Hydrophysical evolution, soil water dynamics, and productivity of *Sphagnum* carpets in a regenerating cutover peatland

by

Neil MacKay Calvin Taylor

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Master of Science
in
Geography

Waterloo, Ontario, Canada, 2014

Abstract

The physical and hydrologic characteristics of cutover peatlands often inhibit the regeneration of typical peatland vegetation, particularly the keystone peat-forming genus *Sphagnum*, in the absence of active rehabilitation measures. Peatland restoration and rehabilitation techniques developed over the past two decades focus on the establishment of a *Sphagnum* carpet on cutover surfaces, largely through amelioration of hydrologic conditions. More recently there has also been increased interest in the use of cutover peatlands as sites for producing *Sphagnum* biomass commercially on a renewable basis, as this can be substituted for the slightly decomposed peat currently used in the production of horticultural growing substrates. As a result, there is interest in better understanding the soil water dynamics and hydrologic controls on productivity in regenerating *Sphagnum*-dominated cutover peatlands, which differ in many regards from natural peatlands. The purpose of this thesis is to describe the structural evolution, hydraulic properties, and productivity dynamics of *Sphagnum* layers regenerating on cutover peat surfaces, ranging from 3-43 years in age. This has applications to *Sphagnum* biomass production as well as to understanding the longer-term trajectory of restored cutover peatlands.

The Shippagan peatland, a block-cut cutover peatland located in northeastern New Brunswick, has been the site of investigations into *Sphagnum* biomass production on cleared cutover surfaces since 2004. Extensive spontaneous regeneration of *Sphagnum* has also occurred across much of the site outside the experimental areas. For this study, plots were established in seven areas of the site where regeneration began at different times. The hydrology (water table depth, distribution of soil moisture, evaporation, precipitation input) of each plot was monitored over the study season (May 24 to August 13, 2013) and gross ecosystem productivity measured frequently using chamber techniques. Following the study season, multiple vertical profiles were extracted from each plot for laboratory determination of the hydrophysical properties (bulk density, porosity, saturated hydraulic conductivity, soil moisture characteristic, unsaturated hydraulic conductivity–pressure relation) of the regenerated layers and underlying cutover peat.

The regenerated layers follow a pattern of evolution whereby the bulk density and retention capacity of the base of the profile (the ~5 cm thick layer directly overlying the cutover peat) increase with age as a result of decomposition and compaction. While the amount of water that can be held against tension within the profile appears to increase with the age of the regenerated layer, there is a general trend towards decreasing near-surface (0-3 cm depth) water content for a given depth of water table as the thickness of the regenerated layer increases. Near-surface water content is strongly

correlated ($p<0.05$; Pearson's Correlation Coefficient, two-tailed test of significance) with water table position at all plots, while canopy retention of precipitation is poor, suggesting the predominance of groundwater as a water source. The water table position remains above the former cutover peat surface for a substantial amount of the growing season (81±8% of study) at the >40 year old plots but not at the <10 year old plots (30±25% of study). This suggests that seasonal water table position may have increased over time relative to initial post-extraction conditions in the spontaneously regenerated areas as a result of the hydrophysical evolution of the profile. The hydrologic regime in these areas may be becoming more similar to that of a natural peatland, where water table fluctuations are confined entirely to the acrotelm. Productivity measurements indicate a broad tolerance within all study plots to observed environmental conditions, and in particular that insufficient supply of water does not limit productivity at the site even when the water table is >40 cm below the surface or when no direct precipitation is received for 16 days. Conversely, productivity may be frequently limited at the site by above-optimal water contents. Based on analysis of productivity response to changes in near-surface water content, a volumetric water content range of 0.13 to 0.50 is identified as optimal for growth.

The spontaneously regenerated layers studied here appear to be on a trajectory of structural and hydrologic evolution favouring peat formation, which is encouraging for the long term prospects of restored cutover peatlands. The *Sphagnum* species studied are tolerant to at least moderate water table drawdowns, though they may be less tolerant to periods of especially high water table, and biomass production operations using these species should take this into consideration. The large predominance of capillarity as a water source, and the hydrologic connectivity between the regenerated layers and cutover peat, imply that control of subsurface water level is an effective means of optimizing hydrologic conditions for biomass production. This study is the first to specifically describe the ecohydrology and long term structural evolution of *Sphagnum* regenerating on cutover peat surfaces.

Acknowledgements

I would like to thank, first and foremost, my advisor, Jonathan Price, for the opportunity to work with him. His mentoring and guidance over the past two years have been invaluable.

I would like to acknowledge funding from Line Rochefort through the NSERC Industrial Research Chair in Peatland Management, as well as from Jonathan Price through the NSERC Discovery Grant.

I would also like to thank Catherine Brown for her assistance with field work and general enthusiasm for life, Maria Strack for her advice on carbon-related matters, and the staff and students at the Wetland Hydrology Laboratory, most notably Colin McCarter and Jonathan Goetz, for their assistance with experiments and equipment.

Table of Contents

List of Figures

List of Tables

Note: Chapters 2 and 3 of this thesis are written as independent manuscripts to be submitted for publication. As a result, some of the text within the manuscripts repeats information stated elsewhere within the thesis.

1.0 Introduction

Canadian peatlands cover an extensive area, estimated at 113 million hectares or roughly 11 percent of the total Canadian landmass, and comprise more than three quarters of all wetlands in Canada by area (Daigle & Gautreau-Daigle, 2001). The accumulation of organic matter as peat is the defining feature of these ecosystems, and is made possible by low rates of decomposition resulting from perennially inundated soils and recalcitrant plant material (Clymo & Hayward, 1982; Clymo, 1984; Rydin & Jeglum, 2009). Of great importance in many types of peatland is the genus *Sphagnum*, which often dominates the landscape in the climax stage of ecological succession owing to its ability to create an environment wherein it can outcompete other plants (Clymo & Hayward, 1982; Kilham, 1982; van Breeman, 1995; Rochefort, 2000). As a result, plant material from *Sphagnum* constitutes a large proportion of Canadian and global peat stocks (Loisel *et al.*, 2014) and it has been suggested that more carbon is stored in dead and living *Sphagnum* tissue than in any other genus of plant (Clymo & Hayward, 1982).

Sphagnum peat is valued for its unique water retention properties, high cation exchange capacity, and sterility, qualities which make it an excellent growing medium for potted plants (Silvan *et al.*, 2012). Though peat is often used as biofuel in other parts of the world, the vast majority of Canadian *Sphagnum* peat is extracted for use in horticultural products (Cleary *et al.*, 2005). The horticultural peat industry is significant in some regions of Canada, notably eastern New Brunswick and the Bas-St-Laurent region of Quebec, generating an estimated $260 million in annual revenue (Natural Resources Canada, 2014). Peat extraction involves the ditching and drainage of sites, the removal of the surface layers of vegetation, and collection of the upper layers of peat. Prior to the 1970s peat was extracted predominantly by hand using traditional block-cut methods. The resulting landscape was one of dug trenches separated by raised baulks where peat blocks were stacked to dry. Since this time, vacuum-extraction techniques employing heavy machinery and necessitating deeper drainage have become the industry standard (Lavoie & Rochefort, 1996; Poulin *et al.*, 2005), although a large number of abandoned block-cut sites still exist (Lavoie *et al.*, 2003).

Peat extraction operations alter the physical and hydrologic conditions at cutover sites with respect to their former state. In natural peatlands, plants grow on layers of their own dead remains that become progressively more decomposed with depth (Clymo & Hayward, 1982; Hayward & Clymo, 1982; Clymo, 1984), creating a corresponding gradient in the hydraulic properties influencing water storage and transmission (Boelter, 1968). In cutover peatlands, the exposure of more highly decomposed peat at the surface results in lower and more variable water tables (Schouwenaars, 1993; Price, 1996) and lowered soil water pressures (Price, 1996, 1997; Price &

Whitehead, 2001) as a consequence of the greater abundance of smaller pore sizes and corresponding lower specific yield in cutover peat (Price, 1996, 1997, 2003). The combination of these factors often inhibits the regeneration of non-vascular *Sphagnum* mosses and other peatland species in the absence of active rehabilitation measures (Lavoie & Rochefort, 1996; Price, 1996). While spontaneous regeneration of *Sphagnum* is generally very poor in vacuum-extracted peatlands (Lavoie *et al.*, 2003; Price *et al.*, 2003; Poulin *et al.*, 2005) the greater abundance of suitably wet microtopography, larger viable seed banks, and less extensive drainage of block-cut peatlands make spontaneous regeneration relatively more common in these environments (Price *et al.*, 2003; Poulin *et al.*, 2005; Triisberg *et al.*, 2011). Nonetheless, large areas of block-cut peatlands can remain devoid of *Sphagnum* decades after abandonment (Van Seters & Price, 2002; Poulin *et al.*, 2005).

Although much less than one percent of Canadian peatlands have been affected by peat extraction (Daigle & Gautreau-Daigle, 2001), cumulative losses in areas like the Bas-St-Laurent have been estimated to be in excess of 70 percent (Laframboise, 1987), and in combination with other land use pressures on peatlands extraction operations can constitute a threat to regional biodiversity (Poulin *et al.*, 1999; Daigle & Gautreau-Daigle, 2001). Additionally, abandoned cutover peatlands tend to become large and persistent sources of atmospheric CO_2 due to vegetation removal and the oxidation of cutover peat (Waddington & Price, 2000; Waddington *et al.*, 2002; Petrone *et al.*, 2003). In response to these concerns, methods have been developed over the past 20 years for restoring cutover sites to functioning, peat-accumulating ecosystems dominated by *Sphagnum* mosses (Ferland & Rochefort, 1997; Rochefort *et al.*, 2003). The main components of the North American method to peatland restoration (Rochefort *et al.*, 2003; Quinty & Rochefort, 2003) are as follows: clearing and leveling of cutover surfaces to bare peat, landscaping of surfaces as necessary to increase on-site retention of water, collection of viable *Sphagnum* diaspores from a donor site, distribution of diaspores across the cutover surface at a 1:10 (donor site: restoration site) areal ratio, covering with straw mulch to improve microclimatic conditions at the surface, and phosphorus fertilization. The creation of a *Sphagnum* carpet on cutover surfaces is seen as imperative both from an ecological and a long-term carbon sequestration perspective to the successful restoration of a site (Ferland & Rochefort, 1997; Rochefort, 2000; Rochefort *et al.*, 2003; Waddington *et al.*, 2010).

The majority of the restoration techniques in the North American method focus on the creation of favourable hydrologic conditions for *Sphagnum* regeneration as *Sphagnum* is poikilohydric, lacking physiological mechanisms to control water loss such as stomata (Proctor, 1982; Titus & Wagner, 1984). Water supply to the capitulum, the uppermost ~1.5 cm of the plant where most growth occurs, is primarily via external capillary flow between pendant leaves along the

outside of the stems (Clymo & Hayward, 1982; Proctor, 1982). The water content in the capitula is the most important control on photosynthesis under non-light-limiting conditions (Busby & Whitfield, 1978; Dilks & Proctor, 1979; Schipperges & Rydin, 1998). If upwards flows cannot balance evaporative demand and the soil water pressure becomes too low at the surface, hyaline cells providing structural support to chlorophyllose cells will drain (Clymo & Hayward, 1982; Lewis, 1988) and photosynthesis will be drastically reduced (Gerdol *et al.*, 1996; McNeil & Waddington, 2003). Photosynthesis can also be reduced by an overabundance of water if the film covering leaves is thick enough to reduce CO_2 diffusion rates (Dilks & Proctor, 1979; Williams & Flanagan, 1998). Due to the reliance on passive water transport and the importance of water content in regulating photosynthesis, establishing a hydrologic regime to support the development of a *Sphagnum* layer is critical to the success of restoration efforts.

While peatland restoration has been adopted widely as a management practice by the Canadian horticultural peat industry (e.g. Canadian Sphagnum Peat Moss Association, 2005**)** and as policy by provincial regulatory bodies (e.g. New Brunswick Department of Natural Resources, 2014), there has been increased interest over the past decade in using cutover sites as locations for producing *Sphagnum* fibre on a commercial scale (Campeau & Rochefort, 2002). Fresh dried *Sphagnum* biomass can be substituted for the slightly decomposed "white peat" currently used by the industry in the production of growing substrates without losses in crop yield (Emmel, 2008). Producing *Sphagnum* biomass in this manner would reduce or eliminate the need to exploit new areas for horticultural peat production, and is thus seen as a more sustainable and climate-friendly alternative to conventional peat production (Boon & Verhagen, 2008; Silvan *et al.*, 2012). However, research into *Sphagnum* biomass production is still at a relatively early stage and many questions remain about the most efficient methods of production, the optimal timescale for production cycles, and the constraints on biomass yields.

1.1 Study Site: The Shippagan Peatland and Experimental *Sphagnum* Farming Station

The Shippagan peatland is located just south of the town of Shippagan, New Brunswick on the Acadian Peninsula (47°40'N, 64°43'W). Mean annual air temperature in Shippagan is 4.8°C and mean annual precipitation is 1077 mm, of which 69 percent falls as rain (Environment Canada, 2014). Approximately 140 ha of the site was mined using block-cutting methods over the mid-twentieth century, and the site was abandoned following the end of operations circa 1970 (Robert *et al.*, 1999). The trenches at the site are approximately 18 m wide with 0.6 – 1 m of residual peat, and

are separated by 5 m wide baulks that are ~1 m higher in elevation than trenches (Robert *et al.*, 1999). Spontaneous revegetation of extracted areas is extensive, with *Sphagnum* species occurring within a large majority of the trench area but mostly absent from baulks. The site appears to be exceptional in the extent of *Sphagnum* regeneration with respect to other block-cut peatlands in eastern North America, where spatial coverage of regenerated areas in trenches is typically less than 30 percent (Poulin *et al.*, 2005). It should be noted, however, that many of these peatlands are located in more continental climatic regions than the Shippagan peatland. Vascular species, mainly ericaceous shrubs and *Eriophorum* spp. have recolonized the baulks and many areas of the trenches at the Shippagan peatland (Robert *et al.*, 1999).

The Shippagan peatland was selected by the Peatland Ecology Research Group (PERG) and its partners in industry as a site for research into *Sphagnum* biomass production under the Natural Sciences and Engineering Research Council (NSERC) Industrial Research Chair in Peatland Management program, which began in 2003 and has since been renewed twice, in 2008 and 2013. The goal of this research is to investigate large scale *Sphagnum* fibre production methods to supply material for renewable commercial growing substrate production as well as donor material for future peatland restoration projects (Pouliot *et al.*, 2014). The existing shallow basins at the site minimized the amount of resurfacing work required, and there was an abundance of potential donor material within the undisturbed and spontaneously regenerated areas of the peatland (Landry & Rochefort, 2009). Two areas within the peatland were selected as experimental basins, where trenches measuring approximately 15 × 90 m were cleared down to bare peat and seeded with *Sphagnum* diaspores following the standard North American approach in the spring of each year, beginning in 2004 (Landry & Rochefort, 2009). Additional production cycles were started in 2006, 2008, 2010, 2011, and 2012.

1.2 Objectives

While the hydrology of cutover peatlands has been the subject of a number of investigations, there is scant research on the development of regenerated *Sphagnum* layers in such environments and how the water storage and transmission properties of these layers evolve over time. Some authors (Schouwenaars & Gosen, 2007; McCarter & Price, 2014) have suggested that the regenerated layer quickly becomes vulnerable to water stress as it grows above the cutover surface owing mainly to low unsaturated hydraulic conductivity. McCarter and Price (2014) reported poor hydraulic connectivity between cutover peat and regenerating *Sphagnum* and proposed that in order for the regenerating layer to access more of the water stored in the underlying peat, the base of the profile

requires sufficient time for decomposition so that the discontinuity in hydrophysical properties is substantially reduced. However, the timescale over which this process might occur is unknown. Furthermore, no studies to date have linked the hydrology of regenerating *Sphagnum* in cutover environments to measurements of productivity on a sub-seasonal timescale, and consequently the optimal hydrologic conditions for *Sphagnum* biomass production and restoration projects remain uncertain. Therefore, the objectives of this research are as follows:

1. To characterize and compare the physical structure and hydraulic properties of regenerated *Sphagnum* and remnant cutover peat in regenerated areas ranging in age from 3-43 years and from 3-40 cm in thickness
2. To determine how the regenerated layers function hydrologically under field conditions and what controls the water content at the surface
3. To determine how soil water dynamics and surface water content relate to the productivity of the regenerated layers

1.3 General Approach

This thesis consists of two separate but related manuscripts on the subject of the hydrophysical properties, hydrologic behaviour, and productivity dynamics of *Sphagnum* at different stages of regeneration on cutover peat surfaces. I was primarily responsible for the design, implementation and execution of field work and laboratory experiments, as well as the writing of both manuscripts. The first manuscript (Soil water dynamics and hydrophysical properties of regenerating *Sphagnum* layers in a cutover peatland) summarizes the hydrophysical properties (bulk density, porosity, saturated hydraulic conductivity, water retention curves, and unsaturated hydraulic conductivity–pressure relations) and hydrologic behaviour of seven regenerated *Sphagnum* layers of differing ages and thicknesses located in different areas of the Shippagan peatland. Intensive field observations of soil water dynamics in regenerated layers are presented in combination with laboratory-determined hydrophysical parameters to help explain the structural evolution of the layers and the consequent changes in the observed hydrologic response to varying environmental conditions. The second manuscript (Hydrologic controls on productivity of regenerating *Sphagnum* in a cutover peatland) links the instantaneous hydrologic conditions observed in the field to the productivity as determined using chamber techniques. Optimal hydrologic conditions for growth are estimated by isolating the effect of water content in the uppermost (0-3 cm) layer on variance in gross ecosystem productivity from the effects of other measured variables using a mixed linear

modeling approach. Together, these two manuscripts represent the first comprehensive description of the structural evolution and ecohydrology of a regenerating *Sphagnum*-dominated cutover peatland.

2.0 Manuscript 1: Soil water dynamics and hydrophysical properties of regenerating Sphagnum layers in a cutover peatland

2.1 Abstract

The physical and hydrologic conditions in cutover peatlands often act as barriers to the regeneration of the keystone peat-forming genus *Sphagnum*. Although previous work has suggested that *Sphagnum* mosses regenerating on cutover peat surfaces quickly become vulnerable to water stress as the thickness of the regenerated layer increases, uncertainties regarding the storage and transmission properties of this layer and how these might evolve over time have made this assertion difficult to evaluate. This study investigates the hydrophysical properties and hydrologic behaviour of regenerating *Sphagnum* layers ranging from 3-43 years in age using both field and laboratory methods. The regenerated layers follow a pattern of structural evolution whereby the bulk density and retention capacity of the basal layers directly overlying the cutover peat increase over time. Capillarity was a much stronger control on surficial water content (θ) than precipitation, which was poorly retained in the *Sphagnum* canopy, suggesting that regulation of water table position is an effective method of controlling θ as a means of optimizing productivity. In general, the θ sustained at a given water table position decreased as layer thickness increased, although this was not always the case. Analysis of water table position relative to the former cutover peat surface suggests that seasonal water table position may have increased at older (>40 year old) areas of the site relative to initial conditions, and that the hydrologic regime may be becoming increasingly similar to that of a natural bog peatland.

2.2 Introduction

The exploitation of bog peatlands for *Sphagnum* peat is an important industry in certain regions of Canada, generating an estimated $260 million dollars in annual revenue (Natural Resources Canada, 2014). *Sphagnum* peat is valued for its high water retention capacity among other properties, and is used within Canada primarily by the horticulture industry as a growing substrate (Cleary *et al.*, 2005). Peat extraction involves site drainage via ditching, the removal of surface vegetation, and extraction of the upper layers of peat. Prior to the 1970s, most peat was extracted by hand using traditional block-cutting methods, resulting in a landscape of wide, shallow extraction trenches separated by narrower baulks on which peat blocks were placed to dry. While this method is no longer used, a large number of abandoned block cut sites still exist (Lavoie *et al.*, 2003). Modern peat extraction operations are mechanized, utilizing specialized machinery to cut and

vacuum peat from the surface. This method requires a deeper and more extensive drainage network and cambering of surfaces to allow heavy machinery to be used on site. In both methods, the prevailing physical and hydrologic conditions following extraction deter natural regeneration of the keystone peat-forming genus *Sphagnum* in most cases without active restoration (Lavoie & Rochefort, 1996; Price, 1996; Poulin *et al.*, 2005).

