested. This is a modified representation of the data in Figure 2, which gives insight into the composition of the pores in a sample. *Sphagnum fuscum* profile 1 2.5 cm was removed because of equipment malfunction.

simulation period showed similar patterns for *S. fuscum*, *S. rubellum* and *S. rubellum* profile 1, in which the ψ nearest the surface never dropped below -100 cm of head and in which depressurization occurred throughout the profile (Figure 5). In contrast, ψ near the surface of *S. magellanicum* dropped to h_{CritA} (-400 cm of head) but only a slight depressurization at depth. Only *S. magellanicum* did not evaporate at the potential rate for the entire simulation.

Surface ψ steadily decreased over the simulation in all profiles (Figure 6). *S. fuscum*'s surface pressure head was the highest throughout the run with its lowest pressure of -73.5 cm occurring during the final evaporation period and -62.4 cm at the end of the simulation. *S. rubellum* (including *S. rubellum* profile 1) followed a similar trend to *S. fuscum*, but with slightly lower ψ . In

contrast, surface ψ of *S. magellanicum* depressurized quicker once an evaporative flux was applied and reached the -400 cm critical limit (h_{CritA}) within the first evaporation cycle. Once the daily evaporation demand ceased, *S. magellanicum*'s surface pressure quickly increased, although not to equilibrium (Figure 6), only to drop again once the flux was reapplied. The final surface pressure head of *S. magellanicum* was -142.3 cm, far below that of the other samples.

Small decreases (less than an order of magnitude) in capitula K_{unsat} occurred in *S. fuscum* and *S. rubellum* (including *S. rubellum* profile 1) between the initial and final 24 h of the simulation (Figure 7). Slight decreases in capitula K_{unsat} occurred at peak evaporation (1500 h), but capitula K_{unsat} then increased to a rate close to its starting value by the end of the non-evaporation period. *S. rubellum*

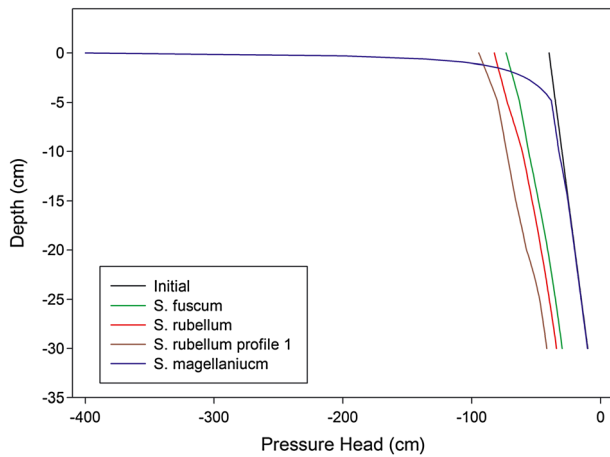


Figure 5. Initial (time=0h, black line) and final evaporation period (time=156h, coloured lines) pressure distribution of each profile from Hydrus-1D. Pressure distributions to the left of the initial pressure distribution indicate depressurization (i.e. dewatering) of the profiles.

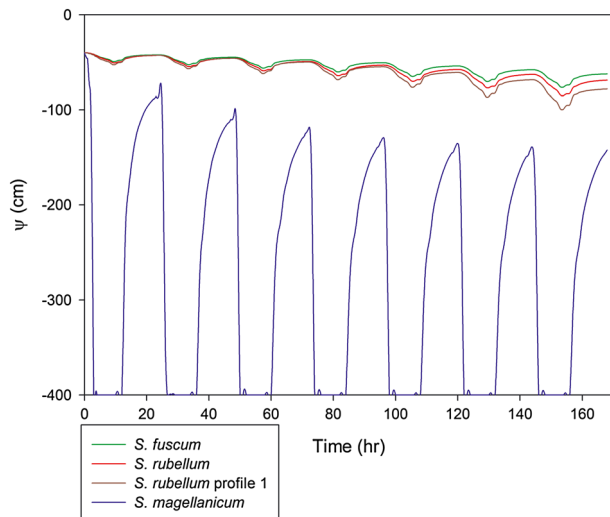


Figure 6. Change in the surface pressure heads over the Hydrus-1D simulation. Values reaching -400 cm of pressure indicate the hyaline cells have drained and evaporation/photosynthesis is limited.

maintained slightly higher capitula K_{unsat} than *S. fuscum* throughout the simulation. Unlike the other species, capitula K_{unsat} in *S. magellanicum* decreased over an order of magnitude ($1.5e^{-4}$ to $9.2e^{-6}$ cm h^{-1}) between the initial and final periods and showed limited rebound of capitula K_{unsat} through the non-evaporation periods.

