RESPONSES OF *SPHAGNUM* PRODUCTIVITY AND NET ECOSYSTEM EXCHANGE OF CO_2 TO MODIFICATIONS OF MOSS MOISTURE CONTENT IN AN OMBROTROPHIC BOG

ANGELA CATHERINE ADKINSON

B. Sc. Environmental and Resource Science (Hons), Trent University,
Peterborough, Ontario, Canada, 2006

A thesis submitted in partial fulfillment of
the requirements for the degree of

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

Department of Geography and Environmental Studies

CARLETON UNIVERSITY
Ottawa, Ontario, Canada

August 2009

ABSTRACT

This study investigates the importance of *Sphagnum* mosses to interannual variability in net ecosystem exchange (NEE) of CO_2 at Mer Bleue bog with varying moss moisture conditions. Precipitation exclusion (PE) and water addition (WA) treatments produced varying moss water contents (WC), and *Sphagnum*, vascular plant, and total ecosystem CO_2 exchange were measured *in situ* using chambers. Despite a relatively low water table at the site, *Sphagnum* mosses were able to maintain average WCs in or near the optimal range for *Sphagnum* net primary productivity (NPP) in all treatments. Consequently, there was no treatment effect on CO_2 exchange. However, in measurements associated with below optimal WCs *Sphagnum* NPP was positive (i.e. net loss) leading to decreased NEE. Water table depth and direct precipitation appear to be equally important controls on *Sphagnum* WC at the site. *Sphagnum* was important to CO_2 exchange, contributing at least one third of gross ecosystem production (GEP) and ecosystem respiration (ER). Dry moss conditions may affect the balance of these components, thereby influencing *Sphagnum* NPP and the moss influence on total NEE in drought years.

ACKNOWLEDGEMENTS

I am very grateful to all who have contributed to this project. In particular, I sincerely thank my supervisor Dr. Elyn Humphreys for her guidance, patience, support and encouragement. I greatly appreciate her consistent enthusiasm for the project and value the time I have spent working with her at Carleton University. I would also like to thank Dr. Sean Carey for his valuable comments and participation in this project as a member of my advisory committee.

This project could not have been completed without the dedication and hard work of Kaitlin Wilson, Samantha Piquette, John Seay, and my brother, Kevin Adkinson, whose assistance in the field is greatly appreciated. Thank you also to Michael Treberg for building and maintaining the custom chambers, and for all of his help and input to this project. I am very appreciative of the comments and interest in this project that were expressed by researchers from McGill University, Trent University, Mount Holyoke College, and participants of the Mer Bleue Working Group and Canadian Carbon Program meetings. Special thanks to Dr. Shaun Watmough and lab group for their friendships and for providing carbon and nitrogen analysis.

I would like to acknowledge the funding agencies that made this research possible: Canadian Foundation for Climate and Atmospheric Sciences (CFCAS), National Sciences and Engineering Research Council (NSERC), Ontario Graduate Scholarship (OGS) program, and Carleton University. Thanks to the National Capital Commission (NCC) of Ottawa for access to the study site.

Finally, I greatly appreciate my family and friends for their interest and encouragement along the way. The support of my peers has been invaluable, so thank

you to all of the friends I have made at Carleton for your support and advice, and for helping me escape from the computer every once in a while. Special thanks to my loving partner and best friend David Dixon, who was very supportive, understanding, and always willing to help. Thanks for following me to Ottawa; it has been a great couple of years.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF SYMBOLS AND ABBREVIATIONS

Symbol	Units	Definition
α	µmol µmol^{-1}	apparent quantum yield
A	m^2	chamber surface area
C_a		collars with some vascular vegetation clipped
C_b		collars with vascular vegetation left intact
CL		control treatment
CLi		control treatment plot number i
dC/dt	µmol mol^{-1} dry air s^{-1}	change in CO_2 mixing ratio with time
D_b	g dry biomass m^{-3}	average bulk density of the 2 cm section below the *Sphagnum* capitula
DOY		day of year
ER		ecosystem respiration
ES		early summer season (DOY 164-206)
F		fall season (DOY 245-311)
F_{CO2}	µmol m^{-2} s^{-1}	CO_2 flux
GEP	µmol m^{-2} s^{-1}	gross ecosystem photosynthesis
GEP_{max}		gross ecosystem photosynthesis at maximum PAR (total ecosystem and vascular plant measurements: PAR > 1000 µmol m^{-2} s^{-1}, *Sphagnum* moss measurements PAR > 500 µmol m^{-2} s^{-1})
GP	µmol m^{-2} s^{-1}	gross photosynthesis
GP_{max}	µmol m^{-2} s^{-1}	gross photosynthesis at maximum PAR
GPP	µmol m^{-2} s^{-1}	gross primary productivity
GPP_{max}	µmol m^{-2} s^{-1}	gross primary productivity at maximum PAR
LAI	m^2 m^{-2}	leaf area index
LS		late summer season (DOY 207-244)
MAT	°C	mean annual temperature
M_{H2O}	mol mol^{-1} dry air	H_2O mixing ratio
NEE	µmol m^{-2} s^{-1}	net ecosystem exchange of CO_2
NEE_{max}	µmol m^{-2} s^{-1}	net ecosystem exchange of CO_2 at maximum PAR
NPP	µmol m^{-2} s^{-1} or g C m^{-2} s^{-1} or g dry biomass m^{-2} s^{-1}	net primary productivity
NPP_{max}	µmol m^{-2} s^{-1}	net primary productivity at maximum PAR
p	Pa	mean air pressure
PAR	µmol m^{-2} s^{-1}	photosynthetically active radiation
PE		precipitation exclusion treatment
PEi		precipitation exclusion treatment plot number i

PG		post-greenup season (DOY 124-145)
PrG		pre-greenup season (DOY 105-109)
Q_{10}		rate of increase in respiration over 10°C, constrained to 2
R	μmol m^{-2} s^{-1}	respiration
R_{ref}	μmol m^{-2} s^{-1}	respiration at reference temperature T_{ref}
R_{10}	μmol m^{-2} s^{-1}	respiration at reference temperature of 10°C
R_d	μmol m^{-2} s^{-1}	dark respiration
R_{bg}	μmol m^{-2} s^{-1}	belowground respiration (includes both heterotrophic and plant root respiration)
R^*	J mol^{-1} K^{-1}	ideal gas constant, 8.3144 J mol^{-1} K^{-1}
T_{air}	°C	plot temperature at 0.5 m above the surface
T	°C	air temperature
T_{ch}	K or °C	mean chamber temperature
T_{ref}	°C	reference temperature (10°C)
T_{2cm}	°C	peat temperature at 2 cm depth
T_{5cm}	°C	peat temperature at 5 cm depth
T_{10cm}	°C	peat temperature at 10 cm depth
V	m^3	chamber volume
WA		water addition treatment
WAi		water addition treatment plot number i
WC	fw dw^{-1}	*Sphagnum* moss water content as ratio of fresh to dry weight

1.0 INTRODUCTION

Approximately 20% to 30% of the carbon (C) in the world's soil is stored in northern peatlands, making them a large potential carbon source (Gorham 1991, Turunen *et al.* 2002). A key component of the peatland carbon balance is net ecosystem exchange (NEE) of carbon dioxide (CO_2), which is the difference between total ecosystem respiration (ER), including both plant and soil respiration, and gross ecosystem photosynthesis (GEP) (Roulet *et al.* 2007). Here the ecosystem is considered the community of organisms and their physical environment.

Although northern peatlands have generally been carbon sinks, climate change is expected to influence many of the environmental controls on both photosynthesis and respiration (e.g. temperature, water availability, atmospheric CO_2 concentration) (Gorham 1991, McCarthy *et al.* 2001). These influences on NEE may reverse peatland carbon budgets, and produce a positive feedback for climate change. Recent multi-year monitoring of NEE at Mer Bleue bog, an ombrotrophic peatland near Ottawa, Ontario, indicates significant interannual variability in CO_2 sequestration in response to variations in weather (Roulet *et al.* 2007).

Sphagnum mosses are the dominant vegetation in many northern peatlands, and contribute to long-term carbon sequestration by taking up atmospheric CO_2 through photosynthesis while being relatively resistant to decomposition. In ombrotrophic bogs, peat is primarily comprised of *Sphagnum* remains because the mosses have slower decomposition rates than canopy vascular plants (Hayward & Clymo 1982, Moore 1989, Gorham 1991, Verhoeven & Toth 1995, Kim & Verma 1996). At Mer Bleue, *Sphagnum* mosses account for roughly 30% of the above-ground biomass (Moore *et al.* 2002), yet it

is uncertain whether *Sphagnum* CO_2 exchange is a key component of annual NEE at the bog, and whether it is, therefore, significant in determining interannual variability of NEE.

There are no known studies that have focused on the influence of *Sphagnum* moss net primary productivity (NPP) (i.e. the difference between *Sphagnum* photosynthesis, or gross primary productivity (GPP), and autotrophic respiration) or on seasonal and interannual variation in peatland NEE. It has been well established in the literature that interannual variability in peatland CO_2 exchange is influenced by drought events (e.g. Arneth *et al.* 2002, Lafleur *et al.* 2003, Roulet *et al.* 2007). The literature also strongly supports, primarily through laboratory experiments, that *Sphagnum* productivity is related to its water content (WC), which is influenced by the depth of the water table (e.g. Silvola & Aaltonen 1984, Rydin 1985, Rydin & McDonald 1985, Shipperges & Rydin 1998, Williams & Flanagan 1998, Weltzin *et al.* 2001, Van Gaalen *et al.* 2007, Robroek *et al.* 2009, Strack & Price 2009). Direct precipitation also influences *Sphagnum* WC and carbon uptake (Robroek *et al.* 2007, Robroek *et al.* 2009). However, there is limited work examining the direct link between peatland hydrology, *Sphagnum* growth, and peatland NEE and there has been little *in situ* study of these relationships.

This study investigates the relative importance of *Sphagnum* CO_2 exchange to NEE at Mer Bleue, particularly in drought conditions that are known to contribute to seasonal and interannual variability in NEE at the bog. An understanding of the influence of water availability on *Sphagnum* productivity is necessary to address this issue. Therefore, the primary objectives of this study are to:

1) Investigate the relationship between *Sphagnum* CO_2 exchange and NEE at Mer Bleue bog.

2) Attempt to represent interannual variation in *Sphagnum* wetness using rain-out shelters in order to observe the effects of moss wetness on NEE and *Sphagnum* NPP.

3) Confirm *in situ* the relationship between *Sphagnum* NPP and moss WC that has been observed in laboratory studies.

4) Examine and compare the influences of water table depth and of direct precipitation on *Sphagnum* WC in the field.

2.0 BACKGROUND

2.1 *Sphagnum* structure, ecology and morphology

Sphagnum is generally comprised of a main stem, branches, and capitulum (Figure 1). Photosynthesis occurs only in the capitulum, a dense cluster of developing branches at the head of the stem, and in the leaves of a small section of stem and branches below it in the living chlorophyllous cells (Bold *et al.* 1980, Rydin & Jeglum 2006). Light penetration is limited to this upper 1 to 2 cm of the moss, restricting photosynthesis below (Robroek *et al.* 2009). *Sphagnum* leaves are only 1 layer of cells in thickness, allowing each cell to be in contact with water outside of the plant (Rydin & Jeglum 2006). Also in the leaves bordering chlorophyllous cells are non-living hyaline

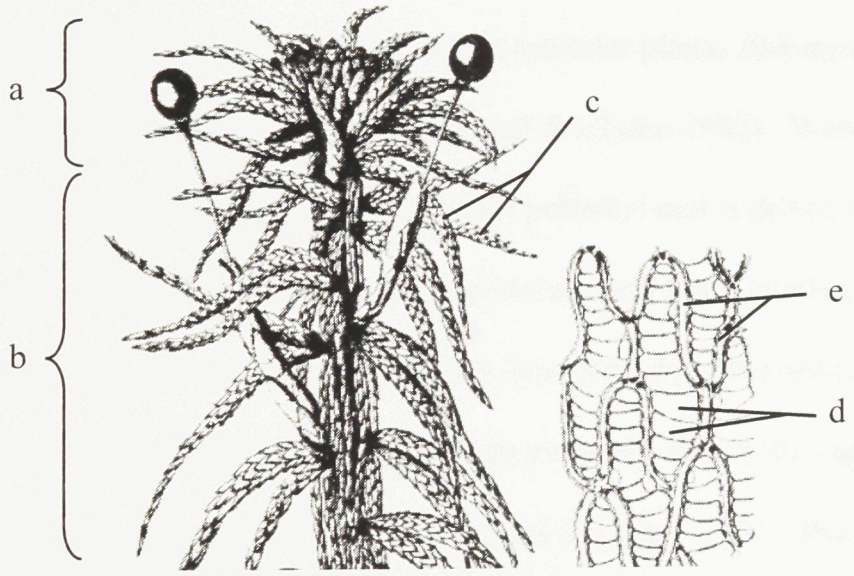

Figure 1. Single *Sphagnum* moss plant, illustrating the location of its (a) capitulum, (b) stem, and (c) branches. Inset diagram is the close-up view of a single layer of leaf cells, illustrating d) the larger non-living hyaline cells, which border e) the living chlorophyllous cells where photosynthesis occurs. Adapted from Schimper (1858) as cited by Rydin & Jeglum (2006).

cells, which are hollow and function to store water (Bold *et al.* 1980, Rydin & Jeglum 2006). Lower portions of the moss stem and clusters of fully developed branches along the stem are primarily comprised of these non-living cells (Rydin & Jeglum 2006). The structure of the moss diminishes with depth as the cells become more decayed and less rigid (Ingram 1983). As the boundary between the living and non-living portions of the stem is not distinct, Clymo (1970) suggests that the moss be divided more practically into capitulum and stem.

The *Sphagnum* stem includes two sections; the inner pith provides support and production and storage of food, while the outer cortical layer is comprised of hyaline cells (Bold *et al.* 1980, Yoshikawa *et al.* 2004). Stem cells are not specialized for water transport, and it is generally believed that neither section of the stem conducts water (Clymo & Hayward 1982, Rydin & Jeglum 2006). Instead water is held in a film between the leaves and the stem and branches of individual and adjacent mosses by capillary forces, providing additional water storage. Unlike vascular plants, *Sphagnum* mosses lack stomata and cannot control their WC (Hayward & Clymo 1982). Water moves through the capillary film along a gradient in water potential that is driven by the atmospheric vapour pressure deficit. Branches protrude both horizontally (spreading branches) and hang somewhat vertically (pendant branches) from the *Sphagnum* stem (Figure 1). Branches and leaves of multiple *Sphagnum* stems within the moss layer overlap like roof shingles (Bold *et al.* 1980, Hayward & Clymo 1982). Because the mosses are in contact with one another and function together in many ways, they are commonly viewed as a unit (i.e. the moss carpet) instead of as individuals.

There is great variability in morphology both among and within species, often making identification difficult. The structures of *Sphagnum* species are adapted to the wetness and light conditions of their particular habitats, and water transport ability varies with structure (Hayward & Clymo 1982, Rydin 1985). For example, species that occupy hummocks (e.g. *S. capillifolium, S. fuscum*) are adapted to living higher above the water table than those that occupy hollows and lawns (e.g. *S. cuspidatum, S. fallax*). Microtopography varies in peatlands, with hummocks being areas in which the peat is raised forming small mounds that are higher above the water table than hollows (i.e. depressed areas) and lawns. Hummock species tend to have longer branches and/or more pendant branches that hang close to the stem and grow in a more dense carpet, producing a more efficient capillary network, more effective water retention capacity, and exposing less surface area for evaporation (Clymo 1973, Rydin 1985, Rydin & Jeglum 2006, Hajek & Beckett 2008). Although water holding capacity varies widely among species, in general the structure of *Sphagnum* mosses allows them to hold up to 20 times their dry weight in water (Rydin & Jeglum 2006). When water is not limiting, productivity of hummock species tends to be lower than hollow species (Gunnarsson 2005, Rydin & Jeglum 2006).

2.2 Environmental controls on *Sphagnum* productivity

Climate change is expected to have an effect on peatland carbon exchange through changes in the environmental controls on both photosynthesis and respiration (Douma *et al.* 2007). North America is predicted to experience a climate warming of between 1°C and 7°C, and Canada in particular is expected to see increases in annual

precipitation with a larger proportion falling as rain (McCarthy *et al.* 2001). While a higher frequency of extreme rainfall events is expected, a decrease in average water tables is predicted as a result of increased air temperatures and evapotranspiration. In order to reliably predict how such changes will affect the carbon balance of peatlands, the environmental controls on photosynthesis and respiration in these ecosystems must be better understood.

Light, temperature, water availability, species, nutrients, competition, and atmospheric CO_2 concentration have all been shown to influence *Sphagnum* productivity (e.g. Silvola 1990, Murray *et al.* 1993, Shipperges & Rydin 1998, Heijmans *et al.* 2001, Dorrepaal *et al.* 2003, Vitt *et al.* 2003, Gunnarsson 2005). While the latter three variables are not likely significant influences over this short term study, the others may all affect short-term variability and/or spatial variability in *Sphagnum* productivity at Mer Bleue. *Sphagnum* species have adapted to differences in environmental conditions (e.g. height above water table, pH, nutrient richness) and as a result tend to be present in microclimates to which they are better suited (Gunnarsson 2005). The effects of other environmental controls on productivity, therefore, often vary with microclimate due to species differences.

2.2.1 Light

The primary limitation to photosynthesis is availability of light. The photosynthetic response to light is commonly described with a rectangular hyperbola relationship (France & Thornley 1984):

(1) $$GP = \frac{\alpha \cdot PAR \cdot GP_{max}}{\alpha \cdot PAR + GP_{max}}$$

in which *GP* is gross photosynthesis, α is the initial slope of the relationship representing photosynthetic efficiency, and GP_{max} is gross photosynthesis at saturating light levels (i.e. maximum photosynthetically active radiation, PAR). Light saturation occurs in *Sphagnum* at intensities well below full sunlight, and at a lower level than most vascular plants. Most studies suggest that light saturation occurs between 300 and 500 μmol m^{-2} s^{-1} in *Sphagnum* (Harley *et al.* 1989, Williams & Flanagan 1996, Titus & Wagner 1984), while light saturation for vascular plants is common at 1000 μmol m^{-2} s^{-1} (Bubier *et al.* 2007). Lower than optimal light levels result in lower photosynthesis, but are not detrimental to *Sphagnum* health (Strack & Price 2009). However, low light in combination with low temperatures, as seen in spring and fall, can drive *Sphagnum* into dormancy (Gerdol 1995). Moderately high light levels (e.g. 800 μmol m^{-2} s^{-1}) have been shown to reduce *Sphagnum* photosynthesis as a result of photoinhibition, and are a suggested primary limiting factor to *Sphagnum* growth (Murray *et al.* 1993, Hajek *et al.* 2009). High light conditions can also exacerbate desiccation of *Sphagnum* during dry periods (Bragazza 2008). *Sphagnum* can reach its maximum capacity for growth under shaded conditions, which eliminate high light stress (Murray *et al.* 1993). *Sphagnum* mosses also have a photosynthetic advantage over vascular plants at times of the day or year when light levels are low (Sommerkorn *et al.* 1999).

Still, despite the advantage of shading to *Sphagnum* productivity, the contribution of *Sphagnum* to ecosystem carbon uptake relative to that of vascular plants is generally negatively affected by canopy shading. In *Sphagnum*-dominated arctic ecosystems,

Douma *et al.* (2007) saw a negative relationship between vascular plant LAI and the contribution of mosses to maximum ecosystem CO_2 uptake ($R^2 = 0.66, p < 0.05$). There is little evidence in the literature as to whether there exists an optimal vascular plant LAI to minimize shading while preventing photoinhibition of mosses, which would maximize *Sphagnum* contribution to ecosystem production.

2.2.2 Temperature

On a global scale increased mean annual temperature (MAT) positively affects *Sphagnum* productivity, explaining 24% of its variation (Gunnarsson 2005). This could be largely due to the increased growing season length associated with increased MAT. At a site-specific scale, temperature can be important in determining growing season length, while there is evidence that during the growing season moisture availability becomes the primary control of moss productivity (Lindholm 1990, Gerdol 1996). Asada *et al.* (2003) concluded growing season *Sphagnum* productivity was more strongly correlated to precipitation and temperature variables together than to precipitation alone, and suggested that precipitation is an important control on growth but temperature is a limiting factor. This study also found that hollow and lawn species were more sensitive to warmer conditions than hummock species. Moore (1989) found weak significant correlations between *Sphagnum* NPP and mean daily temperature at two hummock dominated sites and one lawn dominated site. He also found that MAT explained 31% of the variation in annual *Sphagnum* NPP among temperate to subarctic peatland sites reported in the literature. These results illustrate the limitations of temperature alone in

explaining variability in *Sphagnum* growth, and the importance of other microclimatic and hydrological variables. Douma *et al.* (2007) did not observe a significant effect of moss temperature on photosynthetic characteristics like maximum gross primary production and light use efficiency, and also suggested that growing condition and moss species effects are more important controls.

There is evidence that long-term temperature changes indirectly affect *Sphagnum* growth by inducing changes in the structure of the moss carpet. Dorrepaal *et al.* (2003) manipulated summer temperatures and found a strong positive effect on length growth of *S. fuscum*, but a corresponding decrease in capitulum and sub-capitulum bulk density and little effect on biomass production. The authors point out that decreased bulk density will reduce the effectiveness of the moss' capillary transport system and reduce water supply to the capitulum, which would ultimately decrease *Sphagnum* productivity. These findings could explain some of the variability in *Sphagnum* NPP among peatland sites with different MAT found in other studies.

Temperature is a particularly important control at the beginning and end of the growing season. As *Sphagnum* mosses are evergreen, their growth is not limited by leaf development in spring or leaf drop in fall. Growth at these times of year is therefore primarily limited by the temperature at which growth is possible (Asada *et al.* 2003). In addition, because they do not have roots, *Sphagnum* mosses are only dependent on surface temperature and therefore may begin to assimilate CO_2 when only the surface of the peat profile has thawed (Moore *et al.* 2006). In contrast, winter dormancy of vascular plants results in a longer recovery period during the spring and prevents photosynthesis outside of the growing season.

The temperature limit to *Sphagnum* growth is suggested to be around 0°C (Asada *et al.* 2003). Douma *et al.* (2007) note that growth in arctic mosses has been shown to recover within hours after thawing from a frozen state. Similarly, at Mer Bleue peatland photosynthesis begins immediately following snow melt, and has also been measured when there is only a thin snow cover and in snow free periods during the winter season (Lafleur et al. 2003, Moore et al. 2006). Considering these observations, warmer winter temperatures may extend the spring and fall periods during which mosses are active and vascular vegetation is not. If the frequency of thaw events is increased with warmer temperatures, the relative contribution of mosses to ecosystem production could also be increased due to more frequent periods of *Sphagnum* CO_2 uptake during the winter season. However, *Sphagnum* productivity outside of the growing season is still uncertain. Previous studies have focused on growing season production and no studies are known to have directly measured winter *Sphagnum* growth. This may be partially because it is difficult to accurately measure moss growth in winter with the commonly used cranked-wire method, as the wire that is established as a reference for *Sphagnum* vertical growth may shift due to snow cover and freeze-thaw events (Asada *et al.* 2003).

At a British Columbia peatland that experiences mild winters, Asada *et al.* (2003) estimated winter *Sphagnum* growth from climate variables (i.e. daily precipitation and temperatures). Estimated linear growth varied by *Sphagnum* species and ranged between 5 ± 1 mm (mean ± SE; *S. fuscum*) and 19 ± 3 mm (mean ± SE; *S. pacificum*) between mid-November 1999 and mid-May 2000, and averaged 50% of the growth measured during the growing season. Still, the authors noted that true measurements of winter growth are necessary, as estimates may be affected by differences in winter and growing

season climate-growth relationships due to confounding winter factors like lower solar radiation and snow cover.

Increased winter snow cover has also been shown to have a positive effect on growing season *Sphagnum* growth. Dorrepaal *et al.* (2003) doubled winter snow cover, which resulted in a 33% increase in summer *S. fuscum* production, measured by biomass accumulation. The increased snow cover increased average winter soil temperatures by 0.5–2.8°C and the authors noted that this may have thereby protected *Sphagnum* capitula from frost damage and frost drought. The increase in production may also have been due to enhanced moss hydration during snowmelt in spring, although this was not confirmed with moisture measurements.

Temperature is known to control both plant and soil respiration rates. In general, chemical reaction rates increase with temperature, as described by the Arrhenius equation (Ebbing & Gammon 2002). This is true of the enzymatic processes of respiration, and the exponential increase in respiration rate (R) with temperature (T) can be described as:

$$R = R_{ref} \cdot Q_{10}^{\frac{T - T_{ref}}{10}} \quad (2)$$

in which Q_{10} is the relative change in respiration rate with a 10°C temperature change and R_{ref} *is* respiration at the reference temperature T_{ref} (Tjoelker *et al.* 2001). The typical value of Q_{10} across a wide range of plant species is roughly 2, which is widely used as a fixed Q_{10} in modeling the temperature sensitivity of respiration (Ryan 1991).

