A Method to Determine Unsaturated Hydraulic Conductivity in Living and Undecomposed *Sphagnum* Moss

Jonathan S. Price* Peter N. Whittington

Dep. of Geography Univ. of Waterloo Waterloo, ON, Canada N2L 3G1

David E. Elrick

Land Resource Science Dep. Univ. of Guelph Guelph, ON, Canada N1G 2W1

Maria Strack

Dep. of Geography Univ. of Waterloo Waterloo, ON, Canada N2L 3G 1

Currently at: Dep. of Geography Univ. of Calgary Calgary AB, Canada T2N 1N4

Nathalie Brunet Erica Faux

Dep. of Geography Univ. of Waterloo Waterloo, ON, Canada N2L 3G1

Sphagnum mosses (Sphagnum L.) are the primary peat-forming plant in northern peatlands and rely on capillary transport of water to facilitate physiological processes. The unsaturated hydraulic conductivity of the living, undecomposed, and poorly decomposed mosses is needed to estimate and model water flux to their growing upper layer. This study describes a new apparatus to measure this in the highly porous (~90%) hummock profile where the pore sizes are large and the mosses delicate, in which established methods do not work. Independent tension disks controlled the pressure head (ψ , between 0 and -35 cm of water) and the pressure gradient and thus flow. The uppermost 5-cm layer of moss had a saturated hydraulic conductivity of 1800 μ m s⁻¹, and decreased when unsaturated ($\psi = -25$ cm of water) to $0.03 \,\mu\text{m s}^{-1}$. Moss 25 cm below the surface had equivalent values of 230 and 11.0 μ m s⁻¹ at moisture contents of 0.18 to 0.22 m³ m⁻³. The The soil water retention model RETC provided a good fit for both hydraulic conductivity and water retention when fitted simultaneously, but did not perform well to predict hydraulic conductivity from water retention data alone.

Soil Sci. Soc. Am. J. 72:487-491 doi:10.2136/sssaj2007.0111N Received 20 Mar. 2007.

*Corresponding author (jsprice@fes.uwaterloo.ca).

© Soil Science Society of America

677 S. Segoe Rd. Madison WI 53711 USA

All rights reserved. No part of this periodical may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopying, recording, or any information storage and retrieval system, without permission in writing from the publisher. Permission for printing and for reprinting the material contained herein has been obtained by the publisher. SPHAGNUM MOSSES ARE THE PRIMARY peat-forming plant in northern peatlands (Kuhry et al., 1993), relying on capillary transport of water between closely spaced individual plants within a moss community to facilitate physiological processes (Clymo and Hayward, 1982). There is a poor understanding of the moisture dynamics of in situ sphagnum mosses. It has long been assumed that upward capillary water flow from the water table provides the water required at the growing surfaces (capitula) for plant metabolic processes (Schipperges and Rydin, 1998), and in particular photosynthesis, which takes place in the top several centimeters of the upper moss surface. The moisture content within sphagnum hummocks also controls the rate of soil respiration (plant matter decomposition), which takes place throughout the moss (McNeil and Waddington, 2003). However, while considerable research has been done to characterize the hydraulic properties of undisturbed peat (Silins and Rothwell, 1998; Schwärzel et al., 2006) and peat-soil mixes used in horticultural science (da Silva et al., 1993; Heiskanen, 1995; Caron et al., 2005; Caron and Elrick, 2005), little is known of the hydraulic properties of the mosses themselves. That is, in the uppermost part of the profile, comprising living, dead, and undecomposed mosses, the capillary relations, notably unsaturated hydraulic conductivity (K), are essentially unknown. While water retention characteristics (volumetric soil moisture, θ , vs. pressure head, ψ) of sphagnum mosses have been reported (e.g., Boelter, 1969; Hayward and Clymo, 1982), direct measurement of the unsaturated hydraulic conductivity function, $K(\psi)$ has not been described because of the difficulty in measuring the water pressure and the delicacy of the moss structure. Tensiometers do not work well in this medium, whose porosity can exceed 90% (Boelter, 1969; Cornejo et al., 2005), because of poor contact with the ceramic cup (Kennedy and van Geel, 2000). Lauren and Mannerkoski (2001) reported on hydraulic properties of forest mosses, but these have a different structure than the upper layer of living and undecomposed sphagnum mosses (Proctor, 2000). Sphagnum mosses have a large proportion of easily drainable pores. The theoretical pore-size distribution 5 cm below the surface suggests that 40 to 50% of the pores are >300 μ m and 20 to 30% are >1000 µm (Hayward and Clymo 1982), resulting in air-entry pressures probably in the range of 0 to -1 cm of water.