Sensitivity analysis

The results of the sensitivity analysis stemming from parameter variations revealed that *S. rubellum* and *S. fuscum* were only sensitive to changes in the $K(\psi)$ relationship, whereas *S. magellanicum* responded to changes h_{CritA} and θ in addition to $K(\psi)$ (Figure 8). When K_{unsat} was increased by an order of magnitude, the resulting surface pressures were higher, but *S. magellanicum* still reached the -400 cm limit; however, this occurred for a shorter period than the original simulation (Figure 8). When K was decreased an order of magnitude, all samples reached the -400 -cm critical threshold (h_{CritA}), at which point drainage of the

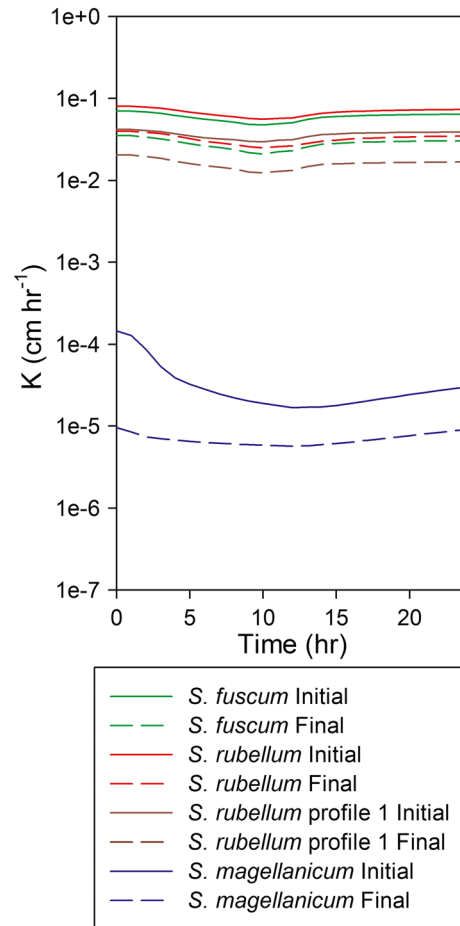


Figure 7. Average K values of the upper 0.9 cm (top 4 nodes) during the initial and final 24-h periods to illustrate changes in K in the capitula during evaporation periods and throughout the entire simulation. Initial time, 0–24 h; final time, 144–168 h.

hyaline cells would occur. *S. magellanicum* recovered less during the non-evaporative times when K was decreased. Because of *S. rubellum*'s higher θ retention values, it did not reach -400 cm until day 5 of the simulation, whereas *S. fuscum* and *S. rubellum* profile 1 depressurized quickly reaching h_{CritA} by days 4 and 3, respectively (Figure 8). Lowering and raising the θ values in RET-C slightly changed the final surface pressure heads of all species; however, the trend of *S. fuscum* retaining the highest surface pressure followed by *S. rubellum*, *S. rubellum* profile 1 and *S. magellanicum* remained the same. Unexpectedly, raising the θ by 0.1, the values resulted in more depressurization of the surface than the original simulation. However, as the $K(\psi)$ relationship was still the original function, relatively low K_{unsat} values occurred at higher θ values; this resulted in limited connectivity within the core because of low K at high θ limiting the movement of water to the surface. However, with the elevated θ , *S. magellanicum* had higher K_{unsat} during the non-evaporation period and was able to better recover its surface pressure head. *S. magellanicum* showed some sensitivity to the lower l parameter; it still reached far lower minimum (-290 cm) and similar final (-68 cm) surface pressure heads compared with that in the other species. *S. magellanicum* was the only species sensitive to the h_{CritA} value (Figure 8, *S. magellanicum*). In every h_{CritA} scenario (-100 , -300 , -500 and -700), *S. magellanicum*

