



WARMING ALTERS PHOTOSYNTHETIC RATES OF SUB-BOREAL PEATLAND VEGETATION



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Master Thesis no. 172

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Abstract

Boreal peatlands are important in the global carbon cycle. Despite covering only 3% of the global land area, peatlands store approximately one third of all soil carbon. Temperature is one of the major drivers in peatland carbon cycling as it affects both plant production and CO₂ fluxes from soils. However, it is relatively unknown how boreal peatland plant photosynthesis is affected by higher temperatures. Therefore, we measured plant photosynthetic rates under two different warming treatments in a poor fen in Northern Michigan. Eighteen plots were established that were divided into three treatments: control, open-top chamber (OTC) warming and infrared (IR) lamp warming. Previous work at this site has shown that there was a significant increase in canopy and peat temperature with IR warming (5°C and 1.4°C respectively), while the OTC's had mixed overall warming. Plots were divided equally into lawns and hummocks. We measured mid-day carbon dioxide (CO₂) uptake on sedges (*Carex utriculata*), shrubs (*Chamaedaphne calyculata*) and *Sphagnum* mosses. *Sphagnum* moss net primary production (NPP) was also measured with cranked wires and compared with CO₂ uptake.

Our results indicate that there was no significant difference in sedge CO₂ uptake, while shrub CO₂ uptake significantly decreased with warming. A significant increase occurred in *Sphagnum* moss gross ecosystem production (GEP), ecosystem respiration (ER) and net ecosystem exchange (NEE). Contrary to the positive CO₂ exchange of *Sphagnum*, overall NPP decreased significantly in hummocks with both warming treatments. The results of the study indicate that temperature partly limits the photosynthetic capacity of plants in sub-boreal peatlands, but not all species respond similarly to higher temperatures.

Key words: Peatlands, CO₂ uptake, Climate change, microtopography

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List of abbreviations

net primary production	NPP
ecosystem respiration	ER
gross ecosystem production	GEP
net ecosystem exchange	NEE
infra-red	IR
open top chamber	OTC
petagram (10^{15} grams)	Pg
infra-red gas analyzer	IRGA
vapor pressure deficit of the leaf	VpdL

Foreword

I would sincerely like to thank the EU-USA funded ATLANTIS program for giving me an opportunity to study in Sweden, Finland and USA and making this thesis possible. This thesis is a dual-degree thesis in cooperation with both Swedish Agricultural University and Michigan Technological University.

My biggest gratitude goes to my advisor, Rod Chimner, for being an example from the beginning to the end of my stay on how to become a great scientist. But more than that, I admire his commitment to his family and his positive attitude to life.

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My regards to my family and friends in Estonia for supporting me mentally while being abroad for such a long time. Big thanks to all the people in wetlands lab for assistance, know-how and for your time in helping out. And to all of the wonderful people I have met on the road for sharing the path with me and giving me the greatest years of my life. I love you all!

Resüme

Borealse kliimavöötme sood on tähtsad globaalses süsinikuringes. Kuigi sood katavad vaid 3% maakera maismaa pindalast, seovad sood kolmandiku maailma mullastikus peituvast süsinikust. Temperatuur on üks peamisi süsinikuringluse mõjuagente, mõjutates nii taimede kasvu kui ka süsinikdioksiidi (CO₂) eraldumist mullastikust atmosfääri (respiratsioon). Samal ajal on vähe teada kuidas boreaalsete soode taimede fotosüntees on temperatuuri poolt mõjutatud.

Seetõttu mõõtsime me taimede fotosünteesitaset kahe erineva soojendusmeetodi mõjul. Mõõtmised toimusid USA-s, Michigani osariigi põhjaosas asuvas siirdesoods. Rajasime kaheksateist platsi, mille jagasime kolme erineva soojendusmeetodi vahel: kontroll, pealt lahtised kasvuhooned ning infrapuna lambid. Eelnev töö katsealal näitas, et nii taimesid ümbritsev õhutemperatuur ja turbatemperatuur tõusis infrapuna soojendusmeetodi abil (5°C ja 1.4°C, vastavalt). Samal ajal pealt lahtised kasvuhooned ei kajastanud selget soojendustrendi. Lisaks jagati katselapid topograafia järgi kõrgemateks ja madalamateks: mätasteks ja mättavahedeks. Me mõõtsime keskpäeva fotosünteesitaset kolmel erineval taimegrupil: tarnad (*Carex utriculata*), põõsad (*Chamaedaphne calyculata*) ja turbasamblad (*Sphagnum*). Turbasammalde kasvuhooaja biomassi juurdekasvu mõõdeti samuti kõikidel katselappidel, et oleks seda võimalik võrrelda fotosünteesiga.