2.2.3 Water

The literature strongly supports that productivity of *Sphagnum* mosses depends greatly on water availability, particularly because they have no ability to control water loss. In laboratory experiments a non-linear parabolic relationship between capitulum WC and moss net photosynthesis has been observed (Figure 2) (Silvola & Aaltonen 1984, Rydin & McDonald 1985, Murray *et al.* 1989a, Williams & Flanagan 1996, Shipperges & Rydin 1998, Van Gaalen *et al.* 2007, Robroek *et al.* 2009). Murray *et al.* (1989a) also saw similar relationships when *Sphagnum* WC was manipulated in the field. Net photosynthesis peaks at an optimal capitulum WC, which varies by *Sphagnum* species, and is limited at both low and high WCs (Table 1). Below optimal WC, desiccation results in a rapid decline in CO_2 uptake (e.g. Silvola & Aaltonen 1984, Silvola 1990,

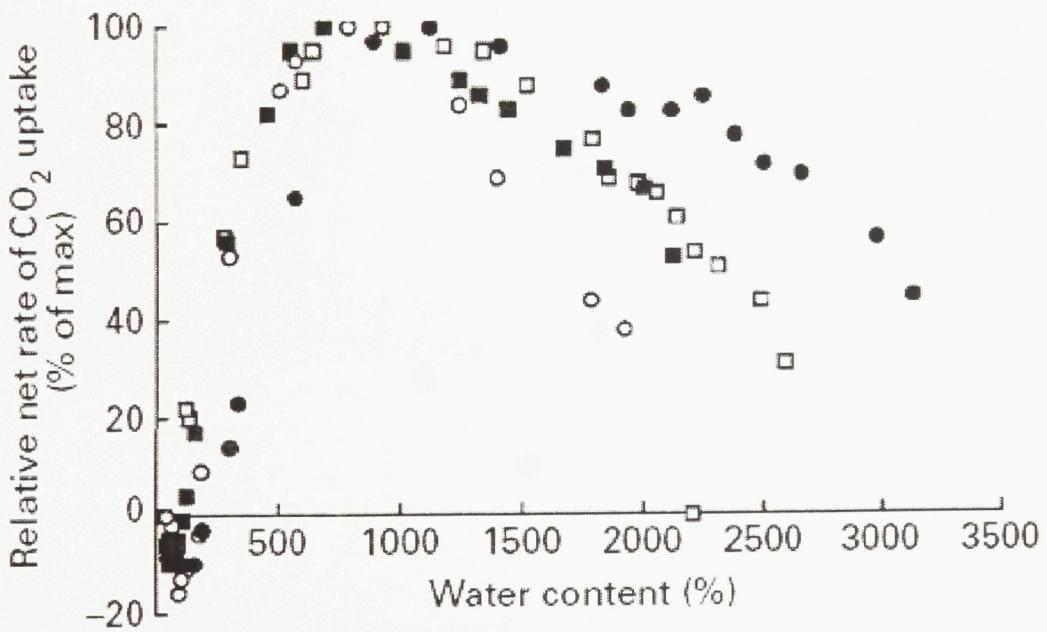

Figure 2. Parabolic relationship between water content and net rate of CO_2 uptake for four *Sphagnum* species: *S. cuspidatum* (■), *S. fuscum* (○), *S. balticum* (□), *S. papillosum* (●) (from Shipperges & Rydin 1998).

Table 1. Optimal capitulum water content (WC) and corresponding maximum net primary productivity (NPP) for *Sphagnum* species seen in the literature. Species are roughly arranged by natural height above the water table in descending order (according to Rydin & Jeglum 2006). Values of maximum NPP are not given where data are expressed in the literature as a proportion of maximum NPP (i.e. approx 100%).

***Sphagnum* species**	**Optimal WC**	**NPP**	**Reference**
	fw dw^{-1}	$\mu mol\ m^{-2}\ s^{-1}$	
section			
Acutifolia	~7	-7	Williams and Flanagan 1996
fuscum	7 to 11[i]	-0.80[ii]	Silvola & Aaltonen 1984
fuscum	~7.5[i]	---	Rydin & McDonald 1985
fuscum	8.7 to 8.9[i]	---	Shipperges & Rydin 1998
fuscum	7 to 9	-0.5 to -2.0[ii]	Silvola 1990
magellanicum	9.2	---	Shipperges & Rydin 1998
angustifolium	10 to 14[i]	-0.82[ii]	Silvola & Aaltonen 1984
angustifolium	8 to 11	---	Murray *et al.* 1989a
papillosum	8.8 to 14[i]	---	Shipperges & Rydin 1998
rubellum	10	approx. -4.3	Robroek *et al.* 2009
tenellum	~9[i]	---	Rydin & McDonald 1985
teres	6 to 11	-1.0 to -1.6	Van Gaalen *et al.* 2007
balticum	7 to 8[i]	---	Rydin & McDonald 1985
balticum	9.3[i]	---	Shipperges & Rydin 1998
cuspidatum	8.2 to 8.8	---	Shipperges & Rydin 1998
cuspidatum	20 to 25	approx. -3.5	Robroek *et al.* 2009
squarrosum	7 to 9	---	Murray *et al.* 1989a
squarrosum	7 to 11	---	Murray *et al.* 1989a

[i]WC converted to fw dw^{-1} from % of dw
[ii]NPP converted to $\mu mol\ m^{-2}\ s^{-1}$ from $mg\ g^{-1}\ h^{-1}$

Williams & Flanagan 1996, Shipperges & Rydin 1998) associated with the draining of hyaline cells and damage to chlorophyllous cells limiting metabolic processes (Gerdol *et al.* 1996, Thompson & Waddington 2008). The decline in CO_2 uptake above optimal WC is more gradual, and is due to decreased gas diffusion, which is limited by the thicker water film on the moss surface (Williams & Flanagan 1998).

Generally, the optimal capitulum WC range observed is from 7 to 11 ratio of fresh weight (fw) (i.e. the weight of the sample before drying) to dry weight (dw^{-1}) (or 600 to 1000% of dw) (Table 1). Still, near maximum NPP has been observed above this range (Shipperges & Rydin 1998, Robroek *et al.* 2009). Maximum net photosynthesis measured at optimal WCs ranges from near zero to -7 $\mu mol\ m^{-2}\ s^{-1}$ (Table 1). Studies have shown that the compensation point in *Sphagnum* (i.e. the WC at which respiration balances photosynthesis resulting in zero net CO_2 uptake) is higher in hummock species (~2.4 to 4.5 fw dw^{-1}) than in hollow species (~2.0 to 2.5 fw dw^{-1}), and CO_2 exchange stops completely at WCs below ~1.2 to 1.9 fw dw^{-1} (Wagner & Titus 1984, Shipperges & Rydin 1998).

Depth to the water table, precipitation, dewfall, and distillation, the condensation of water vapour from lower in the peat profile, influence water availability for *Sphagnum* (Rydin 1985, Shipperges & Rydin 1998, Robroek *et al.* 2009, Strack & Price 2009). There are also strong positive relationships for both capitulum WC and *Sphagnum* CO_2 uptake with evaporation (Robroek *et al.* 2009). Of these controls, the influence of water table has by far been the most widely studied. Thompson & Waddington (2008) provide a useful review linking *Sphagnum* productivity and hydrological functioning related to water table supply. With increasing depth to the water table, capitulum WC generally

declines (Rydin 1985, Gerdol 1995, Strack & Price 2009). As the water table drops, the capillary film becomes thinner and the effectiveness of capillary transport to the surface is reduced, and eventually may reach a point where there is insufficient force to maintain the capillary film. This results in a disconnect between the surface and water table (Price 1997). The relationship between water table and WC varies among *Sphagnum* species, having a more gradual decline in WC with water table decrease in hummock species, and is influenced by environmental conditions (e.g. humidity, bulk density in the profile) (Hayward & Clymo 1982, Rydin 1985, Strack & Price 2009). While there is no defined threshold, WC declines with water table depths of -30 cm to -40 cm, but there appears to be little influence on WC when the water table is below -100 cm (Hayward & Clymo 1982, Strack & Price 2009). The relationship between water table and WC also differs depending on whether the water table is being raised (i.e. the peat is wetting) or lowered (i.e. the peat is drying) (Hayward & Clymo 1982). At a given water table, capitulum WC will be greater when it has reached this water table by drying from a wetter state than when rewetting from a dry state (Hayward & Clymo 1982). This hysteresis effect is strongest in the upper layers of the peat profile.

Numerous studies have assessed the influence of water table fluctuations on *Sphagnum* CO_2 exchange. With lower water tables, generally *Sphagnum* gross photosynthesis decreases and ecosystem respiration increases (Riutta *et al.* 2007, Strack & Price 2009). Strack & Price (2009) saw that while these relationships are linear upon rewetting, with drying they are quadratic, and ecosystem respiration in particular peaks and then begins to fall again at very low water tables. As previous studies have typically measured CO_2 fluxes from *Sphagnum* and the underlying peat as one, or have focused on

NPP of *Sphagnum* stems, there is limited information on effects of water availability on *Sphagnum* autotrophic respiration separate from belowground respiration. Water tables found to correspond with optimal *Sphagnum* WC (e.g. -15 cm to -25 cm, Rydin 1985) or maximum *Sphagnum* CO_2 uptake (e.g. -30 cm to -40 cm, Strack & Price 2009) vary widely, likely due to differences in species and ecosystem characteristics.

Only recently have studies begun to investigate the direct importance of precipitation to *Sphagnum* WC and CO_2 exchange. Robroek *et al.* (2009) suggested that precipitation is equally, if not more, important to peatland CO_2 exchange than are water table variations. The influence of precipitation on growth is greatest when water availability is otherwise limited, and is important in maintaining capitulum WC when the water table is low (Murray *et al.* 1989b, Robroek *et al.* 2007, Robroek *et al.* 2009, Strack & Price 2009). Increases in *Sphagnum* WC immediately following precipitation are greater in moss higher above the water table (Robroek *et al.* 2007, Strack & Price 2009). With a water table very close to the surface (-1 cm), Robroek *et al.* (2009) saw no effect of precipitation on assimilation, suggesting precipitation does not affect WC at such high water tables. However, studies have observed precipitation effects on *Sphagnum* WC and assimilation for water tables from -58 cm up to -10 cm (Robroek *et al.* 2007, Robroek *et al.* 2009, Strack & Price 2009). While water table rise has a more gradual effect on *Sphagnum* CO_2 fluxes, precipitation events produce short-term (2 to 3 day) increases in photosynthesis and respiration (Strack & Price 2009). However, Strack & Price (2009) saw that these increased fluxes can negate one another, resulting in no obvious change in net CO_2 exchange.

Even small precipitation events (e.g. 0.5 to 1 mm) may significantly affect WC (Robroek *et al.* 2007, Strack & Price 2009). Strack & Price (2009) saw WC increase from 4 fw dw^{-1} to 9-11 fw dw^{-1} following small precipitation events (0.5 to 1 mm), and note that this is equivalent to the increase in moisture observed with a water table increase from -40 cm to -20 cm. The influence of small precipitation events is limited to the upper <5 cm of the peat profile, and can be missed by current measurement techniques (e.g. rain gauge or peat volumetric WC measurements) (Strack & Price 2009). Night-time dewfall and distillation accumulation is of similar magnitude to these small precipitation events (approximately 0.5 mm, Garrat & Segal 1988) and may therefore also have an important influence in maintaining *Sphagnum* WC and on assimilation (Shipperges & Rydin 1988, Strack & Price 2009). Strack & Price (2009) noted that the maintenance of higher moisture content by small precipitation events and dewfall could also facilitate capillary water transport from the water table.

2.4 Desiccation recovery

The ability of *Sphagnum* to recover maximum levels of net photosynthesis following desiccation is important to the significance of *Sphagnum* in peatland carbon exchange during dry years. Relative to many other bryophytes, desiccation tolerance in *Sphagnum* is low, and its ability to avoid desiccation is more effective than its ability to recover (Wagner & Titus 1984, Gerdol *et al.* 1996, Shipperges & Rydin 1998). This is particularly true of hummock species, which are able to prevent desiccation longer than hollow species, due to their more efficient capillary transport network and better ability to maintain capitulum WC (Gerdol *et al.* 1996, Shipperges & Rydin 1998). During dry

periods hollow species are, therefore, more susceptible to desiccation, despite being naturally closer to the water table (Wagner & Titus 1984). *Sphagnum* desiccation tolerance also varies among species, but there is disagreement in the literature as to whether tolerance is greater in hummock or hollow species. While is seems reasonable for hummock species to have better desiccation tolerance, and this has been shown in some studies (Clymo 1973, Gerdol *et al.* 1996, Hajek & Beckett 2008), others have observed better tolerance in hollow species (Clymo & Hayward 1982, Wagner & Titus 1984, Shipperges & Rydin 1998). These authors suggest that while hummock species are better adapted for desiccation avoidance, hollow species are more likely to experience desiccation despite inhabiting wetter environments, due to their more limited ability to avoid desiccation, and therefore have developed better desiccation tolerance leading to more efficient recovery. Overall, while there appears to be a better understanding of desiccation avoidance in *Sphagnum*, information on tolerance to desiccation appears to be limited (Wood 2007). The survivability and time to recovery in *Sphagnum* is influenced by the degree and length of desiccation (Wagner & Titus 1984, Gerdol *et al.* 1996). Gerdol *et al.* (1996) observed that cell damage is greater with longer periods of water stress, increasing the length of time required for recovery. The ability of *Sphagnum* to recover is even less with repeated desiccation, as may be observed during a dry summer season, although hummock species appear to be better adapted to repeated desiccation (Shipperges & Rydin 1998). Immediately following rewetting, net CO_2 uptake may continue to decrease for a brief period, possibly due to increased respiration associated with microbial activity or the repair of damaged cells (McNeil & Waddington 2003, Robroek *et al.* 2009). While net gain of CO_2 can return within less than a week, studies

have shown that a much longer period may be required for *Sphagnum* photosynthesis to return to maximum levels (Wagner & Titus 1984, Gerdol 1996, Shipperges & Rydin 1998, McNeil & Waddington 2003, Robroek *et al.* 2009).

The present study focuses in particular on the variability in *Sphagnum* and ecosystem productivity with varying moisture conditions, which has been shown to be one of the most important controls. It aims to provide information on moisture control of both *Sphagnum* WC and productivity under natural field conditions, as the majority of knowledge on this topic has been achieved through laboratory studies of the component relationships in a controlled setting. Intersite and interspecific variability in these relationships has been illustrated in previous studies, and the current study hopes to provide information that is particularly relevant for ongoing carbon cycling research at Mer Bleue and similar peatland sites.

3.0 METHODS

3.1 Site description

Mer Bleue is a 2800 ha ombrotrophic bog located 10 km east of Ottawa, Ontario, Canada (45.41°N lat., 75.48°W long, Figure 3). Three projections that are separated by upland mineral soil extend from the main body of the peatland. A long-term research site is established in the northwest projection (Figure 3). At this site an eddy covariance tower was established to continuously measure NEE of CO_2, water vapour, energy, and momentum from 1998 to present, and has been part of the Fluxnet Canada Research Network (now the Canadian Carbon Program). Over a 6 year period, the bog has been found to be a sink for CO_2 of an estimated -21.5 ± 39.0 g C m^{-2} y^{-1}, although as mentioned NEE is highly variable from year to year due to variations in weather (Roulet *et al.* 2007). Negative values represent CO_2 uptake by the ecosystem.

Roulet *et al.* provide a detailed summary of the events leading to the formation of Mer Bleue bog. The bog lies in a postglacial channel eroded into what was once the floor of the Champlain Sea basin (Lafleur *et al.* 2003, Roulet *et al.* 2007). Following glacial retreat, laminated silt and clay were deposited by Glacial Lake Iroquois over the existing sandy, silty gravel and limestone outcrops (Roulet *et al.* 2007). Next the Champlain Sea deposited silty clay marine sediments, which developed a depth of 40 to 50 m. Eventually the marine waters occupying the area were replaced by fresh waters, and the Ottawa River shaped the current form of the post-glacial channel in which Mer Bleue lies. Peat formation at the bog began approximately 8400 years ago, as the shallow

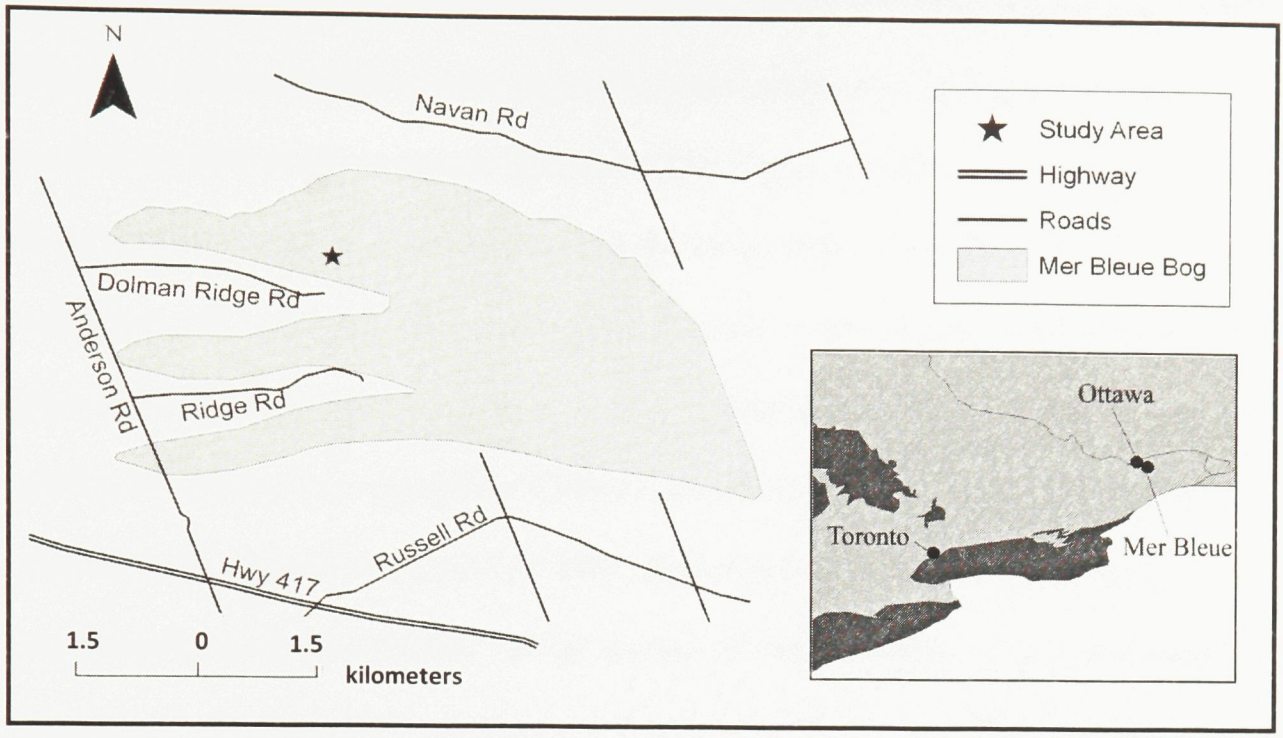

Figure 3. Map of the Mer Bleue bog (45.41°N lat., 75.48°W long), showing the study area location. Inset illustrates the location of the bog in southern Ontario.

lake occupying the basin was replaced by a fen (Roulet *et al.* 2007). Approximately 7100 to 6800 years ago the peatland shifted from a fen to a bog.

At the research site, peat is deepest near the center (> 5 m) and thins toward the edges (< 0.3 m). The bog has a hummock and hollow microtopography, which is influenced by variability in decomposition rates and water transport ability among *Sphagnum* species, as well as variability in the shape and form of vascular plants, which provide support for *Sphagnum* growth and peat development (Malmer *et al.* 1994, Rydin & Jeglum 2006). The average height difference of 25 to 30 cm between the tops of hummocks and bottoms of hollows (Bubier *et al.* 2003). The median diameter of hummocks, which cover approximately 70% of the bog surface, is roughly 1.0 m (Lafleur *et al.* 2003). The surface of the bog is covered by a *Sphagnum* moss layer and an

overstory low shrub layer is also present throughout most of the bog (Moore *et al.* 2002). Dominant moss and shrub species vary with microtopography. *Sphagnum* mosses account for 30% of above ground biomass at Mer Bleue, with dominant species being those typically found relatively high above the water table (*S. capillifolium*, *S. magellanicum*, and *S. fuscum*). *Polytrichum strictum* is also present in the moss layer. Four dominant shrub species make up much of the remaining above ground biomass (61%): *Chamaedaphne calyculata, Kalmia angustifolia, Ledum groenlandicum* and *Vaccinium myrtilloides* (Moore *et al.* 2002, Bubier *et al.* 2007). The remaining vegetation is comprised of other various species of vascular plants, sedges, and some small trees. Additional site description is provided by Roulet *et al.* 2007 and Moore *et al.* 2002.

The climate at Mer Bleue is cool continental, with a mean annual temperature of 6.3 ± 0.8°C, ranging from a mean of -10.8 °C in January to 18.3°C in July measured at the Macdonald-Cartier International Airport (Environment Canada Climate Normals, 1971-2000). On average 944 mm of precipitation fall annually, 78% as rainfall, with 426 mm falling during the growing season (May through September). Snow is typical between December and March, and peak snow depth is typically between 60 and 80 cm (Lafleur *et al.* 2003). Mer Bleue is a relatively dry site compared to other *Sphagnum*-dominated peatlands, with the water table remaining well below the hummock surface, and at or below the hollow surface, throughout the year (Lafleur *et al.* 2003). Between 1998 and 2008, the total range of water table depths observed was -17 cm to -68 cm below the hummock surface. The water table is highly variable among years, with the growing season average ranging between -29 cm and -44 cm. Note that all water table values

presented in this study, including those measured in previous years near the tower, are referenced to the average hummock height within the experimental plot area.

3.2 Experimental design

In situ manipulation experiments were applied to limit water inputs to *Sphagnum* by limiting precipitation. A study area of 529 m^2 (23 m x 23 m) was established just to the north of the eddy covariance tower (Figure 3). Within the study area, nine 1 x 2 m sampling plots were established, each with an additional 0.5 m buffer around the edge to accommodate edge effects (Figure 4). The number of plots was limited by their large size and the need to minimize the area impacted during this study. The minimum distance between sampling plots was 3 m. Elevated boardwalks were installed along the plot edges to minimize disturbance to the vegetation and prevent compaction of the peat. Characteristics of each sampling plot are presented in Table 2.

A completely randomized design with subsamples was applied in this experiment (Steel & Torrie 1980). The nine sampling plots were randomly distributed among a control group (CL) and two treatment groups that were designed to capture the effects of various wetness conditions on *Sphagnum* productivity and NEE (Figure 4). Consequently, each group contained three replicate plots. In each plot, subsamples were measured at two collars for CO_2 exchange measurements (see Section 3.3.1).