Numerous methods are available for determining the unsaturated hydraulic conductivity function (Klute and Dirksen, 1986), which defines K for a range of ψ . For example, direct methods include the instantaneous profile technique (Dirksen, 1991), which evaluates the pressure gradient using tensiometers in a drying soil column with a measured water loss caused by evaporation (Schlotzhauer and Price, 1999; Lauren and Mannerkoski, 2001). The value of $K(\psi)$ can also be estimated directly from steady-state flow methods in which a pressure gradient is established in a soil (substrate) core. Porous membranes fixed at each end of the core permit a negative head to be established by hanging water columns on each end and a hydraulic gradient is established by setting the two hanging water columns at different levels (Richards, 1931; Elrick and Bowman, 1964). Recently, Caron and Elrick (2005) reported on a device (Laval tension disk) to measure the hydraulic conductivity of potting substrates packed into plant pots (approximates field conditions). To determine hydraulic conductivity, the analysis requires homogeneity of the soil above the water table. Thus, this method is inapplicable to living and undecomposed mosses because they are highly anisotropic and vertically heterogeneous (Ingram, 1983).

The value of $K(\Psi)$ can also be estimated indirectly using (i) the inverse method by applying Richard's equation to a laboratory column with imposed boundary conditions and transient outflow from which the hydraulic conductivity function is fitted (Eching et al., 1994), or (ii) from the water retention curve based on the model of van Genuchten (1980), with $K(\Psi)$ being predicted on the basis of pore size distribution derived from water retention experiments (after Mualem, 1976). The latter method, however, can result in considerable error (Khaleel et al., 1995). Since large, vertically oriented pores and water storage cells (hyaline cells) make sphagnum mosses different from mineral soils (Hayward and Clymo, 1982), a priori knowledge of the $K(\Psi)$ function is needed for verification.

The purpose of this study, therefore, was to determine the water retention and unsaturated hydraulic conductivity functions of living and undecomposed sphagnum moss using a new method that is suitable for use in porous materials with large pores and low bulk density. The specific objectives were to (i) develop and test a method for determining unsaturated hydraulic conductivity; (ii) characterize the $\theta(\Psi)$ and $K(\Psi)$ functions for a profile of sphagnum moss; and (iii) test the RETC code (van Genuchten et al., 1991) for matching $K(\Psi)$ on the basis of measured $\theta(\Psi)$ and $K(\Psi)$, and by $\theta(\Psi)$ alone.

MATERIALS AND METHODS

Samples were collected from a raised bog situated in the southern portion of the Luther Marsh Wildlife Management Area, located ~85 km northwest of Toronto near Arthur, Ontario. The bog is characterized by hummock–hollow microtopography comprising primarily *Sphagnum rubellum* Wilson, with a covering of Ericacea including *Chamaedaphne calyculata* (L.) Moench, *Ledum groenlandicum* Oeder, and *Vaccinium* spp. *Sphagnum rubellum* samples were obtained while frozen to avoid compression and sliced into 5-cm-thick sections, then



Fig. 1. Apparatus for measuring the unsaturated hydraulic conductivity function, $K(\psi)$. Upper and lower disks have vertical perforations and are covered by nylon fabric with air-entry pressures of -40 and -35 cm for the lower and upper plates, respectively.

trimmed to snugly fit into 12.7-cm-diameter Plexiglas cylinders, oriented to test the vertical hydraulic conductivity.