Meie tulemused näitavad, et tarnade fotosüntees ei olnud mõjutatud kummagist soojendusmeetodist, samal ajal põõsaste fotosüntees langes soojendamise mõjul. Statistiliselt suurenes nii turbasammalde fotosüntees kui ka taimererespiratsioon. Vastupidiselt suurenenud fotosünteesile, biomassi juurdekasv mätastel langes statistiliselt mõlema soojendusmeetodiga. Meie tulemused osutavad, et temperatuur osaliselt piirab taimede kasvu borealse kliimavööndi soodes kuid mitte kõik taimed ei reageeri samalaadselt kõrgemale temperatuurile.

Võtmesõnad: Sood, fotosüntees, kliima soojenemine, sootaimed.

Introduction

Peatland Types

Peatlands are wetlands where long-term average plant biomass accumulation exceeds decomposition rates (Crum 1992). Peatlands form because perennially saturated soils create anoxic conditions that hinder decomposition. Different countries have different requirements for peat thickness, with minimum thickness ranging between 30 cm to 50 cm (Gorham 1991). Peatland distribution is controlled primarily by climate and topography. Peatlands are most commonly found in cool and moist climates with low evapotranspiration and flat landforms (Sjörs 1980; Wieder and Vitt 2006). For instance, boreal and arctic peatlands (thickness > 30 cm) cover $3.5 \times 10^5 \text{ km}^2$, or about 90% of all peatlands globally (Charman 2002).

Peatlands are often divided into two main types based on source of water and nutrients (Charman 2002). Peatlands that receive all of their water and nutrients from precipitation are called ombrotrophic peatlands, or bogs (Bridgham *et al.* 1999). Since they are cut off from groundwater, which contains minerals, these peatlands are characterized by low pH, low base cation (Ca^{2+} , Mg^{2+} , K^+ , Na^+) content and low nutrient levels (Zoltai and Vitt 1995; Wheeler and Proctor 2000). As a result, they have vegetation that is able to tolerate nutrient poor and acidic conditions and are characterized by the dominance of *Sphagnum* mosses. Peatlands that receive at least a part of their water from groundwater are called minerotrophic peatlands, or fens (Wieder and Vitt 2006). These peatlands have higher concentrations of nitrogen and phosphorus, base cations, and greater pH due to inflow of groundwater (Bridgham *et al.* 2001). Minerotrophic fens are dominated by plants which are not able to tolerate acidity like brown mosses and many types of sedge. Bogs have pH usually <4.0, while fens have pH >4.0 and are divided into poor fens, intermediate fens and rich fens based upon their pH and base cation content (Wheeler and Proctor 2000). Poor fens are acidic, *Sphagnum* dominated but have some influx of ground water (Zoltai and Vitt 1995). Intermediate fens and rich fens have pH>5.5 and are dominated by plants which do not tolerate acidity and lack significant cover of *Sphagnum* (Wieder and Vitt 2006).

Peatland Carbon Cycling

Peatlands are globally important in the terrestrial carbon cycle. What makes these ecosystems special is not their production rates, but the continuous imbalance between the production and decomposition, which over long time periods has resulted in very large carbon pools (Wieder and Vitt 2006). About 98.5% of carbon in peatlands occurs in the form of peat, while the rest is found in vegetation (Gorham 1991). Boreal peatlands cover 3% of the global land mass, (~330,000 km²) (Gunnarsson 2005), but store about one third of all terrestrial soil carbon (Moore *et al.* 1998). Boreal peatlands accumulate carbon at an average rate of 29 g carbon m⁻² yr⁻¹ (Gorham 1991). Boreal peatlands are found within the boreal climatic zone and have been developing since the end of the last ice age (Gignac *et al.* 1998) and have accumulated 300-450 x 10¹⁵ grams of carbon during this period (Gorham 1991). This is about the same amount as currently stored in atmosphere (Houghton *et al.* 1990), and twice as much as forest biomass contains globally (Parish *et al.* 2008). Boreal peatlands have lower values of primary production compared to other ecosystems in the same climatic region. The most important plant genus in terms of carbon storage is *Sphagnum* (Clymo 1970), which contributes the majority of aboveground production in nutrient poor systems like bogs and poor fens, averaging 259 g m⁻² yr⁻¹ (Weltzin *et al.* 2000) compared to average boreal forest biomass accumulation of 424 g m⁻² yr⁻¹ (Gower *et al.* 2001).