The first treatment was a precipitation exclusion treatment (PE) designed to dry *Sphagnum* relative to ambient conditions represented by the control group, while

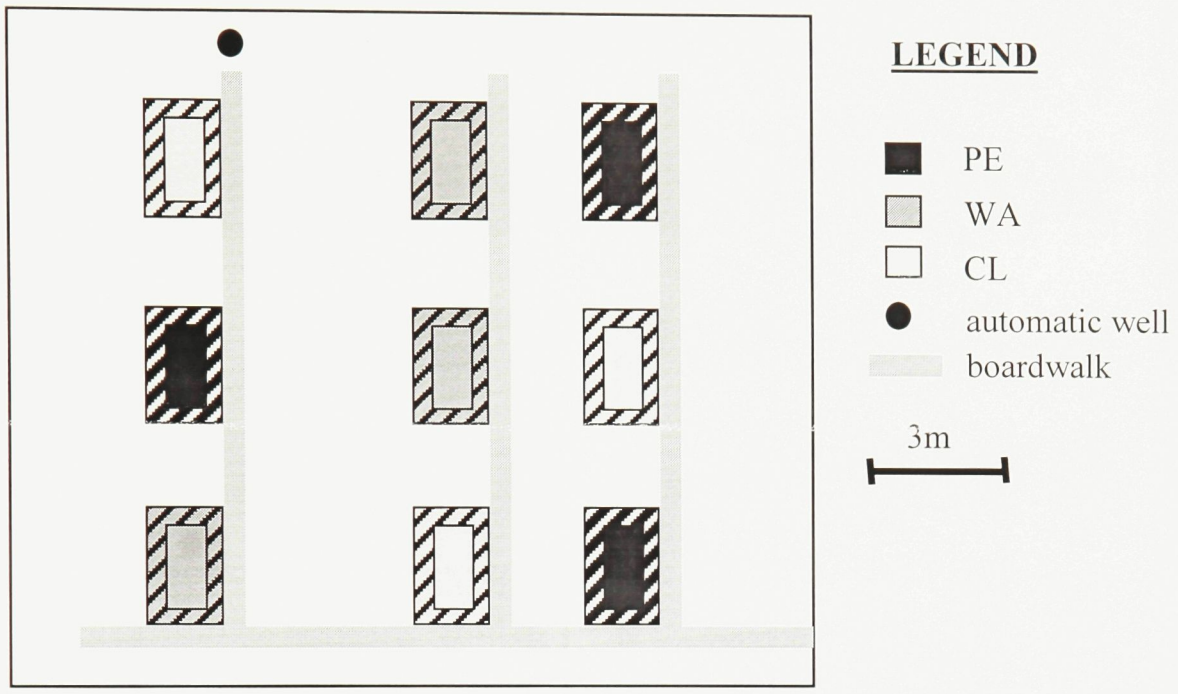

Figure 4. Arrangement of nine 1 by 2 m sampling plots and corresponding treatments within the study area. Each plot has an additional 0.5 m buffer, represented by hatched areas, and groups are at least 3 m apart. Pathways and boardwalks are indicated in light grey. Treatments are precipitation exclusion (PE), water addition (WA), and control (CL).

avoiding complicated manipulations of the water table. Mobile rainout shelters were constructed and used to exclude the majority of precipitation over the measurement period (Figure 5). Each shelter was comprised of two 1 m by 3m frames that were constructed of 1 inch diameter PVC pipe and fittings. Zip-ties were used to attach the two frames lengthwise, and the join was reinforced with contractor's sheathing tape to produce a hinge that allowed for the V-shape of the shelters. The frame was permanently secured using zip-ties on each long side to a 2.4 m long wooden crosspiece attached to posts that were embedded 0.9 m into the peat. Grommets were installed in a 2 m by 3 m sheet of 6-mil clear polyethylene film, producing a tarp that was secured with rope to the frame. The shelter tarps were manually established over the sample plots prior to

Table 2. Characteristics of experimental sampling plots. Dominance (%) of vascular plant and *Sphagnum* moss species in each collar is indicated. Mean (± SE) leaf area index (LAI) of vascular plants (m^2 m^{-2}) and counts of *Sphagnum* and *Polytrichum* mosses (stems m^2) over the study period are given for each sampling collar.

Plot	C_a					C_b					WT
	Vascular plants	***Sphagn.* mosses**	**LAI** m^2 m^{-2}	***Sphagnum*** stems m^{-2}	***Polytrich.*** stems m^{-2}	**Vascular plants**	***Sphagn.* mosses**	**LAI** m^2 m^{-2}	***Sphagnum*** stems m^{-2}	***Polytrich.*** stems m^{-2}	cm
PE1	*KA* 36%, *LG* 30%, *VM* 25%, *CC* 8%	*93% SM, 7% SC*	0.421 (0.036)	15550 (843)	3600 (759)	*KA* 71%, *LG* 14%, *VM* 11%, *CC* 3%	*79% SM, 21% SC*	0.995 (0.080)	18600 (838)	5120 (709)	-30 (-42, -21)
PE2	*CC* 58%, *KA* 27%, *VM* 12%, *LG* 3%	*88% SC, 12% SM*	0.909 (0.047)	21100 (949)	4467 (926)	*CC* 82%, *VM* 9%, *KA* 7%, *LG* 2%	*92% SC, 8% SM*	1.299 (0.072)	25400 (1388)	5067 (382)	-29 (-38, -22)
PE3	*VM* 30%, *LG* 26%, *KA* 25%, *CC* 20%	*93% SC, 7% SM*	0.359 (0.017)	23800 (1878)	5467 (513)	*LG* 67%, *VM* 17%, *KA* 11%, *CC* 5%	*88% SC, 12% SM*	0.067 (0.012)	15700 (452)	3933 (835)	-35 (-47, -26)
WA1	*KA* 51%, *VM* 30%, *CC* 13%, *LG* 6%	*100% SC*	0.399 (0.035)	24950 (2028)	5714 (577)	*CC* 67%, *VM* 18%, *KA* 10%, *LG* 4%	*67% SC, 33% SM*	1.198 (0.112)	19450 (1045)	5257 (1172)	-34 (-42, -27)
WA2	*VM* 41%, *CC* 35%, *KA* 14%, *LG* 10%	*51% SC, 49% SM*	0.864 (0.099)	13150 (780)	4514 (729)	*CC* 80%, *VM* 10%, *LG* 7%, *KA* 3%	*51% SC, 49% SM*	1.213 (0.079)	14250 (1485)	2971 (515)	-31 (-39, -22)
WA3	*KA* 79%, *VM* 14%, *CC* 4%, *LG* 3%	*90% SC, 10% SM*	0.783 (0.090)	22400 (1677)	4667 (625)	*KA* 39%, *CC* 26%, *LG* 18%, *VM* 16%	*66% SC, 34% SM*	0.671 (0.040)	20450 (1672)	11667 (1399)	-30 (-40, -22)
CL1	*KA* 52%, *VM* 27%, *LG* 12%, *CC* 9%	*98% SC, 2% SM*	0.393 (0.028)	22650 (848)	4343 (595)	*KA* 51%, *VM* 32%, *LG* 12%, *CC* 5%	*68% SC, 32% SM*	0.659 (0.075)	16950 (717)	7067 (1026)	-28 (-34, -20)
CL2	*KA* 73%, *VM* 17%, *CC* 6%, *LG* 4%	*68% SC, 32% SM*	0.608 (0.055)	19000 (623)	5200 (756)	*CC* 49%, *KA* 28%, *VM* 21%, *LG* 3%	*75% SC, 25% SM*	0.892 (0.061)	23900 (2086)	7200 (462)	-33 (-45, -25)
CL3	*CC* 49%, *KA* 27%, *VM* 20%, *LG* 5%	*100% SC*	0.719 (0.072)	27550 (1585)	3400 (573)	*CC* 69%, *LG* 11%, *VM* 10%, *KA* 9%	*97% SC, 3% SM*	1.077 (0.079)	24300 (1545)	4733 (891)	-32 (-39, -25)

Note: Water table (WT) is sampling period mean (min, max). PE, precipitation exclusion treatment; WA, water addition treatment; CL, control; C_a, clipped collars; C_b, unclipped collars. *LG*, *L. groenlandicum*; *KA*, *K. angustifolia*; *CC*, *C. calyculata; VM*, *V. myrtilloides*; *SM*, *S. magellanicum*; *SC*, *S. capillifolium*.

Figure 1. Photo of mobile rainout shelter. A frame was permanently erected over each precipitation exclusion (PE) plot. The clear tarp was attached to the frame when precipitation was expected, and removed when no precipitation was expected.

expected precipitation and were removed when there was little risk of precipitation to minimize effects of the shelters on microclimate. A ladder fitted with plywood was laid over the crosspieces at each plot and used as a bridge when establishing or removing the traps and when working over the plots in order to prevent damage to the vegetation. Although the tarps decreased PAR by 24.0 ± 0.4%, the shelters were not established over the plots during flux measurements. This treatment was implemented on May 29, 2008, two weeks prior to the beginning of CO_2 exchange measurements, and was ended on November 6, 2008. Edge effects of the rainout shelter design were assessed on October 22, following heavy rain (15.2 mm) on the previous day. In each of the PE plots,

Sphagnum samples were collected along two perpendicular transects, lengthwise and widthwise across the plot, to determine whether there was a significant gradient in WC from the center of the plots towards the edge. *Sphagnum* samples were collected every 15 cm along the transects for gravimetric WC measurements.

Initially, the second set of treatment plots was reserved as a second control group until the natural wetness conditions of the 2008 growing season could be assessed and the best use for the treatment determined. Beginning on July 25, 2008 a water addition treatment (WA) was implemented on these reserved plots. The spring and early summer of 2008 were particularly wet, limiting the usefulness of this watering treatment to late summer and the fall. This treatment was designed to produce wet moss relative to the control group by simulating a recent rainfall event. Each time gas exchange measurements were made, the WA plots were each watered one hour prior to measuring with 6.5 L of deionized water, as it was not possible to collect a sufficient amount of rainwater for this purpose. This volume distributed over the plot surface area was equivalent to a small rain event of 1.6 mm. As with the PE treatment, the WA treatment was terminated on November 6, 2008.

3.3 Data collection

3.3.1 Chamber measurements of NPP and NEE

Data collection took place from June 12 to November 6, 2008, incorporating the majority of the growing season. Additional spring data collection took place between April 16 and May 25, 2009. Adequately sunny days were required to measure CO_2 exchange, so during some particularly cloudy and/or rainy periods it was not possible to obtain flux measurements. However, when weather was permitting total NEE, vascular plant NPP, and *Sphagnum* NPP were measured at least once per week, between approximately 10 am and 4 pm when photosynthetically active radiation (PAR) was greatest. Fluxes were measured using a set of two custom designed closed chambers and an open-path infra-red gas analyzer system (LI-6400, LI-COR Inc.) (Figure 6). The sensor head of the LI-6400 system was mounted to the largest chamber, and housed the infra-red gas analyzer that measured CO_2 and H_2O, two Peltier Coolers for moderating chamber air temperature, and a mixing fan. An additional fan to mix chamber air and a fine wire thermocouple to measure air temperature were mounted inside the chamber. An external quantum sensor was mounted on a tripod and positioned at the leaf level adjacent to the chamber during measurements (model LI190, LI-COR Inc.). These external PAR measurements were corrected for the attenuation of PAR through the chamber walls in order to more accurately represent light received by the vegetation during measurements. The system measured CO_2 concentration, H_2O concentration, air temperature, pressure, and PAR once per second over the period of measurement.

The larger closed chamber used in total NEE and vascular plant NPP measurements was 24.6 cm in diameter and 30.6 cm high, with a geometric volume of 1.45×10^4 cm^3. The chamber was made of clear acrylic to maximize sunlight penetration, through which an estimated 94% of PAR was transmitted. To minimize leakage of air out of the chamber through the peat, 15 cm deep PVC collars (~25 cm diameter) were inserted into the peat at the beginning of the study, one week prior to

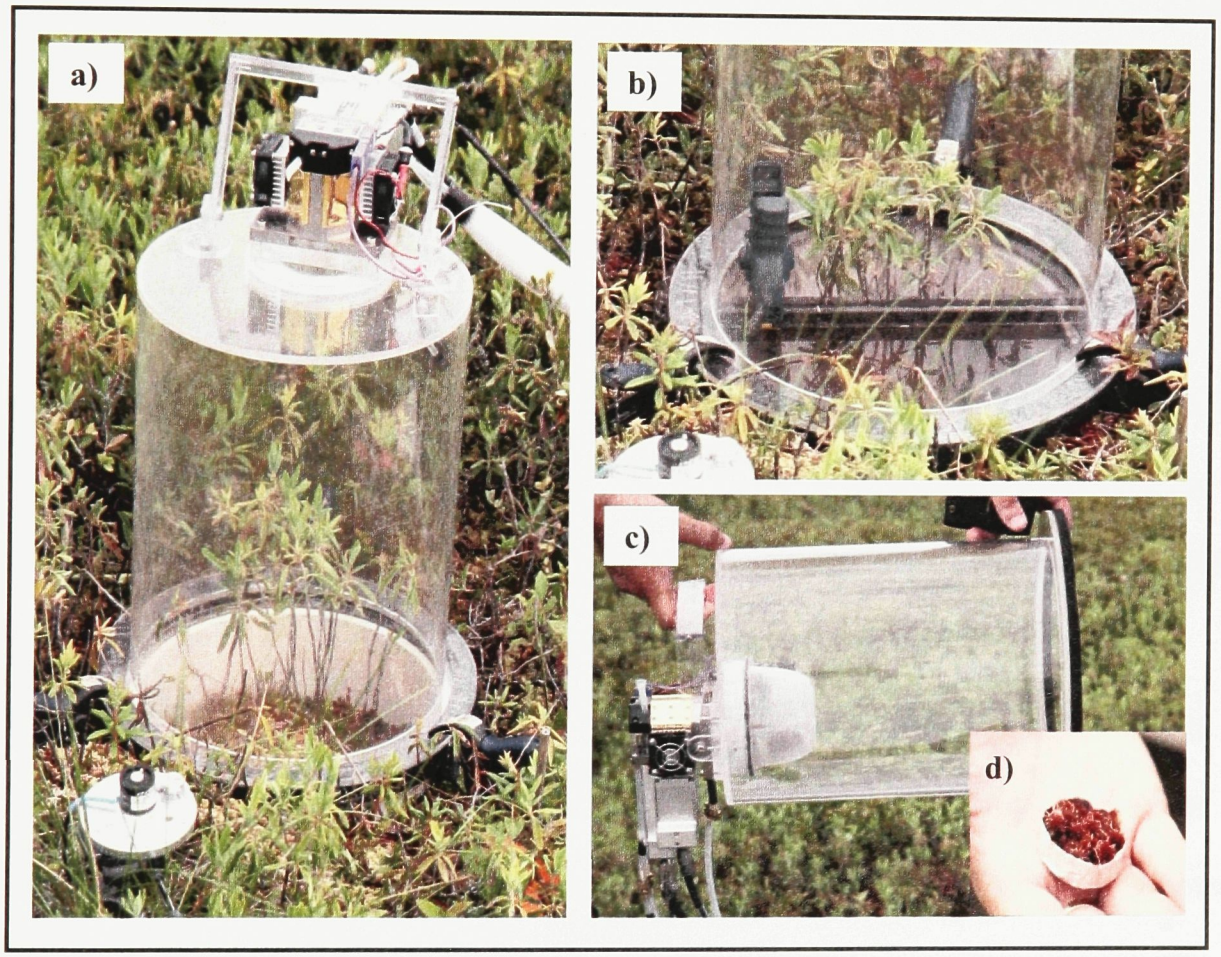

Figure 2. Photos of custom designed chamber system used to measure CO_2 and H_2O exchange by a) the total ecosystem, b) vascular plants, and c) the *Sphagnum* moss. For *Sphagnum* flux measurements, a 3.7 cm diameter circular sample as shown in d) was placed inside the smallest chamber (c).

sampling. A water-filled groove in the collars was used to produce a seal between the collar and chamber during measurements. Two collars were installed in each plot (referred to as C_a and C_b). Collar placement was limited to hummocks, in order to minimize variability in *Sphagnum* species within the sampling area. The collars protruded 3.8 ± 0.3 cm above the surface, slightly increasing the chamber volume for total NEE measurements (~5.6%). When using this chamber for vascular plant NPP measurements, vascular vegetation was clamped at the base of the stems just above the moss surface between two semi-circles of flat acrylic with a combined diameter of 32 cm. This piece was in turn clamped to the chamber, isolating the vascular vegetation within the chamber and excluding the moss carpet (Figure 6). Closed cell foam weather stripping applied between adjacent pieces of acrylic minimized leakage. Any vascular vegetation that could not be clamped into this chamber was removed from the collar prior to the sampling period by clipping it at the stem base, so as to exclude it from total NEE measurements as well. To account for any modification this clipping may have had on other fluxes, only C_a collars were clipped and were used for total NEE and vascular NPP measurements. The C_b collars were left unclipped, and were reserved for total NEE measurements only.

For *Sphagnum* NPP measurements, a 3.7 cm diameter circular sample that was ~1 cm deep and contained on average 22 ± 1 capitula and small portion of the stem below was cut from the *Sphagnum* carpet. This was done by inverting a small metal cup with the same diameter that was ~1 cm deep over the capitula and clipping the stems so that the *Sphagnum* sample was flush with the rim of the cup. The *Sphagnum* sample was then turned right side up into an identical metal cup, which was placed inside a smaller closed

chamber that was then fitted into the larger chamber system (Figure 6). This smaller chamber was made of clear plastic and had a volume of 473 cm^3. Transmission of PAR to the moss sample through the large and small chambers combined was estimated at 78%. Due to initial problems with the method used for *Sphagnum* flux measurement, moss flux data collected prior to July 2 could not be used in analysis. Unless otherwise indicated, *Sphagnum* NPP and total NEE fluxes are expressed as µmol m^{-2} of surface area s^{-1}, while vascular plant NPP is expressed per m^2 of green leaf area.

All NPP and NEE measurements were made in full sun, under two levels of shade (roughly 40% and 15% light transmission associated with 1 and 2 shade cloth(s) respectively) and in the dark to estimate respiration. This was done in order to span a range of light conditions so that the light response of these fluxes could be assessed. Each total ecosystem NEE or vascular NPP measurement was 2.5 minutes long. *Sphagnum* NPP measurements were shorter (1 minute) to limit water loss from the moss sample via evaporation during measurements. Between each measurement the chamber was removed for at least 20 seconds to allow the vegetation to equilibrate to ambient conditions. Due to time constraints all flux measurements could not be made in one sampling day. C_a and C_b collar measurements were made on alternating sampling days, with *Sphagnum* NPP measurements taking place on the C_b collar measurement days.

Cranked wires were used as a secondary method of measuring average total *Sphagnum* NPP over the 2008 measurement period (Clymo 1970). Fifteen cranked wires were initially established within each sample plot, with the cranked portion below the moss surface to anchor the wire. The height of the moss surface was measured relative to a mark 10 cm above the cranked portion periodically throughout the measurement period.

Some wires were badly bent due to interference when working within the plots, and these data were discarded. To estimate accumulated mass from these vertical growth measurements, average bulk density of *Sphagnum* in the 2 cm below the capitulum (D_b) was used. Samples were originally taken to determine D_b, but due to problems with these data D_b for the site was instead calculated from Moore *et al.* 2002. NPP in g dry biomass m^{-2} was estimated as vertical growth multiplied by mean D_b, and then converted to g C m^{-2} assuming 43% carbon, which was the mean carbon content of *Sphagnum* samples.

3.3.2 Sphagnum moisture conditions

Sphagnum WC was determined gravimetrically. Samples taken for *Sphagnum* NPP measurements (see Section 3.3.1) were sealed in plastic bags immediately following flux measurements and then weighed before drying to obtain their fresh weights. To account for possible losses in moisture during flux measurements an additional *Sphagnum* sample, consisting of approximately 5 to 10 capitula and the top 1-2 cm of their stems, was taken at the time of measurement from each plot and sealed immediately in a plastic bag for weighing. Samples were weighed on an electronic balance to ± 0.0001 g. They were then oven dried at 65°C for at least 24 hours before their dry weight was obtained. WCs are expressed as a ratio of fresh weight to dry weight (fw dw^{-1}).

3.3.3 Climate and eddy covariance

Variables presented in Table 3 were measured throughout the study at the frequencies indicated in the table. These variables were measured to monitor the

Table 3. Instrumentation and measurement frequency of climate variables.

Variable	Frequency of Measurement	Measurement Method
water table depth	2-3 times per week	3 wells per plot*
	5 s (averaged every 30 min)	1 well, float and counterweight system
soil temperature (2, 5, 10 cm depths)	5 s (averaged every 30 min)	chromel-constantan thermocouples
air temperature (0.5 m height)	5 s (averaged every 30 min)	chromel-constantan thermocouples
rainfall	automated, varies	tipping bucket rain gauge**
LAI	biweekly	point quadrat method*
moss density	6 times over growing season	manual count in a 25 cm^2 area*

Note: PAR, photosynthetically active radiation; LAI, leaf area index
*manual measurement , ** instrumentation previously established at tower site

environmental controls on NEE and *Sphagnum* NPP, and to assess microclimate differences between treatments. Temperature profiles were established at the centre of each plot using chromel-constantan thermocouples at 2, 5, and 10 cm below the surface and air thermocouples at 0.5 m above the surface. Temperature was measured continuously using a Campbell Scientific 21x micrologger (Campbell Scientific Inc., Logan, UT, USA).

Three wells were established in each plot for manual measurement of water table depth beneath the surface. Depth to the water table was measured every day that chamber measurements were made. Water table was measured periodically on additional days, particularly during periods when chamber measurements were infrequent. In addition, water table was measured continuously at one location in the study area using a float and counterweight system attached to a potentiometer.

The microtopography of the study area was characterized by measuring the average height of a 0.25 m^2 area surrounding each well expressed relative to the lowest well measured. To accomplish this, a water-filled tube was submerged at one end in a bucket of water that was elevated above the highest point within the study area, acting as a temporary zero point. At the open end of the tube, some space was left to allow for movement of water within the tube. As the water at the open end of the tube must be level with that in the bucket, the position of the moss surface at various points within the study area can be measured relative from the surface of water in the bucket, which acts as an arbitrary zero. A 50 x 50 cm quadrat was centered and leveled above each well in turn, and the height of the quadrat above the moss surface was measured in the centre and at each corner. Using the open end of the water-filled tube, the height of the quadrat relative to the water surface in the bucket was also measured at each of these points in order to relate the surface measurements to the zero datum.

The eddy covariance technique is a micrometeorological method that directly measures vertical fluxes of CO_2, water vapour, and energy from terrestrial ecosystems to the atmosphere (Canadell *et al.* 2000). Using this method fluxes were measured at 3.0 m above the hummock surface. Instrumentation and calculations of these fluxes follow Roulet *et al.* (2007) and Lafleur *et al.* (2003). Additional climate measurements made at the tower site included air temperature, relative humidity, and wind speed at 2.0 m, soil temperature at depths from 0.01 to 2.5 m, water table depth, and PAR. Instrumentation used in these measurements is described by Lafleur *et al.* (2003). Data were recorded every 5s on a CR7X datalogger (Campbell Scientific, Logan, UT, USA) and averaged every 30 min.

3.3.4 Vegetation

Shrub height and the density and species composition of both shrubs and *Sphagnum* mosses varied among microsites within the study area. The vegetation characteristics of each plot are summarized in Table 2. Leaf area index (LAI), in m^2 leaf area m^{-2} ground area (m^2 m^{-2}), was estimated every three weeks throughout the 2008 measurement period using the point intercept method of measurement in two permanent 0.36 m^2 subplots that were randomly distributed within the study area (Levy and Madden 1933, Goodall 1952). The 0.6 m by 0.6 m frame had a 5 cm width grid made of fishing line that produced 121 intersection points. The frame was leveled above each plot and at alternating points (61 in total) a pin was dropped perpendicular to the frame until it reached the moss surface. The number of leaves and stems of each species making contact with the pin were recorded at each point. Presence or absence of *Sphagnum* and *Polytrichum* mosses was also noted.

To capture vegetation changes within the collars, leaf area was estimated from counts of green leaves by species. These counts were made at roughly 2 week intervals throughout the 2008 measurement period, and more frequently in spring 2009 to capture the more rapid vegetation changes. Data collected during the 2007 growing season provided statistically significant relationships between number of leaves and leaf area for each species, which were used in these estimates (Table 4; unpublished data). Moss density in each collar was also estimated on these days by counting the number of *Sphagnum* capitula and *Polytrichum* stems in a randomly selected 25 cm^2 area within the collar.

Table 4. Linear regression relationships between number of leaves and leaf area (m^2), presented by species, for data collected during the 2007 growing season. Results are significant for Bonferroni adjusted p-values.

Species	Linear regression relationship†	R^2	p
V. myrtilloides	$A_L = 0.00505 + 0.00012*L$	0.68	< 0.0001
K. angustifolia	$A_L = 0.00050 + 0.00011*L$	0.83	< 0.0001
L. groenlandicum	$A_L = 0.00110 + 0.00006*L$	0.81	< 0.0001
C. calyculata	$A_L = 0.00165 + 0.00006*L$	0.79	< 0.0001

† A_L = leaf area (m^2), L = number of leaves

As ombrotrophic bogs are rain-fed, they are dependent on atmospheric deposition for nutrients. *Sphagnum* total carbon and nitrogen contents were measured to assess whether there was a treatment effect on nutrient availability. Dried *Sphagnum* samples from each plot for five days throughout the measurement period (DOY 177, 199, 235, 268, 289) were ground and analyzed using high temperature decomposition (Elementar© MACRO CNS, Elementar Analysensysteme).

3.4 Data processing and analysis

Flux data were processed in Matlab 7.4.0 (The MathWorks Inc., 2007). CO_2 fluxes (F_{CO2}, µmol m^{-2} s^{-1}) were calculated for each 2.5 minute (total NEE, vascular plant NPP) or 1 minute (*Sphagnum* NPP) measurement as:

(3) $$F_{CO2} = \frac{pV}{R^* T_{ch} A} \frac{dC}{dt} \frac{1}{(1 + M_{H2O})}$$

where M_{H2O} is H_2O mixing ratio (mol mol^{-1} dry air), p is air pressure (Pa), T_{ch} is mean chamber air temperature (°K), R^* is the ideal gas constant (8.3144 J K^{-1} mol^{-1}), V is chamber volume (m^3), and A is chamber surface area (m^2). CO_2 concentration was converted to mixing ratio, and the rate of change in CO_2 mixing ratio in the chamber over the measurement period is dC/dt (µmol mol^{-1} dry air s^{-1}). In some cases a shorter time period was used for the flux calculation to exclude inconsistencies in the rate, which sometimes occurred due to notable changes in PAR (e.g. due to a change in cloud cover) or due to plant stress near the end of the measurement. A negative CO_2 flux represents uptake by the system, while positive indicates a loss to the atmosphere.