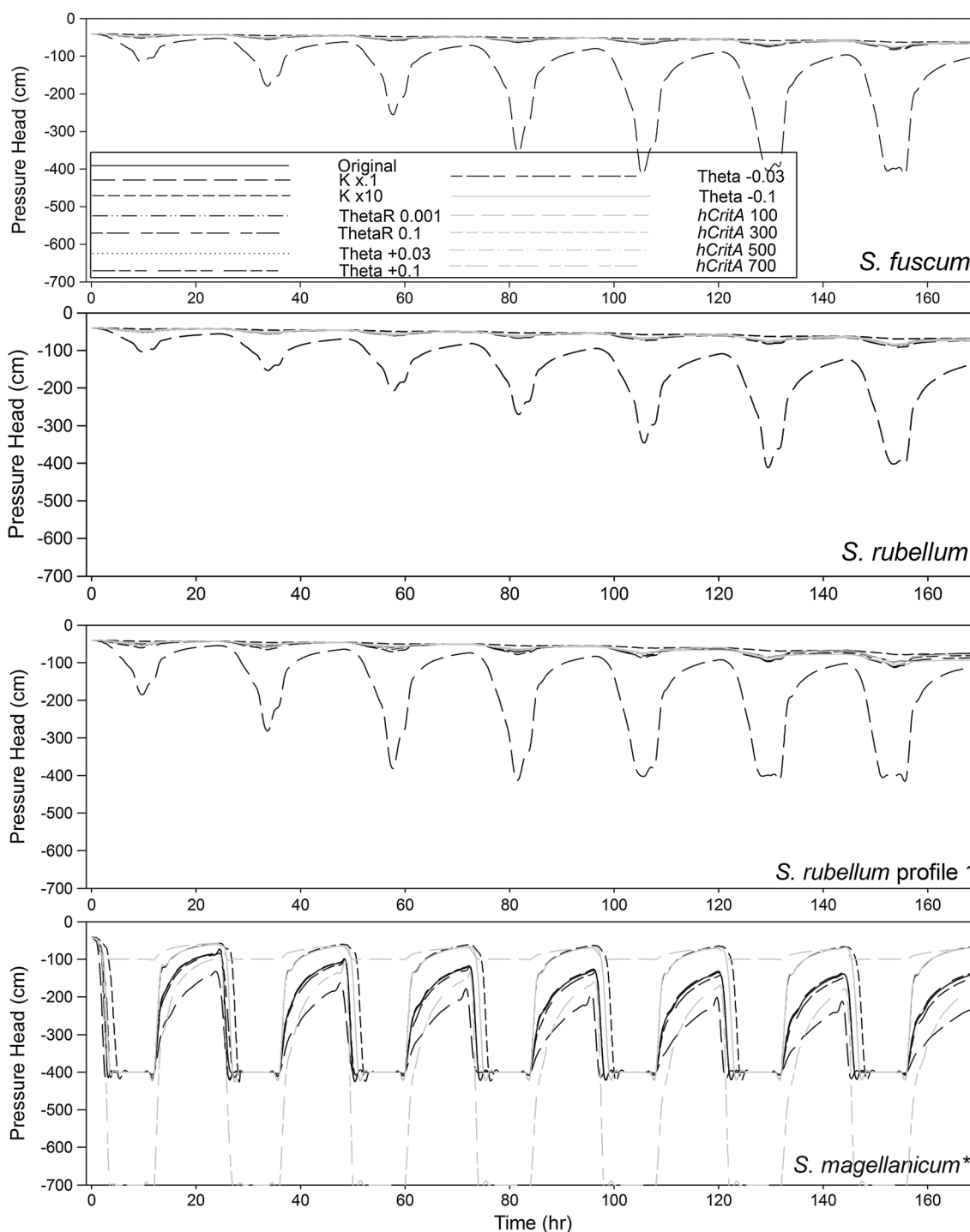


Figure 8. The results of the sensitivity analysis for each *Sphagnum fuscum*, *Sphagnum rubellum*, *S. rubellum* profile 1 and *Sphagnum magellanicum* are shown with the parameter changes. Changes in *K* resulted in the largest deviations from the original simulation. **hCritA* 500, *hCritA* 300 and $\Theta \pm 0.03$ were removed from *S. magellanicum* for clarity. The results plotted between the larger values' (*hCritA* 700, *hCritA* 100 and $\Theta \pm 0.1$, respectively) results and the original results.

reached the critical limit during the evaporation periods (–300 and –500 *hCritA* outcomes were removed in the *S. magellanicum* plot for clarity).