The need to address peatland losses in regions of intense extraction activity led to the development in the 1990s of methods for restoring abandoned sites to functional, carbon-accumulating ecosystems dominated by *Sphagnum* mosses (Ferland & Rochefort, 1997; Rochefort, 2000; Rochefort *et al.*, 2003). More recently, research has also focused on the potential of cutover peatlands as sites for growing *Sphagnum* biomass in order to meet the demand for horticultural substrate without exploiting new areas (Gaudig & Joosten, 2002; Gaudig, 2012; Pouliot *et al*., 2014). *Sphagnum* biomass has been found to be a suitable or even a superior growing media substitute for "white peat", the slightly decomposed *Sphagnum* peat currently used by the industry, and is considered a sustainable alternative (Emmel, 2008; Silvan *et al.*, 2012).

The ability of non-vascular *Sphagnum* mosses to survive desiccation and photosynthesize depends on their ability to maintain adequate moisture content at the capitula (Clymo & Hayward, 1982; McNeil & Waddington, 2003), a cluster of leaves and branches comprising the uppermost part of the plant. This, in turn, is controlled primarily by capillary flow through the underlying layers of peat and moss (Clymo & Hayward, 1982), with the vast majority of flow occurring between overlapping pendant branches and leaves along the outside of the stem (Proctor, 1982). Hyaline cells within the leaves hold water critical for structural support and the maintenance of photosynthetic processes (Clymo & Hayward, 1982). At soil water pressures between -200 and -600 cm, these cells will drain (Clymo & Hayward, 1982; Lewis, 1988) and photosynthesis will essentially cease (Gerdol *et al.*, 1996). In natural peatlands the living mosses grow on layers of dead remains that become progressively more decomposed with depth (Clymo & Hayward, 1982; Hayward & Clymo, 1982; Clymo, 1984), creating a corresponding gradient in the hydraulic properties influencing the storage and transmission of water. By comparison, the hydrophysical properties of highly decomposed cutover peat can present a hostile environment for *Sphagnum* regeneration. Reduced specific yield in cutover peat relative to natural peatland surfaces can lead to low and highly variable water tables below cutover surfaces (Schouwenaars, 1993; Price, 1996). Furthermore, soil water pressures in cutover peat may be below the threshold at which the capillary forces generated by the mosses can extract enough water to offset evaporative losses, preventing recolonization of cutover surfaces (Price & Whitehead, 2001).

It has been suggested by some authors that *Sphagnum* is at increasing risk of water stress as it grows higher above the cutover surface due to low unsaturated hydraulic conductivity of the regenerated layers limiting upwards water fluxes (Schouwenaars & Gosen, 2007; McCarter & Price, 2014). While some studies have examined the hydrological processes operating within *Sphagnum* hummocks (eg. Yazaki *et al.*, 2006; Price & Whittington, 2010), only a couple (McCarter & Price, 2014; Ketcheson & Price, 2014) have looked specifically at processes occurring in the context of regenerating cutover peatlands. The evolution of regenerating *Sphagnum* profiles also has not been well studied, and it is unknown how the water storage and transmission properties may change over time. This presents a barrier to creating optimal hydrologic conditions in bog restoration and *Sphagnum* biomass production operations. An improved understanding of the soil water dynamics of regenerating *Sphagnum* in cutover peatlands is therefore desirable. The specific objectives of this paper are: 1) to demonstrate differences in physical and hydraulic properties of *Sphagnum* profiles at different stages of regeneration; 2) to use differences in properties determined in the laboratory to explain the soil water dynamics within the profiles observed under field conditions, and; 3) to discuss potential implications for water management.

2.3 Methodology

2.3.1 Study Area

Data was collected in a large abandoned cutover peatland located just south of Shippagan, New Brunswick (47°40'N, 64°43'W). Mean annual air temperature in Shippagan is 4.8°C and mean annual precipitation is 1077 mm, of which 69% falls as rain (Environment Canada, 2014). The site was mined using traditional block-cut methods and consequently is characterized by an alternating baulk and trench structure. Trenches ~18 m wide are separated by ~5 m wide and ~1 m high baulks, with residual peat depths ranging from 0.6 – 1 m in the trenches (Robert *et al.*, 1999). The site was abandoned following the end of extraction operations in 1970. In the trenches, but not the baulks, spontaneous regeneration of *Sphagnum* has occurred across most of the site. In this regard the site differs from many other abandoned block-cut peatlands in eastern North America (Poulin *et al.*, 2005) primarily at more continental locations (Gonzalez *et al*., 2013). Natural *Sphagnum* regeneration has been found to be more common at block-cut than at vacuum-extracted sites as the landscape of block-cut peatlands offers a greater variety of microtopographic habitats (Price *et al.*, 2003; Triisberg *et al.*, 2011), although regeneration is generally limited to the wettest parts of the site (Price & Whitehead, 2001). Two sections of the site have been cleared and divided into plots for *Sphagnum* biomass production experiments dating from 2003 (Landry & Rochefort, 2009).

2.3.2 Field Data Collection

Seven plots were established in different areas of the study site for hydrological monitoring and hydrophysical analysis. Three of these plots were in the spontaneously revegetated area of the site, assumed to have begun regeneration at the time of abandonment (plots 1970-A, 1970-B, and 1970-C), and are collectively referred to here as SPONT. These had well-developed *Sphagnum* profiles (hereafter referred to simply as "profiles") ranging from 23 – 40 cm in height above the former cutover peat surface. The other four plots were located within trenches where *Sphagnum* has regenerated on cleared cutover surfaces, having been artificially introduced for biomass production experiments over the period 2003 – 2012 (Landry & Rochefort, 2009). These plots had profile heights of 3 – 17 cm (plots 2004, 2006, 2008 and 2010), and are collectively referred to as EXPER. Plot names denote the year in which regeneration began or was assumed to have begun. Each plot consisted of three replicate sub-plots in close proximity and of apparent homogeneity in structure and species composition. Sub-plots were delineated by metal collars inserted into the profile to a depth of 40 cm, which were also used to measure productivity in a concurrent study not discussed in this paper. All sub-plots were flat and completely covered by regenerating *Sphagnum*. Most areas were characterized by a mix of *Sphagnum* species within section *Acutifolia* (*S. fuscum* (Schimp.) Klinggr., *S. rubellum* Wils., *S. flavicomans* (Sect. *Acutifolia*)), with significant presence of *S. magellanicum* Brid. at many locations. Nomenclature for *Sphagnum* species follows that of Anderson (1990). The relative proportion of species present within each sub-plot was estimated visually, while capitula density was estimated by counting the number of individuals within a 2 cm square quadrant of transparent graphing paper at 16 randomly selected locations within each plot (Table 2-1). At locations where ericaceous shrubs or grasses were present within the sub-plots, the above-ground portion of the plant was clipped and replaced with cuttings of ericaceous branches or grass leaves, as appropriate, so as to maintain similar surface shading and to restrict latent energy exchanges to the moss surface. Cuttings were changed regularly and were removed from the surface during measurements. A system of boardwalks was constructed to prevent disturbance of *Sphagnum* profiles during measurements.

Each plot was instrumented with a well containing a pressure transducer to record water table position (WT), and weighing lysimeters were used in conjunction with data from a meteorological station to estimate evaporation using the Priestley-Taylor method (Priestley & Taylor, 1972) following the approach outlined in Van Seters and Price (2001). Two raingauges, one manual and one automated, recorded precipitation input at the site. A portable WET-Sensor™ (Delta-T Devices, Cambridge, UK) time-domain reflectometry (TDR) device was used to measure the volumetric

moisture content (θ) at the growing surface of each plot. During each measurement, θ was sampled at five locations within each sub-plot and averaged across the three sub-plots to obtain a plot-scale θ value for this layer. Two measurements were taken at each sampling location, one with the 6 cm long probes inserted vertically to full depth and the other with the probes inserted down to a line drawn at half the probe length in order to generate θ values for both the 0-6 cm and 0-3 cm depth layers. TDR calibration curves for individual plots were developed using gravimetrically-determined θ and TDR-derived readings taken from *Sphagnum* samples of known volume as they dried, following the method of Topp *et al.* (1980). Separate calibrations were performed for the 0-6 cm layer and 0-3 cm layer measurements at each plot to account for differences resulting from the partial exposure of the probes to air. Plot- and layer-specific calibration curves were then applied to all readings from the WET-Sensor™.

Three plots (2006, 2010, and 1970-C), taken to be representative of three different stages of regeneration, were fully instrumented with CS605 TDR probes (Campbell Scientific Canada Corp., Edmonton, Alberta) and tensiometers to quantify the moisture regime within and below the regenerated profile. TDR probes were inserted horizontally at regular depth intervals in the *Sphagnum* profile and cutover peat of each sub-plot and connected to dataloggers (Model CR1000, Campbell Scientific Canada Corp.) to record θ of discrete soil layers at 30 minute intervals. Tensiometers were installed in the cutover peat only, as poor contact between the less-decomposed moss and the ceramic cups prevented direct measurement of the soil water pressure in the regenerated layer. Probe depths within the profile are given relative to the growing surface, with positive numbers denoting the depth below the surface. Depths for probes located within the peat are given relative to the top of the cutover peat layer, with negative numbers denoting the depth below the cutover peat. For probes located within the peat, positive numbers in parentheses denote the depth relative to the growing surface.

Direct precipitation was experimentally excluded from all plots during the 16 day period between July 28 and August 13, 2013, to evaluate the effect of the removal of this water source on surface moisture dynamics. This was accomplished using clear plastic sheets tented over the collars at each plot and attached to posts inserted into the peat. Plastic sheets were removed during measurements of θ and other parameters, and were high enough above the collars (~70 cm at the tent peak) so that air temperature and surface shading would not be significantly altered.

Profiles at each plot were sampled for hydrophysical analysis using PVC rings 10 cm in diameter and 5 cm in height. After carefully cutting around the outside of the rings with scissors, the

rings could easily slide down around a sample at a targeted depth. Samples were removed by cutting along the bottom of the ring. This system permitted the preservation of the *in-situ* structure of the moss and partially decomposed plant matter during transport and laboratory analysis. Full profiles of the regenerated *Sphagnum* layer and the top layer of cutover peat were sampled from each sub-plot in 5 cm increments at the end of the study season, for a total of 3 full profiles per plot. Additional 5 cm samples were taken from the surface layer of each plot, from which the top 2 cm (roughly the capitula) were later removed so that they could be analyzed as a distinct layer. This was accomplished by spraying samples with water and freezing to provide the necessary structural stability before cutting with a fine-toothed saw.

2.3.3 Laboratory Analysis

The vertical saturated hydraulic conductivity (K_{sat}), soil water pressure (ψ) – retention curve, unsaturated hydraulic conductivity – ψ (K_{ψ}) curve, bulk density, and porosity of each profile sample was determined in the laboratory. All water used in these analyses was filtered by a reverse osmosis system. K_{sat} was measured using a Darcy permeameter. All samples were wrapped in plaster and sealed with paraffin wax around the sides before being placed in the permeameter so as to leave open a flow face on the top and bottom and eliminate preferential flow around the sides while preserving the structural integrity of the sample (Hoag & Price, 1997). Darcy's Law was used to calculate sample K_{sat} from the rate of discharge across a known hydraulic gradient and flow face area. Bulk density was determined by oven-drying samples at 80°C until they reached a stable mass. Porosity was estimated by placing ground soil samples of known mass in a known volume of kerosene to find the particle density by displacement, then calculating porosity as $(1 - \frac{\text{particle density}}{\text{bulk density}})$ following the liquid pycnometer method outlined by Blake and Hartge (1986).

The ψ – retention and K_{ψ} curves were determined following the method of Price *et al.* (2008) at ψ of -3, -6, -12, -20, and -30 cm. Two samples from select depth intervals (0-2 cm capitulum layer, 0-5 cm, 5-10 cm, profile base, top 5 cm of cutover peat) at each plot were chosen for analysis, as equipment and time constrictions limited the number of samples that could be run simultaneously. Briefly, samples were placed on tension plates covered with 25 μm pore size Nitex™ mesh which were connected to an Erlenmeyer flask beneath. This arrangement allowed the ψ of samples to be controlled by manipulating the height of the flask outlet below the tension surface, effectively creating a hanging column of water beneath the plate. A constant head was maintained within the flask by manually replacing water lost to overflow or evaporation. The flask outlet height was set

relative to the midpoint of the sample to achieve the desired average value of ψ within the sample. Samples were weighed daily and allowed to equilibrate at a given ψ until masses stabilized (<1 $g \cdot day^{-1}$ change), at which point θ for that ψ was determined gravimetrically. K_ψ was measured once all samples had equilibrated to a given ψ. K_ψ measurements used a second Nitex™-covered tension disc placed on top of the sample, connected to a reservoir which was maintained at a constant head value equivalent to the equilibrated ψ at the top of the sample. The beaker outlet was then lowered by half the height of the sample, maintaining the same average ψ within the sample and inducing a constant discharge at a hydraulic gradient of 1. After equilibrating for an hour, the rate of discharge was measured to determine K_ψ using Darcy's Law. All discharge measurements retained for analysis had $r^2>0.9$.

The time intensity of the methods involved limited the number of samples that could be processed, preventing a rigorous statistical comparison of hydrophysical parameters between different plots. Properties of the profiles are therefore compared descriptively in the discussion.

2.4 Results

2.4.1 Hydrophysical Properties

The bulk density of all profiles increased with depth below the surface (Figure 2-1). Both SPONT and EXPER had similar bulk densities in the top 5 cm (average 0.021±0.005 and 0.018±0.005 $g \cdot cm^{-3}$, respectively). However, SPONT had notably greater bulk densities in the 5 cm layer directly overlying the cutover peat (average 0.061±0.013 $g \cdot cm^{-3}$) compared to EXPER (average 0.026±0.009 $g \cdot cm^{-3}$). Peat samples had the highest average bulk density at 0.073±0.012 $g \cdot cm^{-3}$.

The ψ – θ relation for all tested depth intervals is shown in Figure 2-2**.** Water retention capacity for ψ<0 was generally higher in the basal layer than in overlying layers, although the capitulum (0-2 cm) layer had a higher retention capacity than the 0-5 cm and 5-10 cm depths at most plots. The capitulum layer at EXPER plots 2008 and 2010 had markedly higher retention capacity than most other plots, but approached comparable values of θ at ψ=-30 cm. Retention at ψ=-30 cm, the lowest measured pressure, was substantially higher in the basal layer at SPONT (average 0.66±0.10) when compared to the same layer at EXPER (average 0.40±0.09), and both groups had higher retention in the basal layer relative to the surface (0-5 cm) layer (Figure 2-2, bottom right). The difference between SPONT and EXPER was negligible in the surface (0-5 cm and 5-10 cm) layers, with the exception of plot 1970-C, which had much higher θ than other plots across the measured range of ψ.

Bulk density was found to be positively correlated with water retention capacity of samples at $\psi<0$ (Figure 2-3). The relationship between these parameters was best approximated by a linear function at ψ=-30 cm and by a semi-logarithmic function at all higher ψ. After scaled log transformation of θ for the aforementioned ψ values, r^2 of the bulk density – θ relationship was >0.77 across the range of ψ tested. Peat samples showed much less variation in the slope of the bulk density – retention curve throughout this ψ range than did *Sphagnum* samples.

The K_{sat} and porosity of samples showed less distinct patterns of variation with depth. K_{sat} was lower in the basal layer than at the top of the profile at all plots, although there was substantial variability at most depth intervals. Values for *Sphagnum* samples ranged from 6.6×10^{-5} to 1.5×10^{-3} $m \cdot s^{-1}$ while peat samples had values about an order of magnitude lower (average 1.0×10^{-4} $m \cdot s^{-1}$) than surficial *Sphagnum* samples. K_{sat} was weakly negatively correlated with bulk density (r^2=0.53). Porosity for all samples was very high, ranging from 0.91 to 0.99, and tended to decrease with depth. Peat samples had a slightly lower average porosity (0.93±0.01) than *Sphagnum* samples (average 0.97±0.02).

K_ψ curves for all tested samples are shown in Figure 2-4**.** K_ψ dropped by an average of four orders of magnitude between ψ=0 cm (saturation) and ψ=-30 cm. Despite there being differences between samples in other properties, samples tended to follow a similar relationship between ψ and K_ψ, with about one and a half orders of magnitude variability between all samples at any given ψ. The implications of this are explored further in the discussion section.

Plot	*S. flavicomans*	*S. fuscum*	*S. magellanicum*	*S. rubellum*	Capitulum density (count · cm^{-2})	Average layer thickness (cm)
2004	0.00	0.00	0.43	0.57	2.07 ± 0.40	17
2006	0.00	0.36	0.08	0.56	2.44 ± 0.30	10
2008	0.09	0.06	0.50	0.35	1.97 ± 0.21	3
2010	0.42	0.00	0.20	0.39	2.64 ± 0.34	3.5
1970-A	0.00	0.16	0.54	0.30	1.58 ± 0.17	30
1970-B	0.97	0.00	0.00	0.03	2.68 ± 0.36	34
1970-C	0.00	0.00	0.02	0.99	3.31 ± 0.15	24

Table 2-1: The relative proportion of *Sphagnum* species present within the collars at each plot, shown as an average across the three collars. Values are rounded to two digits and may not add exactly to one. Spatial densities of capitula are also shown ±SD.

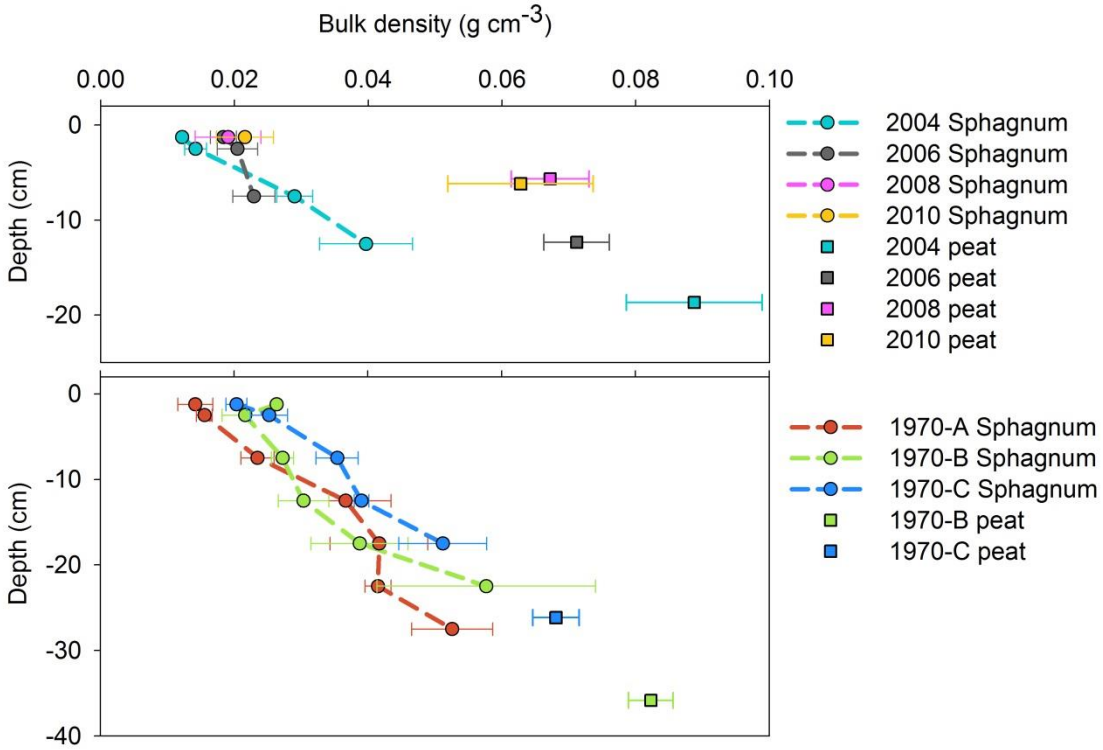


Figure 2-1: Bulk density depth profiles of regenerated *Sphagnum* profiles ("*Sphagnum*") and the upper 5 cm of remnant cutover peat for all sites (*n*=3 for each point). Sampling of cutover peat samples at site 1970-A was prevented by high water table during sampling period. Error bars show ±SD.