To describe variations in NEE or NPP with light and temperature, the following equation combining a rectangular hyperbolic relationship between gross photosynthesis and light (Equation 1) and an exponential relationship between respiration and temperature (Equation 2) was used:

(4) $$NEE = \frac{\alpha \cdot PAR \cdot GP_{\max}}{\alpha \cdot PAR + GP_{\max}} + R_{10} \cdot Q_{10}^{\frac{T - T_{ref}}{10}}$$

in which α is the initial slope of the relationship representing photosynthetic efficiency, GP_{max} is gross photosynthesis at maximum PAR, R_{10} is respiration at a reference temperature of 10°C (T_{ref}), and Q_{10} is the rate of increase in respiration over a temperature change of 10°C. Q_{10} was constrained to 2, which is the typical value found for a wide range of plant species (see Section 2.2.2). In calculations T_{ch} in °C was used

for temperature (*T*). For vascular plant and *Sphagnum* moss fluxes, NPP was substituted for NEE in this equation.

All statistical analyses were completed using JMP 7.0.2 (SAS Institute Inc., 2007). The 2008 data were divided among three measurement periods (from here on called seasons): early summer (ES, DOY 164-206), late summer (LS, DOY 207-244), and fall (F, DOY 245-311). The spring 2009 data were divided into the pre-greenup period (i.e. prior to green leaves on vascular vegetation, PrG, DOY 105-109) and post-greenup period (PG, DOY 124-145). During the early summer season only the PE treatment and CL were active. No treatments were implemented during spring 2009. For each flux measurement GEP or GPP was calculated by subtracting the corresponding dark respiration (R_d) measurement from NEE or NPP. Light/temperature response relationships were calculated for each treatment plot in early summer and late summer for *Sphagnum*, vascular plants, and the total ecosystem. The fit of these relationships was poor for post-greenup and fall season data because there were relatively few data points associated with saturating levels of PAR, and there was not enough data in the pre-greenup period, so light/temperature curve parameters are not included for these periods. In addition, maximum NEE or NPP (NEE or NPP_{max}), maximum GEP or GPP (GEP or GPP_{max}), and mean R_d were calculated for *Sphagnum*, vascular plants, and the total ecosystem in each season. Maximum photosynthesis typically occurs above PAR of 1000 μmol m^{-2} s^{-1} for most vascular plants and above between 250 and 500 μmol m^{-2} s^{-1} for *Sphagnum* mosses (Harley *et al.* 1989, Williams and Flanagan 1996, Bubier *et al.* 2007). NEE or NPP_{max} and GEP or GPP_{max} were therefore calculated as the means for PAR greater than 1000 μmol m^{-2} s^{-1} for vascular plants and the total ecosystem and

greater than 500 μmol m^{-2} s^{-1} for *Sphagnum*. R_d was calculated as mean NEE or NPP in dark conditions (PAR ≈ 0 μmol m^{-2} s^{-1}).

An estimate of total June to September (DOY 152 to 244) carbon exchange was made using light/temperature response relationships. This estimate was made using the combined data from PE and CL plots, as they were shown not to have significantly different light/temperature response relationships (see Section 4.2). The WA treatment data were not included, as this treatment was not started until late July. Half-hourly NEE or NPP was estimated for *Sphagnum*, vascular plants and the total ecosystem for the June to September period using early summer relationships for DOY 152 to 206 and late summer relationships for DOY 207 to 244. Half-hourly PAR measured at the eddy covariance tower and average T_{air} measured in the PE and CL plots (for *T* in Equation 4) were used as predictor variables. The 30 min flux estimates (μmol m^{-2}) were converted to g C m^{-2} and then summed for the June to September period.

Treatment effects were assessed using 2008 data. As the WA treatment was not active in early summer, separate one-way analyses of variance (ANOVA) were performed for each measurement type (*Sphagnum*, vascular plants, total ecosystem) in this season to assess for a treatment effect on light/temperature response curve parameters (GP_{max}, α, R_{10}), NEE or NPP_{max}, GEP or GPP_{max}, R_d, and mean *Sphagnum* WC. Treatment effects in late summer and fall were assessed with Factorial ANOVA (Factors: treatment and season) to reduce multiple testing. For comparisons of total ecosystem fluxes, data measured at both C_a and C_b collars were included, so for these ANOVA tests variance associated with collar subsamples and leaf area as a covariate were included. To test moss recovery, differences in *Sphagnum* fluxes (NEE or NPP_{max}, GEP or GPP_{max}, R_d)

among treatments in spring 2009 were assessed with One-way ANOVA tests. One-way ANOVA was also used to assess for significant differences in microtopography and *Sphagnum* total carbon and nitrogen contents among treatments over the entire measurement period. Comparisons of mean water table, air temperatures (daily mean, maximum, and minimum T_{air}), and soil temperatures (daily mean, minimum, and maximum T_{2cm} and T_{5cm}) were made using Factorial ANOVA (Factors: treatment and season). Differences between C_a and C_b collars in LAI and in total ecosystem flux (NEE_{max}, GEP_{max}, R_d) expressed on a leaf area basis (μmol m^{-2} leaf area s^{-1}) were assessed using a t-test assuming unequal variances, as data transformations did not correct the unequal variances in these data. Pre-greenup season data were excluded from these collar comparisons, as green leaf area was negligible in both collars.

The optimal WC range for *Sphagnum* photosynthesis shown in the literature is roughly 7 to 11 fw dw^{-1} (see Section 2.2.3). As there was little apparent treatment effect on CO_2 fluxes, to determine whether particularly wet or dry moss conditions influence CO_2 exchange the flux data from each season and treatment were pooled and then separated into three groups according to *Sphagnum* WC for further analysis: WC < 5 fw dw^{-1}, WC = 5 to 13 fw dw^{-1}, and WC > 13 fw dw^{-1}. Overall differences in fluxes (NEE or NPP_{max}, GEP or GPP_{max}, and R_d) among WC groups were analysed using multivariate analyses of variance (MANOVA) for *Sphagnum*, vascular plants, and the total ecosystem. Seasonal differences in fluxes (NEE or NPP_{max}, GEP or GPP_{max}, and R_d) for each measurement type were also assessed using MANOVA. Wilks' Lambda was used as the test statistic.

The relationship between *Sphagnum* WC and water table was assessed with simple linear regression analysis. A separate regression test was performed on the data from each treatment group (PE, WA, CL). Linear regression analyses between 2007 leaf area and leaf counts data were also used to produce separate relationships for *C. calyculata*, *V. myrtillodes*, *K. angustifolia*, and *L. groenlandicum*.

Prior to analyses all data were tested for the assumptions of normality and equal variances. All data met the assumption of equal variances, unless otherwise indicated. Non-normal data were transformed, but this did not fully correct the distribution in all cases. In many cases this was due to the small sample size of three replicates per treatment. However, as ANOVA is quite robust to deviations from normality, where transformations were not effective the untransformed data were used (Zar 1999). Post-hoc analyses of significant ANOVA/MANOVA results were performed using Tukey's honestly significant difference (HSD) test. All statistical analyses were tested at a significance level (α_s) of 0.05. To avoid magnified Type I error rates (i.e. the increased chance of rejecting a true null hypotheses) due to the multiple testing in this study, the sequential Bonferroni technique described by Rice (1989) was employed.

4.0 RESULTS

4.1 Water availability and weather conditions

The 2008 water table at the study area was high relative to the long-term average, due to near-record snowfall accumulation in the previous winter, and a particularly wet spring and early summer (Figure 7, Figure 8). Still, with a mean 2008 growing season water table of -31 cm and a range from -21 cm to -39 cm, this was not the wettest year that has been recorded at the site since 1998 (see Section 3.1). The PE shelters excluded an estimated 93.5% of rainfall (Figure 9), and assessment of edge effects indicated that the 0.5 m buffer around each plot was sufficient to prevent rain from reaching the sampling area when the shelters were up (data not shown). Microclimate did not appear to be altered by the shelters, as treatment effects on seasonal mean temperatures (T_{air}: $F = 1.20$, $p = 0.32$; T_{2cm}: $F = 1.31$, $p = 0.29$; T_{5cm}: $F = 1.95$, $p = 1.17$), seasonal minimum temperatures (T_{air}: $F = 1.21$, $p = 0.32$; T_{2cm}: $F = 1.46$, $p = 0.26$; T_{5cm}: $F = 2.09$, $p = 0.15$), or seasonal maximum temperatures (T_{air}: $F = 6.90$, $p = 0.006$; T_{2cm}: $F = 6.37$, $p = 0.008$; T_{5cm}: $F = 0.77$, $p = 0.48$) were not significant for Bonferroni adjusted p-values. *Sphagnum* total carbon (43.3 ± 0.1 % of dry weight) and nitrogen (1.4 ± 0.1 % of dry weight) contents were also not significantly influenced by the treatments ($F = 0.22$, $p = 0.80$ and $F = 0.78$ $p = 0.46$ respectively). Daily mean air and soil temperatures were above 0°C for almost the entire measurement period, but daily temperature of peat at 5 cm and 10 cm depths was below zero throughout the 2009 pre-greenup season (until DOY 111 and 118 respectively) (Figure 10).

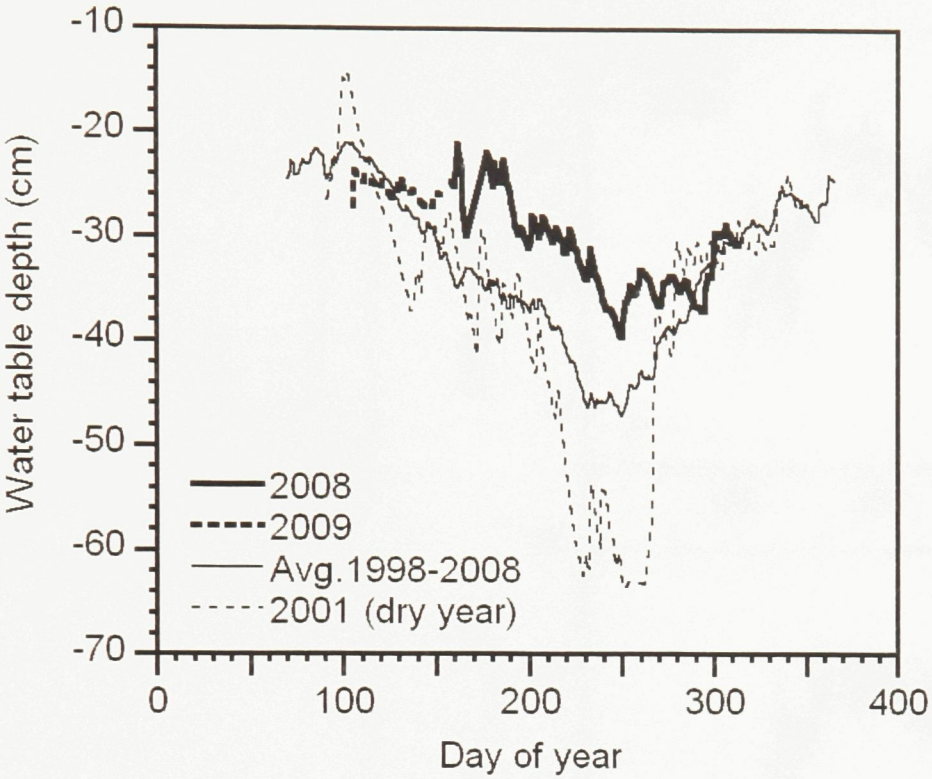

Figure 7. Daily water table depth (cm) at the study area. For comparison, the long term average and water table in a dry year (2001) are also shown. These historical data were recorded at the tower site, but have been adjusted by +6 cm to represent the study area.

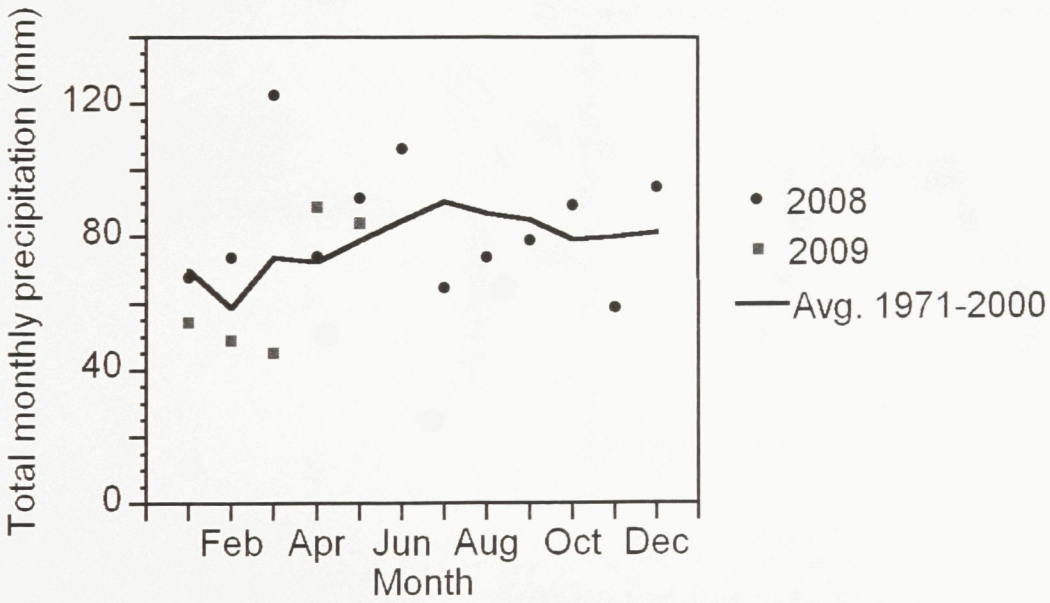

Figure 8. Total monthly precipitation (mm) in 2008 and spring of 2009 compared with the long term average (1971-2000). These data were recorded approximately 12 km southwest of Mer Bleue at the Environment Canada weather station located at the Macdonald-Cartier International Airport.

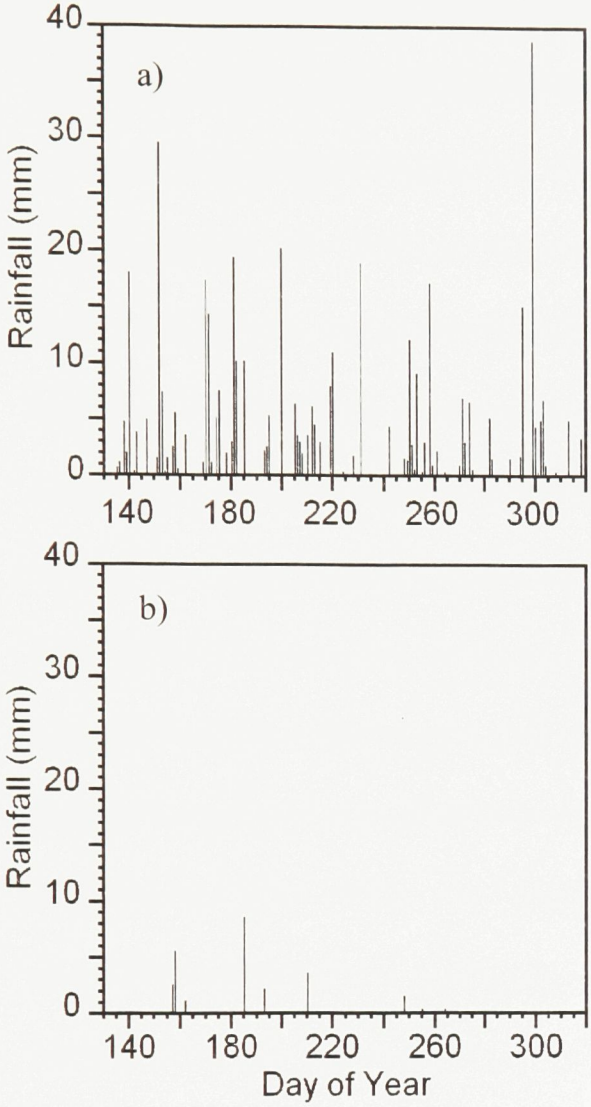

Figure 9. Daily rainfall (mm) a) measured at the tower site and b) estimated for the precipitation exclusion (PE) treatment plots.

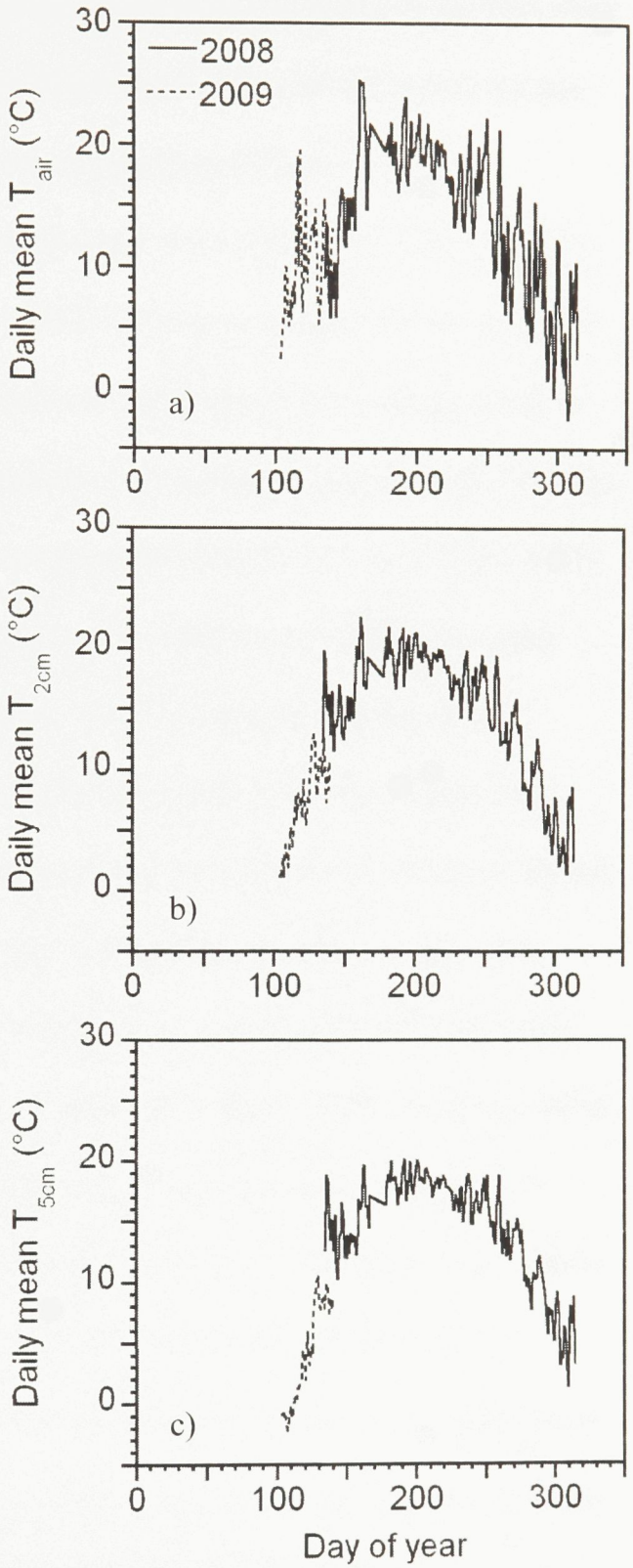

Figure 10. Daily mean a) air temperatures (T_{air}), b) 2cm soil temperatures (T_{2cm}), and c) 5cm soil temperatures (T_{5cm}) for the 2008 and 2009 measurement periods.

Sphagnum WC was significantly lower in the PE plots and higher in the WA plots than in the control, except in the fall when the difference between the PE treatment and CL was not significant (Figure 11). There were no significant differences in microtopography ($F = 0.07$, $p = 0.93$) or seasonal mean water tables ($F = 0.14$, $p = 0.87$) between treatments, suggesting that *Sphagnum* WC differences among plots were due to treatment effects and not produced by differences in the height of the moss above the water table. Seasonal mean WCs for all treatments were within or near the range that has been shown in the literature as optimal for photosynthesis (Figure 11). Still, some white discolouration of the moss, indicating desiccation, was observed throughout the study area, particularly in late summer and fall (Figure 12). This white colour has been associated with dry moss conditions and the emptying of water from the hyaline cells (Hayward & Clymo 1983). Dry patches were seen in all treatments (i.e. were not limited to the PE treatment plots). *Sphagnum* can continue some CO_2 exchange in this state because the living chlorophyllous cells have smaller pores than hyaline cells, allowing them to prevent water loss longer (Clymo 1973, Hajek & Beckett 2008). However, these patches likely corresponded with particularly dry moss samples (WC < 5 fw dw^{-1}) in which NPP was reduced, most of which were taken at this driest time of the year. By the end of the 2008 measurement period, *Sphagnum* within the PE treatment plots also consistently exhibited discolouration from their typical burgundy colour to a light brown (Figure 12). The reason for this is not known, and there do not appear to be any previous studies noting such results in prolonged absence of precipitation.

Changes in *Sphagnum* WC over the 2008 measurement period were controlled at least in part by the depth of the water table, as indicated by the significant relationships

between water table depth and WC for the CL and PE treatment (Figure 13). The greatest proportion of variability in WC was explained by water table ($R^2 = 0.16$) in the PE treatment, where the contribution of precipitation to WC was very minimal. There was no relationship between water table and WC in the WA treatment, because the WC of these samples was likely influenced more strongly by the recent addition of water than by water table depth.

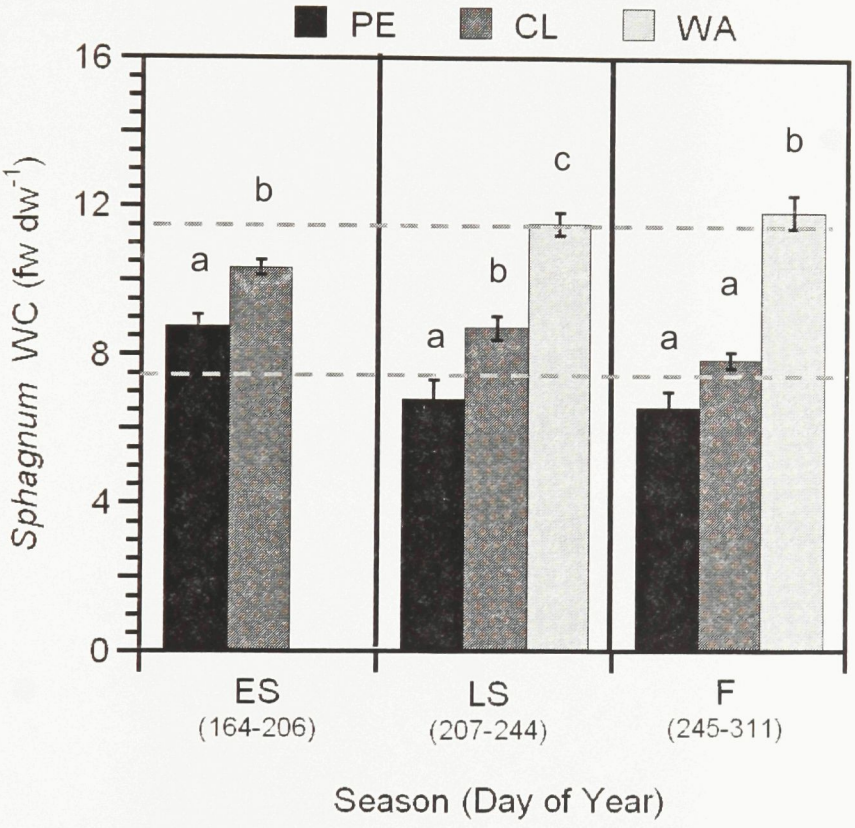

Figure 11. Seasonal mean *Sphagnum* WC presented by treatment. Within each season, treatments with no common letters are significantly different ($p < 0.05$). Results are significant for Bonferroni adjusted p-values. Grey dashed lines indicate the boundaries of the range that has been shown in the literature as optimal for photosynthesis (approximately 7 to 11 fw dw^{-1}). Treatments are defined as in Figure 4. Note: ES, early summer; LS, late summer; F, fall.