The apparatus developed to determine hydraulic conductivity was based on using twin pressure plates (see Fig. 1) modeled after the system described by Elrick and Bowman (1964). The plates were constructed from an 11.4-cm (i.d.) clear Plexiglas cylinder cut into 2.5-cm-high rings. Perforated 0.318-cm-thick disks (\sim 12.4-cm diameter) were affixed (sealed) to both ends of the ring using an acrylic solvent. The disks in contact with the soil were perforated with 115 holes 0.635 cm in diameter, having a total cross-sectional porosity of \sim 36%. A 25- or 35-µm Nitex fabric (21 and 27% total open area, respectively) was glued onto the perforated disks (providing an airentry pressure of about -40 and -35 cm, respectively) for the upper and lower plate, respectively. A brass spigot was inserted into the nonperforated disks and connected to Tygon inflow–outflow tubes. The impedance to flow of the membranes was negligible.

The samples were submerged in deionized water for 5 min before mounting. The two tension disks were filled with water to remove air bubbles. The tube from the lower tension disk (35-µm screen) (see Fig. 1) was connected to the lower outflow spout of a 500-mL plastic beaker and a constant head in the beaker was achieved by adding sufficient water to the beaker to maintain a constant overflow (e.g., Mariotte bottle, not shown in Fig. 1). The sample was transferred from the water and placed onto the lower disk. A 12.7-cm (i.d.) Plexiglas cylinder was slipped over the sample and the disk was lowered, coming to rest on supports anchored into the polyvinyl chloride support pipe. The upper tension disk (25-µm screen) was then placed gently on top of the sample by inserting the upper disk into the Plexiglas cylinder. Because the tension disks were a snug fit in the Plexiglas cylinder, the upper tension disk needed to be pushed gently into position (i.e., friction with the side wall reduced its effective weight) to maintain

> hydraulic contact without causing compression. This is the critical feature of this apparatus that allows it to maintain contact with the sample during every stage of pressure application—at the beginning of each stage, the upper disk was lowered to ensure contact with the upper surface of the sample. Sample height was measured at the end of each stage of pressure. The tube from the upper tension disk was inserted below the water surface in an Erlenmeyer flask that drained into a 10-mL graduated cylinder used to measure outflow. This prevented air from entering the outflow tube of the upper disk while maintaining a constant head.

> The initial starting position had the water level in the source reservoir (beaker) and outflow reservoir (flask) even with the top of the lower tension disk (0 cm) (see Fig. 1). Then, both the flask and beaker were lowered 4 cm. After water stopped flowing, the source reservoir was raised back up to the initial level (0 cm) to create a constant head difference of 4 cm and discharge (Q) was recorded. Once Q became constant, the upper disk and cylinder were removed, the sample was carefully removed and weighed and then placed back on to the lower plate, and the cylinder and upper disk were replaced. Both the source and outflow reservoir were then lowered to the next stage (initially with no head difference) and the

Table 1. Physical, hydraulic, and RETC curve-fitting parameters of the ~5 cm layers of a *sphagnum* hummock. Curve-fitting parameters were estimated with RETC using both the water retention, $\theta(\psi)$, and unsaturated hydraulic conductivity function, $K(\psi)$; the values in parentheses are based on $\theta(\psi)$ only. Predicted values [i.e. using only $\theta(\psi)$] were made only for the plotted 5-, 15-, and 25-cm depths shown in Fig. 2. The RETC code was run with the empirical constant m = 1 - 1/n; simultaneous fitting of hydraulic conductivity (weighting 0.8) and water retention data (van Genuchten et al., 1991) and residual volumetric water content set to 0.02 at -15-m pressure (Boelter, 1969).