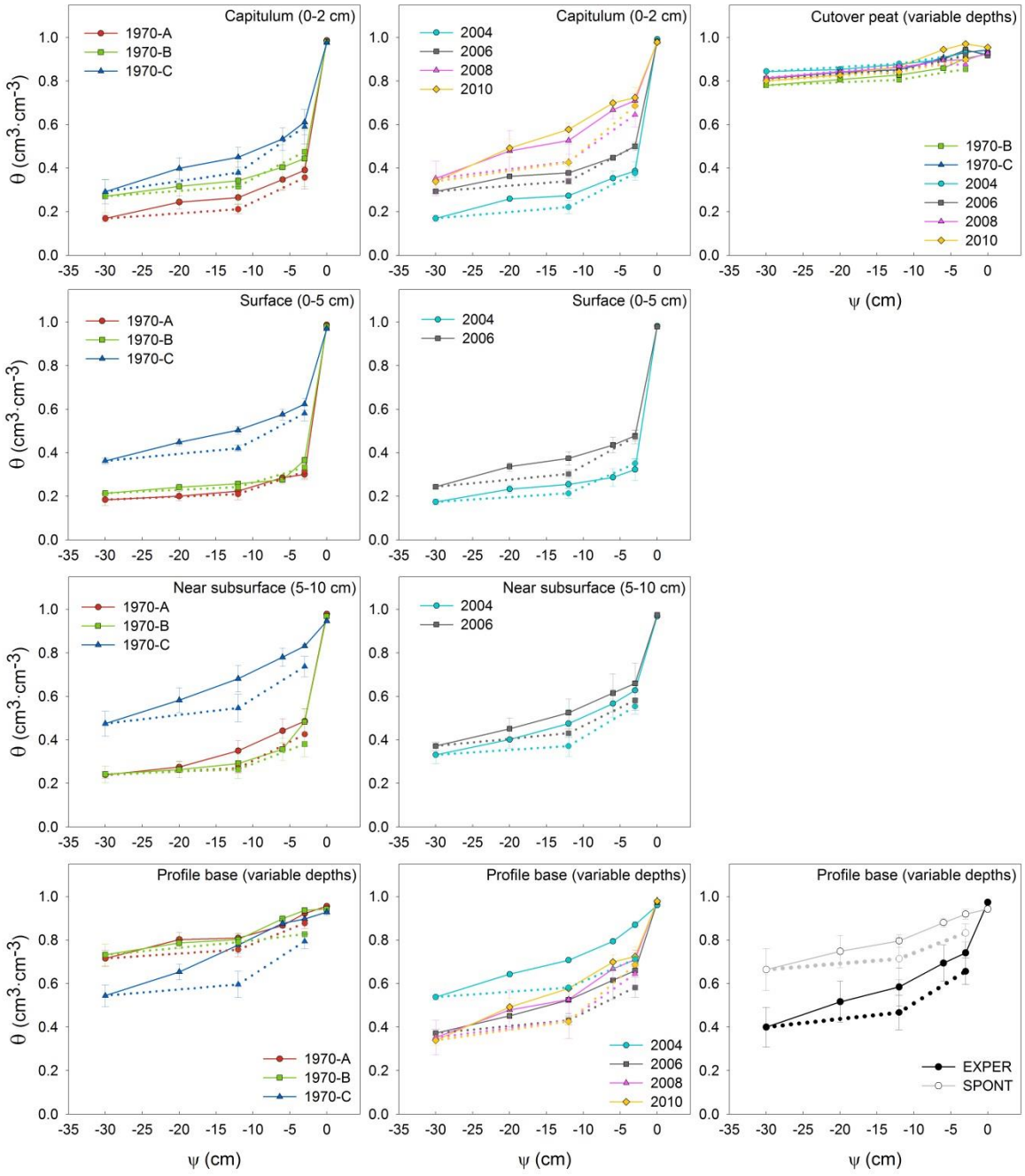


Figure 2-2: Retention curves for samples taken from different profile depth intervals at each site (n=2 for all points except cutover peat values, where n=1). Data for SPONT is shown at left, EXPER in the center column, and cutover peat for all sites at right. The bottom right panel shows group average retention curves for EXPER and SPONT. The profile base refers to the 5 cm layer directly overlying the former cutover peat surface at each site. Values for ψ=0 were derived from sample porosity. Solid lines and dotted lines indicate retention curves during lowering and raising of soil water pressure, respectively. Error bars show ±SD in θ

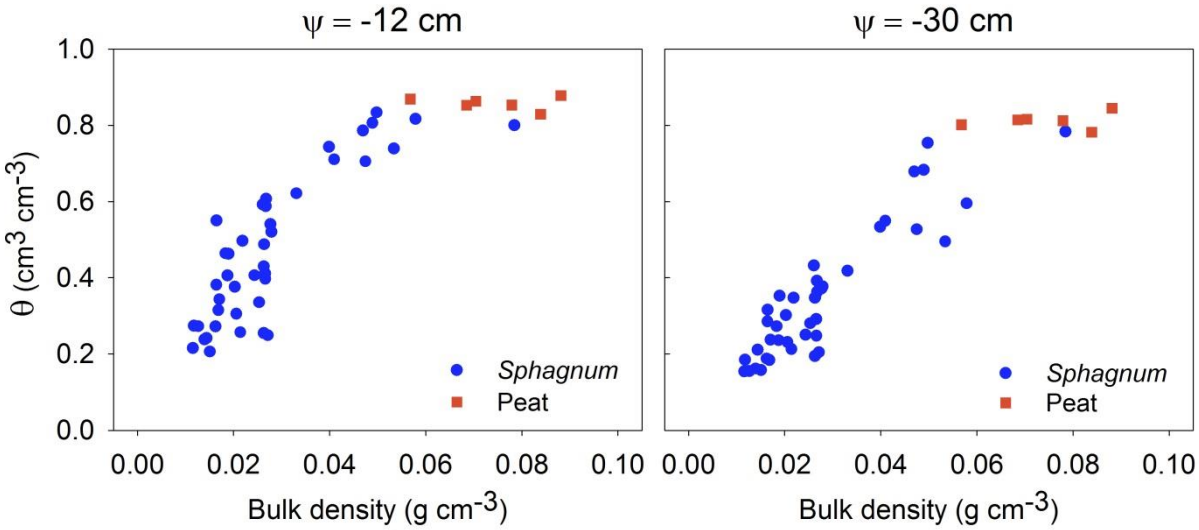


Figure 2-3: Relationship between bulk density and volumetric water content at tension for all samples. Water contents at two tension levels are shown here as typical examples of this relationship. Samples tended to follow a linear relationship at ψ=-30 cm and semi-logarithmic relationship at all other measured ψ.

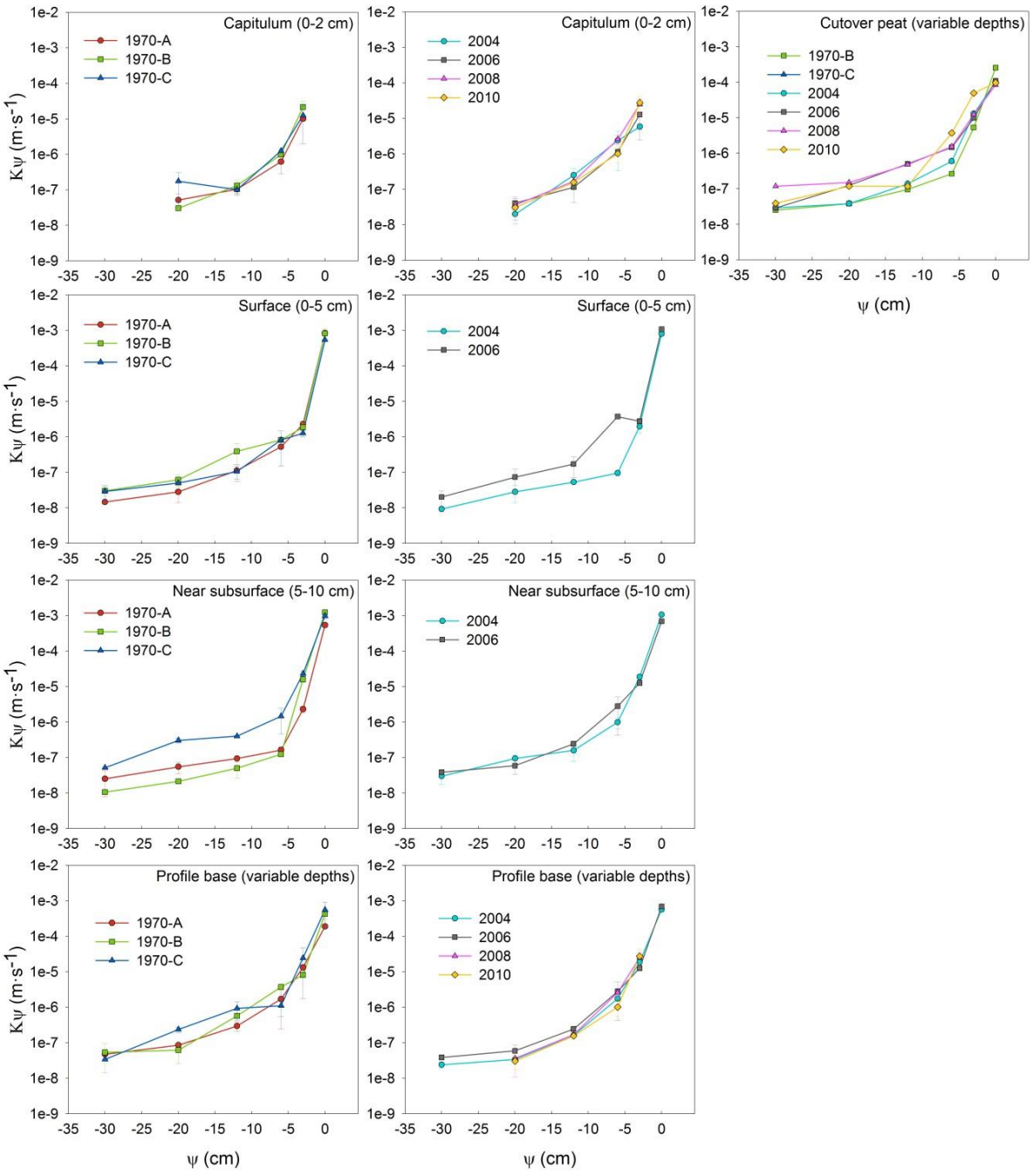


Figure 2-4: Unsaturated hydraulic conductivity (K_ψ) for samples under soil water pressures in the range of 0 to -30 cm (n=2 for all points except cutover peat values, where n=1). Data for SPONT is shown at left, EXPER in the center column and cutover peat for all plots at right. The profile base refers to the 5 cm layer directly overlying the former cutover peat surface at each site. K_ψ values for ψ=0 are determined from the saturated hydraulic conductivity measured in a Darcy permeameter. Error bars represent ±SD in K_ψ.

2.4.2 Soil Water Dynamics under Field Conditions

The study period was characterized by higher than average seasonal precipitation, receiving 227 mm more than would be expected from the 30-year (1981-2010) mean for the 82 day period between May 24 and August 13 (Environment Canada, 2014). More than two-thirds of seasonal precipitation was received in 5 events >30 mm in size, and nearly a quarter was from a single 100 mm event on July 26-27. Precipitation was estimated to exceed evaporation by >110 mm at all plots. Soil water pressures measured by tensiometers set in the cutover peat at plots 2006 and 2010 remained above -15 cm for the entire study season, and WT fluctuations were mostly constrained to within 40 cm of the surface.

Plots exhibited very different responses to WT in θ at the surface (0-3 cm) layer (Figure 2-5). This is evident from the fact that the plots span different regions of the WT–θ graph, implying different surface layer water contents for the same range of WT. The slope of the linear regression for each of these plots represents the change in θ per unit change in WT, and can be taken as an indication of the degree to which surface moisture dynamics are linked to WT. Slopes are given in parentheses in Figure 2-5 as the percent increase in θ per cm rise in WT. The newly-regenerated plots 2008 and 2010 showed a much stronger WT–θ response than all other plots; however, 1970-C also showed a fairly strong response. Plots 2008 and 2010 also showed the highest absolute θ values of all plots when WT was within 20 cm of the surface. At plots 2004, 1970-A and 1970-B, which had profile heights ranging from 16 – 40 cm, slopes approaching zero indicated that changes in WT were only very weakly related to changes in θ. This would suggest that surface moisture dynamics have become somewhat decoupled from WT at these plots. A non-linear response in θ was evident at plots 2006, 2010 and 1970-C, and suggested that the effect of WT on θ diminished as WT decreased.

Time series of θ generated by the static TDR probes inserted in the profiles at 2006, 2010, and 1970-C revealed that θ in the near-surface layers responded differently to precipitation events at different plots (Figure 2-6). At plots 2006 and 1970-C, the response of θ within the profile to WT was much stronger when WT was close to the surface (Figure 2-7). A series of precipitation events between 3.5 and 12 mm in size failed to produce a response in near-surface θ at these plots when WT was at its seasonal low (day-of-year 185 to 205), despite producing a clear response in WT. Near-surface θ remained high during a 16-day period where direct precipitation was excluded from all plots using tented plastic sheeting (day-of-year 209 to 225). θ could be seen to closely mirror WT at these plots. At plot 2010, the profile was not sufficiently thick for a TDR inserted horizontally to measure profile θ without being influenced by the θ of the cutover peat, and so the roaming WET-Sensor™ was used to measure near-surface θ. However, the inherent variability and lower timescale

resolution of this measurement technique made it difficult to establish the response to precipitation at plot 2010. WET-Sensor^{TM} θ measurements (representing the 0-6 cm layer) agreed well with 2.5 cm depth TDR readings at plot 1970-C (representing the 0-5 cm layer), but were systematically ~20% lower than the 2.5 cm TDR readings at plot 2006. The reason for this is unclear.

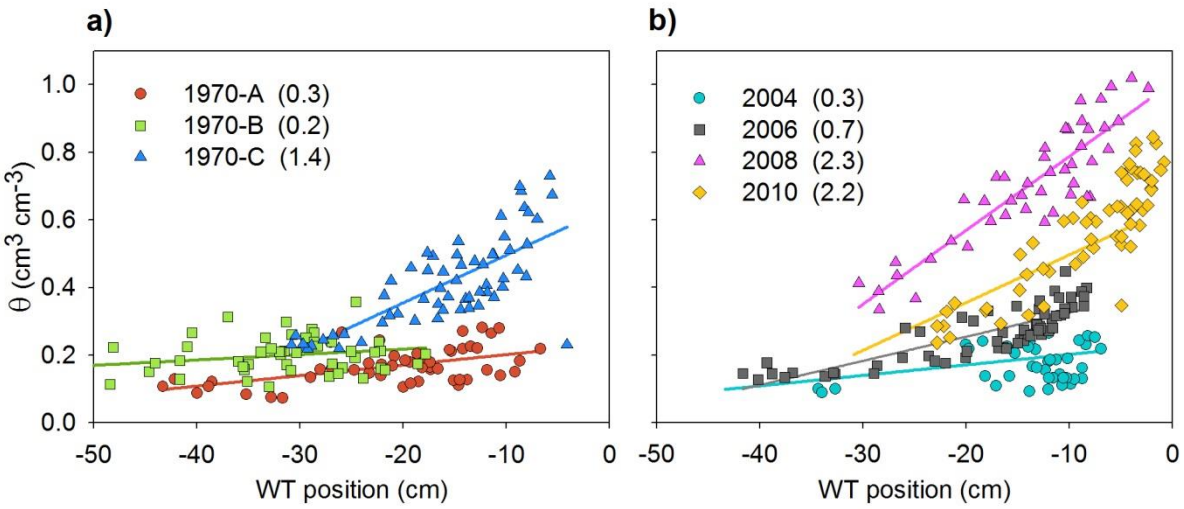


Figure 2-5: Relationship between volumetric moisture content in the surface (0-3 cm) layer (θ) and water table position (WT) relative to the growing surface for **a)** spontaneously regenerated and **b)** experimentally restored *Sphagnum* profiles. Moisture content values were determined using a calibrated portable TDR device. All relationships were significant at the 0.05 level (Pearson's Correlation Coefficient, two-tailed test of significance). Slopes are shown in parentheses as the percent change in θ per cm change in WT.

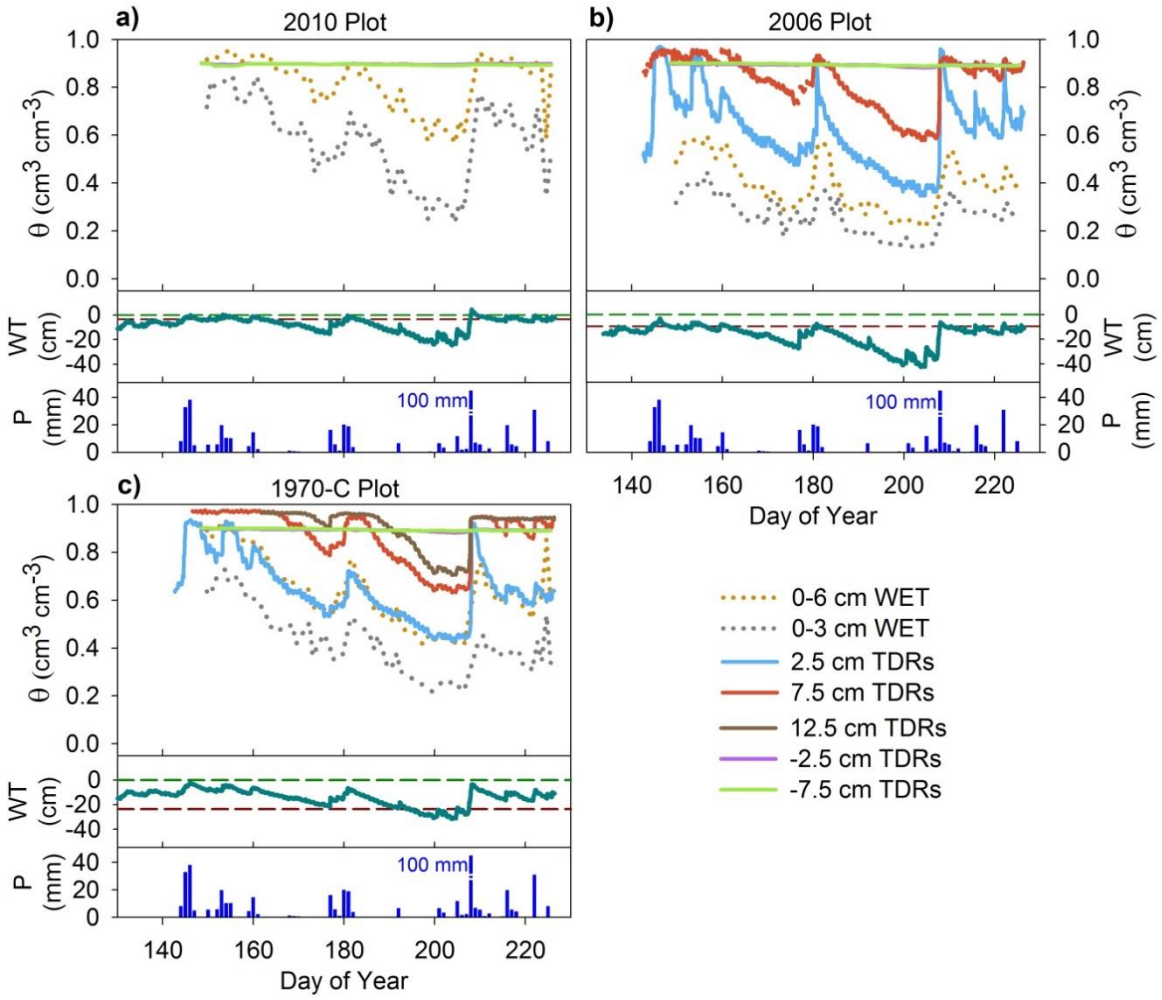


Figure 2-6: Compound figures showing changes in moisture content with depth, WT position, and precipitation over time for 3 different plots: **a)** 2010, **b)** 2006, and **c)** 1970-C. Values for each figure are averaged across 3 replicate profiles at each site. Measurements include both *in-situ* TDRs (solid lines; *n*=3 for all values except 2.5 cm depth where *n*=1) and WET-sensor portable TDR (dotted lines; *n*=15). TDR depths relative to profile surface indicated by positive numbers; negative numbers indicate depth below cutover peat interface. Changes in WT shown with dashed green and red horizontal lines representing the profile surface (0 cm WT datum) and former cutover peat surface, respectively. Profile heights are 3.5 cm (2010 plot), 9.5 cm (2006 plot), and 23.5 cm (1970-C plot). Direct precipitation was excluded experimentally from each of the plots between day 209 and 225.

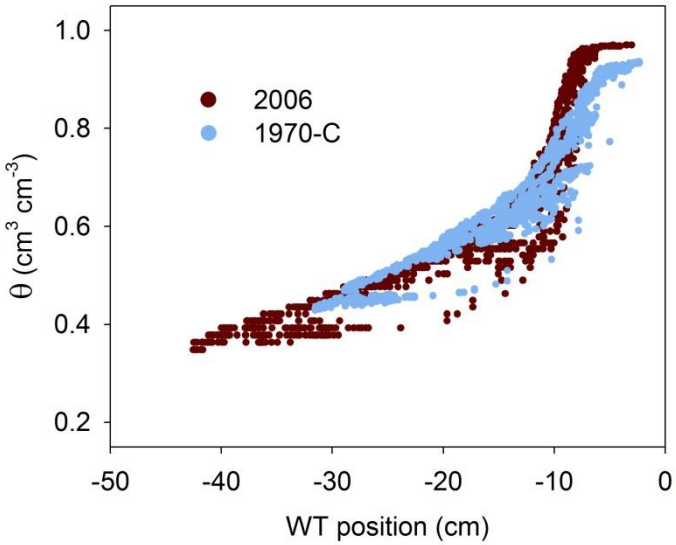


Figure 2-7: Water table position versus volumetric water content (θ) measured by TDRs 2.5 cm below the growing surface (representing roughly the 0-5 cm layer of the regenerated profile) at two plots.