Figure 3. Photos illustrating a) brown discolouration of *Sphagnum* moss in precipitation exclusion (PE) treatment plots, in comparison with b) the natural colour

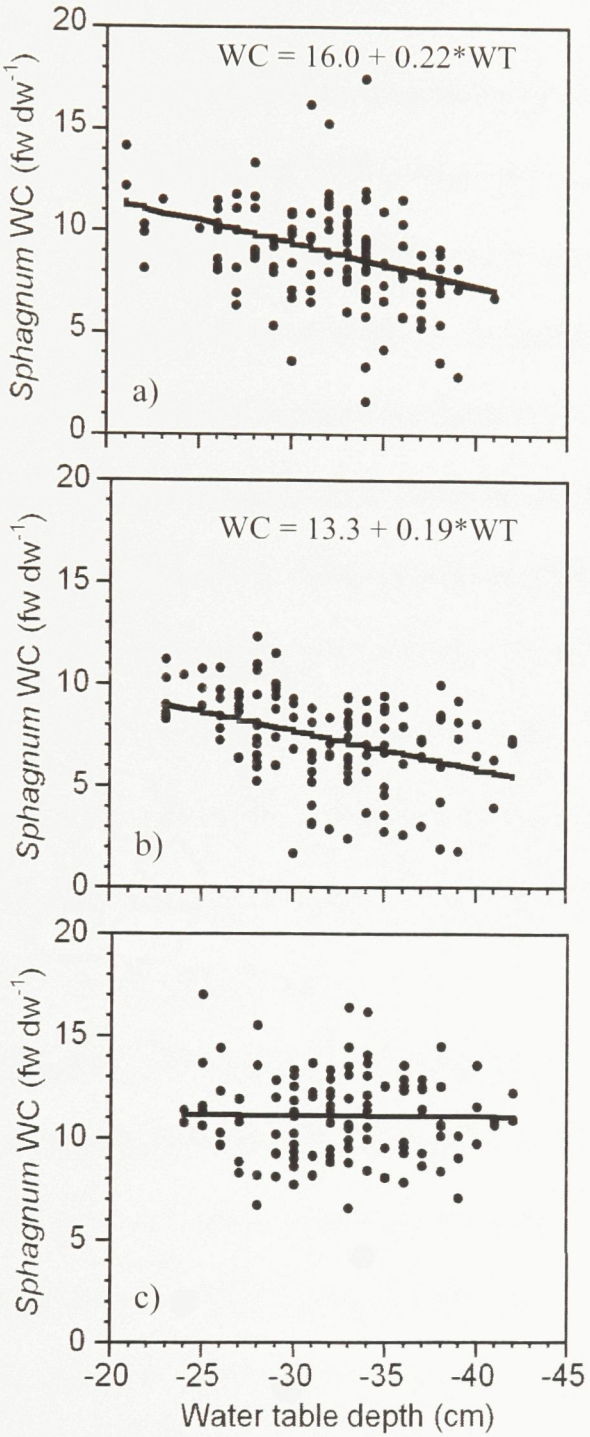

Figure 13. Relationships between water table depth (cm) and *Sphagnum* WC (fw dw^{-1}) for the a) CL ($R^2 = 0.14$, $p < 0.0001$), b) PE treatment ($R^2 = 0.16$, $p < 0.0001$), and c) WA treatment ($R^2 < 0.01$, $p = 0.89$) for the full 2008 measurement period. Results are significant for Bonferroni adjusted p-values. Note that there is not a significant relationship for the WA treatment, and therefore the equation of the line is not presented. Treatments are defined as in Figure 4.

4.2 Moss wetness and CO_2 fluxes

No clear treatment effect on CO_2 fluxes was observed. This is illustrated in Figure 14, where the responses of NEE and NPP to light and temperature were very similar among treatments. Light/temperature response curve parameters (Table 5) were not significantly different among treatments (Table 6). In addition, mean NEE or NPP_{max} and GEP or GPP_{max} were similar among treatments (Figure 15, Table 7 and Table 8). There is some evidence that *Sphagnum* respiration (both R_d and R_{10}) was consistently decreased by the PE treatment (Figure 15, Table 5), although the difference was only significant for late summer and fall season *Sphagnum* R_d (Table 8). There were no significant differences in fluxes in spring 2009 (Table 9, Table 10) suggesting that although there were differences in moss WC, the PE treatments did not result in significant desiccation damage when the treatment was applied nor any damage that carried over into the following growing season.

For measurements associated with very dry *Sphagnum* conditions (WC < 5 fw dw^{-1}), *Sphagnum* GPP_{max} was decreased leading to a small net loss of CO_2 (i.e. positive NEP_{max}) while WC ≥ 5 fw dw^{-1} led to a net uptake of CO_2 (Figure 16). Total ecosystem GEP_{max} also declined with dry moss conditions and total ecosystem net uptake of CO_2 (i.e. NEE_{max}) decreased as a result. These declines in ecosystem uptake appeared to be tied directly to the changes in *Sphagnum* fluxes, as there were no changes in vascular plant fluxes with variations in moss wetness. There were no apparent differences between fluxes associated with near optimal *Sphagnum* WCs (5-13 fw dw^{-1}) and those associated with relatively wet *Sphagnum* (WC > 13 fw dw^{-1}) (Figure 16).

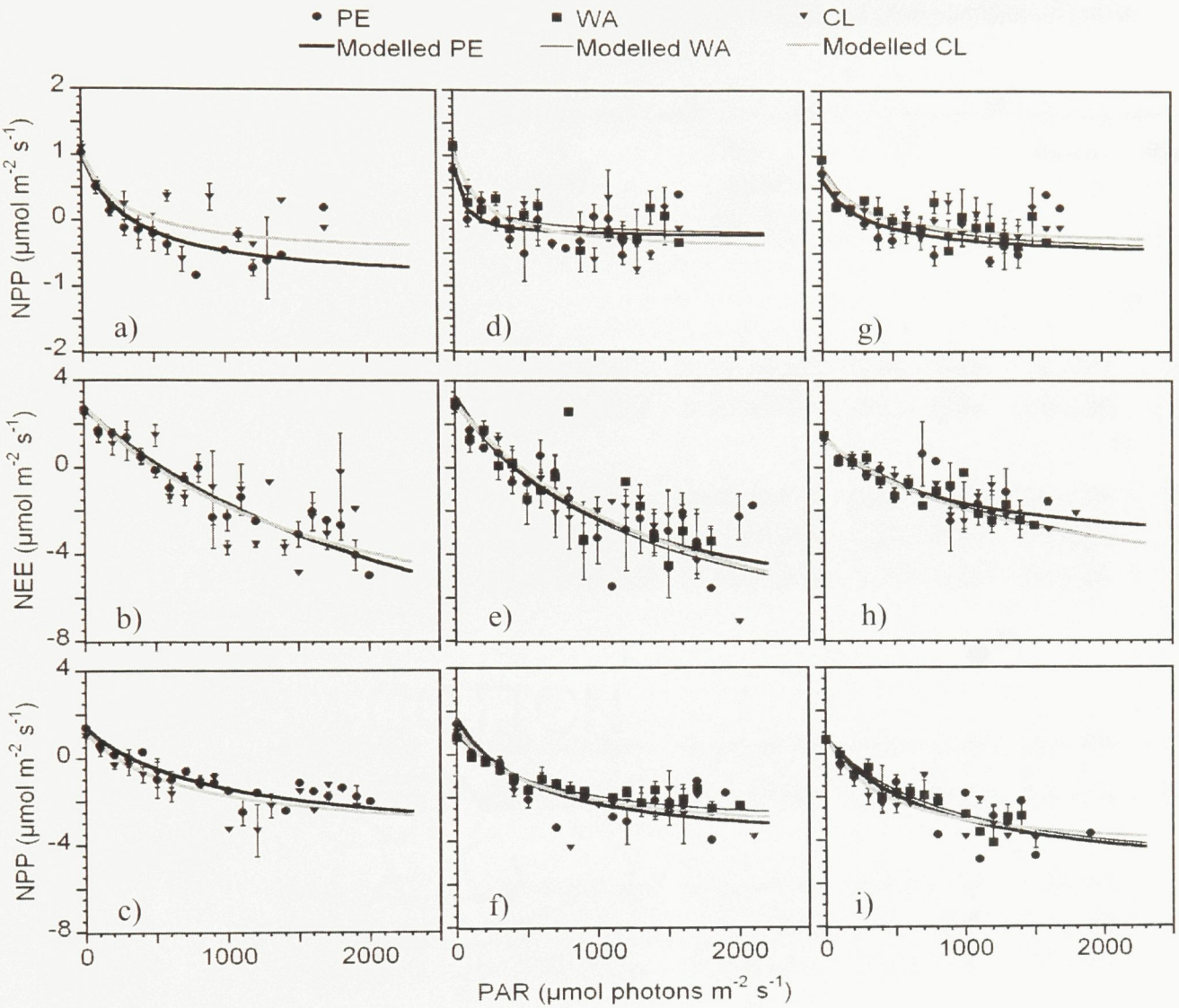

Figure 14. Relationships between bin averaged NEE or NPP data and PAR for *Sphagnum*[‡] (a,d,g), the total ecosystem[‡] (b,e,h), and vascular plants[§] (c,f,i). Separate relationships are presented for the early summer (DOY 164-206) (a-c), late summer (DOY 207-244) (d-f), and fall (DOY 245-311) (g-i) seasons. Bin size is 100 (± SE). Vertical axis scale is not consistent among subfigures. This figure is intended only to illustrate the similarity in these relationships between treatments, and the parameters of the curves are not shown. Light/temperature response relationships were also calculated for each plot separately in early and late summer, and the parameters of these curves (presented in Table 5) were used in statistical comparisons between treatments. Treatments defined as in Figure 4. Note: NEE, net ecosystem exchange of CO_2; NPP, net primary productivity; PAR, photosynthetically active radiation; DOY, day of year
[‡]fluxes expressed m^{-2} surface area; [§]fluxes expressed m^{-2} leaf area

Table 5. Light/temperature response curve parameters (mean ± SE) for 2008 *Sphagnum*[‡], vascular plant[§], and total ecosystem[‡] flux measurements by season and treatment. Number of data points to which curves were fit (n_{curve}) and number of curve parameters averaged for the mean (n_{mean}) are indicated.

Treatment	GP_{max} µmol m^{-2} s^{-1}	α µmol µmol^{-1}	R_{10} µmol m^{-2} s^{-1}	r^2	n_{curve}	n_{mean}
***Sphagnum*[‡]**						
Early summer						
PE	-1.93 (0.21)	-0.006 (0.001)	0.31 (0.02)	0.81 - 0.95	16 - 20	3
CL	-1.51 (0.09)	-0.007 (0.001)	0.35 (0.03)	0.63 - 0.88	15 - 20	3
Late summer						
PA	-1.32 (0.23)	-0.010 (0.001)	0.24 (0.03)	0.62 - 0.81	12 - 23	3
WA	-1.61 (0.07)	-0.011 (0.004)	0.33 (0.03)	0.64 - 0.83	15 - 24	3
CL	-1.77 (0.01)	-0.007 (0.001)	0.34 (0.03)	0.71 - 0.78	14 - 22	3
Vascular plants[§]						
Early summer						
PE	-5.14 (0.46)	-0.007 (0.001)	0.35 (0.03)	0.82 - 0.88	26 - 28	3
CL	-5.20 (1.38)	-0.007 (0.001)	0.36 (0.06)	0.79 - 0.88	19 - 24	3
Late summer						
PE	-6.32 (1.32)	-0.012 (0.002)	0.38 (0.04)	0.84 - 0.97	24 - 32	3
WA	-4.46 (0.24)	-0.008 (0.001)	0.26 (0.03)	0.91 - 0.97	23 - 24	3
CL	-4.62 (0.40)	-0.010 (0.002)	0.27 (0.04)	0.85 - 0.90	20 - 25	3
Total ecosystem[‡]						
Early summer						
PE	-12.55 (2.26)	-0.008 (0.001)	0.76 (0.07)	0.84 - 0.96	14 - 25	6
WA	-12.17 (2.09)	-0.009 (0.001)	0.81 (0.07)	0.86 - 0.97	16 - 35	6
Late summer						
PE	-10.64 (1.69)	-0.011 (0.002)	0.82 (0.13)	0.78 - 0.96	16 - 28	6
WA	-10.83 (1.39)	-0.013 (0.002)	0.91 (0.04)	0.83 - 0.95	19 - 22	6
CL	-10.56 (1.67)	-0.011 (0.001)	0.85 (0.06)	0.78 - 0.95	15 - 26	6

Note: PAR, photosynthetically active radiation; DOY, day of year; PE, precipitation exclusion treatment; WA, water addition treatment; CL, control. Seasons are early summer (DOY 164-206), late summer (DOY 207-244), and fall (245-311).
[‡]fluxes expressed m^{-2} surface area
[§]fluxes expressed m^{-2} leaf area

Table 6. One-way ANOVA results (F-values and p-values) for treatment effects on light/temperature response curve parameters (GP_{max}, α, R_{10}) by measurement type and season. Light/temperature response curves were not produced for the fall season (DOY 245-311). For total ecosystem tests, variance associated with collar subsamples and the covariate leaf area were included. Only treatment effect test results are shown, although in addition whole model degrees of freedom are indicated. No treatment effects were significant.

		GP_{max}		α		R_{10}	
	df - Treatment (Total)	**F**	**p**	**F**	**p**	**F**	**p**
Sphagnum ‡							
Early summer	1 (5)	7.14	0.12	0.57	0.86	0.97	0.43
Late summer	2 (8)	2.23	0.22	0.74	0.53	3.06	0.16
Vascular plants §							
Early summer	1 (5)	<0.01	0.97	0.43	0.58	0.08	0.94
Late summer	2 (8)	1.51	0.32	1.45	0.34	2.69	0.18
Total ecosystem ‡							
Early summer	1 (11)	0.05	0.83	0.70	0.44	0.17	0.70 #
Late summer	2 (17)	1.14	0.36 #	0.06	0.94	0.08	0.93 #

Note: Seasons are early summer (DOY 164-206), late summer (DOY 207-244) and fall (DOY 245-311). Levels of the treatment differ for DOY 164-206 (PE, CL) and DOY 207-244 (PE, WA, CL). DOY, day of year; df, degrees of freedom.

‡fluxes expressed m^{-2} surface area

§fluxes expressed m^{-2} leaf area

#leaf area a significant covariate ($p < 0.05$)

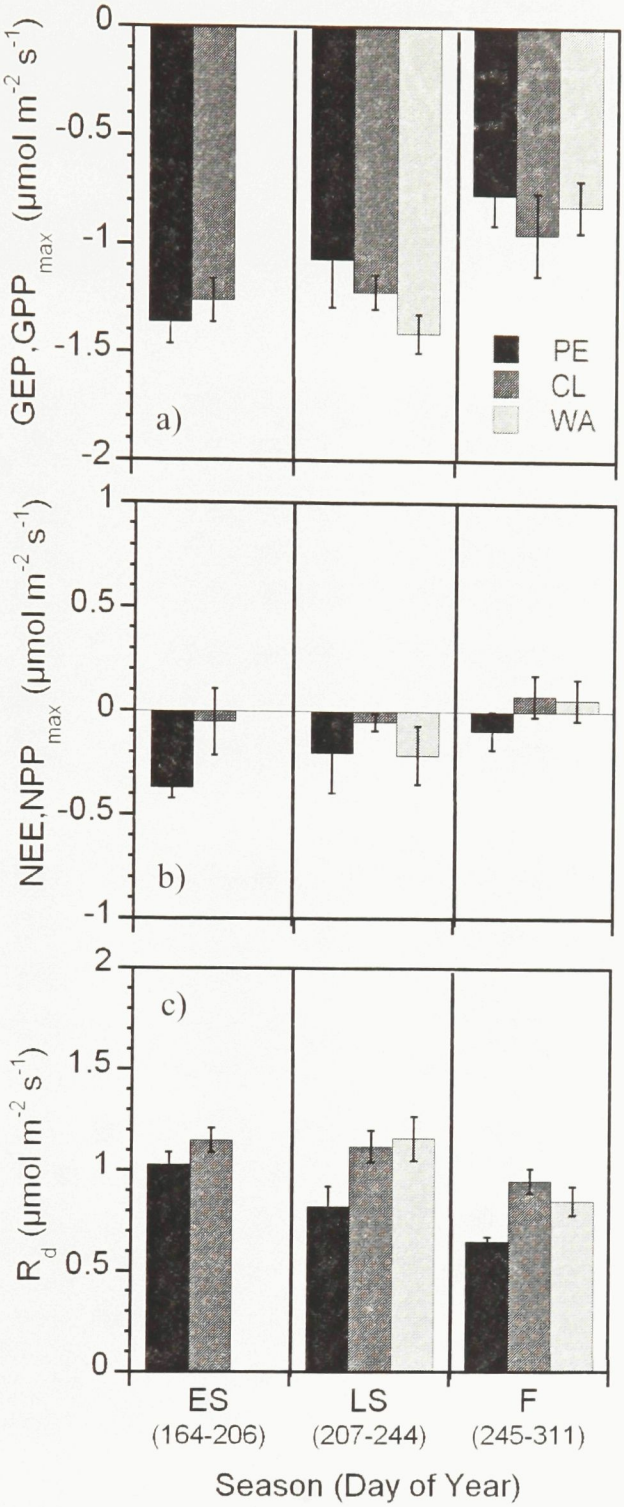

Figure 15. Mean (± SE) NEE or NPP_{max}, GEP or GPP_{max} and R_d for *Sphagnum*‡ flux measurements (µmol m^{-2} s^{-1}) by season and treatment. Corresponding vascular plant and total ecosystem flux data are presented in Table 7. There were no statistically significant differences among treatments, and results of statistical testing are presented in Table 8. Note: GEP or GPP_{max}, maximum gross ecosystem productivity (GEP) or gross primary productivity (GPP); NEE or NPP_{max}, maximum net ecosystem exchange of CO_2 (NEE) or net primary productivity (NPP); R_d, dark respiration. Seasons as defined in Figure 11. ‡fluxes expressed m^{-2} surface area

Table 7. Mean (± SE) NEE or NPP_{max}, GEP or GPP_{max} and R_d for 2008 vascular plant[§], and total ecosystem[‡] flux measurements (μmol m^{-2} s^{-1}) by season and treatment. Corresponding *Sphagnum* flux data are presented in Figure 15.

	Treatment	NEE,NPP_{max}	GEP,GPP_{max}	R_d
Vascular plants[§]				
Early summer	PE	-1.79 (0.17)	-3.25 (0.22)	1.42 (0.08)
	CL	-2.17 (0.52)	-3.26 (0.56)	1.24 (0.20)
Late summer	PE	-2.64 (0.79)	-4.31 (0.79)	1.55 (0.12)
	WA	-2.11 (0.24)	-3.02 (0.22)	0.84 (0.12)
	CL	-2.30 (0.11)	-3.71 (0.17)	1.11 (0.15)
Fall	PE	-2.93 (0.59)	-3.76 (0.54)	0.78 (0.10)
	WA	-3.30 (0.70)	-4.12 (0.81)	0.88 (0.14)
	CL	-3.26 (0.40)	-4.42 (0.63)	0.99 (0.20)
Total ecosystem[‡]				
Early summer	PE	-2.74 (0.53)	-5.43 (0.76)	2.69 (0.28)
	CL	-2.44 (0.54)	-5.03 (0.61)	2.52 (0.18)
Late summer	PE	-2.86 (0.81)	-5.58 (1.03)	2.87 (0.48)
	WA	-3.01 (0.82)	-6.38 (0.75)	3.23 (0.06)
	CL	-2.75 (0.73)	-5.70 (0.77)	2.91 (0.07)
Fall	PE	-1.92 (0.70)	-3.60 (0.68)	1.49 (0.33)
	WA	-2.70 (0.45)	-4.54 (0.44)	1.66 (0.12)
	CL	-2.25 (0.60)	-4.15 (0.650	1.48 (0.26)

Note: GEP or GPP_{max}, maximum gross ecosystem productivity (GEP) or gross primary productivity (GPP); NEE or NPP_{max}, maximum net ecosystem exchange of CO_2 (NEE) or net primary productivity (NPP); R_d, dark respiration. Seasons are early summer (DOY 164-206), late summer (DOY 207-244), and fall (DOY 245-311).

[‡]fluxes expressed m^{-2} surface area

[§]fluxes expressed m^{-2} leaf area

Table 8. One-way[+] and Factorial[¥] ANOVA results (F-values and p-values) for treatment effects on 2008 NEE or NPP_{max}, GEP or GPP_{max}, and R_d by measurement type and season. Treatment effect in early summer (DOY 164-206) was tested separately from Factorial ANOVAs, because levels of the treatment differ (PE, CL) from later seasons (PE, WA, CL). For total ecosystem tests, variance associated with collar subsamples and leaf area as a covariate were included. Only treatment and season effect test results are shown, although in addition whole model degrees of freedom are indicated. Significant results for Bonferroni adjusted p-values are emphasized in bold. There were no significant interaction effects between season and treatment ($p > 0.05$).

	Effect	df - Treatment (Total)	NEE,NPP_{max} F	NEE,NPP_{max} p	GEP,GPP_{max} F	GEP,GPP_{max} p	R_d F	R_d p
Sphagnum[‡]								
Early summer[+]	Treatment	1 (5)	2.21	0.28	0.30	0.64	3.14	0.22
Late summer	Treatment	2(17)	0.83	0.46	0.91	0.43	7.19	**0.01**
and fall[¥]	Season	1(17)	2.79	0.13	9.50	**0.01**	9.19	**0.01**
Vascular plants[§]								
Early summer[+]	Treatment	1 (5)	0.38	0.60	<0.01	0.98	1.14	0.40
Late summer	Treatment	2(17)	0.02	0.98	0.43	0.66	2.07	0.18
and fall[¥]	Season	1(17)	3.81	0.08	0.75	0.41	5.51	0.04
Total ecosystem[‡]								
Early summer[+]	Treatment	1 (11)	0.26	0.63	0.30	0.61	0.18	0.69
Late summer	Treatment	2(35)	0.51	0.61[#]	1.90	0.17[#]	0.38	0.69
and fall[¥]	Season	1(35)	3.48	0.07	0.19	0.67	15.98	**<0.001**

Note: Seasons are early summer (DOY 164-206), late summer (DOY 207-244) and fall (DOY 145-311). WA, water addition treatment; PE, precipitation exclusion treatment; CL, control; DOY, day of year; df, degrees of freedom.
[§]fluxes expressed m^{-2} leaf area, [#]leaf area a significant covariate ($p < 0.05$)

Table 9. Mean (± SE) NEE or NPP_{max}, GEP or GPP_{max} and R_d for spring 2009 vascular plant[§], and total ecosystem[‡] flux measurements (μmol m^{-2} s^{-1}) by season and treatment. Treatments were not active during these spring measurement periods.

	Treatment	NEE/NPP_{max}	GEP/GPP_{max}	R_d
Sphagnum[‡]				
Pre-greenup	PE	0.04 (0.15)	-0.62 (0.11)	0.64 (0.17)
	WA	0.06 (0.16)	-0.53 (0.11)	0.67 (0.13)
	CL	0.09 (0.27)	-0.45 (0.23)	0.61 (0.06)
Post-greenup	PE	0.11 (0.09)	-1.23 (0.02)	1.30 (0.09)
	WA	0.26 (0.07)	-1.40 (0.09)	1.58 (0.06)
	CL	-0.08 (0.13)	-1.53 (0.11)	1.44 (0.07)
Vascular plants[§]				
Pre-greenup	PE	0.07 (0.08)	-0.76 (0.47)	0.83 (0.47)
	WA	0.23 (0.11)	-0.75 (0.09)	0.98 (0.18)
	CL	0.03 (0.38)	-0.65 (0.46)	0.68 (0.09)
Post-greenup	PE	-0.74 (0.37)	-1.23 (0.48)	0.49 (0.12)
	WA	-0.96 (0.14)	-1.49 (0.23)	0.53 (0.09)
	CL	-0.96 (0.31)	-1.45 (0.31)	0.49 (<0.01)
Total ecosystem[‡]				
Pre-greenup	PE	-0.16 (0.18)	-1.54 (0.18)	1.51 (0.21)
	WA	-0.31 (0.19)	-1.29 (0.31)	1.24 (0.32)
	CL	-0.57 (0.16)	-1.48 (0.20)	1.38 (0.22)
Post-greenup	PE	-1.99 (0.29)	-3.91 (0.40)	1.92 (0.15)
	WA	-2.12 (0.19)	-4.41 (0.28)	2.28 (0.11)
	CL	-2.24 (0.21)	-4.44 (0.30)	2.15 (0.17)

Note: GEP or GPP_{max}, maximum gross ecosystem productivity (GEP) or gross primary productivity (GPP); NEE or NPP_{max}, maximum net ecosystem exchange of CO_2 (NEE) or net primary productivity (NPP); R_d, dark respiration. Seasons are pre-greenup (DOY 105-109) and post-greenup (DOY 124-145).