Depth+	Bulk density	Saturated $\boldsymbol{\theta}$	α‡	<i>n</i> ‡	L§	Hydraulic conductivity		
						Saturated	-25 cm pressure head	
cm	g cm ⁻³					μm s ⁻¹		
5	0.040	0.89	10.47 (10.24)	2.53 (1.28)	-0.81	1830	0.04 (0.00012)	
10	0.034	0.88	0.47	2.21	-1.99	245	0.37	
15		0.90	0.47 (3.00)	2.00 (1.25)	-2.14	319	0.063 (0.002)	
20	0.038	0.90	0.27	2.36	-2.20	331	3.7	
25		0.92	0.10 (0.13)	2.82 (1.54)	-1.79	235	11.1 (2.4)	

+ Mid-depth of 5-cm samples.

 $\ddagger \alpha$ and *n* are empirical constants that affect the shape of the (predicted) water retention curve.

§ L is a parameter in Mualem's model that accounts for pore tortuosity and connectivity.

above sequence repeated until the outflow flask was ${\sim}32$ cm below the base of the sample and the source beaker 28 cm below. Thus a constant head gradient (-4 cm [difference between flask and beaker]/5 cm [height of core] = -0.8) was maintained for all tests, but with variable pressure. Pressure (ψ) was calculated as the average of the lower and upper tension disk pressure heads, nominally referenced to the mid-depth of the sample (approximately -6, -10, -14, down to -32 cm). The smaller fabric size (25 μ m) was used on the upper disk because the outflow (flask) location was always 5 cm (thickness of core) plus 4 cm (head difference) lower than the inflow beaker and thus a lower (more negative) air entry pressure (Ψ_{a}) was needed; otherwise the system would leak as air entered the plate. The hydraulic conductivity function, $K(\psi)$, was calculated at each ψ from the imposed gradient, sample length, and discharge by applying Darcy's law (Elrick and Bowman, 1964). Water content (θ) was determined gravimetrically using standard methods (Gardner, 1986) based on the original field sample volume, the sample mass at specified pressure intervals, and the dry mass.

Water retention was determined as part of the $K(\Psi)$ analysis, since the samples were weighed at each progressive head setting. Saturated hydraulic conductivity (K_s) was determined on the same samples in a cylinder lined with a rubber sleeve like those commonly used in triaxial tests (Franklin and Hoeck, 1970). The sleeve was inflated by injecting it with water, using a syringe, to provide sufficient lateral compression to prevent leaks down the sidewall. A unit (upward) hydraulic gradient was applied to produce a measured outflow, and K_s was determined using Darcy's law.

The RETC code (van Genuchten et al., 1991) with the model of Mualem (1976) for determining unsaturated hydraulic conductivity was used to fit curves to the $\theta(\psi)$ and log-transformed $K(\psi)$ relationships, and then to predict $K(\psi)$ on the basis of $\theta(\psi)$ only.

RESULTS

The sphagnum moss from the hummock had a bulk density (ρ_b) typically around 0.04 g cm⁻³, and saturated water content (θ_s) 0.89 to 0.92 m³ m⁻³ (Table 1). The water retention capacity was similar at the 5- and 15-cm depths but was notably greater at 25-cm depth (Fig. 2a). The RETC curves fit well for all water retention data ($r^2 = 0.99$).

The value of K_s in the uppermost layer was almost an order of magnitude greater than in the lower layers, dropping from 1830 to

235 μ m s⁻¹ with depth. The unsaturated hydraulic conductivity at Ψ = -25 cm of water ($K_{\Psi-25}$) had the opposite trend, being higher in the deeper (25-cm) sample (11.1 μ m s⁻¹) than in the upper (5-cm) sample (0.040 μ m s⁻¹) (Fig. 2b). The RETC code also did a good job of replicating the observed data when fitted simultaneously with retention and $K(\Psi)$ data (Fig. 2b). Using only water retention data in RETC to predict the $K(\Psi)$ function, however, resulted in errors of up to two orders of magnitude at Ψ = -25 cm of water, seriously underpredicting the measured values for the 5- and 15-cm layers (Fig. 2c). The predicted $K(\Psi)$ function for the 25-cm layer underpredicted the measured value by almost an order of magnitude throughout most of the applied pressure range. The RETC parameters for all three depths are provided in Table 1, along with those of the intermediate layers.