2.5 Discussion

In general, the hydrophysical properties of the regenerated profiles show that the greatest differences between the spontaneously regenerated and experimentally regenerated plots occur closer to the profile base. This is most likely due to the fact that at SPONT, where plots were assumed to have begun regenerating >40 years before present, decomposition and compression from the weight of overlying layers have compacted the moss fibre. More decomposed and compacted plant matter generally possesses a greater abundance of small pore sizes (Boelter, 1968) imparting a stronger capillary force. This has resulted in a higher bulk density and water retention capacity, and slightly lower K_{sat} , at SPONT compared to the same layer at the <10 year old EXPER plots. Whereas an abrupt transition in hydrophysical properties exists at the interface between the regenerating layer and the cutover peat at EXPER, at SPONT the basal layer is approaching levels of bulk density and retention capacity comparable to the cutover peat. Interestingly, plot 2004 showed a basal layer bulk density and retention capacity only slightly lower than that of the SPONT plots, suggesting that some degree of compaction and decomposition had already taken place after only 9 years of growth.

Cutover peat samples had higher average bulk density and greater retention capacity than *Sphagnum* samples. While *Sphagnum* profiles exhibited a wide range of θ in the field, the TDR probes at the three instrumented plots show that θ variance within the cutover peat was remarkably small and that this layer remained close to saturation for the entire study season. Peat samples also showed little variance in θ across the range of ψ tested in the laboratory, which encompassed the ψ range observed in the field within peat at similar depths (a seasonal minimum of -14 cm). Regenerating *Sphagnum* at plots 2008 and 2010, consisting of only a thin (3-4 cm) layer directly overlying the cutover peat, maintained the highest average surface θ over the study period. This would suggest that at these plots the water stored in the cutover peat can be easily accessed by capillary flow to maintain photosynthesis, at least within the relatively narrow range of ψ observed in the field.

Direct precipitation appeared to be poorly retained within the upper regenerating layer. This is supported by field observations of θ in the near-surface layer at plots 2006 and 1970-C, which showed very little response to substantial (up to 12 mm) precipitation events during periods of lower WT (Figure 2-6). When WT was within about 20 cm of the surface, near-surface θ mirrored the position of the water table very closely. Furthermore, logging TDR probes at the 2.5 cm depth level showed clear hysteretic loops on a θ–WT graph and a relatively narrow variance in θ for a given WT, suggesting the strong predominance of WT as a control on near-surface θ (Figure 2-7). This said, it has been demonstrated that small (<1 mm) atmospheric inputs of water such as dewfall can be crucial to maintaining metabolic processes during highly water-limiting conditions (Csintalan *et al.*, 2000; Strack & Price, 2009), which were not observed in this study. The 16 day period of precipitation exclusion for all plots in this study, during which mosses remained healthy and productive, shows that *Sphagnum* can maintain adequate moisture for photosynthesis in the absence of precipitation inputs for at least this long, although it is noted that WT was also near its seasonal high during the first several days of this period. The large variations in θ observed within the profiles during this period can thus be attributed exclusively to WT fluctuations and, to a lesser extent, evaporation, in the absence of significant atmospheric inputs of water. The magnitude of diurnal variations in WT was noticeably greater when WT was below the cutover interface than when it was within the profile (most evident for plot 1970-C), most likely as a result of the lower specific yield of the cutover peat relative to the *Sphagnum*.

While WT dynamics were closely tied to near-surface (0-3 cm) θ at plots 2008 and 2010, the effect of WT on θ in this layer tended to diminish with increasing profile height. Plot 2006, with a regenerated layer thickness of 10 cm, showed a θ-WT relationship that was clear but weaker (had a

lower slope) than that of plots 2008 and 2010 (Figure 2-5). The regenerated layers were >15 cm thick at all other plots and the θ-WT relationship slopes approached horizontal, indicating that WT was a relatively poor predictor of θ in the near surface at these plots (plots 2004, 1970-A and 1970-B). Plot 1970-C was an important exception to this.

The profile at plot 1970-C was notably different from the other well-developed *Sphagnum* profiles in that surface moisture dynamics were more strongly linked to WT than at any other plots besides 2008 and 2010, especially in relation to the other plots at SPONT where all profiles exceeded 20 cm in height. Samples from 1970-C also had a much greater water retention capacity than other plots in the 0-5 cm and 5-10 cm profile depth intervals across the range of ψ tested, and had marginally higher bulk density than the other SPONT plots throughout the regenerated profile. This may be attributable to the fact that this plot had both a significantly ($p<0.05$; One-way ANOVA with Tukey's HSD Post-hoc tests) higher density of capitula (3.31 cm^{-2}) and a greater proportion of *S. rubellum* Wils. (98.5%) than all other plots (Table 2-1). This area of the peatland also had a visually distinctive regenerated surface relative to other areas of the site, with a denser appearance, more even surface contour, and very little ericaceous plant cover. It is well established that hummock species are able to remain productive at higher elevations above the water table than lawn or hollow species due to the greater capillarity afforded by tighter spacing of individuals (Hayward & Clymo, 1982; Luken, 1985; Rydin, 1993). *Sphagnum rubellum* has also been found to have a higher water retention capacity than *S. magellanicum* (McCarter & Price, 2012), a species that was present at most plots in varying proportions. While the heterogeneous array of species at most plots and the small number of plots in this study made it impossible to isolate the effects of individual species on soil water dynamics, it appears very likely that the differences in hydrophysical properties and WT connectivity observed at 1970-C are attributable to the particular community architecture of the dense *S. rubellum* Wils. carpet that has developed there. Although all other plots where the regenerated layer thickness exceeded 15 cm had reduced WT connectivity and generally low near-surface θ, plot 1970-C demonstrated that WT connectivity and capillarity of regenerating *Sphagnum* layers are not simply a function of age but are controlled by factors such as species composition and community architecture as well.

An analysis of the observed range of WT relative to the regenerating *Sphagnum* – cutover peat interface at each plot (Figure 2-8) revealed that at SPONT, WT remained above the cutover peat for 81±8% of the study season, whereas at EXPER, WT was above the cutover peat for only 30±25% of the time. Although this cannot be used as evidence that seasonal WT has increased over the time

period of regeneration as data on initial conditions are lacking, the fact that the site was abandoned after peat extraction and that drainage ditches remained active during this time means it is unlikely that the water table was above the cutover surface at the start of regeneration. This suggests that the seasonal WT has increased at SPONT and that spontaneously regenerated areas are able to constrain WT fluctuations largely to within the regenerated moss profile. Several studies (McNeil & Waddington, 2003; Lucchese *et al.*, 2010; McCarter & Price, 2013) have identified the latter observation as significant, because once WT fluctuations are constrained entirely to within the regenerated layer, the hydrologic regime of the plots functions much more similarly to that of a natural bog peatland. There are two main feedback processes which could account for this observation. Firstly, as the retention capacity of the profile base increases and K_{sat} decreases (albeit only slightly), a greater proportion of precipitation is retained in the regenerated layer. Secondly, there may be an evaporation-limiting feedback (Waddington *et al.*, 2014) occurring, whereas the thickness of the regenerated layer increases, the vertical K_{ψ} decreases as the upper layers dry, limiting upwards transfer of water and thus reducing evaporative losses. A combination of these two processes could account for the perceived increase in seasonal WT at SPONT.

The relationship between ψ and K_{ψ} between samples did not exhibit as much variability as expected, given the substantial variation in other hydrophysical properties. This was surprising given the large differences in θ between samples at a given ψ, as hydraulic conductivity is often assumed to be a function of θ as explained by differences in water-filled pore diameter and pore connectivity for a given level of saturation (Buckingham, 1907). The relationship between θ and K_{ψ} for all samples as a group was quite weak, with an average r^2 across all tensions of 0.16. This presents two possible interpretations. One is that as ψ decreases, the connectivity between the remaining saturated pores decreases more rapidly in some samples than in others (or flowpath tortuosity increases more rapidly, or a combination of the two). In the peat samples for example, which maintained θ>0.77 throughout the analysis, it may be that the largest pores which drain at ψ of -3 to -12 are capable of transmitting much more water than those pores which are only slightly smaller due to dramatically lower connectivity between these pores. This would account for the fact that K_{ψ} values for peat are within an order of magnitude of values for surficial *Sphagnum* samples at the lowest levels of ψ despite having a water content >50% higher. An alternative explanation is that a large proportion of the water remaining in the samples at lower pressures was immobile, such as that stored in hyaline cells, and that differences in θ between samples at a given ψ are attributable primarily to differences in immobile water content rather than mobile water content. This would explain the similarity in K_{ψ} across samples, while differences in θ could result from differences in the bulk volume of hyaline

cells within a sample. We propose that these differences derive from differences in species morphology and capitula density, although no known studies to date have examined this proposition. Regardless of the explanation, the results show that K_ψ in regenerating moss layers drops precipitously between 0 and -30 cm ψ, corresponding to an approximate 30 cm WT decline below a given point within the profile.

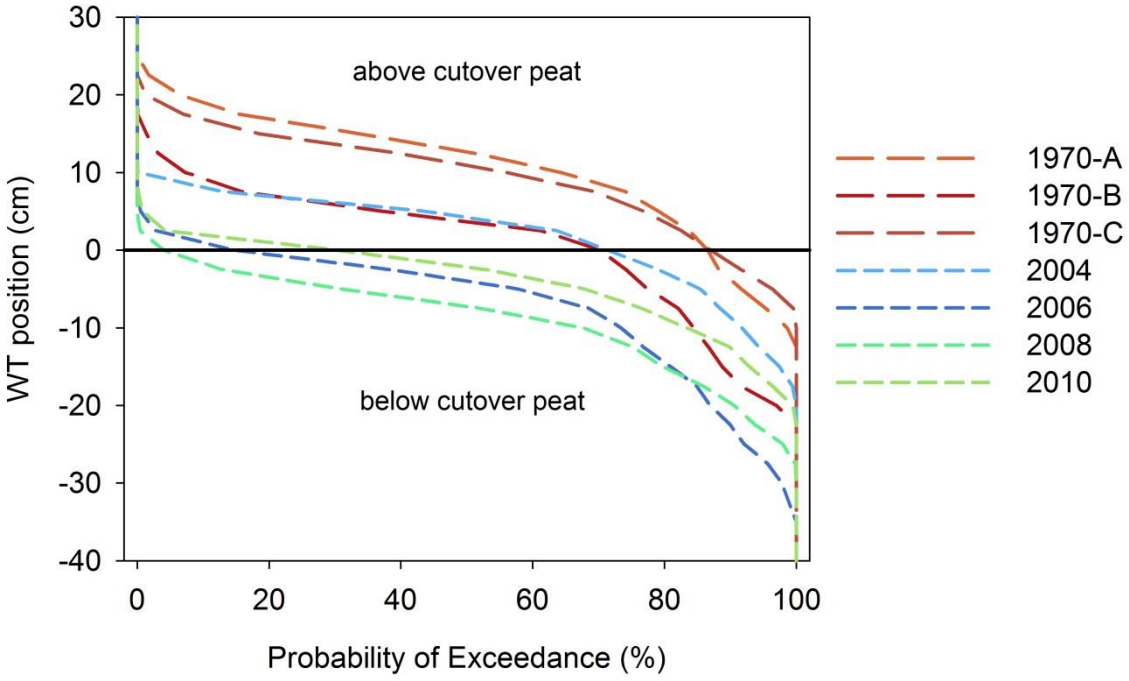


Figure 2-8: Probability of exceedance of a given water table position on the y-axis over the study period. The interface between the old cutover peat and the regenerating moss layer is used as the 0 cm datum for all plots and is also indicated here by the black horizontal line, with positive values signifying water tables above the interface. Spontaneously regenerated (SPONT) plots are represented by long dashed lines and experimentally restored (EXPER) plots by short dashed lines to emphasize differences between the two groups.

2.6 Conclusion

This study is the first to describe the evolution of regenerated *Sphagnum* layers in terms of their specific hydrophysical properties and hydrologic behaviour. *Sphagnum* regenerating on cutover peat surfaces appears to follow a pattern of structural evolution whereby the bulk density and water retention capacity of the layers directly overlying the cutover peat increase over time. These properties were consistently greater in the basal layer at the older SPONT plots than in the same layer at EXPER because the longer period of growth has allowed more time for decomposition and compaction of the moss. The high bulk density and retention capacity of the nine year old 2004 plot relative to the other EXPER plots suggest that the development of this water-retaining basal layer may proceed more quickly than previously thought. The ability of the basal layer to hold more water against tension may be important for maintaining capillary flow during periods of low WT.

Direct precipitation appeared to be poorly retained in the *Sphagnum* canopy and near-surface. Changes in WT position were strongly correlated with θ in the near-surface at all plots, and the relatively narrow variance in the TDR-derived water contents for a given WT suggests that capillarity was a much stronger control on surficial θ than precipitation. However, large differences between plots in the WT–θ relationship show that the ability of the profiles to convey water to the surface differs greatly between different profile structures. Six of the seven plots demonstrated a pattern of hydrophysical evolution whereby the surficial θ that can be sustained at a given WT decreases as the thickness of the regenerated layer increases. Plot 1970-C was an exception to this trend, and while this area may or may not be unique within this peatland or other cutover sites, it shows that community architecture and species composition have the potential to be more influential than layer thickness in determining profile capillarity. The K_ψ curves observed here could not account for the large differences in upwards water transmission observed in the field, but demonstrated the rapid (>4 orders of magnitude) reduction in K_ψ that occurs as soil water pressures drop to -30 cm.

The data shown here strongly support the conclusion that WT is an effective regulator of near-surface θ in regenerating *Sphagnum* when WT is within 30 cm of the surface and possibly at lower positions as well. The data of Ketcheson and Price (2014) also support this conclusion. This implies that regulation of WT is an effective means of optimizing hydrologic conditions for *Sphagnum* biomass production, especially at the thinner <9 year old layers most relevant to biomass production cycles, even when WT remains below the cutover peat surface. WT fluctuations remained within the profile for a substantially longer proportion of the growing season at SPONT than at EXPER, and seasonal WT seems to have increased over time at SPONT. This suggests that

layer structure is evolving such that it may at some point be able to fully constrain WT to within the regenerated profile, which several studies (McNeil & Waddington, 2003; Lucchese *et al.*, 2010; McCarter & Price, 2013) have identified as a critical criterion for hydrological restoration as well as net carbon sequestration in restored bog peatlands. High near-surface θ was sustained in the absence of direct precipitation for at least 16 days; however, the response of the layers to more water-limiting conditions is unknown, as field observations occurred in a season where measured precipitation greatly exceeded estimated evaporation. Future work should integrate soil water dynamics with CO_2 measurements, and attempt to quantify the resilience of regenerating *Sphagnum* in cutover environments to drought or water table drawdown to establish hydrologic limits of tolerance. A numerical modelling approach using the hydrophysical parameters described here may prove useful in determining both the limiting and optimal hydrologic conditions for growth.

3.0 Manuscript 2: Hydrologic controls on productivity of regenerating Sphagnum in a cutover peatland

3.1 Abstract

In addition to ecological restoration as a post-industrial use of mined peatlands, recent research into the production of *Sphagnum* biomass on cutover sites has highlighted the need for an improved understanding of the ecohydrology of *Sphagnum* regenerating in these environments. Previous work suggested that limited connectivity between surficial layers and the underlying partially decomposed plant matter and peat would result in water stress and inhibited growth. This study links the soil water dynamics of regenerated layers ranging in age from 3-43 years and from 3-40 cm in thickness to the productivity of *Sphagnum* in order to determine the hydrologic controls on productivity and the optimal range of water content for producing *Sphagnum* biomass. Productivity was never observed to be limited by insufficient supply of water, including during periods where water table was >40 cm below the surface and periods of 16 days without measured precipitation. While layers of different ages and thicknesses were able to sustain adequate water supply to remain productive under a range of conditions, the ability of layers to transmit water upwards differed greatly. Water content in the near-surface inhibited productivity during wetter periods, especially at newly regenerating sites where the layer was <5 cm thick. This has important implications for biomass production using the *Sphagnum* species studied here. Using a mixed linear modeling approach to isolate the effects of water content on variance in productivity from those of other measured variables, a volumetric water content range of 0.13 to 0.5 is identified as optimal.

3.2 Introduction

The drainage and mining of peatlands for *Sphagnum* peat represents a significant localized disturbance to peatland ecosystems in certain regions of Canada, most notably southeastern Québec and northeastern New Brunswick (Lavoie & Rochefort, 1996; Daigle & Gautreau-Daigle, 2001; Poulin *et al.*, 2005). Peat extraction involves site drainage and the removal of the surface layer of vegetation and the upper layers of peat. Following extraction operations, the altered physical environment and hydrology of sites impede the recolonization of the primary peat-forming genus *Sphagnum* in most cases (Lavoie & Rochefort, 1996; Poulin *et al.*, 2005), and the oxidization and decomposition of the formerly saturated peat can convert sites from sinks of atmospheric CO_2 to large and persistent sources (Waddington & Price, 2000; Waddington *et al.*, 2002; Petrone *et al.*, 2003). Motivated by concern over regional peatland losses and the degradation of carbon-rich soils,

restoration techniques were developed over the past two decades to return these cutover sites to productive ecosystems dominated by *Sphagnum* mosses (Ferland & Rochefort, 1997; Rochefort, 2000; Rochefort *et al.*, 2003). The primary aim of the North American method to peatland restoration is the creation of hydrologic conditions which favour the establishment of a *Sphagnum* carpet on cutover surfaces (Rochefort *et al.*, 2003; Quinty & Rochefort, 2003). This is seen as a critical restoration criterion from both an ecological perspective and a long-term carbon sequestration perspective (Ferland & Rochefort, 1997; Rochefort, 2000; Rochefort *et al.*, 2003; Waddington *et al.*, 2010).

In addition to ecosystem restoration as an after-use of cutover peatlands, there has been increased interest over the past decade in the potential commercial production of *Sphagnum* biomass on cutover sites, particularly in Germany (Gaudig & Joosten, 2002; Gaudig, 2012). Canadian *Sphagnum* peat is extracted primarily for horticultural use as a growing substrate (Cleary *et al.*, 2005), but research has suggested that dried *Sphagnum* biomass can be substituted for the only slightly decomposed "white peat" currently preferred by industry without any reduction in crop yield (Emmel, 2008). Additionally, it may be a lower carbon emission alternative to mined peat as it does not require the exploitation of undisturbed peatlands (Gaudig, 2012; Silvan *et al.*, 2012).

Water availability is crucial for the growth and survival of *Sphagnum*, and the lack of a sufficient and stable water supply often constrains regeneration on cutover surfaces (Price, 1997; McNeil & Waddington, 2003; Price *et al.*, 2003). Being non-vascular and also lacking the ability to regulate water loss (Proctor, 1982; Titus & Wagner, 1984), *Sphagnum* relies on passive external capillary transport of water to the capitula – the cluster of branches and leaves comprising the top ~1 cm of the plant – to sustain photosynthesis (Clymo & Hayward, 1982; Proctor, 1982). If upwards flows are consistently less than evaporative demand the plants will desiccate (McCarter & Price, 2012) and photosynthesis will be severely reduced (Gerdol *et al.*, 1996; McNeil & Waddington, 2003). Hyaline cells store water important for plant structural integrity and leaf photosynthetic capacity. Water is extracted from the narrow pore openings of these cells when soil water pressures drop below a threshold value in the range of -200 to -600 cm (Clymo & Hayward, 1982; Lewis, 1988). However, Price & Whitehead (2001) found that *Sphagnum* was absent from areas where seasonal soil water pressures dropped below -100 cm on a cutover bog abandoned for 30 years. Lower specific yield in the formerly saturated deep peat can increase the variability of water table fluctuations below cutover surfaces relative to natural peatland surfaces, reducing soil water pressures and thus moisture availability for *Sphagnum* (Price, 1996). While high atmospheric water demands and constraints on capillary transport can limit productivity, too high a water content in the

capitulum can also be limiting as the rate of CO_2 diffusion is reduced as the film of water covering leaves becomes thicker (Dilks & Proctor, 1979; Williams & Flanagan, 1998). Furthermore, the stability of the water supply is important in supporting growth processes, as repeated drying cycles negatively affect photosynthetic rates and drastically increase respiration following re-wetting (Schipperges & Rydin, 1998; McNeil & Waddington, 2003).