DISCUSSION

Water retention has long been assumed to be the controlling factor in *Sphagnum* moss' preferential habitat and growth (Hayward and Clymo, 1982; Rydin, 1985;

Schipperges and Rydin, 1998; Robroek *et al.*, 2007a). Accordingly, hummock species with higher capitula densities have a greater resistance to desiccation (Clymo, 1973; Hayward and Clymo, 1982; Luken, 1985; Li *et al.*, 1992). In this study, *S. fuscum* had the highest capitula density, whereas *S. magellanicum* had the lowest, as seen in previous studies (Li *et al.*, 1992; Robroek *et al.*, 2007a; Thompson and Waddington, 2008; Turetsky *et al.*, 2008). *S. magellanicum*'s lower soil-water retention characteristics

in the upper 5 cm lead to substantial depressurization in the simulation and subsequent dewatering of the capitula layer. This is seen during dry periods in natural settings as *S. magellanicum* tends to desiccate and turn white, whereas hummock species continue to retain moisture (Hayward and Clymo, 1982; Thompson and Waddington, 2008). The larger capitula of *S. magellanicum* create larger pore spaces that drain more thoroughly at a given pressure head (Figure 2) than other hummock-forming species. The pores of *S. magellanicum* are visibly connected through the capitula themselves, thus draining easily. However, the vertical shrinkage noted while draining could increase the moisture content (i.e. remain photosynthetically active) during times of low water table *in situ*, although not observed in laboratory experiments. The bulk density data (Figure 1) and visual inspection confirmed the more tightly packed capitula layer of *S. fuscum* and *S. rubellum* generally imparted a higher water retention capacity to the upper layer. This behaviour was not evident in *S. magellanicum*, whose bulk density was low in the top layer (Figure 1), affording it poorer water retention capacity (Figure 2). Although the K_{unsat} at a given moisture content in *S. magellanicum* was similar to *S. fuscum* and *S. rubellum*, at any given time in a field setting, this moss will have drained more and be at a lower pressure, thus with lower K_{unsat} . The simulations show (Figure 5 and 6) that unlike *S. fuscum* or *S. rubellum*, water movement in the *S. magellanicum* profile was limited by its relatively poor water retention characteristics. The potential flux generated by evaporation was greater than the moss' ability to supply water to the surface due to strongly decreased K_{unsat} ; thus, critical depressurization of the surface occurred (−400 cm). This illustrates why *S. magellanicum* depends on a higher water table to avoid desiccation compared with *S. fuscum* or *S. rubellum*. Conversely, *S. fuscum* and *S. rubellum* (including *S. rubellum* profile 1) did not reach the critical depressurization threshold because of larger K_{unsat} values and higher θ at the same ψ .

The small differences in the water retention and hydraulic conductivity of *S. fuscum*, *S. rubellum* and *S. rubellum* profile 1 (Figures 2 and 3) do not clearly explain the differences in habitat and growth form seen in nature. Although retaining less water at a given pressure, *S. fuscum* was better able to supply the capitula with water because of higher average K_{unsat} throughout the profile. The larger K_{unsat} values increased water availability at the capitula more than in *S. rubellum* and *S. rubellum* profile 1 during times of evaporative loss (Figure 6). This suggests that it may be the pore geometry controlling K_{unsat} (and hence the rate of water flow) and not only water retention as previously thought.