DISCUSSION

The newly developed $K(\Psi)$ apparatus provides the only known published values of unsaturated hydraulic conductivity for sphagnum mosses. While saturated hydraulic conductivity of living and undecomposed mosses may be too high to determine using field methods (Boelter, 1965), undecomposed mosses at 0.15- to 0.25-m (Boelter, 1965) and 0.20- to 0.30-m (Hoag and Price, 1995) depths have been reported to be 0.38 and 16 mm s⁻¹, respectively. Saturated hydraulic conductivity values reported in this study are between these values. Vertical hydraulic conductivity in bog peats is typically 1 to 10 times lower (Chason and Siegel, 1986). The results show a very steep decrease in hydraulic conductivity as the sample drained from 0- to -35-cm pressure. In the upper layer, K dropped nearly five orders of magnitude as ψ was decreased. In the lower layers, the drop was about one order of magnitude. The sharp change in unsaturated hydraulic conductivity is caused by the initially rapid drainage of the mosses that occurs when the pressure head is reduced-the air-entry pressure (Ψ_{2}) was essentially 0 m³ m⁻³. In the 5- and 15-cm-depth samples, more than half the water drained out at the first stage of desaturation $(\psi = -6 \text{ cm})$ (Fig. 2). In the 25-cm-depth sample, water retention was greater, and this imparted a notably greater unsaturated hydraulic conductivity. We attribute this to the greater water retention that occurs with depth in mosses (Hayward and Clymo, 1982) so the flow path becomes less tortuous because of the presence of more and thicker water films through which flow can occur.



Fig. 2. (a) Water retention and (b) hydraulic conductivity predicted with RETC using both the water retention, $\theta(\psi)$, and the unsaturated hydraulic conductivity function, $K(\psi)$, measured with the apparatus; and (c) $K(\psi)$ predicted on the basis of $\theta(\psi)$ only.

The rapid decline in moisture content on drainage of the upper moss layers has been noted previously (e.g., Boelter, 1969). In the upper layers, θ became more constant at relatively high Ψ (about –10 cm). At Ψ values lower than this, the water films that conduct flow are very thin (hence the low unsaturated hydraulic conductivity), and the residual water is mostly held within the hyaline cells of sphagnum mosses (Ingram, 1983). According to Hayward and Clymo (1982), water in these hyaline cells is drained when Ψ drops below about –200 cm and represents about 10% of the space in a moss carpet. In the samples tested here, with $\rho_b = 0.04 \text{ g cm}^{-3}$, the moss comprised about 3% of the volume; thus, as little as 7% of the volume contributed to flow when ψ was less than approximately -20 cm.

The RETC code provides a useful way of representing the characteristic curves, but only if both $\theta(\psi)$ and $K(\psi)$ are used to generate curve-fitting parameters (Table 1). The predicted $K(\psi)$ based on $\theta(\psi)$ data alone underestimated $K_{\psi-25}$ by several orders of magnitude in the 5- and 15-cm layers. This suggests that the theoretical pore-size distribution model (Mualem, 1976) does not represent well the structure of mosses.

The measurement apparatus is cheap to construct and worked relatively quickly (several hours to do each run); however, there are limitations to the method caused by the high ψ_a of the nylon mesh we used. The minimum average pressure we could consistently achieve was about -35 cm. Our original intention was to minimize flow resistance by using the largest mesh size practical (i.e., to achieve a sufficiently low ψ_2 ; however, the mesh used (25 and 35 µm) could produce a flow several orders of magnitude larger than the highest unsaturated hydraulic conductivity we measured, thus using different mesh sizes on upper and lower screens proved unnecessary. Moreover, given the low resistance to flow, a smaller mesh size could possibly be used to achieve a greater range of ψ . After several uses, however, there was a measurable decrease in the flow that a single plate could deliver because the pores on the mesh became clogged. Flow could be restored by scrubbing lightly.