[‡]fluxes expressed m^{-2} surface area

[§]fluxes expressed m^{-2} leaf area

Table 10. One-way ANOVA results (F-values and p-values) for treatment effects on spring 2009 recovery of NEE or NPP_{max}, GEP or GPP_{max}, and R_d by measurement type and season. For total ecosystem tests, variance associated with collar subsamples and leaf area as a covariate were included. Only treatment effect test results are shown, although in addition whole model degrees of freedom are indicated. No treatment effects were significant.

	df - Treatment (Total)	NEE,NPP_{max}		GEP,GPP_{max}		R_d	
		F	p	F	p	F	p
Sphagnum [‡]							
Pre-greenup	2 (8)	0.01	0.99	0.16	0.86	0.06	0.95
Post-greenup	2 (8)	2.78	0.14	3.11	0.12	3.57	0.10
Vascular plants [§]							
Pre-greenup	2 (8)	0.19	0.83	0.03	0.97	0.25	0.78
Post-greenup	2 (8)	0.19	0.83	0.15	0.86	0.07	0.94
Total ecosystem [‡]							
Pre-greenup	2 (17)	1.38	0.28	0.3	0.74	0.28	0.76
Post-greenup	2 (17)	0.37	0.7[#]	0.89	0.43[#]	1.52	0.25

Note: Seasons are pre-greenup (DOY 105-109) and post-greenup (DOY 124-145).
DOY, day of year; df, degrees of freedom.
[§]fluxes expressed m^{-2} leaf area
[#]leaf area a significant covariate ($p < 0.05$)

It is important to note that despite these observed trends, MANOVA did not show significant differences for *Sphagnum* (Wilks F = 1.61, p = 0.14), vascular plant (Wilks F = 1.30, p = 0.20), or total ecosystem (Wilks F = 1.44, p = 0.20) fluxes among WC groups, possibly due in part to the small proportion of observations with very dry (5.3%) or wet (8.0%) moss conditions.

To reduce the considerable scatter in the individual flux measurements, *Sphagnum* flux data were bin averaged to reveal non-linear trends in both *Sphagnum* GPP_{max} and NPP_{max} with WC (Figure 17). *Sphagnum* photosynthesis and net CO_2 uptake both began to decline at WCs between 5 and 10 fw dw^{-1}. It was not possible to deduce whether *Sphagnum* photosynthesis similarly declined at high WC, as the data did not extend far into the range of WCs considered high for *Sphagnum* mosses. There was a weak linear decline in R_d with decreasing *Sphagnum* WC.

It is known that water relationships in *Sphagnum* can vary among species (Rydin 1985, Rydin and Jeglum 2006), and in this study the dominant *Sphagnum* species varied between *S. capillifolium* and *S. magellanicum* among plots (Table 2). However, species type did not appear to be a significant control on variability in *Sphagnum* fluxes throughout the study period as a whole. Linear regression analysis showed that coverage of *S. capillifolium* in relation to *S. magellanicum* in *Sphagnum* gas exchange samples (expressed as % *S. capillifolium* stems) was not significantly related to *Sphagnum* NPP_{max} ($R^2 < 0.01$, $p = 0.21$), GPP_{max} ($R^2 < 0.01$, $p = 0.72$), or R_d ($R^2 < 0.01$, $p = 0.79$).

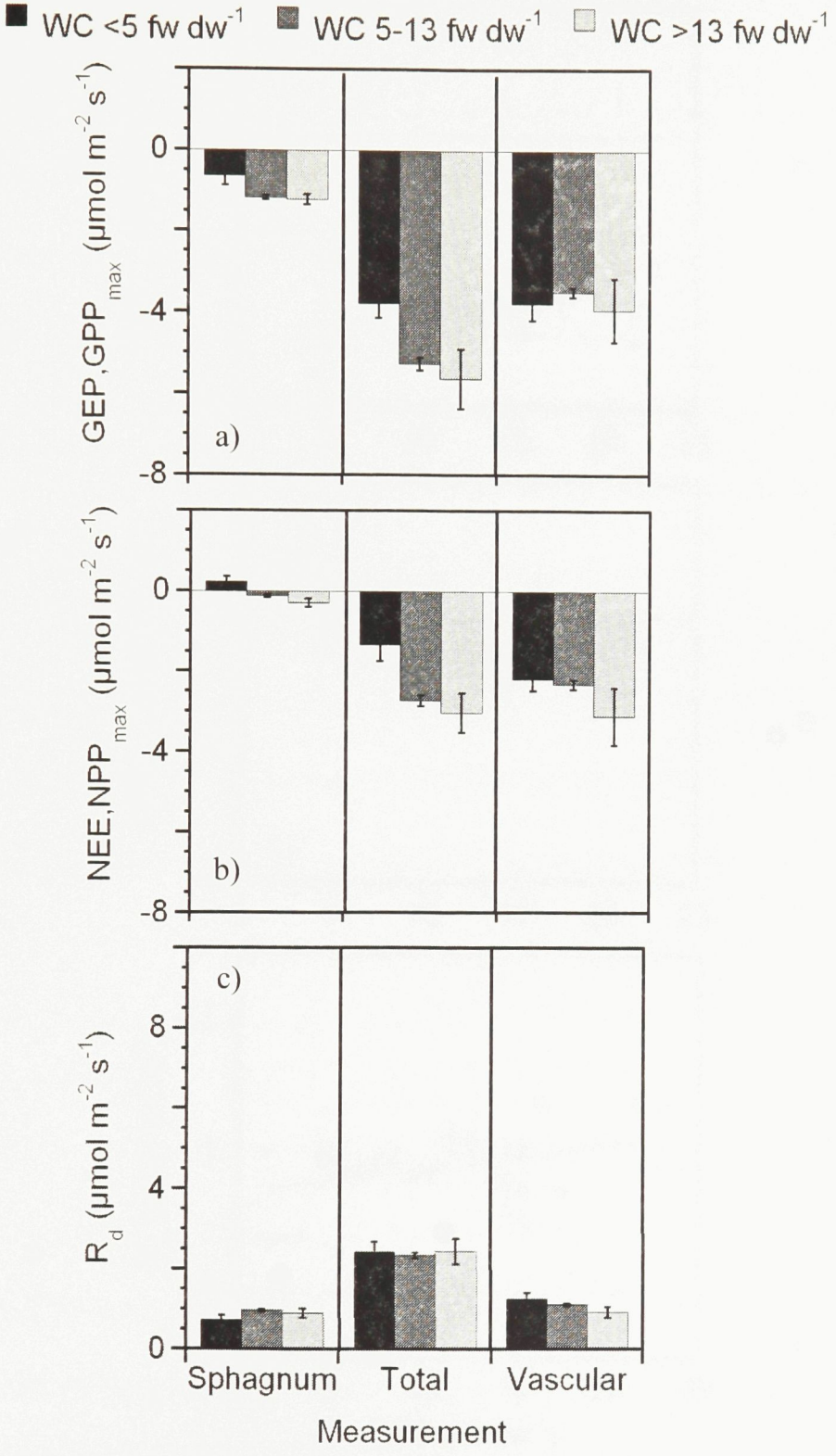

Figure 16. Mean (± SE) a) GEP or GPP_{max}, b) NEE or NPP_{max}, and c) R_d for *Sphagnum*[‡], vascular plant[§], and total ecosystem[‡] flux measurements (µmol m^{-2} s^{-1}) by water content (WC) range. Mean water contents for the WC < 5 fw dw^{-1}, WC 5-13 fw dw^{-1}, and WC > 13 fw dw^{-1} are 3.21 ± 0.25 (n = 16), 9.08 ± 0.12 (n = 261), and 14.44 ± 0.45 (n = 21) respectively. Flux terms as defined in Figure 15.
[‡]fluxes expressed m^{-2} surface area; [§]fluxes expressed m^{-2} leaf area

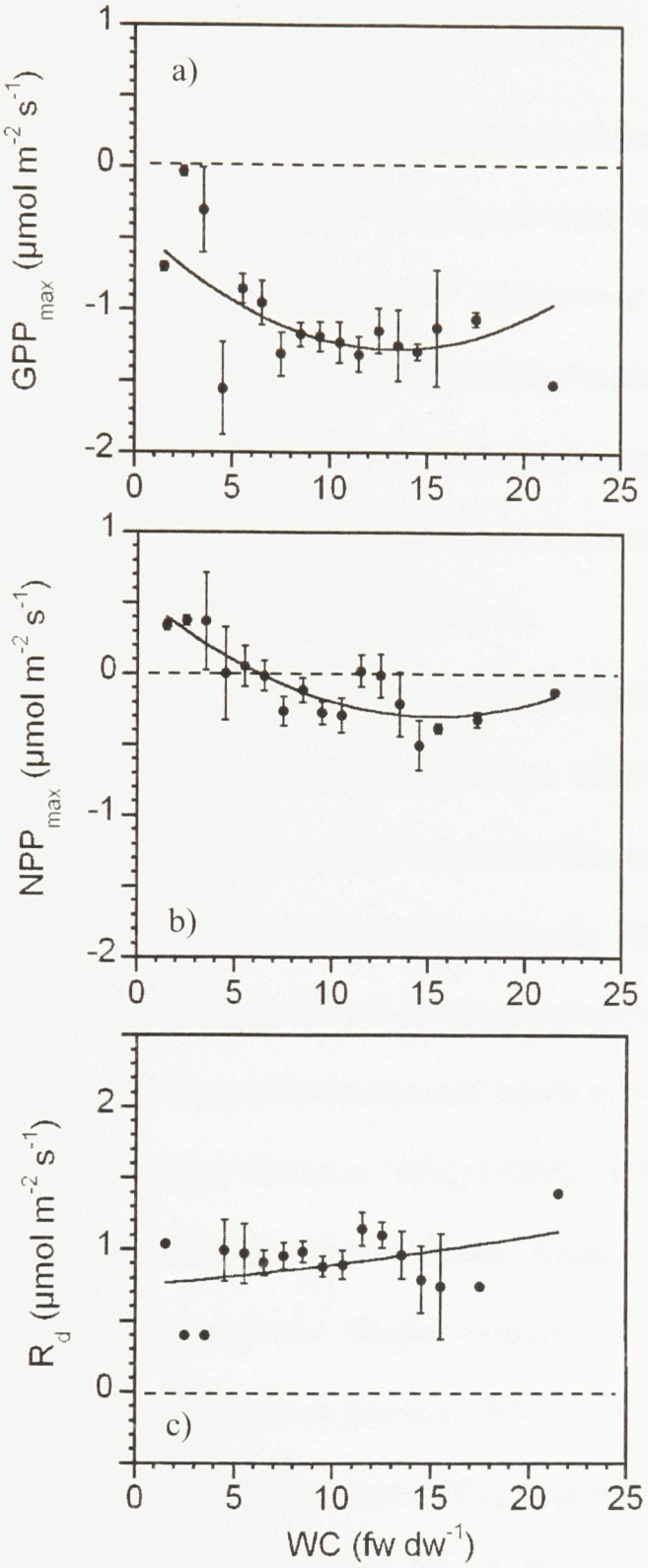

Figure 17. Relationships between *Sphagnum* water content (WC) and bin averaged a) *Sphagnum* GPP_{max}, b) *Sphagnum* NPP_{max}, and c) *Sphagnum* R_d data. Bin size is 1.0 (± SE). Quadratic and linear relationships were fit to raw data. Only the relationship between WC and NPP_{max} is significant ($R^2 = 0.05$, $p = 0.01$). Relationships are not significant for GPP_{max} or R_d ($p > 0.05$), but lines are included to illustrate trends. Flux terms as defined in Figure 15.

4.3 Seasonal trends in CO_2 fluxes

As expected, the PAR threshold for maximum photosynthesis in *Sphagnum* occurred at PAR of approximately 500 μmol m^{-2} s^{-1}, a lower value than what is common for most vascular plants (e.g. PAR > 1000 μmol m^{-2} s^{-1}, Bubier *et al.* 2007) (Figure 14). In vascular plants in this study, maximum uptake occurred above 600 to 1000 μmol m^{-2} s^{-1}. The rectangular hyperbolic curve applied to the data cannot account for decreased NEE or NPP at high light (Letts & Lafleur 2005), but upon visual examination of the data there was no evidence of photoinhibition at high light levels.

Figure 18 illustrates the seasonal trends in average CO_2 fluxes at maximum light levels for *Sphagnum*, vascular plants, and the total ecosystem. Belowground respiration from the peat (heterotrophic and plant root respiration) was estimated as the difference between total R_d and the sum of vascular plant and *Sphagnum* R_d. There was a significant seasonal effect on fluxes, as shown by MANOVA results presented in Table 11. *Sphagnum* and vascular plants showed different seasonal trends in NPP_{max}, GPP_{max} and R_d. As expected, the trends in R_d were similar to those of GPP_{max} (Figure 18). *Sphagnum* GPP_{max} and NPP_{max} showed less variability than in vascular plants, and GPP_{max} and R_d peaked earlier during the post-greenup period. Higher *Sphagnum* R_d in the post-greenup season was statistically significant, while post-greenup GPP_{max} was not significantly different from the summer seasons. Vascular plant GPP_{max} and total ecosystem GEP_{max} and R_d were significantly higher in summer (Table 11). As expected, vascular plant fluxes were low in spring when vascular plant leaf area was low. Overall, fall R_d was similar to spring, but vascular plant GPP_{max} and total GEP_{max} tended to be slightly greater in fall (Figure 18, Table 11).

The seasonal trend in total NEE_{max} was produced primarily by seasonal trends in vascular plant NPP_{max} and belowground respiration from the peat. Although there was seasonal variation in *Sphagnum* GPP_{max} and R_d, they were similar in magnitude and so *Sphagnum* NPP_{max} was small and not significantly different among seasons (Figure 18, Table 11). Despite higher spring GPP_{max} in *Sphagnum* than in vascular plants, vascular NPP_{max} was greater than *Sphagnum* NPP_{max} in all seasons except PrG. Belowground respiration was estimated to peak in late summer, when water table was lowest and temperatures were relatively high. Regardless of seasonal variability in the magnitude of CO_2 fluxes, NEE_{max} was negative (i.e. net uptake of CO_2) in all seasons.

Variations in NEE_{max} were explained in part by seasonal changes in vascular plant leaf area within the collars (Figure 19, Figure 20). In the unclipped collars (C_b), total NEE_{max} peaked in summer and fall when GEP_{max} was high enough to overcome respiration. However, lower total GPP_{max} in summer and fall in the clipped collars (C_a), which had significantly lower leaf area than the unclipped collars ($t = 8.49$, $p < 0.0001$), resulted in less total NEE_{max} in summer. Still, NEE_{max} did not differ significantly between the post-greenup, summer and fall seasons in either C_a or C_b. When expressed on a leaf area basis ($\mu mol\ m^{-2}$ leaf area s^{-1}) there was not a significant difference in NEE_{max} between collars ($t = 0.11$, $p = 0.91$), despite greater GEP_{max} and R_d in C_a ($t = 9.35$, $p < 0.0001$ and $t = 6.89$, $p < 0.0001$ respectively) that may have been due to decreased shading in these collars. In general, total GEP_{max} and R_d were significantly higher in late summer than in fall, when LAI began to notably decline (Table 11, Figure 19).

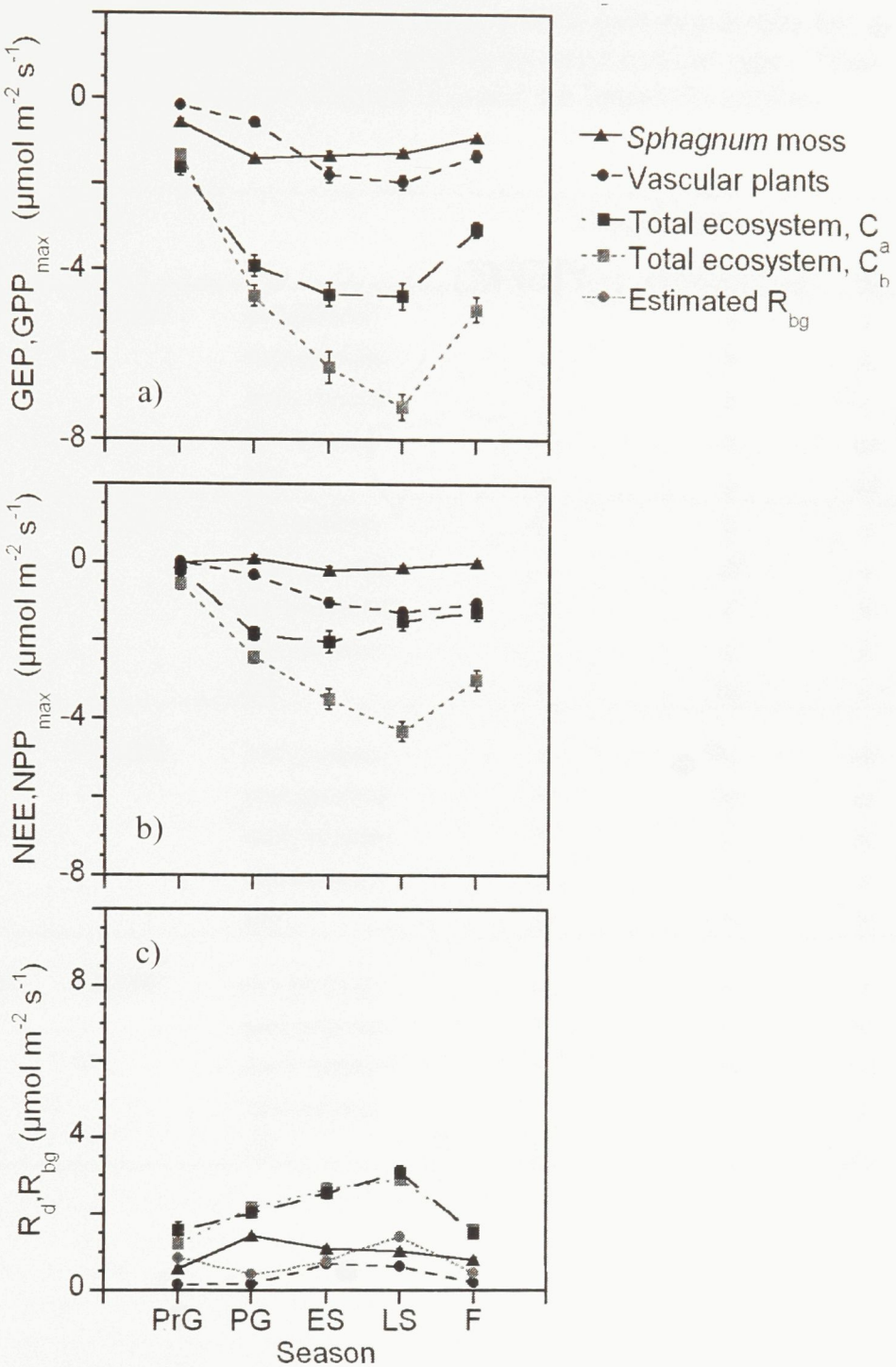

Figure 18. Seasonal trends in mean (± SE) a) GEP or GPP_{max}, b) NEE or NPP_{max}, and c) R_d for *Sphagnum*, vascular plant, and total ecosystem flux measurements (µmol m^{-2} s^{-1}). All fluxes are expressed in µmol m^{-2} surface area s^{-1}. Total ecosystem fluxes are separated into data for clipped (C_a) and unclipped (C_b) collars, for better comparison with vascular plant fluxes. Estimated belowground respiration (R_{bg}) is included in (c). Flux terms are as defined in Figure 15 and statistical analyses of seasonal differences in measurements are presented in Table 11. Spring data are from 2009 (pre-greenup, PrG; post-greenup, PG), while early summer (ES), late summer (LS) and fall (F) data are from 2008.

Table 11. MANOVA (F-values and p-values) and Tukey's HSD post-hoc results for season effects on NEE or NPP_{max}, GEP or GPP_{max}, and R_d by measurement type. Total ecosystem fluxes are separated into data for clipped (C_a) and unclipped (C_b) collars. MANOVA df(num, den) = 12, 93.

	MANOVA			Tukey's HSD tests		
	F	p		NEE,NPP_{max}	GEP,GPP_{max}	R_d
Sphagnum	8.25	< 0.0001	pre-greenup	a	a	a
			post-greenup	a	b	b
			early summer	a	b	c
			late summer	a	b	cd
			fall	a	a	ad
Vascular plants	8.05	< 0.0001	pre-greenup	a	a	a
			post-greenup	a	ab	a
			early summer	b	c	b
			late summer	b	c	b
			fall	b	bc	a
Total ecosystem, C_a	8.23	< 0.0001	pre-greenup	a	a	ab
			post-greenup	b	bc	ab
			early summer	b	c	ac
			late summer	b	c	c
			fall	b	b	b
Total ecosystem, C_b	12.64	< 0.0001	pre-greenup	a	a	a
			post-greenup	b	b	bc
			early summer	bc	bc	bd
			late summer	c	c	d
			fall	bc	b	ac

4.4 Relative proportions of total ecosystem CO_2 fluxes

As expected, vascular plants had a greater influence on total GEP_{max} in summer when vascular leaf area was high, while *Sphagnum* contributed a larger proportion in spring before vascular plants were fully active (Figure 21). Vascular plant leaf area did not begin to decline until late in the fall season (Figure 19), so the proportion of GEP_{max} attributed to vascular plant GPP_{max} remained high in the fall (Figure 21). *Sphagnum* may become more important to GEP_{max} after leaf area declines, but these results show that the timing of vascular plant leaf drop influences the relative importance of *Sphagnum* and vascular plants in the fall. The influence of vascular plants on GEP_{max} was more variable throughout the measurement period than that of *Sphagnum*, accounting for roughly 10% to 40% and 25% to 35% of total GEP_{max} respectively. The opposite trend was found in R_d, with a more variable proportion of *Sphagnum* R_d (~35% to 70%) than vascular plant R_d (~10% to 20%). Following the trend in GPP_{max}, the influence of vascular plants on R_d was low in spring and higher in summer and fall. The influence of vascular plant NPP_{max} on total NEE_{max} was highest in summer and fall (56% to 86%) and lowest in spring (-11% and 17% for pre-greenup and post-greenup seasons respectively), again following a similar trend to GPP_{max} and R_d. Interestingly, *Sphagnum* R_d was consistently the greater proportion of total R_d, despite the greater contribution of vascular plants to GEP in summer and fall. The *Sphagnum* proportion of total R_d was particularly high in the post-greenup season.

Residual R_d includes belowground respiration (R_{bg}), comprised of heterotrophic respiration from microorganisms in the peat and plant root respiration (Figure 21). This respiration was included in total R_d and NEE measurements, but unlike *Sphagnum* and

vascular plant fluxes was not separately measured. Increasing residual R_d from post-greenup to late summer could be associated with increasing belowground respiration with warming temperatures. High residual R_d in spring does not follow this pattern, and may be explained by the release of built up CO_2 from thawing peat or increased microbial activity stimulated by freeze-thaw dynamics (Alm *et al.* 1999, Bubier *et al.* 2002).

There is evidence that some of the non-photosynthetic section of *Sphagnum* stems and branches may have been incorporated in the samples taken for flux measurements, leading to excess respiration in the *Sphagnum* flux samples and an underestimation of *Sphagnum* NPP_{max}. *Sphagnum* NPP_{max} at optimal WC (-0.12 ± 0.04 μmol m^{-2} s^{-1}) was lower than shown in previous studies for both hummock and hollow species (Table 1), supporting that it may be underestimated in this study. *Sphagnum* and vascular plant respiration accounted for 70-80% of ecosystem respiration in some seasons, leaving a residual that is often smaller than expected based on previous estimates of the annual heterotrophic contribution to ecosystem respiration (~50%; Moore *et al.* 2002), although there are no known estimates of belowground respiration in summer alone at the site. So while *Sphagnum* NPP_{max} was on average 5 ± 3% of total NEE_{max}, this may be a low estimate and must be considered with caution. Furthermore, *Sphagnum* GPP_{max} was similar to that found in other studies (see Section 5.3), suggesting that the low NPP_{max} did not result from lower than expected GPP_{max}. The residual may also be attributed partly to error produced by the variability around seasonal means. All residual fluxes include fluxes from *Polytrichum* moss, which was present in the moss carpet but not included in *Sphagnum* flux measurements.

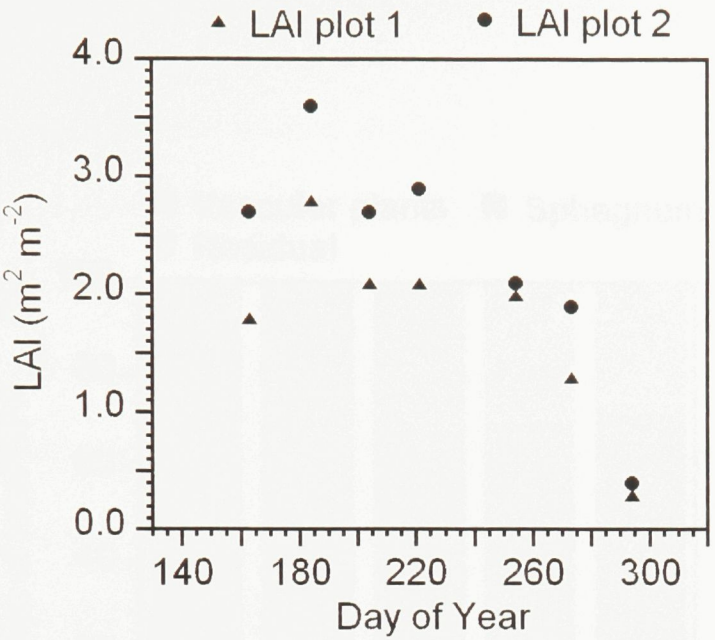

Figure 19. Vascular plant leaf area index (LAI) over the 2008 measurement period in two permanent plots within the study area measured using the point-frame method.