The relationship between water content and *Sphagnum* productivity has been the subject of a number of studies. Many of these have looked at this relationship in a laboratory setting, using either individual capitula (Rydin & McDonald, 1985; Murray *et al.*, 1989; Williams & Flanagan, 1996; Schipperges & Rydin, 1998) or small samples of *Sphagnum* (Silvola, 1992; Gerdol *et al.*, 1996; Robroek *et al.*, 2007; Van Gaalen *et al.*, 2007; Robroek *et al.*, 2009; Strack & Price, 2009), while *in-situ* field studies are comparatively rare (Luken, 1985; Murray *et al.*, 1989; McNeil & Waddington, 2003; Strack *et al.*, 2009). Furthermore, many field studies quantify productivity using seasonal timescale measures such as crank wires (e.g. Luken, 1985; McNeil & Waddington, 2003) which miss finer scale variations in productivity and water content, and often use destructive sampling methods to determine capitulum water content (e.g. Luken, 1985; Murray *et al.*, 1989) which prohibits frequent repeated measurement of the same area. Additionally, the structure and soil water dynamics of regenerating *Sphagnum* layers in cutover peatlands may differ substantially from that of natural peatlands (see Chapter 2) and reduced bulk density and unsaturated hydraulic conductivity have been found to limit upwards water transfer to the capitula (Schouwenaars & Gosen, 2007; McCarter & Price, 2014). The specific hydrologic conditions under which *Sphagnum* regenerating on cutover surfaces can remain productive are unclear. This study seeks to evaluate the *in-situ* productivity of *Sphagnum* regenerating in a cutover peatland in relation to instantaneous hydrologic conditions using non-destructive measures of capitulum water content. The specific objectives are: 1) to evaluate and contrast the influence of capitulum water content and canopy air temperature on the productivity of regenerating *Sphagnum* profiles of different ages, and 2) to identify the range of capitulum water content that maximizes productivity.

3.3 Methodology

3.3.1 Study Site

Data was collected between May 24 and August 13, 2013 at a large abandoned cutover peatland located on the Acadian Peninsula near Shippagan, New Brunswick (47°40'N, 64°43'W). The 30-year (1980-2010) mean annual precipitation in Shippagan is 1077 mm, of which rain comprises 69%, and the mean annual air temperature is 4.8°C (Environment Canada, 2014). The site

was mined using block cutting techniques and was abandoned following the end of extraction operations around 1970. Because of the extraction method used, the site is characterized by an alternating baulk-and-trench structure, where trenches ~20m wide are separated by baulks ~5 m wide and ~1 m higher in elevation than the trenches (Robert *et al.*, 1999). *Sphagnum* has spontaneously recolonized the majority of the area within the trenches but is absent on the baulks. The degree of spontaneous recolonization in this peatland is much higher than at many other block-cut peatlands in more continental climates, where large areas can remain devoid of *Sphagnum* decades after abandonment (Poulin *et al.*, 2005; Gonzalez *et al.*, 2013). In two regions of the peatland, *Sphagnum* biomass production experiments have been ongoing since 2004 (Landry & Rochefort, 2009). Within these trenches, sections measuring roughly 15 × 90 m were cleared of any vegetation that had spontaneously regenerated in the period since abandonment, leaving a surface of bare cutover peat. A new *Sphagnum* cover was then established on these surfaces based on the North American method for bog restoration outlined in Quinty and Rochefort (2003).

Seven plots were established at the site for CO_2 measurements and hydrologic monitoring, each plot consisting of three replicate sub-plots delineated by square metal collars with sides of 60 cm and a height of 40 cm. Collars were cut into the peat until the top was sitting just above the surface of the regenerated layer. Sub-plots are referred to as "collars" hereafter. The collars at each plot were located within a 2 m radius of one another and were installed in areas entirely covered by *Sphagnum* where the regenerated profile appeared to be homogenous in thickness and species composition. Boardwalks were constructed in the vicinity of collars to reduce the impact of accessing collars for measurements on the regenerated profiles. Four of the seven plots were within the experimentally regenerated areas of the site, collectively referred to here as EXPER (plots 2004, 2006, 2008 and 2010), where *Sphagnum* was introduced on cleared cutover surfaces in the spring of each year (Landry & Rochefort, 2009). At the time of this study (2013), these plots ranged in age from 3 to 9 years since the start of regeneration, while the vertical thickness of the regenerated moss profiles varied from 3.5 to 17 cm. The other three plots were located in areas where regeneration was assumed to have taken place spontaneously at the time of abandonment in 1970, referred to collectively as SPONT (plots 1970-A, 1970-B and 1970-C). These plots were well-developed and had profile thicknesses of between 23 and 40 cm.

Species abundance, expressed as a relative proportion of total spatial coverage within collars, was evaluated by visual estimation. Capitulum density was estimated by counting the number of individuals within a 2 cm square quadrant of transparent graphing paper at 16 randomly selected locations within the collars at each plot (Figure 3-1). Plots were generally characterized by a mix of

Sphagnum species within the section *Acutifolia* (*S. fuscum* (Schimp.) Klinggr., *S. rubellum* Wils., *S. flavicomans* (Sect. *Acutifolia*)) and *S. magellanicum* Brid., with *S. rubellum* as the most prevalent species at the site and the only species of the four occurring at all plots. Nomenclature for *Sphagnum* follows that of Anderson (1990).

3.3.2 CO_2 Flux Measurements

Net ecosystem CO_2 exchange (NEE) was measured approximately twice a week at each collar using a 0.108 m^3 dynamic Plexiglas chamber coupled with an infrared gas analyser (IRGA) (Model-EGM4; PP Systems, Hitchin, UK), following the method of Griffis *et al.* (2000). NEE was expressed in g $CO_2 \cdot m^{-2} \cdot day^{-1}$ and was calculated using:

$$NEE = \frac{\Delta CO_2 \cdot M_m}{M_v} \cdot \frac{V}{A} \cdot C \qquad \textbf{Eq. 3-1}$$

where ΔCO_2 is the change in CO_2 concentration over time ($ppm \cdot s^{-1}$), M_m is the molar mass of CO_2 (44.01 $g \cdot mol^{-1}$), M_v is the molar volume of a gas at standard temperature and pressure (0.224 $m^3 \cdot mol^{-1}$), V is the temperature-corrected combined volume of the chamber and the void space between the *Sphagnum* surface and the open bottom of the chamber (m^3), A is the ground surface area within each collar (m^2), and C is a conversion factor to convert concentration from ppm to mol and time from seconds to days (0.0864). Each chamber run was 120 seconds in duration, and all runs retained for analysis had $r^2 > 0.9$ except where the change in concentration was ≤2 ppm in which case runs were retained as long as the change was monotonic. Two fans within the chamber ensured that air within the chamber was well-mixed and a water-filled trough running along the outside of the collar created a seal between the collar and chamber. Although temperature was not controlled within the chamber, chamber air temperature remained within 1°C of ambient temperature in 96.3% of runs. Photosynthetic photon flux density (PPFD, μmol photons $\cdot m^{-2} \cdot s^{-1}$) within the chamber at 10 cm above the growing surface was recorded during each measurement, and the air temperature within the *Sphagnum* canopy (T_C) and the water content of the top 3 cm of the profile were recorded immediately before or after each chamber measurement. T_C was measured using a 1 cm copper constantan wire thermocouple probe inserted just below the surface in three randomly selected locations within the collar and left to equilibrate. The methodology for determining water content is described below along with the methodology for other hydrologic measurements.

Gross ecosystem productivity (GEP) was determined by subtracting the ecosystem respiration (ER) component of CO_2 flux from the NEE under non-light-limiting conditions. An opaque (PPFD = 0) blind was placed over the chamber to determine ER after each full-light NEE measurement. For this investigation, chamber measurements where PPFD exceeded 750 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were considered to be light-saturated. Published estimates of the light saturation point for *Sphagnum* range from 250 to 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Harley *et al.*, 1989; Williams & Flanagan, 1996). All chamber measurements were performed between 10 AM and 4 PM. CO_2 concentrations inside the chamber were allowed to return to ambient levels between each measurement. Any vascular vegetation inside the collars was clipped so CO_2 measurements reflected only the NEE of *Sphagnum*. Clipped vascular plants were replaced with cuttings of fresh ericaceous shrub branches that were changed periodically. This was done to ensure that similar surface shading was maintained within the collar and that latent heat exchanges were restricted to the moss surface.

3.3.3 Hydrologic Measurements

Precipitation was measured and evaporation estimated in order to quantify the primary hydrologic inputs and outputs of the regenerated *Sphagnum* profiles. Precipitation was recorded by one manual and one automated tipping-bucket raingauge, while a pair of weighing lysimeters containing peat-*Sphagnum* monoliths was used at each plot in combination with data from a meteorological station at the site to estimate evaporation using the Priestley-Taylor method (Priestley & Taylor, 1972) following the approach outlined in Van Seters and Price (2001). Pressure transducers in wells recorded water table position (WT) at 30 minute intervals at each plot, and multiple string-level measurements of the vertical distance between the well top and the growing surface allowed for the position of the water table relative to the surface to be determined for each individual collar. Volumetric water content (θ) in the top 3 cm of the profile, taken to be representative of the moisture content in the capitulum, was measured using a WET-Sensor™ portable time-domain reflectometry (TDR) device (Delta-T Devices, Cambridge, UK). The prongs of the device were inserted to a depth of 3 cm and readings taken at five points throughout the collar to provide a representative θ value of this layer at the time of chamber measurement. Recorded WET-Sensor θ values were later transformed by calibration equations, which were determined by relating WET-Sensor readings of known-volume cylindrical *Sphagnum* samples to the gravimetrically-determined θ of these samples, following the method of Topp *et al.* (1980). Two *Sphagnum* samples from each plot were used to derive plot-specific calibration curves to account for the influence of any differences in bulk density, capitula density or other parameters on the

measurement of θ. Unless otherwise stated, θ refers here to the volumetric water content of only the 0-3 cm layer.

The pH, electrical conductivity (EC), and salinity of groundwater in sampling wells close to the collars at each plot were recorded immediately before or after chamber measurements using a multi-parameter probe (model PCTestr 35; Oakton Instruments, Vernon Hills, USA) to determine if these parameters were a confounding factor in evaluating differences in CO_2 exchange. Tensiometers set in the cutover peat 2.5 and 7.5 cm below the former cutover surface at two of the plots provided an estimate of soil water pressure beneath the regenerated layer.

A rainfall exclusion experiment was carried out over a 16 day period between July 28 and August 13, 2013, to investigate the effects on productivity of removing direct precipitation as a source of water. Precipitation was excluded using tented clear plastic sheets attached to posts inserted into the peat around the collars at each plot. Plastic sheeting was removed during measurements of GEP and other environmental variables, and was installed at least 70 cm above the collars at the tent peak to minimize the disturbance to evaporation dynamics.

3.3.4 GEP Modeling and Statistical Analysis

To determine the most important controls on variations in GEP, a mixed linear model (IBM® SPSS® Statistics 20.0, IBM Corp, 2011) was used with θ in the 0-3 cm layer, air temperature within the *Sphagnum* canopy (T_C), plot, and their interactions as fixed effects, as well as a random effect of plot (at the "collar" level). This approach was best suited to analysing the data because it considers correlated errors arising from repeated measurements of the same experimental units through the random effect, and also allows for nested study designs. Data for groundwater chemistry were too sparse to use in the model as data collection for these parameters did not begin until midway through the study season; this was justified as variance in pH, EC, and salinity was low and uncorrelated with GEP (see results). WT was not included in the model as it was considered to be a proxy for capitulum water content, a parameter that was more closely approximated by θ. The model was validated by visually assessing the normality and homogeneity of the residuals of the predicted values. Model selection is described in the results section along with the output.

Friedman's 2-way Analysis of Variance by Rank (related samples) was used with a significance threshold of 0.05 to assess the statistical significance of differences between plots in the distributions of the measured parameters (GEP, θ, WT, T_C). This test was selected as data was typically non-normal for one or more plots within each parameter and sample sizes nearly always differed. All analyses were performed in IBM® SPSS® Statistics 20.0.

3.4 Results

3.4.1 Field Data

The study season (May 24 to August 13, 2013) was characterized by extremely wet conditions, receiving 227 mm more than the 30-year (1980-2010) mean for the same period (Environment Canada, 2014). More than two-thirds of seasonal precipitation was received in 5 events >30 mm in size, and nearly a quarter was from a single 100 mm event on July 26-27. Soil water pressures within the cutover peat remained above -15 cm at all measured plots and depths, and precipitation exceeded estimated evaporative water losses by >110 mm at all plots.

The range of GEP values recorded during light-saturated chamber runs throughout the study season is shown for each plot in Figure 3-2, along with the range of T_C during chamber runs and the seasonal range of WT and θ at each plot. There were significant differences ($p<0.05$) between different plots in terms of GEP, θ, and WT, while T_C did not differ appreciably between plots. Plot 2008 was significantly less productive than all other plots, and also had significantly higher mean seasonal capitulum water content (0.70) than all other plots except 2010, which was also quite high (0.57). Plots 2004, 2006, 1970-A and 1970-C had similar (not significantly different) levels of GEP. The differences in mean seasonal θ were striking in that both the means and the ranges showed substantial variation between plots, especially when the relatively small, though statistically significant, absolute differences in WT ($n\geq2228$) between many of the plots are considered. Plot 1970-B experienced the lowest mean seasonal and absolute WT, reaching a seasonal low of 57 cm below the growing surface, while at all other plots WT remained within 30 cm of the surface 87% of the time or more. Groundwater chemistry data collection did not begin until midway through the study season, and as sample sizes were small ($n=8$ per plot) a statistical comparison of sites was not performed. Nonetheless, there was little variation in the measured parameters across the site, with average values of 4.53±0.19 for pH, 75.8±13.9 μS for EC, and 56.1±8.9 ppm for salinity. None of these parameters was significantly correlated with GEP (Pearson's Correlation Coefficient, two-tailed test of significance ; $p\geq0.69$ for all parameters).

GEP values were plotted against near-surface θ and T_C recorded at the time of chamber measurement (Figure 3-3). Individual plots tended to cluster in distinct regions of the GEP–θ graph. Plots 2008, 2010, and 1970-C were wetter and had greater variance in θ than the other four plots, and had a negative relationship with GEP. There was a high degree of scatter in the GEP–θ relationship, but a negative relationship was evident for higher values of θ (>~0.7). Within the lower range of θ (plots 2004, 2006, 1970-A and 1970-B) no clear relationship was apparent, although the two driest

plots (2004 and 1970-A) had positive relationships with GEP. For the GEP– T_C relationship, all plots had positive linear correlations, four of which were statistically significant at the 0.05 level.

The presence of the plastic sheeting above the collars during the 16-day rainfall exclusion experiment reduced incoming PPFD by an average of 222±92 μmol·m^{-2}·s^{-1} and had no measurable effect on air temperature (n=20). The reduction in light intensity was assumed to have been too small to have had a meaningful influence on moss physiological condition or collar evaporation dynamics (<10 percent of typical full-light conditions of ~2400 μmol·m^{-2}·s^{-1}). GEP measurements taken during this time were not significantly different for 5 of the 7 sites (Related Samples Wilcoxon Signed Rank Test, p>0.05), while plots 2006 and 2008 had significantly lower GEP (p<0.05).

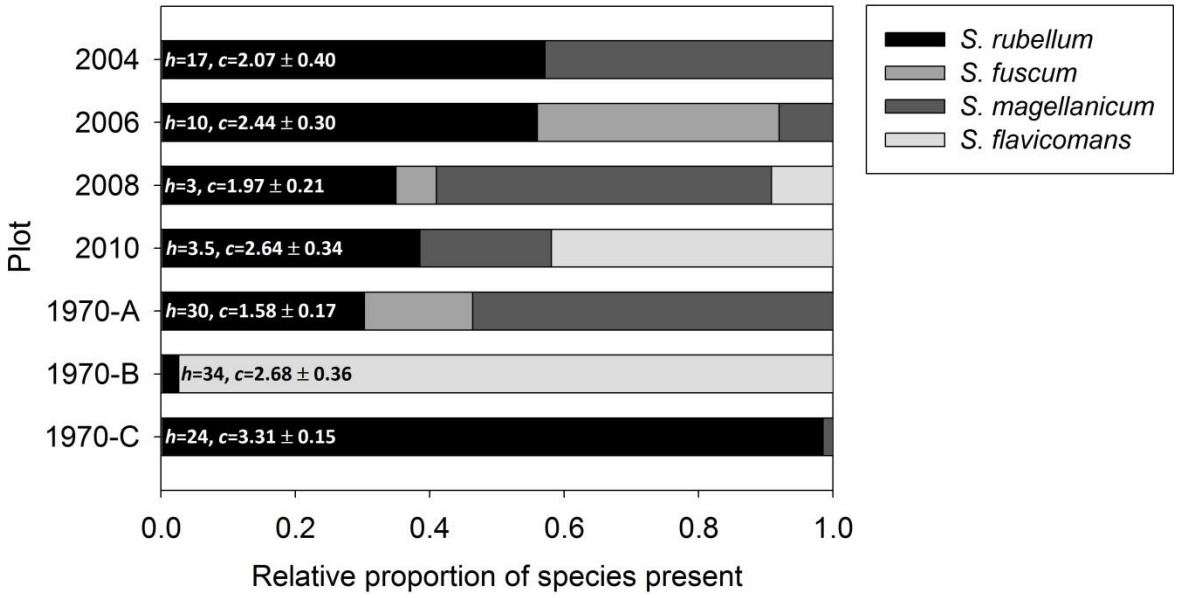


Figure 3-1: Bar graph showing the relative proportion of species present at each plot, taken as an average of the three collars. Numbers on bars show average layer thickness in centimeters (*h*) and density of capitulum per square centimeter (*c*) at each plot ± SD (n=16 per plot).

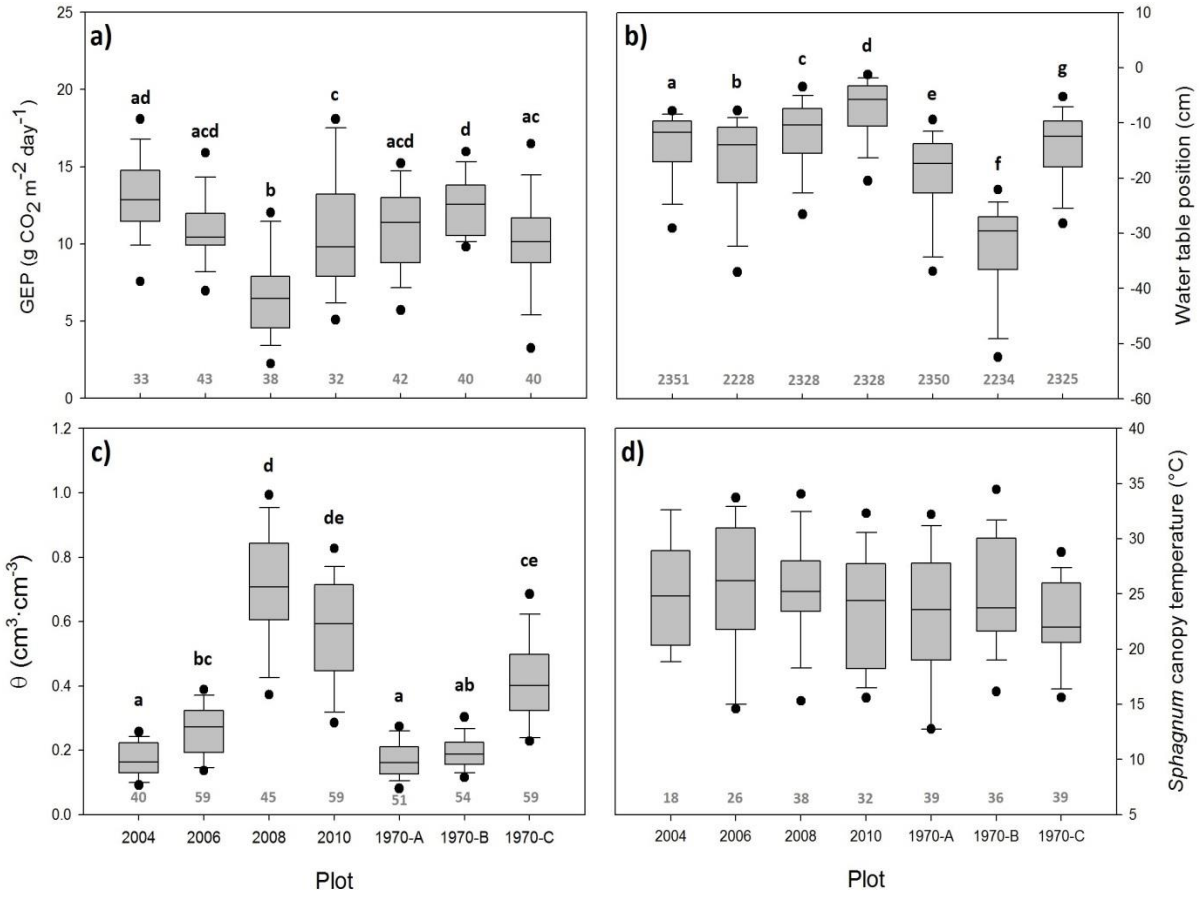


Figure 3-2: Box plots of data grouped by plot, showing **a)** Gross Ecosystem Productivity (GEP) during full light measurements, **b)** water table position relative to the growing surface over the study season, **c)** volumetric water content (θ) in the 0-3 cm layer over the study season, and **d)** air temperature in the *Sphagnum* canopy (T_C) measured during full light GEP measurements. Box plot whiskers show 90th and 10th percentiles, dots represent 95th and 5th percentiles. Boxes sharing the same letter are not significantly different from one another (no significant differences found for panel d). Significance of differences was tested using Friedman's 2-way Analysis of Variance by Rank for related samples and a significance threshold of 0.05. Grey letters below boxes denote *n* values.