The imbalance between production and decomposition itself is fragile. Around 90% of the carbon accumulated annually by plants is lost through decomposition, resulting in only 10% of plant biomass being stored over longer time periods (Gorham 1988; Vasander 1982). Peatlands are therefore sensitive to decreases in net primary production (NPP) or increases in ecosystem respiration (ER), which is the main loss of carbon to the atmosphere (Dorrepaal *et al.* 2009). Shifts in the carbon balance of these ecosystems could start releasing stored carbon back in the atmosphere as CO₂; further accelerating the “greenhouse effect”. For example, a 1°C increase was found to raise ER rates 56%, with 69% of this increase coming from the bottom of the active layer in a permafrost peatland (Dorrepaal *et al.* 2009).

Primary productivity is the major input of carbon to a peatland (Rydin and Jeglum 2006). Net primary production is defined as a difference between gross primary production, total amount of organic carbon fixed by a plant, and autotrophic respiration which is the total amount of carbon lost by a plant (Woodwell and Whittaker 1968). Plants acquire carbon from CO₂ taken up through photosynthesis (Lambers *et al.* 1998). The amount of CO₂ assimilated by a vegetated surface is called gross ecosystem production (GEP) (Wofsy *et al.* 1993). For photosynthesis to occur, plants need sufficient source of water, sunlight and CO₂. Each plant species has different requirements for optimum photosynthesis to occur. Photosynthesis is influenced directly by the light intensity and air temperature, which alters vapor pressure deficit, electron transport rate and photosynthetic enzyme production (Lloyd and Farquhar 2008). Light intensity (irradiance) relates to photosynthesis through the amount of captured photons (units of light), greater irradiance results in enhanced CO₂ uptake (Lambers *et al.* 1998). Therefore if warming enhances photon capture, plant is able to fix more CO₂ resulting in higher net biomass production.

Carbon outputs from peatlands are from efflux of CO₂, methane and leaching of dissolved organic carbon (Davidson and Janssens 2006). Some of the carbon plants fix through photosynthesis is lost through plant respiration, defined as autotrophic respiration (Lambers *et al.* 1998). Heterotrophic respiration is a combination of fungal and microbial respiration and other organic matter decaying organisms (Shaver *et al.* 2000). Autotrophic and heterotrophic respiration together form ecosystem respiration, which is the total amount of CO₂ lost from an ecosystem at a given time period (Davidson and Janssens 2006; Moore *et al.* 1998). Net ecosystem exchange (NEE) is the difference between the carbon gained by an ecosystem (GEP) minus the loss of carbon from ER.

Peatland Warming

Increased greenhouse gas concentrations are expected to increase surface temperatures and alter regional precipitation patterns (IPCC 2007). It is predicted that higher concentrations of atmospheric CO₂ concentrations will lead to greater

photosynthesis and plant growth in most ecosystems (Norby *et al.* 2001), in nutrient poor ecosystems, increased CO₂ concentration are predicted to have negligible effect on NPP (Hoosbeek *et al.* 2001).