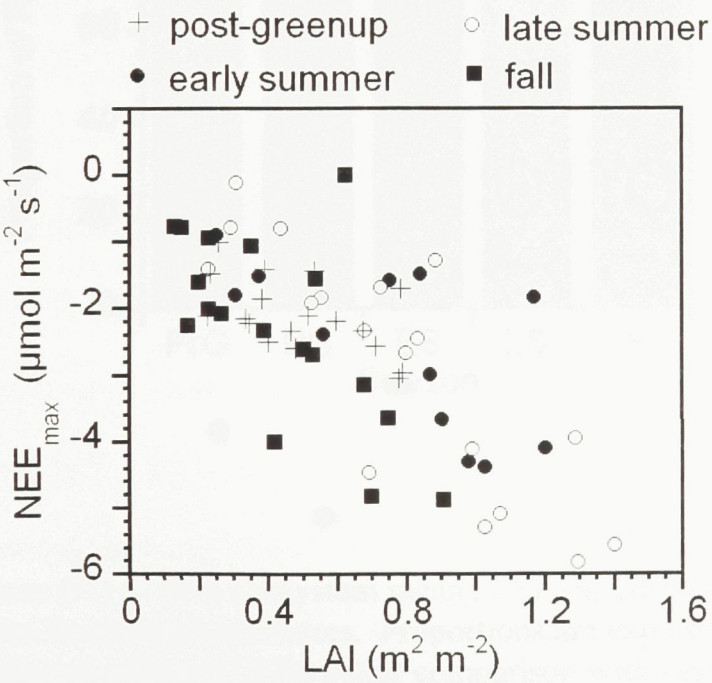

Figure 20. Decrease in NEE_{max} with mean collar vascular plant LAI, estimated from leaf counts, for four seasons in the 2008 (early summer, late summer, fall) and 2009 (post-greenup) measurement periods. Data for 2009 pre-greenup season are not included, as green leaf area was negligible. Flux terms as defined in Figure 15.

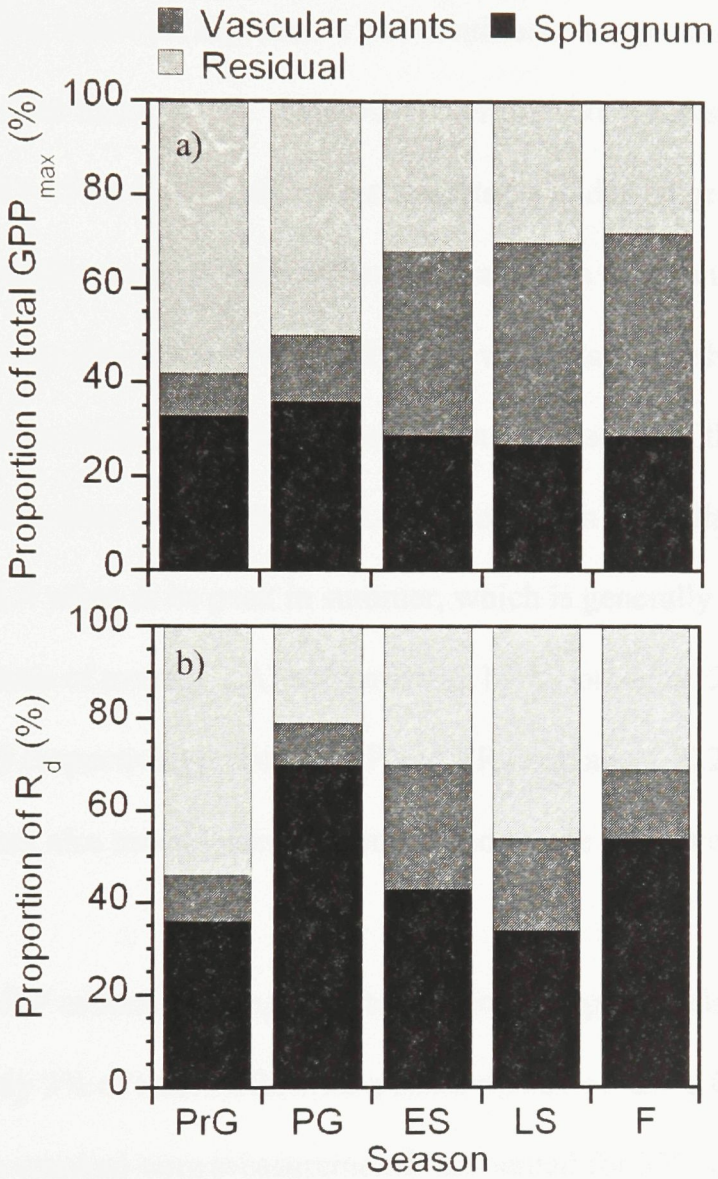

Figure 21. Proportions (%) of total ecosystem mean (± SE) a) GEP or GPP_{max}, and b) R_d that are *Sphagnum* and vascular plants fluxes. Proportions are expressed relative to mean fluxes measured in clipped collars (C_a) for better comparison with vascular plant fluxes. Residual R_d includes error and both heterotrophic and plant root respiration. Flux terms are as defined in Figure 15. Spring data are from 2009 (pre-greenup, PrG; post-greenup, PG), while early summer (ES), late summer (LS) and fall (F) data are from 2008.

4.5 Estimates of June to September total carbon exchange

There was an estimated total NEE of -69.7 g C m^{-2} from June 1 to September 31 in the PE and CL plots, based on Equation 4 and continuous temperature and PAR data measured at the site (see Section 3.4). This was lower than NEE measured at the EC tower for this period (-157 g C m^{-2}), which incorporated a wider range of ecosystem conditions than the study area (e.g. hollows/lawns in addition to hummocks and some trees). Shrub cover was also lower in the study area, with relatively short plants compared to other areas of the bog, which could account for some of the difference between tower and chamber measurements. LAI estimated in the collars from leaf counts ranged from 0.2 to 1.4 when at its peak in summer, which is generally lower than previous measurements of average LAI at Mer Bleue by Moore *et al.* 2002 and Bubier *et al.* 2007 (1.3 and 2.3 respectively). Total GEP and ER estimates (-222.1 and 152.4 g C m^{-2} respectively) were also much lower than measured by the EC tower (-603 and 447 g C m^{-2} respectively).

Sphagnum NPP estimated using light/temperature response relationships accounted for roughly 3% of total NEE, with a small uptake of -2.3 g C m^{-2}. *Sphagnum* NPP estimated from cranked-wire measurements, accounted for 35% of this total NEE, with a flux of -24.3 g C m^{-2}. Estimates of *Sphagnum* NPP for 1998 and 1999 (-13.6 and -17.7 g C m^{-2} respectively) based on cranked-wire measurements (Moore *et al.* 2002) and a 43% carbon content were slightly less than those obtained in the present study. This suggests again that *Sphagnum* NPP measured in the chambers may have been underestimated due to additional respiration and/or the chamber methodology. June to

September *Sphagnum* GPP and R_d were very similar in magnitude, at -53.0 and 50.7 g C m^{-2}, accounting for 24% and 33% of total GEP and ER.

Estimated vascular plant NPP for June to September was -68.4 g C m^{-2} leaf area, and GPP and ER were -123.9 and 55.5 g C m^{-2} respectively. These fluxes are expressed per m^2 leaf area and are not directly comparable to the NEE estimate. Using the average collar LAI for the June to September period (0.8), estimates of vascular plant NPP, GPP, and R_d expressed relative to surface area were approximately -54.7, -99.1, and 44.4 g C m^{-2} (78%, 45%, and 29% of total fluxes respectively). Residual fluxes for the June to September period are explained similarly to Section 4.3, and support that *Sphagnum* NPP may be underestimated to some extent.

5.0 DISCUSSION

5.1 Controls on *Sphagnum* capitulum WC

Water table was a significant control of *Sphagnum* capitulum WC, as has been widely supported in previous studies (Hayward & Clymo 1982, Rydin 1985, Gerdol 1995, Strack & Price 2009). Compared with the control plots, the relationship between water table and *Sphagnum* WC was slightly stronger in the PE treatment, where precipitation influence was almost entirely absent (Figure 13). This and the lack of a significant relationship in the WA treatment suggest that water table alone is not a sufficient predictor of capitulum WC under field conditions.

The small degree of sensitivity of *Sphagnum* WC to water table position, as shown by the shallow slopes in the relationships between these variables in both the PE treatment and control (Figure 13), is similar to that shown in previous studies for hummock species experiencing the same range in water table variations (Gerdol 1995, Strack & Price 2009). Strack & Price (2009) suggest that this illustrates the ability of hummock species to efficiently supply water to the capitulum through capillary transport and to maintain capitulum WC as the water table declines. At higher water tables, *Sphagnum* show greater sensitivity to changes in water table (Hayward & Clymo 1982, Rydin 1985, Strack & Price 2009), possibly because there is a more rapid change in the distribution of capillary water near the surface with changes in higher water tables as shown by Hayward & Clymo (1982). However, it is unlikely hummock *Sphagnum* at Mer Bleue would experience such higher water tables, as the maximum hummock water table depth observed since 1998 at the site was -17 cm. There is limited information on the influence of very low water tables on *Sphagnum* WC, as most studies have typically

focused on those greater than -40 cm (e.g. Rydin 1985, Gerdol 1995, Robroek *et al.* 2009, Strack & Price 2009), which is considered to be quite low at most peatland sites. At Mer Bleue, hummock water table is rarely above the range seen in the present study, and is on average well below the levels recorded in 2008. The relationships developed here may not be applicable below the range observed, as the capillary film will eventually be disrupted causing the surface to become disconnected from the water table (Price 1997). A better understanding of the WC/water table relationship at lower water tables is needed to predict how desiccated *Sphagnum* may become in drought years at Mer Bleue. The relationships found in the present study also do not likely hold true for other *Sphagnum* species, like those found in the lawns and hollows at the bog. Previous studies show that species adapted to hollows or lawns tend to experience more rapid changes in WC with water table, because these species are not as well adapted to maintaining high capitulum WCs in dry conditions (Rydin 1985, Strack & Price 2009).

Only a few studies have addressed the importance of precipitation to *Sphagnum* capitulum WC, but those that have suggest that precipitation is at least as influential as water table (Robroek *et al.* 2007, Robroek *et al.* 2009, Strack & Price 2009). This study similarly provides strong support for the importance of even quite small precipitation events (~1.6 mm) to *Sphagnum* WC. While its influence is greatest during and immediately following precipitation events (Robroek *et al.* 2007, Strack & Price 2009), the amount of precipitation received over the growing season also has a significant direct influence (i.e. not only through water table changes) on the average *Sphagnum* WC. This is shown by the significantly greater mean WC in the control plots than in PE treatment plots (Figure 11), as water table was not significantly different between them.

Precipitation influenced *Sphagnum* WC even when the water table was high (i.e. early summer). Similarly, Robroek *et al.* (2009) observed the influence of precipitation effects on *Sphagnum* WC when water table was only 10 cm below the surface, which is considerably higher than the maximum hummock water table recorded at Mer Bleue. Only when the water table nears the surface (e.g. -1 cm) precipitation has little influence on *Sphagnum* WC (Robroek *et al.* 2009). This would suggest that precipitation would have little effect on the WC of species on hollows or lawns, where at Mer Bleue the water table can reach the surface at wet times of year. Since hummocks occupy an estimated 70% of the surface area at Mer Bleue (Lafleur *et al.* 2003), precipitation is an important control on *Sphagnum* WC over the full length of the growing season.

The influence of water table position on *Sphagnum* WC was completely removed when WC was assessed soon after simulated precipitation events in the WA treatment (Figure 13). This suggests that within the range of water tables observed, precipitation is the dominant control immediately following rain events. It also stresses the importance of frequent small rain events in maintaining capitulum WC when water table is low (Grosvernier *et al.* 1997, Strack & Price 2009). Strack & Price (2009) found that small precipitation events (0.5 to 1.0 mm) can raise capitulum WC by 5 to 7 fw dw^{-1}, which was equivalent in their study to raising the water table from -40 to -20 cm. The present study supports these findings, as the WC in the WA treatment was approximately 6 fw dw^{-1} higher than in the PE treatment when the water table was -40 cm, which also corresponds to roughly an increase in water table position from -40 to -20 cm (Figure 13). When the water table was high (e.g. -25 cm), there was little difference between WC in the WA and PE treatments. Previous studies have also seen that even larger precipitation

additions (5 mm) than was used in this study have a weakened effect when the water table is closer to the surface (Robroek *et al.* 2007, Strack & Price 2009). However, while precipitation may not substantially increase WC at higher water tables, it may still be important in maintaining capitulum WC. For example, Robroek *et al.* (2009) saw *Sphagnum* WC decline in absence of precipitation at a relatively high water table of -10 cm. The interception capacity of *Sphagnum* is not well known, but was estimated by Frolking *et al.* (2002) to be 8 mm. Further study of interception capacity of the *Sphagnum* capitulum is necessary to better understand the influence of precipitation on WC, as no known studies have measured it and it likely varies with moss moisture conditions.

Sphagnum WC measurements were not made frequently enough in this study to clearly reveal the length of time following precipitation events for which the influence of precipitation is sustained, although comparing WC in the PE and CL plots suggests that it is at least a few days. Previous studies suggest that WC may increase for 1 to 3 days following precipitation (Robroek *et al.* 2007, Strack & Price 2009), but it is likely that other environmental conditions influencing the rate of evaporation from the moss surface must also be considered and further study of the relationships between water table, precipitation, and *Sphagnum* capitulum WC under various environmental conditions is needed. In very hot dry years, precipitation events may be more important to *Sphagnum* WC but their effects could be short lived due to faster evaporation rates. More study is needed to better understand the conditions under which *Sphagnum* water content is likely to drop below the optimal water content range. It would also be useful for future work to

investigate the range of water contents that occur at Mer Bleue in dry summers when the site becomes a carbon source.

5.2 Moss moisture effects on *Sphagnum* and ecosystem CO_2 exchange

Although the treatments had a significant effect on *Sphagnum* capitulum WC, it is unlikely that they fully replicated the variations in moss moisture that would be seen between the extremes of wet and dry years at Mer Bleue. While Mer Bleue is a relatively dry peatland site, the dominant *Sphagnum* species, *S. capillifolium* and *S. magellanicum*, are able to survive at the site because they are adapted to living high above the water table. As the water table positions observed during the study were above average for the site, the moss was readily able to maintain average capitulum WCs within or very near to the optimal range in all treatments (Figure 11). Since the treatments did not produce extremely wet or dry moss conditions, this could explain why there was no noticeable treatment effect on CO_2 fluxes from either *Sphagnum* or the total ecosystem.

Although one would expect *Sphagnum* WC to drop below the optimal range for photosynthesis in particularly hot and dry years, it is clear that it is necessary to confirm with field measurements that this is true. During a dry summer period (August 1999) at Mer Bleue, in which water table was approximately -60 cm, Moore *et al.* (2002) surprisingly found WCs of hummock *Sphagnum* near the optimal range (6 fw dw^{-1}). Roulet *et al.* (2007) also found near-average annual NEE at the site in 1999. However, in other dry years (e.g. 2001 and 2002), when summer water table was similarly low (-60 to -70 cm), NEE was small and when combined with methane and dissolved organic carbon

losses there was a net loss of carbon from the peatland. Precipitation in the summers of 2001 and 2002 was notably lower than the long-term average summer precipitation measured over 66 years (1938-2004) in the Mer Bleue area. Precipitation may have helped maintain *Sphagnum* WC in 1999, as summer precipitation in this year was not significantly lower than the long-term average. The summer of 1999 was also colder than the average, unlike 2001 and 2002 in which summer temperatures were near or above the average, and evaporation rates may therefore have been lower, allowing the moss to maintain near optimal WC.

Other studies show that while *Sphagnum* NPP declines at high and low capitulum WCs, NPP is fairly constant when at maximum levels in the optimal WC range (e.g. Williams & Flanagan 1996, Shipperges & Rydin 1998). In this study, only the measurements of *Sphagnum* fluxes associated with below optimal WC revealed the decreases in gross and net photosynthesis that are expected with dry moss conditions (Figure 16) (Williams & Flanagan 1996, Shipperges & Rydin 1998, Strack & Price 2009). The net loss of CO_2 (i.e. positive NPP_{max}) from *Sphagnum* at WC < 5 fw dw^{-1} is consistent with some previous studies that saw a switch from uptake to loss between WCs of approximately 2 and 5 fw dw^{-1} (Titus *et al.* 1983, Silvola & Aaltonen 1984, Murray *et al.* 1989a). Total ecosystem gross and net photosynthesis also declined by approximately 30% and 50% respectively with *Sphagnum* WC < 5 fw dw^{-1}, suggesting that dry moss conditions could influence the ecosystem carbon budget in dry years. However, further study is needed to confirm these trends as very few samples fell outside of the optimal WC range, resulting in poor representation of the populations in high and low WC groups. This also produced unequal sample sizes, which decreases the ability of

ANOVA tests to distinguish factor effects, although the robustness of MANOVA to unbalanced designs is not as well known (Shaw & Mitchell-Olds 1993, Scheiner & Gurevitch 2001)

With wet moss conditions (WC > 13 fw dw^{-1}), fluxes were similar to those at optimal WC (Figure 16). *Sphagnum* NPP has been observed to decline with greater than optimal water conditions, but the decline is much more gradual than that observed for drying moss, particularly in hummock species (Titus *et al.* 1983). The upper end of the optimal WC range for *Sphagnum* photosynthesis is therefore not as clearly defined as the lower end of the range. At the mean WC of wet moss samples in this study (14.4 fw dw^{-1}) some studies have observed relatively high NPP (e.g. Silvola 1990, Titus *et al.* 1983, Williams & Flanagan 1996). Strack & Price (2009) suggest that even at quite high water tables (e.g. – 5 cm) *Sphagnum* WC may not be high enough to considerably limit diffusion of CO_2 and decrease *Sphagnum* NPP. It is unlikely that hummock *Sphagnum* at Mer Bleue would ever experience much greater WCs than those observed in either the control or WA treatments in this study. These results agree with Lafleur *et al.* (2003), who saw similar NEE at Mer Bleue in wet and average years and Roulet *et al.* (2007) who did not report decreased NEE in wet years, emphasizing that dry years are more important to the bog's carbon budget.

There is limited information on the effects of water availability on *Sphagnum* respiration separate from ecosystem respiration, because it is very difficult to accurately separate the two. McNeil & Waddington (2003) estimated *Sphagnum* respiration as the difference between total and soil respiration, and found that it decreased with decreasing surface moisture. In the present study, the decreasing trend in *Sphagnum* respiration with

WC supports previous findings (Figure 17), but was weak and not statistically significant. *Sphagnum* respiration decreased in late summer and fall in the drier PE treatment, but no difference was found between respiration in dry moss (WC < 5 fw dw^{-1}) and those at optimal WC. As *Sphagnum* GPP was not significantly less in the PE treatment, it is possible that the decreased *Sphagnum* respiration in this treatment may have actually been the result of decreased heterotrophic respiration instead of decreased autotrophic respiration. As previously mentioned, some of the dead *Sphagnum* stem, and some aerobic bacteria, may have been incorporated in *Sphagnum* samples. If this were the case, in PE treatments the consistently drier surface conditions may have been particularly unfavourable for these bacteria. *Sphagnum* samples with WC < 5 fw dw^{-1} were not only associated with the PE treatment, and dry surface conditions for these moss may have been less prolonged and therefore less detrimental to the bacteria, which could explain why respiration was not significantly lower in these samples.

The effect of lower water table on heterotrophic respiration is complicated, but in general increased oxygen diffusion into peat and the higher efficiency of aerobic respiration (Blodau *et al.* 2004, Lafleur *et al.* 2005) likely account for the higher ecosystem respiration seen in studies of *Sphagnum* and peat columns with water table decline (McNeil & Waddington 2003, Lafleur *et al.* 2005, Strack *et al.* 2006, Strack & Price 2009). Heterotrophic respiration is believed to account for a large fraction of peatland ecosystem respiration (~50% annually, Moore *et al.* 2002), and so any increase in ecosystem respiration with dry conditions could overshadow a decline in *Sphagnum* respiration that may have occurred in dry moss in these studies.

Rapid rewetting following dry periods (e.g. during and shortly after precipitation events) is associated with what has been termed 'resaturation respiration' (McNeil & Waddington 2003, Robroek *et al.* 2009, Strack & Price 2009), a pulse of respiration that may be caused by recovery of damaged moss tissue (Gerdol *et al.* 1996). Strack & Price (2009) found that this occurred even with small precipitation events that only affected surface moisture, supporting the idea that the increased respiration is at least in part associated with *Sphagnum*. Considering these observations, increased respiration might be expected in the WA treatment, but was not observed (Figure 15, Table 5). It is known that the moss did not become thoroughly desiccated during this study, and were therefore likely not damaged prior to precipitation additions, which could explain why higher respiration was not seen following water additions.

The non-linear parabolic relationship between capitulum WC and *Sphagnum* NPP that has been established by previous studies was observed to some extent in this field study (Figure 17). However, there was a great deal of scatter in flux and WC data. In other studies, these relationships have typically been developed using individual *Sphagnum* stems or small sample sizes that were repeatedly measured while being wetted or dried (e.g. Shipperges & Rydin 1998, Williams & Flanagan 1996, Van Gaalen *et al.* 2007). The relationship can vary quite significantly among individual *Sphagnum* stems (Van Gaalen *et al.* 2007). *Sphagnum* samples in the present study were taken throughout the plots while water table was measured in fixed locations, thus including the spatial variability inherent in moss carpet structure, moss density, shading, microtopography and other environmental conditions which could all contribute to spatial variability in CO_2 fluxes. With greater sample sizes and sampling areas, the variability in *Sphagnum* fluxes

increases, blurring the relationship between *Sphagnum* NPP and WC (e.g. Robroek *et al.* 2009, Strack & Price 2009). Laboratory studies have also typically focused on sample(s) drying from saturation, but the WC/NPP relationship is known to differ under wetting or drying conditions (Hayward & Clymo 1982, Strack & Price 2009). Field measurements in this study do not account for this hysteresis, which could also weaken an overall WC/NPP relationship in the data. In the present study, the results suggest that capitulum WC alone does not predict instantaneous *Sphagnum* NPP as strongly in the field as has been shown in laboratory studies. Interestingly, Robroek *et al.* (2009) saw stronger relationships between NPP and whole microcosm WC (0 to 11 cm depth) than with capitulum WC, and it is possible that WC of the whole unsaturated zone may be less variable than capitulum WC and be a better predictor of *Sphagnum* NPP in the field.

While the shape and magnitude of the *Sphagnum* WC/NPP relationship can vary by species (Titus *et al.* 1983, Shipperges & Rydin 1998, Robroek *et al.* 2009), the composition of the *Sphagnum* community did not influence NPP_{max} in the present study. Some studies have seen similar effects of water table on *S. magellanicum* fluxes to those on *S. fuscum*, which occupies similar habitat to *S. capillifolium* (Grosvernier *et al.* 1997, Strack & Price 2009). *S. magellanicum* is known to be quite plastic in its morphology, having looser carpet structure at wetter sites and more dense structure with improved capillary transport at drier sites (Rydin 1985, Li *et al.* 1992). It is possible that at Mer Bleue, where *S. magellanicum* grows in a similar habitat with *S. capillifolium* (i.e. on hummocks and often in mixed carpets), the species have adapted similar carpet structure, accounting for the lack of noticeable interspecific differences in NPP_{max} in this study.