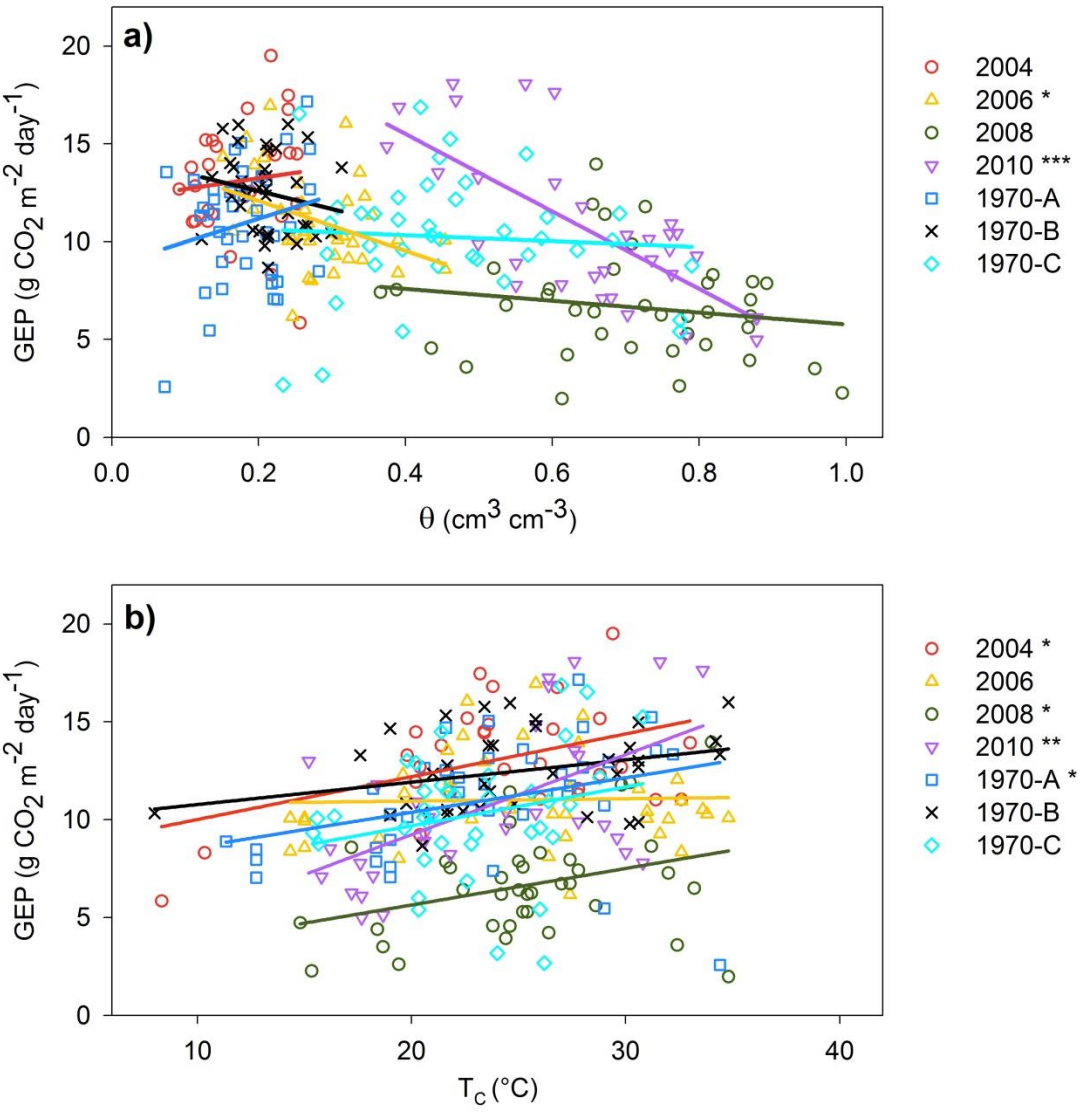


Figure 3-3: Relationship between **a)** GEP and θ in the 0-3 cm layer **b)** GEP and T_C. Each point represents a single measurement from one collar within a plot. Plots are depicted separately to emphasize differences in relationships between plots, and lines of best fit are overlaid to illustrate potential interaction effects between plot and the independent variables. Significance of relationships are shown in the legend (* <0.05; ** ≤0.01; ***≤0.001).

3.4.2 GEP Model

A number of different mixed linear models were compared for their explanatory power. Model fit was assessed by the Bayesian Information Criteria (BIC) of the model output. Briefly restated, the models used for comparison had fixed effects of θ in the 0-3 cm layer, T_C, and plot (denoted hereafter by "Plot", capitalized, for clarity) as a categorical factor with a corresponding random effect of plot, as well as different combinations of these variables as fixed interaction effects. The interaction between θ and T_C was ruled out as an explanatory variable in the interest of model simplicity, as the interaction was not of primary interest and the exclusion of this interaction did not greatly influence model fit. The final model contained the fixed and random effects described above along with a single interaction effect of θ and Plot. The significance of the effects of the relative abundance of the four species of *Sphagnum* at the site could not be assessed using this method due to zero degrees of freedom within any plot (zero variance in species abundance). When included in the model, there were no significant differences between species in the predicted fixed coefficients ($p>0.11$ for all pairwise comparisons). Because the significance of species effects could not be assessed and there were no significant differences in the predicted fixed coefficients of species, species parameters were not included in the model despite a very modest improvement in BIC.

Model output was validated by examining residuals to ensure that normality and homogeneity of variance were achieved, and that all explanatory variables met the assumptions of independence. The selected predictor variables were able to explain nearly half (48%) of the variance in GEP. The F-statistics and corresponding significance of the fixed effects are given in Table 3-1. Plot, T_C, and the interaction between Plot and θ were determined to be significant effects ($p<0.05$), while θ alone was not a significant predictor of GEP.

Parameter	F	df numerator	df denominator	p
Overall Model	11.170	14	236	<.0005
Plot	5.471	6	236	<.0005
T_C	22.121	1	236	<.0005
θ	0.000	1	236	.994
Plot * θ	4.822	6	236	<.0005

Table 3-1: Estimated F-statistics and corresponding p-values of the fixed effects within the linear mixed model used to predict GEP ($r^2 = 0.48$).

3.5 Discussion

3.5.1 Moisture and Temperature Controls on GEP

The relationship observed between GEP and capitulum water content (as approximated by θ in the top 3 cm of the *Sphagnum* profile) appeared to follow a roughly parabolic distribution when data from all plots was considered together, with a wide central range where water content is non-limiting and a gradual decline in GEP towards higher θ. This is similar to what has been observed in laboratory studies of *Sphagnum* productivity (Rydin & McDonald, 1985; Murray *et al.*, 1989; Williams & Flanagan, 1996; Schipperges & Rydin, 1998; Van Gaalen *et al.*, 2007; Robroek *et al.*, 2009) where carbon fixation rates declined above and below an optimal range of capitulum water content. Plots experienced significantly different and in some cases non-overlapping ranges of near-surface θ over the study season. As the underlying "true" GEP–θ function most likely follows a parabolic distribution, this would account for the high degree of significance in the interaction of Plot and θ in the GEP model as data from different plots fall along discrete ranges of this function (see Figure 3-3, a). Conditions where GEP was limited by low water contents were not observed in the field, despite the fact that a pale brittle appearance of capitula indicative of desiccation was observed during drier periods across sizable areas of the collars at several plots (2004, 1970-A, 1970-B), and that WT at plot 1970-B dropped below -50 cm. Additionally, the exclusion of direct precipitation from plots for 16 days did not significantly affect GEP at 5 of the 7 plots. The reduction in GEP at the other 2 plots (2006 and 2008) is more likely explained by an overabundance of water limiting the rate of CO_2 diffusion than by a water deficit, as WT and θ at all measured depths were close to their seasonal maximums during this period. The relatively wet conditions at the site and higher than normal rainfall precluded productivity measurements during very dry conditions when GEP would be substantially reduced. However, the slopes of the driest sites (2004 and 1970-A) show productivity to decline with decreasing water content (Figure 3-3, a).

A regression between the TDR–derived θ of the 0-3 cm layer (using the WET-Sensor^{TM}) and the wet mass (field water content) : dry mass ratio (W:D) of capitula (defined here as the top 1.5 cm of the profile) cut in a 3 cm radius from the point of TDR measurement revealed that the two measures of capitulum water content were only moderately coupled (r^2=0.45, $p<0.001$; Figure 3-4). W:D of the top 1-2 cm of living *Sphagnum* has typically been used to quantify θ in investigations of the moisture-productivity relationship, with studies reporting optimal productivity at W:D of 6-15 dependent on species and ambient conditions (Titus *et al.*, 1983; Silvola & Aaltonen, 1984; Rydin & McDonald, 1985; Murray *et al.*, 1989; Silvola, 1990, 1992; Gerdol *et al.*, 1996). Below this optimal range, productivity rapidly declines, while above it the decline is typically slower. Using the linear

regression equation shown in Figure 3-4 to estimate θ in the top 1.5 cm of the profile, W:D of 6-15 corresponds to an optimal TDR-derived θ range of 0.07 – 0.23, which is roughly the minimum range of θ observed during the study season (5^{th} percentile of $\theta \approx 0.11$). It therefore appears that capitulum water content was rarely, if ever, too low to limit GEP during the study, while it may have frequently been limiting during wet periods of high θ. For example, the three plots with the highest seasonal average near-surface θ had the lowest seasonal average GEP, and plot 2008 was both the wettest and least productive plot on average.

The relationship between TDR-derived θ in the top 3 cm of the profile and W:D of 1.5 cm capitula was weaker than might have been expected. Part of the reason for this may be due to morphology, as the dense cluster of branches comprising the capitula has a much higher water-holding potential than the more sparsely-branched stems (Hayward & Clymo, 1982). Robroek *et al.* (2009) reported a relatively weak correlation between the gravimetric water content of the 0-2 cm and 2-4 cm layers of *Sphagnum* monoliths sectioned in a laboratory, particularly for low water table treatments, suggesting that water content can vary greatly over a short distance in the uppermost few centimeters of the profile. Hayward and Clymo (1982) note that even the measurement of W:D introduces some uncertainty as water may be lost during collection. Accurate quantification of capitulum water content in the field is difficult, and the scatter in the TDR-derived θ–W:D relationship likely accounts for some proportion of the variance observed in the GEP–θ relationship.

The effect of ambient temperature on growth has not been studied as well as that of moisture content, and can be confounded by changes in water content when increased evaporative losses are not controlled for (e.g. Gunnarsson *et al.*, 2004). Harley *et al.* (1989) found that responses to temperature in three species of *Sphagnum* were broad, with optimal GEP at approximately 20°C and GEP at or above 75% of the maximum rate between 13 and 30°C. Robroek *et al.* (2007) observed higher vertical growth rates in the four species studied at 20°C than at 15°C. The findings of this study are in general agreement with previous work. All seven plots had positive linear correlations between GEP and T_C over a measured range of about 15-35°C, and four of these were statistically significant at the 0.05 level (Figure 3-3, b).

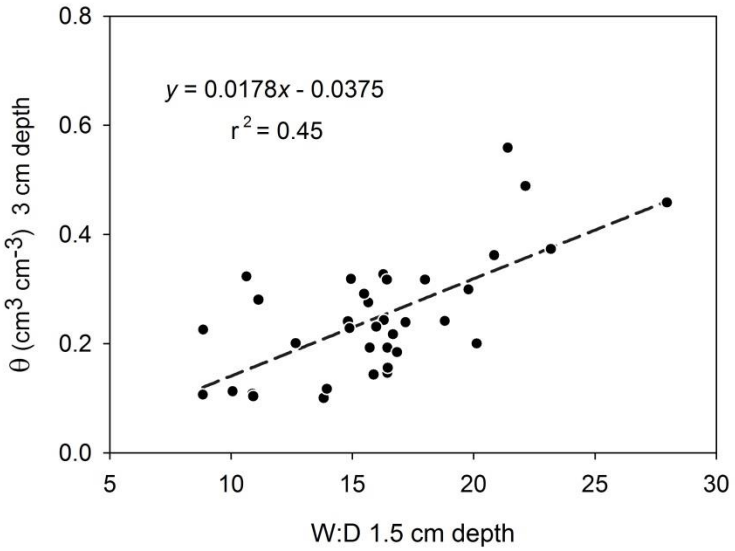


Figure 3-4: Plot of volumetric water content (θ) in the 0-3 cm layer, measured using a WET-Sensor™ portable TDR device, against the wet mass : dry mass ratio (W:D) of capitulum samples (top 1.5 cm layer) extracted from the same location. Sampling locations (*n*=36) were chosen randomly within a single trench with a similar species composition and capitulum density.

3.5.2 Role of Profile Age and Species Composition

The role of species composition was difficult to parse out from that of θ and the regenerated *Sphagnum* profile age as these variables were somewhat confounded. While it could be argued that species composition was similar at the four EXPER plots and between EXPER and 1970-A, within SPONT there were large differences in species composition (Figure 3-1). There are few reports of photosynthetic responses of different *Sphagnum* species with which to compare GEP values, and comparisons can be difficult as laboratory studies tend to report values normalized per unit dry sample mass whereas field studies are generally expressed per unit surface area. The following statements refer to studies of water content and photosynthesis in *S. fuscum*, *Sphagnum* section *Acutifolia* spp., and *S. magellanicum* (Silvola & Aaltonen, 1984; Silvola, 1990, 1992; Williams & Flanagan, 1996; Schipperges & Rydin, 1998), and apply to the species present at the study site. There is general agreement that photosynthetic responses at low water contents are similar across species, and that at higher water contents the shape of the GEP–capitulum water content function is species-specific. There is some disagreement over whether or not there are meaningful differences in

maximum potential carbon assimilation rate between these species, but most studies would suggest that there are.

There were no clear correlations between species relative abundance and GEP in this study, and there is some reason to doubt that species differences were significant in explaining differences in GEP. For instance, plots 2004 and 2008 had fairly similar species compositions but 2004 had the highest seasonal average GEP while 2008 had the lowest. Similarly, there were no statistically significant ($p<0.05$) differences in GEP at plots 2004, 2006, 1970-A and 1970-B despite the fact that 1970-B had virtually no species in common with the first three. While the effect of species composition was not clear and may not have been especially significant on a seasonal timescale, it is very likely that differences in species contributed to differences in the response to θ and other parameters, particularly at higher water contents (Silvola, 1992). Different response curves and tolerances to saturation and desiccation in the species present at each collar could account for some of the unexplained variance in the GEP model.

Though there were no statistically meaningful correlations between the age of a regenerated layer and GEP, there were clear differences between plots in their ability to convey water to the surface. This is evident from the fact that θ in the near surface was very different between plots for a given WT (Figure 3-5), suggesting different degrees of capillarity. It is well documented that in natural peatlands, *Sphagnum* species exist in particular ecological niches dictated primarily by their ability to conduct water to the capitulum (see the extensive literature review by Rydin, 1993). This is understood to be a function of community traits, such as capitulum density, and individual shoot morphology (Clymo & Hayward, 1982; Titus & Wagner, 1984; Elumeeva *et al.*, 2011), as well as the properties of the underlying substratum (e.g. degree of decomposition with depth) (Clymo & Hayward, 1982; Clymo, 1984). As previously discussed, the structure of the substrate differs dramatically between natural and cutover peatlands, and thus patterns of growth influencing capillarity may also differ, although this has not been well studied. It appears here that the more recently regenerated *Sphagnum* layers (plots 2008 and 2010, with thicknesses of 3-4 cm) maintain a very high θ throughout the range of WT observed, and that θ is strongly linked to WT at these plots, as indicated by a steeper slope (greater change in θ per unit rise in WT). This is likely a function of the properties of the cutover peat directly underlying the regenerated layers. Plot 2006, aged 7 years with a *Sphagnum* profile height of ~10 cm, had a strong θ–WT connection when WT was within ~20 cm of the surface, whereas at all other plots with profile heights >10 cm there was little relation between θ and WT (θ was near-constant for a wide range of WT). This was not true, however, at plot 1970-C, where θ dynamics at the surface were clearly linked to WT. We propose that this is due to

the much higher capitulum density and dominance of *S. rubellum* Wils. at the plot. A full analysis of the soil water dynamics within the plots and the reasons for the differences between them is beyond the scope of this paper and is addressed in a concurrent study (see Chapter 2). To summarize, although there was no obvious simple effect of profile age on GEP, there were clear differences in capillarity between plots which were reflected in the large differences in near-surface θ, and corresponding differences in GEP can certainly be at least partially attributed to this effect.

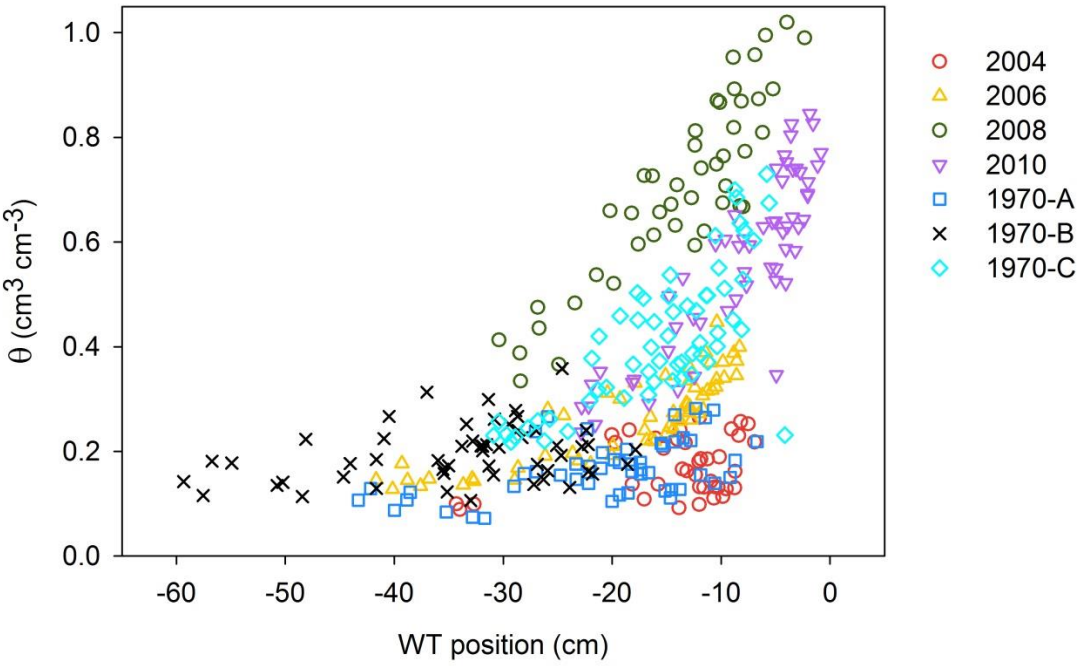


Figure 3-5: Water table position relative to the growing surface versus volumetric water content in the top 3 cm of the regenerated layer. All relationships were significant at the 0.05 level (Pearson's Correlation Coefficient, two-tailed test of significance).