Boreal peatlands are ecosystems characterized by generally low temperatures, short growing seasons, and low soil nutrient contents (Arft *et al.* 1999). Average global temperatures are predicted to increase 0.6 - 6°C by the end of 21st century compared with the temperatures a century before (IPCC 2007). The greatest increases are predicted to occur at high latitudes of the Northern Hemisphere, especially in the arctic, where temperature increase could be even higher than average (Houghton *et al.* 1990; Houghton *et al.* 1995; Maxwell and Barrie 1989). Higher temperatures in northern peatlands could be seen as a large-scale disturbance with implications on growing conditions of the plants (Alm *et al.* 1999). Higher temperatures have the potential to increase evapotranspiration rates, which will lower water table and make oxygen more available for microbial decomposition (Faubert 2004; Gorham 1991). Both plant and soil microbial respiration rates could be positively influenced by higher temperatures (Dorrepaal *et al.* 2009). Heterotrophic respiration counts for 80% of soil respiration and increases more than autotrophic respiration in short time scale warming experiments (Melillo *et al.* 2002). Plant production could also be influenced either positively or negatively by increasing temperatures. Boreal peatlands are therefore, sensitive to either increases in decomposition or decreases in plant production (Wieder 2001), and could shift from carbon sinks to sources (Hoosbeek *et al.* 2001). If decomposition values exceed the CO₂ uptake by plants, the carbon released to the atmosphere may result in positive feedback of rising CO₂ concentrations in atmosphere (Oechel *et al.* 1993). Increase in both temperature and ER through lowered water tables will result in increased CO₂ emissions to the atmosphere (Moore *et al.* 1998). It has been suggested that daytime CO₂ uptake will be influenced less by temperature than ER (Houghton and Woodwell 1989). Therefore, peat accumulation in most sub-boreal peatlands may decrease or even cease (Gignac and Vitt 1994).

Peatlands at the southern end of boreal region (sub-boreal) could be especially vulnerable to climate change. The plant communities in these peatlands are

accustomed to a moist and cold climate, and increasing temperature could affect their growing conditions. As the boreal forest zone is predicted to move northwards, and boreal peatlands are highly linked with the boreal forest zone (Gignac *et al.* 1998), peatland distribution could move northwards too. This was illustrated by (Prentice *et al.* 1991), who used a forest succession model to predict that in central Sweden boreal zone evergreen trees like Norway spruce (*Picea abies*) will be replaced by broadleaved temperate trees like beech (*Fagus sylvatica*) and common oak (*Quercus robur*), which require longer growing season and higher summer temperatures. Similarly, boreal peatland plants in sub-boreal zone could already be at their temperature threshold and any increase in temperature could result in northward movement of peatlands and changes of species composition of peatlands in former sub-boreal zone. It has been shown that with increased temperatures at high latitudes, areas currently unvegetated will have plant cover (Myneni *et al.* 1997), giving further evidence to movement of ecosystems following suitable conditions. Species will follow the shifting climate northwards to higher latitudes as much as the dispersal and resource availability allow (Aerts *et al.* 2006).

Water table level is the most important factor controlling decomposition rates in peatlands (Bridgham and Richardson 2003). Upland soils are well aerated and therefore have low carbon stocks (Davidson and Janssens 2006). If rising temperatures or lower precipitation in the future lower the water table, increased microbial activity is expected to occur in the peat (Clymo 1992). Plant photosynthesis responds to temperature almost immediately, which can result in higher NPP (Shaver *et al.* 2000). Higher temperatures have positive effects on overall soil respiration rates (Lloyd and Taylor 1994) since microbial decomposition is reduced under low temperatures (Allison *et al.* 2010; Woodwell and Whittaker 1968). In nutrient poor ecosystems like boreal peatlands, warming enhanced soil respiration results in higher nutrient availability over long time periods (Chapin 1983). Plant growth in most boreal peatlands is nutrient limited (Shaver *et al.* 2000), especially by nitrogen (Aerts *et al.* 1992). Most of the nutrients are tied up in plant biomass or peat. Nutrient availability is crucial for plant growth and warming induced changes in nutrient dynamics could result in changes in plant communities (Aerts *et al.* 2006). Nitrogen

availability could increase through faster decomposition of organic matter (Shaver *et al.* 2000). Nitrogen availability has also increased through increased atmospheric N deposition (Aber *et al.* 1998). Increased N supply possesses more positive growth response on fast growing sedges and deciduous shrubs and decreases the abundance of slow growing mosses (Aerts *et al.* 2006). If plant species composition changes, so does litter composition and quality. Tissue quality (e.g. cellulose, lignin and nutrient composition) can be more important on decomposition rates than temperature or pH (Bartsch and Moore 1985). For example, because of their low tissue quality, *Sphagnum* species decompose more slowly than sedges (Toet *et al.* 2006). This is one of the reasons why *Sphagnum* spp. is one of the major peat forming plant genus and its remains store more carbon than any other plant genus on the globe (Clymo 1970). Peatlands dominated by *Sphagnum* mosses typically store more carbon than sedge dominated peatlands (Thormann and Bayley 1997). *Sphagnum* has unique properties in acidifying the substrate it is living in, resists decay, and being able to live in extremely nutrient poor conditions (Clymo 1964; Verhoeven and Liefveld 1997). *Sphagnum*'s ability to acidify its environment is thought to help it reduce the competition and gain competitive advantage (Andrus 1986). In boreal peatlands, vascular plant growth is limited by presence of *Sphagnum*, which dominates the lower layer of vegetation (Arft *et al.* 1999). Vascular plants have to invest into height growth not to become overgrown by *Sphagnum* (Rydin 1997). Therefore, shifts in species composition could result in peatland transformation from carbon sink to source if *Sphagnum* is outcompeted with sedges, shrubs or other mosses that are able to respond more rapidly to available nutrients, decay at faster rates, and do not acidify the soil (Toet *et al.* 2006).