Following these experiments, we built new tension plates that were much thinner (\sim 8 mm), so that the potential for inadvertently compressing the sample is reduced. In the experiments reported here, some shrinkage occurred as the sample dried-from about 1 to 7% in the tested ψ range. During the first stage of drainage, the volume change is primarily vertical (and also the greatest), thereafter becoming triaxial. The volume change can be considerably reduced by ensuring that the sample is not oversaturated to start the test. In fact, assessing θ_s is problematic. The sample can swell beyond field volume if too much water is added to cause saturation, even to the point where calculated θ_s is >1 m³ m⁻³. We attempted to constrain our samples to field volume to calculate θ_s , which made those values several percentage points lower than some other values reported in the literature (e.g., 0.95 m³ m⁻³; Boelter, 1969). The design of the instrument, with the "suspended" upper plate, accommodates the volume change, as it can be pushed into firm contact with the subsiding surface following each step in reduc-

ing ψ ; however, θ may be underestimated by a few percentage points because the end volume of the sample is smaller than the starting volume used to calculate moisture content. In the field, the upper layer of moss in hummocks is rarely saturated (e.g., Price, 1996), so the effective volume change is not so important.

ACKNOWLEDGMENTS

Funding by the Natural Science and Engineering Council (NSERC) of Canada is appreciated.

REFERENCES

Boelter, D.H. 1965. Hydraulic conductivity of peats. Soil Sci. 100:227-231.

- Boelter, D.H. 1969. Physical properties of peats as related to degrees of decomposition. Soil Sci. Soc. Am. Proc. 33:606–609.
- Caron, J., and D.E. Elrick. 2005. Measuring the unsaturated hydraulic conductivity of growing media with a tension disc. Soil Sci. Soc. Am. J. 69:783–793.
- Caron, J., D.E. Elrick, R. Beeson, and J. Boudreau. 2005. Defining critical capillary rise properties for growing media in nurseries and greenhouses. Soil Sci. Soc. Am. J. 69:794–806.
- Chason, D.B., and D.I. Siegel. 1986. Hydraulic conductivity and related physical properties of peat, Lost River peatland, northern Minnesota. Soil Sci. 142:91–99.
- Clymo, R.S., and P.M. Hayward. 1982. The ecology of sphagnum. p. 229–290. *In* A.J.E. Smith (ed.) Bryophyte ecology. Chapman & Hall, London.
- Cornejo, C., D.Z. Haman, and T.H. Yeager. 2005. Evaluation of soil moisture sensors and their use to control irrigation systems for containers. Pap. 054056. *In* ASAE Annu. Int. Meet., Tampa, FL. 17–20 July 2005. Am. Soc. Agric. Eng., Saint Joseph, MI.
- da Silva, F.F., R. Wallach, and Y. Chen. 1993. Hydraulic properties of sphagnum peat moss and tuff (scoria) and their potential effects on water availability. Plant Soil 154:119–126.
- Dirksen, C. 1991. Unsaturated hydraulic conductivity. p. 209–269. *In* K.A. Smith and C.E. Mullins (ed.) Soil analysis: Physical methods. Marcel Dekker, New York.
- Eching, S.O., J.W. Hopmans, and O. Wendroth. 1994. Unsaturated hydraulic conductivity from transient multistep outflow and soil water pressure data. Soil Sci. Soc. Am. J. 58:687–695.
- Elrick, D.E., and D.H. Bowman. 1964. Note on an improved apparatus for soil moisture flow measurements. Soil Sci. Soc. Am. Proc. 28:450–453.
- Franklin, J.A., and E. Hoeck. 1970. Developments in triaxial testing technique. Rock Mech. 2:223–228.
- Gardner, W.H. 1986. Water content. p. 493–544. *In* A. Klute (ed.) Methods of soil analysis. Part 1. Physical and mineralogical methods. SSSA Book Ser. 5. SSSA, Madison, WI.
- Hayward, P.M., and R.S. Clymo. 1982. Profiles of water content and pore size in *Sphagnum* peat, and their relation to peat bog ecology. Proc. R. Soc. London, Ser. B 215:299–325.
- Heiskanen, J. 1995. Physical properties of two-component growth media based on *Sphagnum* peat and their implications for plant-available water and aeration. Plant Soil 172:45–53.
- Hoag, R.S., and J.S. Price. 1995. A field-scale, natural gradient solute transport experiment in peat at a Newfoundland blanket bog. J. Hydrol. 172:171–184.