3.5.3 Modeled GEP and Estimation of Optimal Water Content

There are several possible sources for the variance in the GEP model not explained by the measured environmental parameters. While it is generally accepted that water availability is the most important factor affecting *Sphagnum* productivity under non-light-limiting conditions (Busby & Whitfield, 1978; Dilks & Proctor, 1979; Schipperges & Rydin, 1998), studies have also evaluated the

effects of other environmental parameters on *Sphagnum* productivity such as groundwater pH (e.g. Clymo, 1973) or atmospheric nitrogen deposition (e.g. Granath *et al.*, 2012). However, given the close spatial proximity of the plots (<1km), the ombrotrophic nature of the site, and the limited range of pH, EC, and salinity (see results), it was thought to be unlikely that these would account for any significant proportion of the unexplained variance controlling GEP. More likely explanations for this variance are the differences in water relations between species and the potential error in the measurement of capitulum water content, as already discussed. A further potential source of variance is the hysteretic relationship between water content and GEP that has been observed (Silvola, 1992; Schipperges & Rydin, 1998), where GEP at a given water content is dependent to some degree on antecedent conditions (note that the drying cycles in these studies were likely more severe than any experienced in this study). Nonetheless, the measured model inputs were able to account for roughly half of the variance in GEP.

Based on the predicted values of GEP derived from the mixed linear model, the range of θ for optimum productivity of regenerating *Sphagnum* was estimated. Modeled GEP values are shown plotted against θ in Figure 3-6. The range of θ containing the top 10% of modeled GEP values (n=25) was selected as the optimal productivity range. GEP values in this range were ≥ 85% of the maximum modeled value. This corresponded to a θ range of 0.13 to 0.50, which is both broader and higher than the θ range determined from the literature (0.07 – 0.23; see sources above, section 3.5.1). The likely presence of multiple optimal θ values for different species is the most probable cause for the broad optimal range observed here.

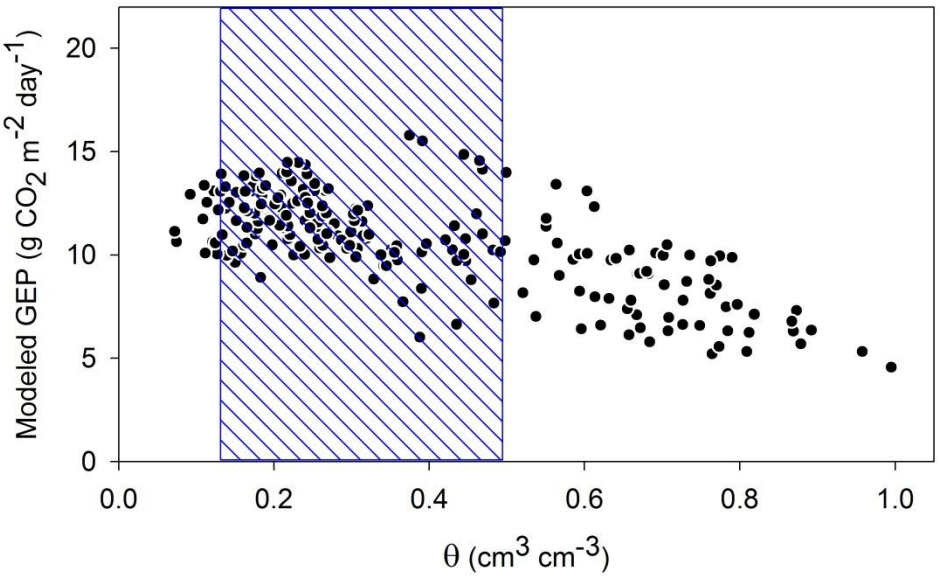


Figure 3-6: Plot of θ against GEP values predicted by the mixed linear model. The shaded blue region shows the range of θ containing the highest ten percent (*n*=25) of predicted GEP values (θ values range from 0.13 to 0.50). All GEP values in this range were ≥85% of the maximum predicted value. This is considered to be the theoretical maximum productivity range of water content.

3.6 Conclusion

Sphagnum regenerating on cutover peatland surfaces can remain productive under a variety of hydrologic conditions. In this study productivity was never observed to be limited by an insufficient supply of water, including during periods where the water table was more than 40 cm below the surface and periods where no direct precipitation was received for up to 16 days. Conversely, the water content in the near surface was high enough to limit productivity during wetter periods, sometimes severely. This was particularly apparent for thinner regenerating layers < 5 cm in thickness. This has important implications for the production of *Sphagnum* biomass on cutover surfaces using the species studied here, which are typical of hummocks and drier lawns in the study region. It must be noted that conditions of extended low water table were not observed in this study, and the response of regenerating *Sphagnum* to these conditions remains uncertain. However, this may not be an issue at sites where seasonal water table drawdown is limited by irrigation or other water management practices.

Based on the model used to determine the relative influence of the measured environmental parameters on GEP, a volumetric water content range in the 0-3 cm layer of about 0.13 to 0.50 was determined to be the optimal range for maximizing productivity. The species studied here may have narrower optima within this range, but the presence of multiple species within each study plot made it impossible to identify these from the data. Regenerated *Sphagnum* layers of a variety of ages and thicknesses were able to maintain sufficiently high water content to remain productive during all conditions observed in this study. However, the ability of layers of different thicknesses and community structures to transmit water to the surface clearly differed. The depth of water table needed to achieve optimal capitulum water content will therefore vary as a function of the properties of the peat substrate, the species, and the thickness of the regenerated layer.

The quantification of water content in the capitulum layer is extremely sensitive to measurement depth. Future studies attempting to measure this parameter using TDR or other non-destructive methods need to consider the fine spatial scale on which water content can vary in the top few centimeters of growing *Sphagnum* and refine measurement techniques to focus on this layer.

4.0 Conclusion and Implications

This study is the first to specifically describe the long term structural evolution and ecohydrology of *Sphagnum* regenerating on cutover peat surfaces. Regenerated layers appear to follow a trajectory of structural evolution whereby the bulk density and water retention capacity of the layer immediately above the former cutover peat surface increase substantially over time owing to decomposition and compaction. This was quite evident at the >40 year old spontaneously regenerated plots, where basal layer retention capacity was on average 65 percent greater at the lowest measured soil water pressure (-30 cm) than at the younger plots, but could also be seen to a lesser degree at the 2004 plot which was only nine years old at the time of data collection. The greater water storage capacity at tension in the older more developed basal layers may be significant in maintaining water supply for capillary flow during drier periods. Additionally, the structure of the regenerated layer at plot 2004 suggests that this process of decomposition and compaction, and the resultant increase in storage capacity at tension, may begin to occur after less than a decade of growth.

Analysis of water table position relative to the former cutover surface at each plot suggests that seasonal water table positions may have increased relative to initial post-extraction conditions at the spontaneously regenerated plots (WT above cutover peat 81±8% of study) but not at the <10 year old experimentally regenerated plots (WT above cutover peat 30±25% of study). If this is indeed the case, it indicates that the older plots are developing a soil water regime more similar to that of a natural bog peatland, where the water table is always maintained above catotelmic peat, but that this process is still incomplete after >40 years of regeneration. Nonetheless, the older regenerated *Sphagnum* layers seem to be developing properties conducive to peat formation, which bodes well for the long-term regeneration prospects of these cutover peatlands.

Near-surface (0-3 cm layer) water content was statistically significantly related ($p<0.05$; Pearson's Correlation Coefficient, two-tailed test of significance) to water table position at all studied plots. This fact, along with TDR time series data detailing the hydrologic response of layers to specific events, demonstrates the poor retention of precipitation in the *Sphagnum* canopy and the relatively greater importance of groundwater as a water source. The seven different regenerated layers studied here clearly differ in their ability to transmit water to the surface. Although six of the seven plots support the idea that the near-surface water content for a given depth of water table decreases as a function of the thickness of the regenerated layer, one of the plots (plot 1970-C) does not fit this model. This is very likely attributable to the overwhelming dominance of *S. rubellum* and relatively higher capitulum density of this particular area of the site, which have imparted the

regenerated layer there with a higher retention capacity in the upper (0-10 cm) depth ranges and the ability to maintain a much higher near-surface water content for a given water table depth than other similarly thick regenerated layers. Plot 1970-C shows that while layer capillarity may perhaps generally be a function of thickness, factors such as community architecture can supersede layer thickness in importance.

Based on field chamber measurements of CO_2 exchange, this research demonstrates that regenerated *Sphagnum* layers are broadly tolerant to a range of hydrologic conditions, and are able to remain highly productive during periods where the water table is >40 cm below the surface and during periods where no precipitation is received for 16 consecutive days. Insufficient supply of water does not appear to limit productivity under these conditions, but productivity may be considerably limited by an overabundance of water during wet periods. Using a mixed linear model approach to isolate the effect of capitulum water content on light-saturated productivity from the effects of canopy temperature, plot, and their statistical interactions, a volumetric water content range of 0.13 to 0.50 is identified as optimal for growth. It is likely that this range can be further refined by increasing the precision of TDR measurements to reflect the water content of only the capitulum layer (uppermost ~1.5 cm of the profile), as well as by isolating individual species responses from the response of the heterogeneous species arrays observed here.

This research has several important implications for *Sphagnum* biomass production using the species studied here, which are typical of hummocks and lawns in the peat extraction areas of eastern New Brunswick. Firstly, that water table position is an effective means of controlling water content in the near-surface. This suggests that subsurface irrigation schemes aimed at maintaining a constant water table below the cutover peat surface, such as those now in development in eastern Canada, will be successful in creating optimal conditions for *Sphagnum* growth provided that the correct water table depths are used. The depth of water table needed to achieve the optimal range of water content will naturally vary as a function of the peat substrate properties, the thickness of the regenerated layer, and the particular species used. However, the relationships developed here between water table depth and average near-surface water content for a given layer thickness should prove useful to this end.

The second implication of this work is that it is entirely possible for conditions on cutover surfaces to be too wet for optimal *Sphagnum* growth. While restoration and rehabilitation techniques generally focus on ensuring sufficient water supply to *Sphagnum* diaspores, flooded conditions or even periods where the water table is just beneath the cutover peat surface have the potential to substantially reduce levels of productivity in the species studied here. This seems to be most relevant

to the newly-regenerating layers <5 cm in thickness, which are also likely the most relevant to biomass production cycles.

Finally, it is clear from this work that the hydraulic properties of the regenerating layers change relatively quickly as the layer thickness increases. The water table depth corresponding to the optimal capitulum water content range will likely differ for a *Sphagnum* layer 4 cm thick as compared to a layer 14 cm thick, although this is likely only relevant to production cycles >5 years in duration. Production cycles should take this into account either by changing water table levels at different stages of growth or by harvesting at suitable time intervals so that near-optimal hydrologic conditions are maintained throughout the production cycle.

Appendix: WET-Sensor Calibration and Lysimeter Data

WET-Sensor Calibration

This section describes the calibration of the WET-sensor™ portable TDR probe (Delta-T Devices Ltd., model WET-2) to determine volumetric water content in living and partially decomposed *Sphagnum* moss as well as peat. Calibration generally follows the approach outlined in Topp *et al.* (1980).

For field measurements of water content, a custom setting was used instead of the sensor's "organic" factory setting to increase the sensitivity of the probe to the range of low water contents encountered in the near-surface of *Sphagnum* hummocks (which, on the organic setting, tended to read between 5 and 8% water content). On the custom setting, the two sensor parameters b0 (offset parameter) and b1 (scaling parameter) were set to 1 and 6, respectively, in accordance with the operable value ranges outlined in the sensor manual (Delta-T Devices, 2005). These parameters govern the conversion of the measured apparent dielectric constant of a given material to the water content.

To determine the volumetric water content (θ) of the 0-6 cm and 0-3 cm layers at each plot, four samples were extracted from the near-surface of each of the seven plots in 10 cm diameter PVC rings, two for the full depth (0-6 cm) and two for the partial exposure (0-3 cm) layer calibrations (for a total of 28 samples). Samples were large enough in both cases to ensure that the probes were >2.5 cm from the sides of the containers to prevent interference (Kellner & Lundin, 2001). The experimental set-up is shown in Figure A-1 below. Samples were slowly wet up to saturation over a period of 24 hours to minimize entrapment of air in pores. Samples were weighed and concurrent sensor measurements were taken twice daily as samples dried with the aid of a fan. At the end of the calibration, samples were dried at 80 °C until masses stabilized to determine the dry sample mass, and the dry sample and container masses were then subtracted from each total mass recorded to determine the mass of water in each sample at that time. Gravimetric water contents were converted to θ by assuming that 1 g water = 1 cm^3, and θ was then plotted against the sensor reading at each measurement. Finally, a third-order polynomial function (Topp *et al.*, 1980) was fit to the calibration data from each plot and layer. The equation, along with plots and estimates of the parameters for each calibration, is shown in Figure A-2.

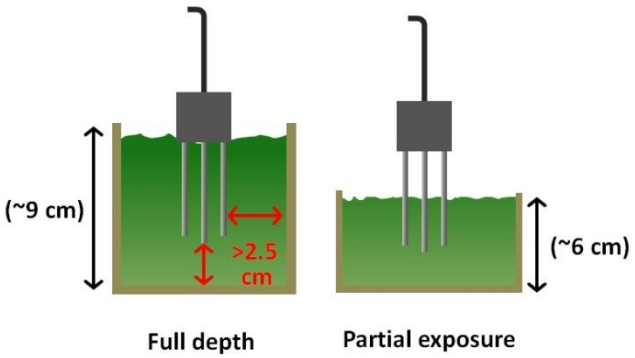
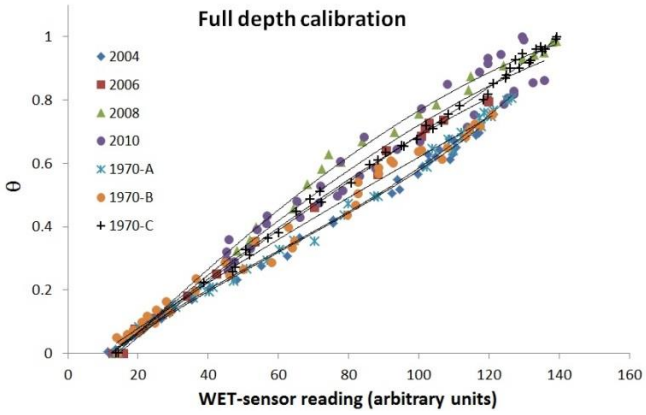
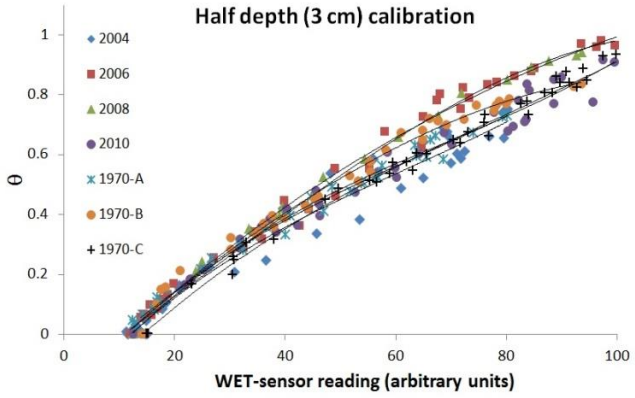


Figure A-1: Diagram showing experimental set-up used during the calibration of the WET-sensor for both full depth (0-6 cm layer) and partial exposure (0-3 cm layer) calibrations



Site:	*a*	*b*	*c*	*d*
2004	2.41 E-7	-4.40 E-5	8.77 E-3	-1.01 E-1
2006	-7.37 E-8	5.89 E-7	8.60 E-3	-1.06 E-1
2008	-6.56 E-8	-1.19 E-5	1.10 E-2	-1.52 E-1
2010	-8.33 E-8	-1.81 E-7	9.22 E-3	-1.16 E-1
1970-A	2.91 E-7	-5.16 E-5	9.10 E-3	-9.91 E-2
1970-B	2.88 E-8	-1.21 E-5	7.86 E-3	7.44 E-2
1970-C	1.15 E-7	-3.20 E-5	1.04 E-2	-1.46 E-1



Site:	*a*	*b*	*c*	*d*
2004	1.06 E-6	-1.98 E-4	2.07 E-2	-2.23 E-1
2006	-6.29 E-7	5.15 E-5	1.23 E-2	-1.36 E-1
2008	1.32 E-7	-7.96 E-5	1.86 E-2	-2.00 E-1
2010	1.06 E-6	-2.20 E-4	2.31 E-2	-2.53 E-1
1970-A	9.88 E-7	-1.94 E-4	2.10 E-2	-2.11 E-1
1970-B	-3.32 E-7	-1.71 E-5	1.51 E-2	-1.49 E-1
1970-C	5.74 E-7	-1.39 E-4	1.99 E-2	-2.57 E-1

Figure A-2: Calibration curves for each plot for both 0-6 cm (top) and 0-3 cm (bottom) layers. Volumetric water content (θ) was approximated by a third-order polynomial equation, $\theta = ax^3 + bx^2 + cx + d$, where x is the sensor reading and a, b, c and d are parameters estimated from the data. Estimated parameter values are shown for each calibration at right.

Lysimeter Data and Priestley-Taylor Evaporation Coefficient Estimates

Evapotranspiration was estimated for each plot by relating the equilibrium evapotranspiration (ET_{eq}), estimated using net radiation, air temperature and ground heat flux data recorded by a meteorological station at the site, with the actual evapotranspiration (ET_a) over a given time period measured by a pair of weighing lysimeters. This approach is known as the Priestley-Taylor method (Priestley & Taylor, 1972). The slope of the $ET_{eq} - ET_a$ relation, referred to as the alpha parameter (α), represents a multiplier coefficient that is applied to the seasonal ET_{eq} to generate a calibrated plot-specific estimate of total seasonal evapotranspiration. Data used to generate plot α values are shown in Figure A-3 below. The lysimeters were made out of buckets, approximately 22 cm in diameter by 30 cm depth, filled with peat-*Sphagnum* monoliths extracted from within a close vicinity of the study plots. Water was added or removed, as necessary, following rain events or during extended dry periods to maintain near-surface water content in the lysimeters to within 5–10 percent of the average water content measured at a given plot. ET_a was taken as the average depth of water lost (determined from mass difference between readings, density of water, and lysimeter surface area) over the two lysimeters at each plot. Measurement periods for ET_a ranged from roughly 12 to 72 hours, and all measurement periods used for calculating α values contained no precipitation and had a measured difference in ET_a of <30 percent between lysimeters at a given plot. Two lysimeters were also installed in an area of bare cutover peat for comparative purposes.

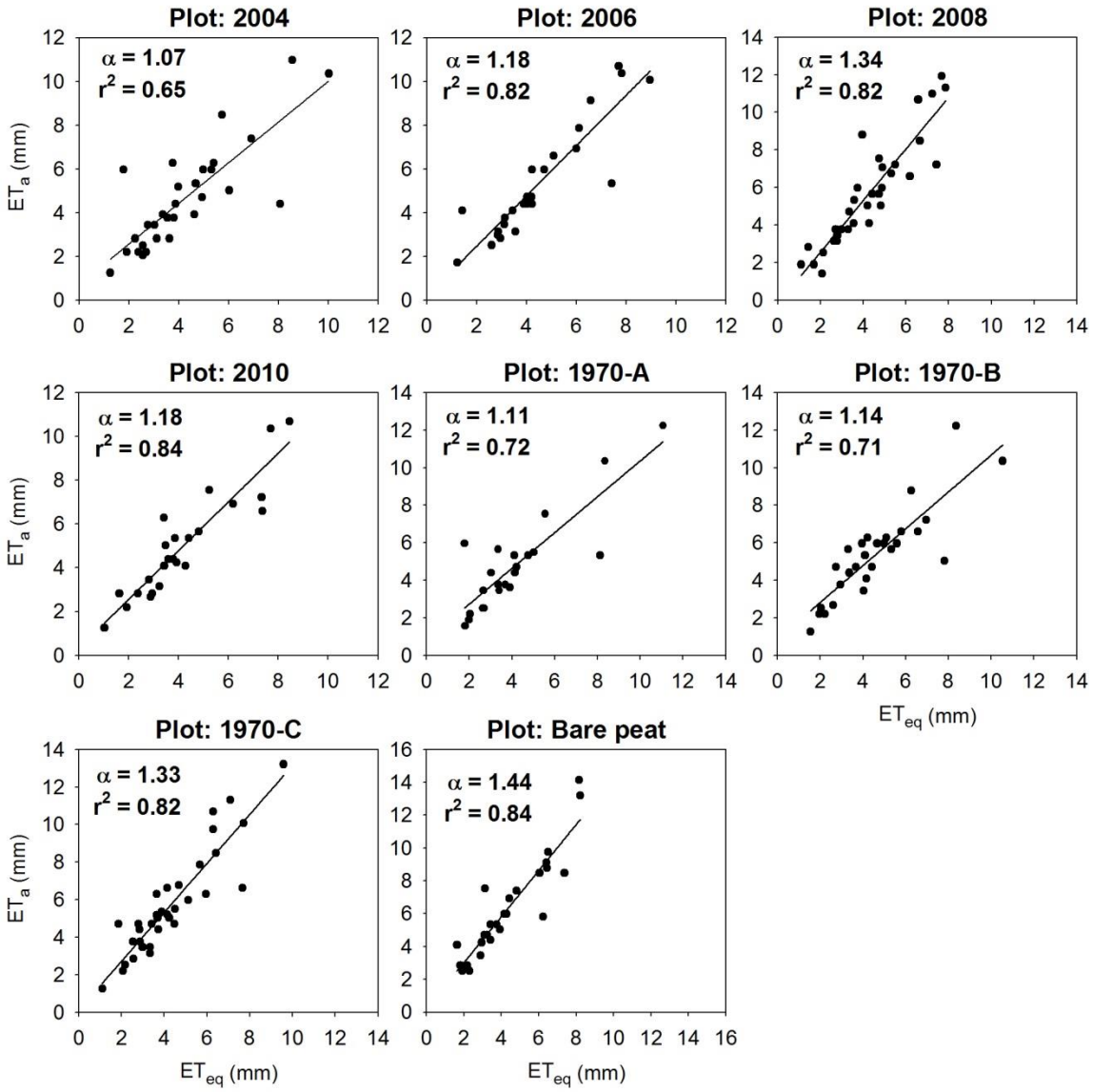


Figure A-4: Plots of equilibrium evapotranspiration (ET_{eq}) estimated from meteorological station data for a given time period against the actual evapotranspiration (ET_a) measured over the same period at a given plot. Alpha parameters (slopes) are shown for each plot, along with r^2 values.