Net primary production, increment of organic matter over time, is the most common metric to quantify warming on peatland plants (Dorrepaal *et al.* 2004; Szumigalski and Bayley 1997). Probable reasons for using NPP is because of limited accessibility of many arctic and boreal peatlands, and NPP measurements can be done with few field days. However, NPP measurements do not allow for monitoring short-term plant physiological responses to changes in temperature. Because NPP measurements may miss smaller time scale changes in plants, like reduced

photosynthesis due to desiccation, CO₂ flux measurements (leaf or ecosystem level) are commonly conducted to quantify these processes. The common method for measuring CO₂ exchange between an ecosystem and the atmosphere has been to use small chambers (Alm *et al.* 1999; Gunnarsson *et al.* 2004; Kivimaki *et al.* 2008; Laine *et al.* 2007; Moore *et al.* 2002). These chambers allow monitoring photosynthesis and respiration of peatlands at community scale, which can thereafter be extrapolated to bigger areas. The problem with the method is that it neglects the response of individual plant groups within that community. Measuring CO₂ uptake on a plant level gives the opportunity to quantify the differences between species or plant groups within the community. This is helpful in determining the possible shift in species composition in the future.

Methodology Background

In our study, we categorized plants as either woody (shrubs), graminoids (sedges) or bryophytes (*Sphagnum* spp.) to quantify changes in CO₂ uptake under increased temperature.

How peatlands and peatland plants will behave under future climates has been under intensive study since it was realized how important peatlands are to the global carbon cycle. Artificial warming is the most common method used to study the effect of warming on ecosystem processes in peatlands (Arft *et al.* 1999; Marion *et al.* 1997). Artificial warming can be divided into two functionally different groups, active and passive. Active treatments use an artificial energy source to heat the soil or plant canopy (Aronson and McNulty 2009). Passive warming treatments utilize the sun's energy to heat the canopy during the daytime and reduce heat loss during the night (Marion *et al.* 1997). In our study, we used standard ITEX (International Tundra Experiment) (Henry and Molau 1997) passive warming open top chambers (OTC's) and active warming infra-red (IR) lamps (Aronson and McNulty 2009) as treatments to monitor changes in plant CO₂ uptake. IR lamps are elevated above the vegetation and distribute IR energy evenly to the canopy, while OTC's act as a greenhouse that is open at the top. They trap the IR wavelengths and reduce their re-radiation back to the

atmosphere further warming the air inside the chamber (Marion *et al.* 1997). Although OTC's alter air temperature, they have relatively little impact on disturbing gas exchange, light and moisture (Arft *et al.* 1999). The IR lamps were constantly on during the growing season and warmed the plots during days and nights, whereas OTC's provide heating effect only during daytime. Since global temperature increase will raise nighttime temperatures (Luxmoore *et al.* 1998), it has been suggested that IR-lamps are more accurate in simulating future higher temperatures (Aronson and McNulty 2009). In Arctic peatlands, OTC's have been shown to increase the average temperature by about 2°C (Marion *et al.* 1997). Two functionally different warming treatments enabled us to monitor the differences these two treatments were having on vegetation CO₂ uptake. Changes in basic metabolism of a plant like acclimation to temperature occurs within a year (Shaver *et al.* 2000). Therefore short time period warming experiments enable monitoring plant physiological changes without influencing long term changes in the ecosystem like soil nutrient availability.