5.3 Importance of *Sphagnum* to whole ecosystem CO_2 exchange

Sphagnum NPP has been shown to vary widely both interannually and among peatland sites, due to variability in environmental controls like wetness and species differences as discussed in Section 2.3. In an extensive review of 68 *Sphagnum*-dominated wetland sites, including 31 different *Sphagnum* species in total, Gunnarsson (2005) observed mean moss net productivity of -259 ± 206 g dry biomass m^{-2} y^{-1} (mean ± SD) and an overall range from -8 to -1450 g dry biomass m^{-2} y^{-1}. This substantial variability is conceivable considering the wide range in geographical locations, including sites at low and high latitudes around the world. Gerdol (1995) also observed wide ranges of NPP for *S. capillifolium*, *S. magellanicum*, and *S. fallax* in the literature (-69 to -454 g dry biomass m^{-2} y^{-1}, -8 to -540 g dry biomass m^{-2} y^{-1}, and -348 to -670 g dry biomass m^{-2} y^{-1} respectively). In a summary of eight boreal and cool-temperate bogs from North America and Europe, Moore *et al.* (2002) observed quite a range in *Sphagnum* NPP (-188 ± 127 g dry biomass m^{-2} y^{-1}, mean ± SD), as well as in shrub and total above-ground NPP. As measurements were not made between November and April in the present study, an estimate of annual *Sphagnum* NPP could not be made, however Moore *et al.* (2002) found that *Sphagnum* NPP at Mer Bleue estimated from biomass measurements (-170 g dry biomass m^{-2} y^{-1}) was near the average of these reviewed sites.

There are several methods that have been used to estimate *Sphagnum* NPP, which could also account for some of the variability in the values presented in the literature. By far the most widely used method has been the simple cranked wire method described by Clymo (1970). Waddington *et al.* (2003) compared this method to destructive sampling and gas exchange methods, and found that the gas exchange method gave similar

measurements of *Sphagnum* NPP to the destructive sampling method, but higher estimates than the cranked wire method. In the present study, *Sphagnum* NPP was greater when estimated with the cranked wires, but Waddington *et al.* (2003) suggest that cranked wire estimates may have been unreliable in their study, as they were made in a restored peatland with a very thin *Sphagnum* mat over expanding and contracting peat. Unlike the present study, Waddington *et al.* (2003) measured *Sphagnum* NPP in collars set into the peat where there was no other vegetation. The influence of heterotrophic respiration was removed by assuming it was 15% of total respiration, as seen by McNeil (2001) as the difference between total respiration and that over bare peat, and was also determined using litter bags to measure decomposition. The benefit of this method is that *Sphagnum* NPP is measured without destructive sampling, but this is not a direct measure of *Sphagnum* NPP as *Sphagnum* respiration is not measured directly. In the method used in the present study, *Sphagnum* NPP was measured directly, but it was assumed that the moss samples contained only the photosynthetically active portion of the moss carpet. As discussed in Section 4.4, *Sphagnum* NPP may be underestimated due to excess non-photosynthetic tissue in moss samples, which could partially explain the difference in estimates between the cranked wire and gas exchange methods.

Few studies have addressed the contribution of *Sphagnum* to total peatland ecosystem CO_2 fluxes. It is likely that *Sphagnum* is an important component of total NEE in some peatland ecosystems, although its contribution may vary among sites and with environmental conditions. Using cranked wires and estimating vascular production from accumulated biomass, Szyumigalski & Bayley (1997) found *Sphagnum* to be more important than vascular plants to total annual aboveground production at an open bog

peatland site. They also saw that *Sphagnum* NPP was ≥ 40% of total NPP (i.e. vascular NPP + *Sphagnum* NPP) at wooded bog and poor fen sites. It is possible that the shorter growing season at these more northern sites limits the annual production of vascular plants, which could allow *Sphagnum* to be a more significant component of total production for a larger part of the year. In the present study, *Sphagnum* was found to be a significant component of both GEP and ER at Mer Bleue, but *Sphagnum* NPP_{max} was quite small relative to total NEE_{max} because GPP_{max} and R_d were similar in magnitude. *Sphagnum* contributed roughly 30% of total GEP_{max} and at least 35% of total R_d. The proportion of total GEP_{max} attributed to *Sphagnum* was much higher than found by Moore *et al.* (2002), who estimated *Sphagnum* contributed only 6% of GEP at the site. Few studies have separated *Sphagnum* NPP into its components GPP and R_d. *Sphagnum* GPP_{max} found in this study (Figure 15, Table 9) was comparable to that measured by Swanson & Flanagan (2001) in a boreal forest ecosystem (-1 to -4 μmol m^{-2} s^{-1}), but generally higher than that measured by McNeil & Waddington (2003) at a bog (-0.5 to -0.6 μmol m^{-2} s^{-1}). *Sphagnum* R_d was also comparable to that measured in previous studies (~1 μmol m^{-2} s^{-1}, Williams & Flanagan 1998; ~0.2 to 0.7 μmol m^{-2} s^{-1}, McNeil & Waddington 2003; ~1 to 4 μmol m^{-2} s^{-1}, Swanson & Flanagan 2001). Although *Sphagnum* was a significant component of GEP and ER, the influence of *Sphagnum* to total NEE in dry periods will depend on how this balance between GPP and R_d shifts with decreasing WC. However, the importance of *Sphagnum* to these component CO_2 fluxes individually suggests that *Sphagnum* could be quite influential to NEE in dry years.

Understanding the contribution of *Sphagnum* mosses to ecosystem CO_2 exchange is important in understanding the carbon budget at Mer Bleue, of which NEE is the

largest and most variable component (Roulet *et al.* 2007). The dissolved organic carbon (DOC) flux is a significant but smaller and less variable component than NEE, while loss of carbon as methane (CH_4) at Mer Bleue is quite small. Total annual NEE at Mer Bleue is influenced by the timing of spring and fall conversions between net CO_2 sink and source (Lafleur *et al.* 2003) It has been suggested that *Sphagnum* contributions to NEE may be particularly important at these times when vascular plant leaves are underdeveloped (Douma *et al.* 2007). As expected, *Sphagnum* was most important to GEP and R_d in spring when vascular plant leaves were not yet fully developed. These fluxes peaked in the post-greenup season when shading by vascular plants was low, but temperatures were more ideal for growth than in the pre-greenup season. However, vascular plants remained the dominant proportion of GEP_{max} in the fall season, probably because vascular plant leaf area did not decline substantially until the end of the fall measurement period (Figure 19). Flux measurements were stopped shortly after vascular plant leaf area began to decline due to snowfall and time limitations, but *Sphagnum* is likely important to NEE in fall at times when vascular leaf area is low as was shown for the spring. Also, vascular plant production was not inhibited by drought stress in fall during this study, since the maximum rooting depth for vascular plants on hummocks at Mer Bleue is 50 to 60 cm (Lafleur *et al.* 2005) and water table was well above these depths. It is uncertain at exactly what water table depth the capillary film supplying *Sphagnum* capitula becomes disconnected from the water table, but it may be above the maximum rooting depth of vascular plants (Lafleur *et al.* 2005). Sphagnum is likely more dependent on the direct influence of precipitation than vascular plants, which are more dependent on water table depth and don't experience moisture stress until the water

table is quite low at the site (i.e. below -50 to -60 cm). This study did not confirm the higher magnitude of *Sphagnum* growth in spring and fall at Mer Bleue measured by Moore *et al.* (2002). Although *Sphagnum* GPP_{max} and R_d varied among seasons, *Sphagnum* NPP_{max} did not differ significantly among seasons as seen in some previous studies (Figure 18, Table 11) (e.g. Clymo 1973, Swanson & Flanagan 2001, Moore *et al.* 2002).

Overall, annual NEE at Mer Bleue is largely determined by NEE during the August and September period ($R^2 > 0.81$, $p = 0.001$) (E.R. Humphreys, unpublished data). This period is when water table and moss WC vary most among years, while vascular leaf area has not yet decreased, suggesting that *Sphagnum* NPP could be influential despite its relatively smaller contribution to NEE. In particularly dry years, the influence of vascular plants will likely be greatest if the water table declines below their maximum rooting depth during this period.

6.0 CONCLUSION

This study is one of a few to address the direct links between peatland hydrology, *Sphagnum* growth, and peatland NEE, and to study moisture controls on *Sphagnum* NPP under field conditions. The relative importance of *Sphagnum* and vascular plants to interannual variability in NEE at Mer Bleue is still uncertain, although it seems likely that both play a significant role. While vascular plants contribute more to NEE, the influence of *Sphagnum* may become important in dry years if moss WC is low.

Many *Sphagnum* dominated ecosystems like peatlands and other types of wetlands are currently not included in the terrestrial carbon cycle models used in global climate simulations (St-Hilaire *et al.* 2008). There is potential for peatland ecosystems to shift from sinks to sources of carbon with changes in moisture conditions and, considering the large carbon stocks contained in these ecosystems, this could become a significant positive feedback for climate change. The results of this study support previous findings that suggest dry conditions can reduce peatland NEE (e.g. Arneth *et al.* 2002, Lafleur *et al.* 2003, Roulet *et al.* 2007), potentially reversing the peatland carbon budget (Roulet *et al.* 2007).

It is clear from the results of this study that peatland carbon cycling models should incorporate the dynamics of *Sphagnum* CO_2 exchange, in addition to those of vascular plants, as *Sphagnum* fluxes are important components of total GEP and ER and could be important to interannual variability in NEE. Direct precipitation was shown to be a strong control of *Sphagnum* capitulum WC, which suggests that an accurate representation of this relationship in addition to that with water table depth is required when modeling *Sphagnum* WC and NPP. Therefore, models that represent *Sphagnum*

WC as only a function of water table depth (e.g. PCARS, Frolking *et al.* 2002) may not fully describe *Sphagnum* CO_2 fluxes. The hummock *Sphagnum* species at Mer Bleue were resilient to relatively low water tables, but this is not the case for all *Sphagnum* species. A better understanding of species-specific water relationships is also needed in order to understand the influence of drought conditions on *Sphagnum* CO_2 exchange at different peatland and wetland sites.

The results of this study also show that while laboratory studies provide insight on the processes involved with *Sphagnum* moisture dynamics and controls on NPP, in natural environments these relationships are complex and field studies are necessary for a more complete understanding. Manipulation experiments such as this are useful for studying variation that occurs in ecosystems over longer periods when time allotted for study is limited. They are also useful for isolating a specific variable for study. However, in manipulation studies such as this where only one variable is changed, the others may not reflect the typical conditions associated with the manipulation. This study explored only one variable associated with drought conditions (i.e. water availability through intercepted precipitation). As a result, further work is necessary to investigate the relative importance of the influence of deep water table positions and high temperatures, conditions also associated with drought years, which tend to lead to net losses of carbon from Mer Bleue.

7.0 REFERENCES

Alm J, Saarnio S, Nykanen H, Silvola J, Martikainen PJ (1999) Winter CO_2, CH_4, and N_2O fluxes on some natural and drained boreal peatlands. *Biogeochemistry,* **44**(2), 163-186

Arneth A, Kurbatova J, Kolle O *et al.* (2002) Comparative ecosystem-atmosphere exchange of energy and mass in a European Russian and central Siberian bog II: interseasonal and interannual variability of CO_2 fluxes. *Tellus*, **54B**, 514–530.

Asada T, Warner BG, Banner A (2003) Growth of mosses in relation to climate factors in a hypermaritime coastal peatland in British Columbia, Canada. *The Bryologist*, **106**, 516-527.

Blodeau CB, Basiliko N, Moore TR (2004) Carbon turnover in peatland mesocosms exposed to different water table levels. *Biogeochemistry*, **67**, 331-351.

Bold HC, Alexopoulos CJ, Delevoryas T (1980) *Morphology of Plants and Fungi* (4th ed.) Harper & Row Publishers, New York.

Bragazza L (2008) A climatic threshold triggers the die-off of peat mosses during an extreme heat wave. *Global Change Biology*, **14**, 2688-2695.

Bubier J, Crill P, Mosedale A (2002) Net ecosystem CO_2 exchange measured by autochambers during the snow-covered season at a temperate peatland. *Hydrological Processes,* **16**, 3667-3682.

Bubier JL, Bhatia G, Moore TR, Roulet NT, Lafleur PM. (2003) Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems*, **6**, 353-367.

Bubier JL, Moore TR, Bledki LA (2007) Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Global Change Biology*, **13**, 1-19.

Canadell JG, Mooney HA, Baldocchi DD, *et al.* (2000) Carbon metabolism of the terrestrial biosphere: a multitechnique approach for improved understanding. *Ecosystems*, **3**, 115-130.

Clymo RS (1970) The growth of *Sphagnum*: methods of measurement. *The Journal of Ecology*, **58**, 13-49.

Clymo RS (1973) The growth of *Sphagnum*: some effects of environment. *The Journal of Ecology*, **61**(3), 849-869.

Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: *Bryophyte Ecology* (ed. Smith AJE), pp. 229–289. Chapman & Hall, New York.

Dorrepaal E, Aerts R, Cornelissen JHC, Callaghan TV, van Logtestijn RSP (2003) Summer warming and increased winter snow cover affect *Sphagnum fuscum* growth, structure and production in a sub-arctic bog. *Global Change Biology*, **10**, 93-104.

Douma JC, van Wijk MT, Lang SI, Shaver GR (2007) The contribution of mosses to the carbon and water exchange of arctic ecosystems: quantification and relationships with system properties. *Plant, Cell and Environment*, **30**, 1205-1215.

Ebbing D, Gammon D (2002) *General Chemistry* (7th ed.) Houghton Mifflin, Boston, MA.

France J, Thornley JM (1984) *Mathematical Models in Agriculture*. Butterworths, London, UK.

Frolking S, Roulet NT, Moore TR, Lafleur PM, Bubier JL, Crill PM (2002) Modelling seasonal to annual carbon balance at Mer Bleue Bog, Ontario, Canada. *Global Biogeochemical Cycles,* **16**(3), DOI: 10.1029/2001GB001457.

Garratt JR, Segal M (1988) On the contribution of atmospheric moisture to dew formation. *Boundary-Layer Meteorology,* **45**, 209–36.

Gerdol R (1995) The growth dynamics of *Sphagnum* based on field measurements in a temperate bog and on laboratory cultures. *Journal of Ecology*, **83**, 431– 437.

Gerdol R (1996) The seasonal growth pattern of *Sphagnum magellanicum* Brid. in different microhabitats on a mire in the southern Alps (Italy). *Oecologia Montana*, **5,** 13–20.

Gerdol R, Bonora A, Gualandri R, Pancaldi S (1996) CO_2 exchange, photosynthetic pigment composition, and cell ultrastructure of *Sphagnum* mosses during dehydration and subsequent rehydration. *Canadian Journal of Botany,* **74**, 726-734.

Gorham, E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, **1,** 182-195.

Goodall, DW (1952) Some considerations in the use of point quadrats for the analysis of vegetation. Australian Journal of Scientific Research, Series B, **5**(1), 1-41.

Grosvernier P, Matthey Y, Buttler A (1997) Growth potential of three *Sphagnum* moss species in relation to water table level and peat properties with implication for their restoration in cut-over bogs. *Journal of Applied Ecology*, **34**, 471-483.

Gunnarsson U (2005) Global patterns of *Sphagnum* productivity. *Journal of Bryology*, **27**, 269-279.

Hajek T, Beckett R (2008) Effect of water content components on desiccation and recovery in *Sphagnum* mosses. *Annals of Botany*, **101**, 165-173.

Hajek PC, Tuittila ES, Ilomets M, Laiho R (2009) Light responses of mire mosses – a key to survival after water-level drawdown? *Oikos*, **118**, 240-250.

Harley PC, Tenhunen JD, Murray KJ, 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**(2), 251-259.

Hayward PM, Clymo RS (1982) Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London B*, **215**, 299-325.

Hayward PM, Clymo RS (1983) The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. *The Journal of Ecology*, **71**(3), 845-863.

Heijmans MMPD, Klees H, Berendse F (2001) Competition between *Sphagnum magellanicum* and *Eriphorum angustifolium* as affected by raised CO_2 and increased N deposition. Oikos, **97**(3), 415-425.

Ingram HAP (1983) Hydrology. In *Mires: swamp, bog, fen, and moor, Vol. 4B* (ed. Gore AJP). Elsevier, Amsterdam, Netherlands, pp. 67-158

Kim J, Verma SB (1996) Surface exchange of water vapour between an open *Sphagnum* fen and the atmosphere. *Boundary-Layer Meteorology*, **79**, 243-264.

Lafleur PM, Roulet NT, Bubier JL, Frolking S, Moore TR (2003) Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles*, **17**, 1036, doi:10.1029/2002GB001983.

Lafleur PM, Moore TR, Roulet NT, Frolking S (2005) Ecosystem respiration in a cool temperate bog depends on peat temperature but not on water table. *Ecosystems*, **8**, 619-629.

Letts MG, Lafleur PM (2005) On the relationship between cloudiness and net ecosystem carbon dioxide exchange in a peatland ecosystem. *Ecoscience*, **12**(1), 53-59.

Levy EB, Madden EA (1933) The point method of pasture analysis. *New Zealand Journal of Agriculture*, **46**, 267-279.

Li Y, Glime JM, Liao C (1992) Responses of two interacting *Sphagnum* species to water level. *Journal of Bryology*, **17**(1), 59-70.

Lindholm T (1990) Growth dynamics of the peat moss *Sphagnum fuscum* on hummocks on a raised bog in southern Finland. *Annales Botanici Fennici*, **27,** 67–78.

Malmer N, Svensson BM, Wallén B (1994) Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. *Folia Geobotanica*, **29**(4), 483-496.

McCarthy JJ, Canziani OF, Leary NA, Dokken DJ, White KS (eds) (2001) *Climate Change 2001: Impacts, Adaptation and Vulnerability*. Cambridge University Press, New York, NY.

McNeil P (2001) Limits to *Sphagnum* Growth on a Cutover Peatland. M.Sc. Thesis, School of Geography and Geology, McMaster University, Hamilton, Ontario.

McNeil P, Waddington JM (2003) Moisture controls on *Sphagnum* growth and CO_2 exchange in a cutover bog. *Journal of Applied Ecology*, **40**, 354-367.

Moore TR (1989) Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. *Canadian Journal of Botany*, **67,** 1203–1207.

Moore TR, Bubier JL, Frolking SE, Lafleur PM, Roulet NT (2002) Plant biomass and production and CO_2 exchange in an ombrotrophic bog. *Journal of Ecology*, **90**, 25-36.

Moore TR, Lafleur PM, Poon DMI, Heumann BW, Seaquist JW, Roulet NT (2006) Spring photosynthesis in a cool temperate bog. *Global Change Biology*, **12**, 2323-2335.

Murray KJ, Harley PC, Beyers J, Walz H, Tenhunen JD (1989a) Water content effects on photosynthetic response of *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia*, **79**(2), 244-250.

Murray KJ, Tenhunen JD, Kummerow J (1989b) Limitations on *Sphagnum* growth and net primary production in the foothills of the Philip Smith Mountains, Alaska. *Oecologia*, **80**, 256-262.

Murray KJ, Tenhunen JD, Nowak RS (1993) Photoinhibition as a control on photosynthesis and production of *Sphagnum* mosses. *Oecologia*, **96**, 200-207.

Price JS (1997) Hydrology and microclimate in a partially restored cutover bog, Quebec. *Hydrological Processes*, **10**, 1263-1272.

Rice WR (1989) Analyzing tables of statistical tests. *Evolution*, **43**(1), 223-225.

Riutta T, Laine J, Tuitilla ES (2007) Sensitivity of CO_2 exchange of fen ecosystem components to water level variation. *Ecosystems*, **10**, 718-733.

Robroek BJM, Limpens J, Breeuwer A, van Ruijven J, Schouten MGC (2007) Precipitation determines the persistence of hollow *Sphagnum* species on hummocks. *Wetlands*, **27**(4), 979-986.

Robroek BJM, Schouten MGC, 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.

Roulet NT, Lafleur PM, Richard PJH, Moore TR, Humphreys ER, Bubier JL (2007) Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland. *Global Change Biology*, **13**, 397-411.

Ryan MG (1991) Effects of climate change on plant respiration. *Ecological Applications*, **1**(2), 157-167.

Rydin H (1985). Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna*. *Oikos*, **45**, 374-379.

Rydin H, Jeglum J (2006) *Sphagnum* – the builder of boreal peatlands, In: *The Biology of Peatlands*. Oxford University Press, New York, pp. 58-74.

Rydin H, McDonald AJS (1985) Photosynthesis in *Sphagnum* at different water contents. *Journal of Bryology*, **13**, 579-584.

Scheiner SM, Gurevitch J (2001) *Design and Analysis of Ecological Experiments (2nd ed.)*. Oxford University Press, Oxford.

Schimper WP (1858) *Versuch einer Entwickelungs-Geschichte der Torfmoose (Sphagnum) und einer Monographie der in Europa vorkommenden Arten dieser Gattung*. E. Schweizerbart's Verlagsbuchhandlung, Stuttgart.

Shaw RG, Mitchell-Olds T (1993) ANOVA for unbalanced data: an overview. *Ecology*, **74**(6), 1638-1645.

Shipperges 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.

Silvola J (1990) Combined effects of varying water content and CO2 concentration on photosynthesis in *Sphagnum fuscum*. *Holarctic Ecology*, **13**, 224-228.

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

Sommerkorn M, Bölter M, Kappen L (1999) Carbon dioxide fluxes of soils and mosses in wet tundra of Taimyr Peninsula, Siberia: controlling factors and contribution to net system fluxes. *Polar Research*, **18**, 253-260.

St-Hilaire F, Wu J, Roulet NT, Frolking S, Lafleur PM, Humphreys ER, Arora V (2008) McGill Wetland Model: evaluation of a peatland carbon simulator developed for global assessments. *Biogeosciences Discussions*, **5**, 1689-1725.

Steel RGD, Torrie JH (1980) *Principles and Procedures of Statistics: a Biometrical Approach (2nd ed.)*. McGraw-Hill, Inc, New York, NY.

Strack M, Waddington JM, Rochefort L, Tuittila ES (2006) *Journal of Geophysical Research,* **111**, DOI: 10.1029/2005JG000145.

Strack M, Price JS (2009) Moisture controls on carbon dioxide dynamics of peat-*Sphagnum* monoliths. *Ecohydrology*, **2**, 34-41.

Swanson RV, Flanagan LB (2001) Environmental regulation of carbon dioxide exchange at the forest floor in a boreal black spruce ecosystem. *Agricultural and Forest Meteorology*, **108**, 165-181.

Szumigalski AR, Bayley SE (1997) Net aboveground primary production along a peatland gradient in central Alberta in relation to environmental factors. *Ecoscience*, **4**(3), 385-393.

Thompson DK, Waddington JM (2008) *Sphagnum* under pressure: towards and ecohydrological approach to examining *Sphagnum* productivity. *Ecohydrology*, **1**, 299-308.

Titus JE, Wagner DJ (1984) Balance for two *Sphagnum* mosses: water balance resolves a physiological paradox. *Ecology*, **65**(6), 1765-1774.

Titus JE, Wagner DJ, Stephens MD (1983) Contrasting water relations of photosynthesis for two *Sphagnum* mosses. *Ecology*, **64**(5), 1109-1115.

Tjoelker MG, Oleksyn J, Reich PB (2001) Modelling respiration of vegetation: evidence for a general temperature-dependent Q_{10}. *Global Change Biology,* **7**, 223-230.

Turunen J, Tomppo E, Tolonen K, Reinikainen A (2002) Estimating carbon accumulation rates of undrained mires in Finland – application to boreal and subarctic regions. *The Holocene*, **12**(9), 69-80.

Van Gaalen KE, Flanagan LB, Peddle DR (2007) Photosynthesis, chlorophyll fluorescence and spectral reflectance in *Sphagnum* moss at varying water contents. *Oecologia*, **153**, 19-28.

Verhoeven JTA, Toth E (1995) Decomposition of *Carex* and *Sphagnum* litter in fens: effect of litter quality and inhibition by living tissue homogenates. *Soil Biology and Biochemistry*, **27**, 271-275.

Vitt DH, Wider K, Halsey LA, Turetsky M (2003) Response of *Sphagnum fuscum* to nitrogen deposition: a case study of ombrogenous peatlands in Alberta, Canada. *The Bryologist*, **106**, 235-245.

Waddington JM, Rochefort L, Campeau S (2003) *Sphagnum* production and decomposition in a restored cutover peatland. *Wetlands Ecology and Management*, **11**, 85-95.

Wagner DJ, Titus JE (1984) Desiccation tolerance of two *Sphagnum* mosses. *Oecologia*, **62**(2), 182-187.

Weltzin JF, Harth C, Bridgham SD, Pastor J, Vonderharr M (2001) Production and microtopography of bog bryophytes: response to warming and water-table manipulations. *Oecologia*, **128**, 557-565.

Williams TG, Flanagan LB (1996) Effects of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in *Pleurozium* and *Sphagnum*. *Oecologia*, **108**, 38-46.

Williams TG, Flanagan LB (1998) Measuring and modeling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*. *Plant, Cell and Environment*, **21**, 555-564.

Wood AJ (2007) The nature and distribution of vegetative desiccation-tolerance in hornworts, liverworts and mosses. *The Bryologist*, **110**(2), 163-117.

Yoshikawa K, Overduin PP, Harden JW (2004) Moisture content measurements of moss (*Sphagnum* spp.) using commercial sensors. *Permafrost and Periglacial Processes*, **15**, 309-318.

Zar JH (1999) *Biostatistical Analysis (4th ed.)*. Prentice Hall, Upper Saddle River, NJ.