References

Anderson, L. 1990. A checklist of Sphagnum in North America north of Mexico. *The Bryologist* **93** : 500–501.

Blake, G. & Hartge, K. 1986. Particle density. In *Methods of soil analysis. Part 1: Physical and mineralogical methods*. A. Klute, ed. SSSA: Madison, WI, pp. 377–382.

Boelter, D. 1968. Important Physical Properties of Peat Materials. In *Proceedings of the 3rd International Peat Congress*. Quebec City, QC, pp. 150–156.

Boon, H. & Verhagen, J. 2008. Growing media for the future. In *After Wise Use - The Future of Peatlands. Proceedings of the International Peat Symposium, Tullamore, Ireland, 8-13 June, 2008, Vol. 1, Oral Presentations*. C. Farrell & J. Feehan, eds. International Peat Society, pp. 142–143.

van Breeman, N. 1995. How Sphagnum bogs down other plants. *Tree* **10** : 270–275.

Buckingham, E. 1907. *Studies on the movement of soil moisture. Bulletin 38*. USDA Bureau of Soils: Washington, D.C.

Busby, J. & Whitfield, D. 1978. Water potential, water content, and net assimilation of some boreal forest mosses. *Canadian Journal of Botany* **56** : 1551–1558.

Campeau, S. & Rochefort, L. 2002. Possibilities and limits to Sphagnum farming. In *Proceedings of the International Peat Symposium: Peat in Horticulture. Quality and environmental challenges.* G. Schmilewski & L. Rochefort, eds. Int. Peat Society: Jyväskylä, Finland, pp. 264–269.

Canadian Sphagnum Peat Moss Association. 2005. Preservation and Reclamation Policy. Accessed on September 19, 2014 at www.peatmoss.com

Cleary, J., Roulet, N.T. & Moore, T.R. 2005. Greenhouse gas emissions from Canadian peat extraction, 1990-2000: A life-cycle analysis. *Ambio* **34** : 456–461.

Clymo, R.S. 1973. The growth of Sphagnum : Some effects of environment. *Journal of Ecology* **61** : 849–869.

Clymo, R.S. 1984. The limits to peat bog growth. *Philosophical Transactions of the Royal Society B: Biological Sciences* **303** : 605–654.

Clymo, R.S. & Hayward, P.M. 1982. Ecology of Sphagnum. In *Bryophyte Ecology*. A. Smith, ed. Chapman and Hall: London, U.K., pp. 229–289.

Csintalan, Z., Takács, Z., Proctor, M., Nagy, Z. & Tuba, Z. 2000. Early morning photosynthesis of the moss Tortula ruralis following summer dew fall in a Hungarian temperate dry sandy grassland. *Plant Ecology* **151** : 51–54.

Daigle, J.-Y. & Gautreau-Daigle, H. 2001. *Canadian peat harvesting and the environment, 2nd ed.* North American Wetlands Conservation Council Committee: Ottawa, ON.

Delta-T Devices. 2005. WET-sensor user manual v1.3. Cambridge, U.K.: Delta-T Devices.

Dilks, A.T.J.K. & Proctor, M.C.F. 1979. Photosynthesis, respiration and water content in bryophytes. *New Phytologist* **82** : 97–114.

Elumeeva, T.G., Soudzilovskaia, N.A., During, H.J. & Cornelissen, J.H.C. 2011. The importance of colony structure versus shoot morphology for the water balance of 22 subarctic bryophyte species permafrost insulation and carbon sequestration functions. *Journal of Vegetation Science* **22** : 152–164. DOI: 10.1111/j.1654-1103.2010.01237.x

Emmel, M. 2008. Growing ornamental plants in Sphagnum biomass. *Acta Horticulturae* **779** : 173–178.

Environment Canada. 2014. Canadian Climate Normals 1981-2010. Accessed on May 9, 2014 at http://climate.weather.gc.ca/.

Ferland, C. & Rochefort, L. 1997. Restoration techniques for Sphagnum-dominated peatlands. *Canadian Journal of Botany* **75** : 1110–1118.

Van Gaalen, K.E., Flanagan, L.B. & Peddle, D.R. 2007. Photosynthesis, chlorophyll fluorescence and spectral reflectance in Sphagnum moss at varying water contents. *Oecologia* **153** : 19–28. DOI: 10.1007/s00442-007-0718-y

Gaudig, G. 2012. Sphagnum farming in Germany: 10 years on the road to sustainable growing media (extended abstract). In *Proceedings of the 14th International Peat Congress*. Stockholm, Sweden.

Gaudig, G. & Joosten, H. 2002. Peat moss (Sphagnum) as a renewable resource - an alternative to Sphagnum peat in horticulture. In *Proceedings of the International Peat Symposium: Peat in Horticulture. Quality and environmental challenges.* G. Schmilewski & L. Rochefort, eds. Int. Peat Society: Jyväskylä, Finland, pp. 117–125.

Gerdol, R., Bonora, A., Gualandri, R. & Pancaldi, S. 1996. CO2 exchange , photosynthetic pigment composition , and cell ultrastructure of Sphagnum mosses during dehydration and subsequent rehydration. *Canadian Journal of Botany* **74** : 726–734.

González, E., Rochefort, L., Poulin, M. 2013. Trajectories of plant recover in block-cut peatlands 35 years after peat extraction. *Applied Ecology and Environmental Research* **11** : 385–406.

Granath, G., Strengbom, J. & Rydin, H. 2012. Direct physiological effects of nitrogen on Sphagnum: a greenhouse experiment. *Functional Ecology* **26** : 353–364. DOI: 10.1111/j.1365-2435.2011.01948.x

Griffis, T.J., Rouse, W.R. & Waddington, J.M. 2000. Scaling net ecosystem CO2 exchange from the community to landscape-level at a subarctic fen. *Global Change Biology* **6** : 459–473.

Gunnarsson, U., Granberg, G. & Nilsson, M. 2004. Growth, production and interspecific competition in Sphagnum: effects of temperature, nitrogen and sulphur treatments on a boreal mire. *New Phytologist* **163** : 349–359. DOI: 10.1111/j.1469-8137.2004.01108.x

Harley, P.C., Tenhunen, J.D., Murray, K.J. & Beyers, J. 1989. Irradiance and temperature effects on photosynthesis of tussock tundra Sphagnum mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia* **79** : 251–259.

Hayward, P.M. & Clymo, R.S. 1982. Profiles of water content and pore size in Sphagnum and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society B: Biological Sciences* **215** : 299–325. DOI: 10.1098/rspb.1982.0044

Hoag, R. & Price, J.S. 1997. The effects of matrix diffusion on solute transport and retardation in undisturbed peat in laboratory columns. *Journal of Contaminant Hydrology* **28** : 193–205.

IBM Corp. 2011. IBM SPSS Statistics for Windows, Version 20.0. IBM Corp: Armonk, NY.

Ketcheson, S.J. & Price, J.S. 2014. Characterization of the fluxes and stores of water within newly formed Sphagnum moss cushions and their environment. *Ecohydrology* **7** : 771–782.

Kellner, E. & Lundin, L-C. 2001. Calibration of time domain reflectometry for water content in peat soil. *Nordic Hydrology* **32** : 315–332.

Kilham, P. 1982. The biogeochemistry of bog ecosystems and the chemical ecology of Sphagnum. *The Michigan Botanist* **21** : 159–168.

Laframboise, M. 1987. *Origine et évolution de deux terres noires de la MRC du Haut-Saint-Laurent, Québec. M. Sc. Thesis*. Université de Montréal, Montréal, Québec.

Landry, J. & Rochefort, L. 2009. *Experimental Sphagnum farming station, Shippagan, New Brunswick: Activity report 2003-2008*. Peatland Ecology Research Group, Université Laval: Québec, QC.

Lavoie, C., Grosvernier, P., Girard, M. & Marcoux, K. 2003. Spontaneous revegetation of mined peatlands : An useful restoration tool? *Wetlands Ecology and Management* **11** : 97–107.

Lavoie, C. & Rochefort, L. 1996. The natural revegetation of a harvested peatland in southern Québec : A spatial and dendroecological analysis. *Écoscience* **3** : 101–111.

Lewis, A.M. 1988. A test of the air-seeding hypothesis using Sphagnum hyalocysts. *American Journal of Botany* **87** : 577–582.

Loisel, J., Yu, Z., Beilman, D., Camill, P., Alm, J., Amesbury, J., Anderson, D. ... Zhou, W. 2014. A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *The Holocene* **24** : 1028-1042. DOI: 10.1177/0959683614538073

Lucchese, M., Waddington, J.M., Poulin, M., Pouliot, R., Rochefort, L. & Strack, M. 2010. Organic matter accumulation in a restored peatland: Evaluating restoration success. *Ecological Engineering* **36** : 482–488. DOI: 10.1016/j.ecoleng.2009.11.017

Luken, J.O. 1985. Zonation of Sphagnum mosses : Interactions among shoot growth, growth form, and water balance. *The Bryologist* **88** : 374–379.

McCarter, C.P.R. & Price, J.S. 2012. Ecohydrology of Sphagnum moss hummocks: mechanisms of capitula water supply and simulated effects of evaporation. *Ecohydrology* **7** : 33–44. DOI: 10.1002/eco.1313

McCarter, C.P.R. & Price, J.S. 2013. The hydrology of the Bois-des-Bel bog peatland restoration: 10 years post-restoration. *Ecological Engineering* **55** : 73–81. DOI: 10.1016/j.ecoleng.2013.02.003

McCarter, C.P.R. & Price, J.S. 2014. The hydrology of the Bois-des-Bel peatland restoration: hydrophysical properties limiting connectivity between regenerated Sphagnum and remnant vacuum harvested peat deposit. *Ecohydrology*. DOI: 10.1002/eco.1498

McNeil, P. & Waddington, J.M. 2003. Moisture controls on Sphagnum growth and CO2 exchange on a cutover bog. *Journal of Applied Ecology* **40** : 354–367.

Murray, K.J., Harley, P.C., Beyers, J., Walz, H. & Tenhunen, J.D. 1989. Water content effects on photosynthetic response of Sphagnum mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia* **79** : 244–250.

Natural Resources Canada. 2014. Mineral production of Canada, by province and territory. Accessed on July 14, 2014 at http://sead.nrcan.gc.ca/.

New Brunswick Department of Natural Resources. 2014. Peat Mining Policy. Accessed on September 20, 2014 at http://www.gnb.ca.

Petrone, R.M., Waddington, J.M. & Price, J.S. 2003. Ecosystem-scale flux of CO2 from a restored vacuum harvested peatland. *Wetlands Ecology and Management* **11** : 419–432.

Poulin, M., Rochefort, L. & Desrochers, A. 1999. Conservation of bog plant species assemblages: assessing the role of natural remnants in mined sites. *Applied Vegetation Science* **2** : 169–180.

Poulin, M., Rochefort, L., Quinty, F. & Lavoie, C. 2005. Spontaneous revegetation of mined peatlands in eastern Canada. *Canadian Journal of Botany* **83** : 539–557. DOI: 10.1139/B05-025

Pouliot, R., Hugron, S., Rochefort, L. 2014. Sphagnum farming: A long-term study on producing peat biomass sustainably. *Ecological Engineering* **74** : 135–147.

Price, J.S. 1996. Hydrology and microclimate of a partly restored cutover bog, Québec. *Hydrological Processes* **10** : 1263–1272.

Price, J.S. 2003. Role and character of seasonal peat soil deformation on the hydrology of undisturbed and cutover peatlands. *Water Resources* **39** : 1–10.

Price, J.S. 1997. Soil moisture, water tension, and water table relationships in a managed cutover bog. *Journal of Hydrology* **202** : 21–32.

Price, J.S., Heathwaite, A.L. & Baird, A.J. 2003. Hydrological processes in abandoned and restored peatlands: An overview of management approaches. *Wetlands Ecology and Management* **11** : 65–83.

Price, J.S. & Whitehead, G.S. 2001. Developing hydrologic thresholds for Sphagnum recolonization on an abandoned cutover bog. *Wetlands* **21** : 32–40.

Price, J.S. & Whittington, P.N. 2010. Water flow in Sphagnum hummocks: Mesocosm measurements and modelling. *Journal of Hydrology* **381** : 333–340. DOI: 10.1016/j.jhydrol.2009.12.006

Price, J.S., Whittington, P.N., Elrick, D.E., Strack, M., Brunet, N. & Faux, E. 2008. A Method to Determine Unsaturated Hydraulic Conductivity in Living and Undecomposed Moss. *Soil Science Society of America Journal* **72** : 487. DOI: 10.2136/sssaj2007.0111N

Priestley, C. & Taylor, R. 1972. On the assessment of surface heat flux and evaporation using large scale parameters. *Monthly Weather Review* **100** : 81–92.

Proctor, M. 1982. Physiological ecology: water relations, light and temperature responses, carbon balance. In *Bryophyte Ecology*. A. Smith, ed. Chapman and Hall: London, U.K. pp. 333–382.

Quinty, F. & Rochefort, L. 2003. *Peatland Restoration Guide, Second Edition*, Canadian Sphagnum Peat Moss Association and New Brunswick Department of Natural Resources and Energy: Québec, Québec.

Robert, É.C., Rochefort, L. & Garneau, M. 1999. Natural revegetation of two block-cut mined peatlands in eastern Canada. *Canadian Journal of Botany* **77** : 447–459.

Robroek, B.J.M., Limpens, J., Breeuwer, A. & Schouten, M.G.C. 2007. Effects of water level and temperature on performance of four Sphagnum mosses. *Plant Ecology* **190** : 97–107. DOI: 10.1007/s11258-006-9193-5

Robroek, B.J.M., Schouten, M.G.C., Limpens, J., Berendse, F. & Poorter, H. 2009. Interactive effects of water table and precipitation on net CO2 assimilation of three co-occurring Sphagnum mosses differing in distribution above the water table. *Global Change Biology* **15** : 680–691. DOI: 10.1111/j.1365-2486.2008.01724.x

Rochefort, L. 2000. Sphagnum : A keystone genus in habitat restoration. *The Bryologist* **103** : 503–508.

Rochefort, L., Quinty, F., Campeau, S., Johnson, K. & Malterer, T. 2003. North American approach to the restoration of Sphagnum dominated peatlands. *Wetlands Ecology and Management* **11** : 3–20.

Rydin, H. 1993. Interspecific competition between Sphagnum mosses on araised bog. *Oikos* **66** : 413–423.

Rydin, H. & Jeglum, J. 2009. *The biology of peatlands*, Oxford University Press: New York, NY.

Rydin, H. & McDonald, A.J.S. 1985. Photosynthesis in Sphagnum at different water contents. *Journal of Bryology* **13** : 579–584.

Schipperges, B. & Rydin, H. 1998. Response of photosynthesis of Sphagnum species from contrasting microhabitats to tissue water content and repeated desiccation. *New Phytologist* **140** : 677–684.

Schouwenaars, J.M. 1993. Hydrological differences between bogs and bog-relicts and consequences for bog restoration. *Hydrobiologia* **265** : 217–224.

Schouwenaars, J.M. & Gosen, A.M. 2007. The sensitivity of Sphagnum to surface layer conditions in a re-wetted bog: a simulation study of water stress. *Mires and Peat* **2** : 1–19.

Van Seters, T.E. & Price, J.S. 2001. The impact of peat harvesting and natural regeneration on the water balance of an abandoned cutover bog , Quebec. *Hydrological Processes* **15** : 233–248.

Van Seters, T.E. & Price, J.S. 2002. Towards a conceptual model of hydrological change on an abandoned cutover bog , Quebec. *Hydrological Processes* **16** : 1965–1981. DOI: 10.1002/hyp.396

Silvan, N., Silvan, K., Näkkilä, J., Tahvonen, R. & Reinikainen, O. 2012. Renewability, use and properties of Sphagnum biomass for growing media purposes (extended abstract). In *Proceedings of the 14th International Peat Congress*. Stockholm, Sweden.

Silvola, J. 1990. Combined effects of varying water content and CO2 concentration on photosynthesis in Spagnum fuscum. *Holarctic Ecology* **13** : 224–228.

Silvola, J. 1992. Moisture dependence of CO2 exchange and its recovery after drying in certain boreal forest and peat mosses. *Lindbergia* **17** : 5–10.

Silvola, J. & Aaltonen, H. 1984. Water content and photosynthesis in the peat mosses Sphagnum fuscum and S. angustifolium. *Annales Botanici Fennici* **21** : 1–6.

Strack, M. & Price, J.S. 2009. Moisture controls on carbon dioxide dynamics of peat-Sphagnum monoliths. *Ecohydrology* **2** : 34–41. DOI: 10.1002/eco

Strack, M., Waddington, J.M., Lucchese, M.C. & Cagampan, J.P. 2009. Moisture controls on CO2 exchange in a Sphagnum-dominated peatland: results from an extreme drought field experiment. *Ecohydrology* **2** : 454–461. DOI: 10.1002/eco

Titus, J.E. & Wagner, D. 1984. Carbon balance for two Sphagnum mosses: water balance resolves a physiological paradox. *Ecology* **65** : 1765–1774.

Titus, J.E., Wagner, D.J. & Stephens, M.D. 1983. Contrasting water relations of photosynthesis for two Sphagnum mosses. *Ecology* **64** : 1109–1115.

Topp, G., Davis, J. & Annan, A. 1980. Electromagnetic determination of soil-water content: Measurements in coaxial transmission lines. *Water Resources Research* **16** : 574–582.

Triisberg, T., Karofeld, E. & Paal, J. 2011. Re-vegetation of block-cut and milled peatlands : an Estonian example. *Mires and Peat* **8** : 1–14.

Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K. & Moore, P.A. 2014. Hydrological feedbacks in northern peatlands. *Ecohydrology*. DOI: 10.1002/eco.1493

Waddington, J.M. & Price, J.S. 2000. Effect of peatland drainage, harvesting, and restoration on atmopsheric water and carbon exchange. *Physical Geography* **21** : 433–451.

Waddington, J.M., Strack, M. & Greenwood, M.J. 2010. Toward restoring the net carbon sink function of degraded peatlands: Short-term response in CO2 exchange to ecosystem-scale restoration. *Journal of Geophysical Research* **115** : G01008. DOI: 10.1029/2009JG001090

Waddington, J.M., Warner, K.D. & Kennedy, G.W. 2002. Cutover peatlands: A persistent source of atmospheric CO2. *Global Biogeochemical Cycles* **16** : 1–7.

Williams, T.G. & Flanagan, L.B. 1996. Effect of changes in water content on photosynthesis, transpiration and discrimination against 13C02 and C180160 in Pleurozium and Sphagnum. *Oecologia* **108** : 38–46.

Williams, T.G. & Flanagan, L.B. 1998. Measuring and modeling environmental influences on photosynthetic gas exchange in Sphagnum and Pleurozium. *Plant Cell and Environment* **21** : 555–564.

Yazaki, T., Urano, S. & Yabe, K. 2006. Water balance and water movement in unsaturated zones of Sphagnum hummocks in Fuhrengawa Mire, Hokkaido, Japan. *Journal of Hydrology* **319** : 312–327. DOI: 10.1016/j.jhydrol.2005.06.037