The large θ changes observed in *S. magellanicum* and *S. rubellum* profile 1 at 2.5 cm (Figure 2) with minimal decrease in ψ indicate a greater abundance of large-diameter pores than in *S. fuscum* or *S. rubellum*. It would be expected that *S. rubellum* profile 1 mimics *S. magellanicum*'s surface depressurization (Figure 6) if soil-water retention was the only factor preventing *Sphagnum* desiccation. However, the pore geometry (i.e. tortuosity, connectivity and distribution)

can also impact the ability to transmit water to the capitula and avoid desiccation. The slopes (i.e. amount of water drained over a specified range of pore diameters) of the theoretical pore-size distributions (Figure 4) are not distinct between species, which suggests a similar number of pores in this pore-size range. However, most of the water in *S. magellanicum* drained from larger pores (>495 μm) resulting in low θ and few pores <82 μm filled with water. *S. fuscum* and *S. rubellum* had fewer large pores (shown by limited initial desaturation) and a greater proportion of smaller pores (<82 μm) that remained filled and contribute to water flow as the sample desaturated, thus leading to a higher K_{unsat} at a given pressure less than −24 cm than *S. magellanicum*. In addition to pore diameter (which controls water retention), pore connectivity and tortuosity also affected the water retention/ K_{unsat} relationships, hence the ability of *Sphagnum* to supply the capitula with water.

Pore connectivity and tortuosity are expressed in the van Genuchten/Mualem model as the l parameter (van Genuchten, 1980), which is not a physical parameter but rather is a scaling factor related to the level of pore connectivity and tortuosity. Lower l values (i.e. more negative) denotes that K_{unsat} will decrease less as θ decreases, resulting in higher K_{unsat} values at a given pressure < 0 (Mualem, 1976; van Genuchten, 1980; Schaap and Leij, 2000). As l decreases, the pore connectivity increases and tortuosity is reduced; hereafter, for simplicity, this will be referred to solely as 'pore connectivity'. Average profile l values for *S. fuscum*, *S. rubellum* and *S. rubellum* profile 1 are not statistically different from each other, while being statistically different than *S. magellanicum* ($p < 0.001$ for *S. fuscum* and *S. rubellum* and $p < 0.05$ for *S. rubellum* profile 1). The sensitivity analysis on l showed that raising pore connectivity (lowering l) reduced *S. magellanicum*'s surface depressurization so that it avoided desiccation and allowed for better recovery of its surface pressure head during the non-evaporative periods. Although lower l values prevented the simulated desiccation in *S. magellanicum*, the results show that *S. magellanicum* still is not as effective as the other species at avoiding low and potentially harmful capitula pressures. In addition to having more larger diameter pores (low θ in the 2.5-cm core) than *S. fuscum* and *S. rubellum*, *S. rubellum* profile 1 had lower l values than *S. magellanicum* (Table 1), signifying that the pore connectivity is higher than in *S. magellanicum* and more similar to *S. fuscum* and *S. rubellum*. This indicates that there are dramatically different pore networks in *S. rubellum* profile 1 than *S. magellanicum* that allow for a higher level of connectivity between pores, resulting in more efficient water transmission to the capitula. The higher pore connectivity in *S. rubellum* profile 1 led to dramatically higher surface pressure heads than *S. magellanicum* (Figure 6), even with similar pore-size distributions and the resulting poor water retention. Although there is no statistical difference in pore connectivity between *S. rubellum* profile 1 and *S. fuscum*/*S. rubellum*, there are large differences in water retention, which explain *S. rubellum* profile 1's slightly lower surface pressures heads (Figure 6) and how it avoided depressurization of the capitula layer. *S. rubellum* profile 1 further illustrates that

pore geometry (i.e. pore connectivity and tortuosity) in addition to water retention (and pore diameter) controls water migration in *Sphagnum*, and ultimately the maximum height *Sphagnum* will grow above the water table.

It is assumed that the moss capitula layer's hydraulic properties strongly control evaporation from, and water retention in, the moss profile. *Sphagnum* moss enters a state of desiccation that greatly reduces the evaporative and photosynthetic fluxes, while increasing soil respiration once their hyaline cells drain of water (Hayward and Clymo, 1982; Titus *et al.*, 1983; Lewis, 1988; Williams and Flanagan, 1996; Schipperges and Rydin, 1998; McNeil and Waddington, 2003; Strack and Price, 2009). However, the results of these simulations indicate that it is the entire profile's ability to transmit and retain water that is critical to maintaining higher surface pressure heads (i.e. higher moisture contents) and healthy capitula. If the surface becomes desiccated, there is little (if any) moisture available for evaporation; however, as there is no available water to evaporate, a flux cannot be generated and the surface is unable to access water stored below. *S. fuscum* was best able to maintain high surface and bottom soil-water pressure heads compared with the other species, demonstrating that it can more easily access the stored water within the profile. Unlike *S. fuscum* and *S. rubellum* (including *S. rubellum* profile 1), *S. magellanicum* was unable to access the water stored in the soil profile primarily because of the limited connectivity between the upper and lower layers.