Several different methods have been used to measure CO₂ exchange of plants, soil or the whole ecosystem. They all follow the same basic concept of analyzing the incoming and outgoing gas concentrations in the air and velocity of air movement between ecosystem and atmosphere. Eddy covariance towers are the primary means for monitoring the whole ecosystem fluxes (Baldocchi 2003). Since eddy covariance towers require uniform vegetation structure, flat landforms, big land areas and are biased during the nighttime they are unsuitable for use in all ecosystems (Baldocchi 2003). They cannot also be used for small experiment units with many treatments (Sullivan *et al.* 2008). Therefore manual chambers are often used to monitor smaller areas and areas with less uniform landscapes (Oechel *et al.* 1993). These kinds of chambers enable monitoring of differences in gas concentrations and humidity within the chamber. Chambers are put on top of the soil with vegetation enclosed into it, gas is directed into it while air is circulated at constant speed to mix the air (Vourlitis *et al.* 1993). Infra-red gas analyzer measures the difference between incoming and outgoing CO₂ concentration in the chamber and calculates flux rates (Vourlitis *et al.* 1993). The reduction in gas concentration (CO₂) indicates uptake by plant

photosynthesis from within the chamber. Manual chamber techniques have been found to give comparable results with eddy covariance method (Oechel *et al.* 1998).

We separated our treatments equally between two microtopographic features, hummocks and lawns. Their importance comes from the height of the water table, which influences soil moisture, biogeochemical cycling, and species composition (Moore *et al.* 2002). Hummocks are elevated higher up from the water table than lawns and typically have higher vascular plant biomass and less *Sphagnum* dominance (Vasander 1982). Hummocks are 20-50 cm above the water table, whereas lawns are only 0-10, and during some part of the growing season might even be submerged by water. Hummocks and lawns tend to have different *Sphagnum* moss composition and growth forms. At our study site, the species dominating the hummocks, *Sphagnum fuscum*, was rarely found on lawns. Microtopography is vitally important in determining *Sphagnum* growth and decomposition (Wieder and Vitt 2006). *Sphagnum* is dependent on the height of the water table and moisture content of the capitulum determines the growth rate of *Sphagnum*. Lawn species tend to have higher growth rates as illustrated by (Weltzin *et al.* 2001), who found that lawn species showed 100% higher primary production than hummock species and 50% higher production than intermediate microtopography. Since hummock *Sphagnum* species are farther away from the water table and they have no roots, they utilize their better capillary water transport and have denser growing forms than lawn species (Murray *et al.* 1989; Wieder and Vitt 2006). *Sphagnum* species are also known for their water holding capacity as they can hold up to 25 times more water than their own weight (Clymo and Hayward 1982). Even though the higher production in hollows could indicate that the microtopography would eventually become evened out, the hummock hollow dynamics seem to be maintained by lower decomposition rates of hummock species (Rocheffort *et al.* 1990).

Methods

Site Description

We conducted a field experiment to test the influence of two different types of warming (IR-lamps vs. OTC'S) on peatland carbon cycling. The study occurred in a poor fen in Pequaming (46.85°N 88.37°W, elevation 193m), in the western half of Michigan's Upper Peninsula (Figure 1). The poor fen is 170 ha in size (EPA 2010), and occurs in a tombolo on the Keweenaw Bay, Lake Superior. A tombolo forms when sediments from waves create a land bridge connecting an island to a mainland. The Pequaming tombolo has a ridge on both lake sides, which act as barriers that keep most of the lake water out of the tombolo (Boisvert 2009).

The growing season in this region is 110 to 130 days (Eichenlaub 1990), with average minimum winter temperature of -17° C and average maximum summer temperature of 26° C (IDcide 2010). Mean annual precipitation ranges from 760 to 910 centimeters, with heavy lake-effect snowfalls up to 5 meters per year (Albert 1995).

Peat cores indicate that the peat is 200-250 cm thick with a ¹⁴C basal age of 2,225 +/- 105 years, consisting of humic *Carex* and *Sphagnum* remains (Boisvert 2009). The bottom layer of peat from 110-200 cm is mainly remnants of *Carex* ssp. The upper layer of peat (20-110 cm) is mostly *Sphagnum* with some undecomposed *Carex* ssp. (Boisvert 2009). Peat humification increased with increasing peat depth, with the uppermost 20 cm of peat consisting of undecomposed woody material and *Chamaedaphne calyculata*, *Carex* ssp. and *Sphagnum* moss.