- Ingram, H.A.P. 1983. Hydrology. p. 67–224. In A.J.P. Gore (ed.) Ecosystems of the World 4A. Mires: Swamp, bog, fen and moor. Elsevier, Amsterdam.
- Kennedy, P., and P.J. van Geel. 2000. Hydraulics of peat filters treating septic tank effluent. Transp. Porous Media 41:47–60.
- Khaleel, R., J.F. Relyea, and J.L. Conca. 1995. Evaluation of van Genuchten– Mualem relationships to estimate unsaturated hydraulic conductivity at low water contents. Water Resour. Res. 31:2659–2668.
- Kuhry, P., B.J. Nicholson, L.D. Gignac, D.H. Vitt, and S.E. Bayley. 1993. Development of *Sphagnum* dominated peatlands in boreal continental Canada. Can. J. Bot. 71:10–22.
- Klute, A., and C. Dirksen. 1986. Hydraulic conductivity and diffusivity: Laboratory methods. p. 687–734. *In* A. Klute (ed.) Methods of soil analysis. Part 1. SSSA Book Ser. 5. SSSA, Madison, WI.
- Lauren, A., and H. Mannerkoski. 2001. Hydraulic conductivity of mor layers in Finland. Scand. J. For. Res. 16:429–441.
- Mualem, Y. 1976. A new model for predicting the hydraulic conductivity of unsaturated porous media. Water Resour. Res. 122:513–522.
- McNeil, P., and J.M. Waddington. 2003. Moisture controls on *Sphagnum* growth and CO₂ exchange on a cutover bog. J. Appl. Ecol. 40:354–367.
- Price, J.S. 1996. Hydrology and microclimate of a partly restored cutover bog, Quebec. Hydrol. Processes 10:1263–1272.
- Proctor, M.C.F. 2000. Physiological ecology. p. 225–247. In A.J. Shaw and B. Goffinet (ed.) Bryophyte biology. Cambridge Univ. Press, Cambridge, UK.
- Richards, L.A. 1931. Capillary conduction of liquids through porous mediums. Physics 1:318–333.
- Schipperges, B., and H. Rydin. 1998. Response of photosynthesis of *Sphagnum* species from contrasting microhabitats to tissue water content and repeated desiccation. New Phytol. 140:677–684.
- Schlotzhauer, S.M., and J.S. Price. 1999. Soil water flow dynamics in a managed cutover peat field, Quebec: 1. Field and laboratory investigations. Water Resour. Res. 35:3675–3683.
- Schwärzel, K., J. šimnek, H. Stoffregen, G. Wessolek, and M.Th. van Genuchten. 2006. Estimation of the unsaturated hydraulic conductivity of peat soils: Laboratory versus field data. Vadose Zone J. 5:628–640.
- Silins, U., and R.L. Rothwell. 1998. Forest peatland drainage and subsidence affect water retention and transport in an Alberta peatland. Soil Sci. Soc. Am. J. 62:1048–1056.
- van Genuchten, M.Th. 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. Soil Sci. Soc. Am. J. 44:892–898.
- van Genuchten, M.Th., F.J. Leij, and S.R. Yates. 1991. The RETC code for quantifying the hydraulic functions of unsaturated soils. EPA/600/2– 91/065. USEPA, Ada, OK.