Although these simulations indicate that pore geometry plays a role in controlling the evaporation rate of the mosses, they are unable to account for other field-scale factors. For example, evaporation has shown to be highly variable over bog microforms (i.e. hummocks and hollows) (Mölder and Kellner, 2002), which was attributed to varying aerodynamic resistance between different *Sphagnum* growth forms (i.e. tightly vs loosely packed canopy) (Kettridge and Baird, 2010; Kettridge *et al.*, 2012) and could be extrapolated to coincide with different species of *Sphagnum* moss (hummock vs hollow species). Unlike *S. fuscum* and *S. rubellum*, which have a relatively low aerodynamic resistance (Kettridge and Baird, 2010) and are more tightly packed, *S. magellanicum* has a relatively high aerodynamic resistance (Kettridge and Baird, 2010) and loose canopy structure, thus a greater potential for evaporation if it can maintain the water supply. However, given its inability to supply water to the surface, this explains the tendency for *S. magellanicum* to desiccate.

The considerable time and equipment required to complete the hydraulic analysis for multiple species and depths limited the number of replicates, thus precluded a broader statistical analysis. As can be seen from Figure 2, the retention characteristics for a given species encompass a range of values for a given pressure, but nevertheless clearly demonstrate the lower water retention capacity for *S. magellanicum*. The hydraulic conductivity profiles (Figure 3) were not notably different from each other in the range tested. This range was limited by the method of analysis (Price *et al.*, 2008), and to perform the simulations, it was necessary to extrapolate beyond the measured

hydraulic conductivities, particularly for *S. magellanicum*. Given the relatively small changes in θ and K_{unsat} at low values of ψ , we are confident in the main findings regarding the behaviour of the various species.

CONCLUSIONS

Extensive surface sampling showed the profiles used for simulations had capitula density and bulk density not significantly different from those occurring at the same site. Notwithstanding the relatively small sample size for the hydraulic analysis, and the necessity to extrapolate to pressures beyond the tested range, these simulations are consistent with field observations that *S. magellanicum* reaches a critical threshold and dries far quicker than other hummock species. Within the profiles tested, there were distinct patterns of water retention associated with each species (although we note the deviation of one profile, *S. rubellum* profile 1, from this trend). The simulations illustrate that along with water retention capacity, pore geometry and pore connectivity control the redistribution of water within the monolith and ultimately the species' ability to supply the capitula with water to avoid desiccation. For instance, *S. magellanicum*'s upper 5 cm substantially dewatered with a -40 -cm water table, whereas *S. fuscum* is able to maintain relatively moist capitula with the same water table because of a larger number of smaller pores. These data mimic the general ecological habitats of the species with *S. fuscum* growing the furthest above from the water table, followed by *S. rubellum*, and *S. magellanicum* closest to the water table (Robroek *et al.*, 2007a). In these simulations, *S. fuscum* was able to maintain the highest soil-water pressures at the surface. Although reaching lower simulated surface pressures than *S. fuscum*, *S. rubellum* still maintained surface soil-water pressure well above -100 cm of head, thus with little or no water stress. *S. magellanicum* is far more constrained to higher water tables (higher soil-water pressures) to maintain sufficiently moist capitula as demonstrated in the simulations. The ability to remain wet and photosynthesize under dry conditions has implications for carbon accumulation (i.e. better for *S. fuscum* and *S. rubellum*). Furthermore, bogs dominated by *S. magellanicum* hollows or hummocks could have a higher net loss of carbon during periods of low water table than bogs dominated by *S. rubellum* and *S. fuscum* because of poor water retention characteristics (i.e. larger pore diameters) resulting in a drier unsaturated zone. These results illustrate the long-held belief that the principal survival mechanism in hummock species is not solely due to soil-water retention but also includes pore geometry, pore connectivity and pore-size distribution to allow hummock species to grow higher above the water table and avoid desiccation.

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