Vegetation composition was surveyed during the summer of 2009 using a grid intercept method in the middle of each plot. A 1 m x 1 m grid was used with 100 points in each plot. An aluminum frame with a movable crossbar mounted with laser was used for sampling. All vascular plants and bryophytes hit by a laser pointer were identified, counted, and the number of hits was divided by 100 to get the percent cover of each species. Vascular plants and bryophytes were treated as two different vegetation layers, both summing up to 100%. In summary, vegetation at the site is

similar to other poor fens in the region (Table 1). The main vascular plants on the hummocks were *Chamaedaphne calyculata*, *Vaccinium oxycoccos* and *Picea mariana*. The dominant vascular plants in the lawns were *Vaccinium oxycoccos*, *Carex exilis*, *Carex oligosperma* and *Chamaedaphne calyculata*. *Sphagnum fuscum* was the dominant moss on the hummocks, constituting almost 60% of the cover, followed by *Sphagnum magellanicum* and *Sphagnum rubellum*. *Sphagnum rubellum* was the most common bryophyte in the lawns followed by *Sphagnum papillosum*.



Figure 1. Location of the study site. (Source: 2011 Google. Available from maps.google.com)

Experimental Design

Eighteen plots were established in 2008 and divided into three treatments with equal numbers of IR heating lamps (lamps), OTC's, and unwarmed control plots (Figure 2). The warming experiment ran from late 2008 through October 2010. The 6 replicates of each warming treatment were split equally among hummocks and lawns. Boardwalks were installed to all plots to minimize impacts.



Figure 2. Site set-up at Pequaming field site, 2010. *Photo by: Arvo Aljaste.*

Air and soil temperatures were manipulated on six lamp plots by using adjustable, thermal infrared heating lamps [~ 2 m in length, Kalglo Inc. IR lamps (120V, 1500 W, 12.5 amps)] suspended 1.25 m above the moss surface (Figure 3). The lamps were operational 24 hours per day until the end of the growing season,

from April to middle of October. Lamps were disassembled for the winter and stored in the lab until used again the following year.

Six plexiglass hexagon OTC's were designed according to ITEX (International Tundra Experiment) specifications (Henry and Molau 1997). The OTC's were 2.08 m wide from the bottom, 0.5 m in height, the sides were at 60° angle and the open top was 1.5 meters wide (Figure 4). OTC's were assembled and put out at the same time with lamps and disassembled in mid-October.

IR lamps in our study increased average daily soil temperatures by about 1.4°C compared to OTC and control plots, but warmed even more during the night since the lamps were constantly operating (Chris Johnson, unpublished data).

Precipitation was measured on site using tipping-bucket rain gauge (TE525WS, Texas Instruments, Dallas, TX). Water table depth beneath the surface was monitored daily using a 10.16 cm wide and 1.5 m long PVC pipe well which had pressure transducers (Levellogger Junior, Solinst, Georgetown, Ontario) and a barometric logger (Barallogger Gold, Solinst, Georgetown, Ontario) installed into it. I-Buttons were installed to all plots (I-Buttons, Maxim Integrated Products, Sunnyvale, CA) 5 cm beneath the moss surface to monitor hourly temperature. Volumetric water content of the top 12 cm beneath the *Sphagnum* moss surface was measured manually with a HydroSense® Water Content Sensor (Campbell Scientific Inc., Australia).

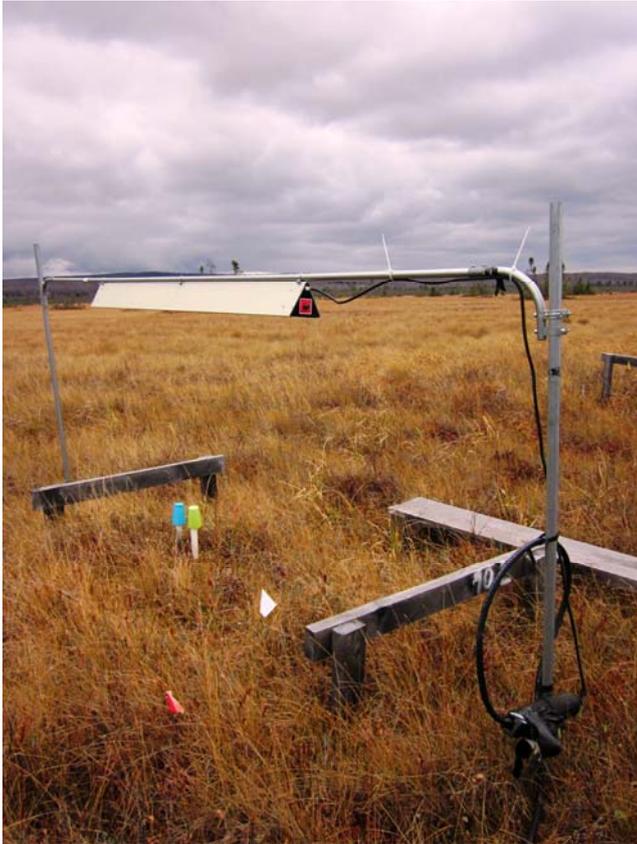


Figure 3. Infra-red lamp at Pequaming field site, 2010. *Photo by: Arvo Aljaste.*



Figure 4. Open top chamber (OTC) at Pequaming field site, 2010. *Photo by: Arvo Aljaste.*

Gas exchange of vascular plants

Gas exchange measurements of two different vascular plant species [leatherleaf (*Chamaedaphne calyculata*) and sedge (*Carex utriculata*)] were conducted. *C. calyculata* was chosen to represent shrub and *C. utriculata* sedge plant functional groups. The photosynthetic rate of these two species was measured over the growing season (end of April to the start of October 2010) using a Licor-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA), equipped with a 6400-2B LED Light Source (Figure 5). The light source provided a constant photosynthetically active radiation (PAR) during the measurements and was set to 1500 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. The reference CO_2 concentration was set to 400 $\mu\text{mol per mole}$ and the flow was set to a constant rate of 400 $\mu\text{mol per second}$. Leaf temperature and humidity were not controlled during the measurements.



Figure 5. Measuring CO_2 uptake with Licor 6400 infra-red gas analyzer. *Photo by: Arvo Aljaste.*



Figure 6. Permanent plastic collars inserted into peat which had chamber on them during the measurements. Collars had to be lifted up several times since *Sphagnum* moss was overgrowing the collars. The purpose was to have identical chamber volume during every measurement. *Photo by: Arvo Aljaste.*

To determine leaf area in cm^2 , a requirement to calculate CO_2 uptake, sedge leaf width was multiplied by 3 cm (longest side of IRGA's chamber). For leatherleaf, a common mathematical formula for ovals was used, where the area of the oval (cm^2) equals the width (cm) x length (cm) x 0.8. In most cases, the leaf area for the leather leaf was relatively small, ranging from 0.7 to 3.36 cm^2 with the mean 1.61 cm^2 . The average leaf area for sedges was more evenly balanced with values between 1.0-2.67 cm^2 with a mean value of 1.72 cm^2 .

Measurements of vascular plant CO_2 uptake were performed twice monthly between 9AM and 4PM. Cloudy and rainy days were avoided because the purpose was to diminish differences in environmental conditions surrounding the leaves between measurements and to simulate days when the leaf's photosynthetic capacity was high.

Gas exchange of Sphagnum moss

Due to difficulties with measuring *Sphagnum* spp. with a Licor 6400, chamber methods (Moore *et al.* 2002) were used instead to measure the gas exchange of *Sphagnum* moss. A small clear cylindrical plexiglass chamber was used with diameter of 10.46 cm and inner volume of 1.295 dm³. Permanent round plastic collars (diameter of 10.46 cm and 10 cm deep) were installed into the peat at all plots, where the chamber was mounted on during the measurements (Figure 6). Sites for collars were chosen with very few vascular plants, but if any occurred in the collars they were picked or cut out to eliminate the photosynthetic gas exchange from vascular plants. The chamber was mounted with a battery operated fan for the mixing of air. Field measurements were done using an EGM-4 environmental gas monitor (PP-Systems; Amesbury, Massachusetts, USA), which monitors the CO₂ concentrations in the chamber. Both light (NEE) and dark measurements (ER) were carried out with the chamber. Before the measurements started, the chamber was placed on a collar and left to equilibrate until steady mixing ratio occurred. Typically for 20-30 seconds, which was indicated by steady increase or decrease in CO₂ concentration inside the chamber (Chimner *et al.* 2010). NEE measurements were conducted first and lasted 120 seconds with readings recorded every 5 seconds. After the measurement the chamber was taken off from the collar and flushed with ambient air for ~2 minutes since chambers cannot be held on place for extended periods because they start to alter evapotranspiration and temperature (Goulden and Crill 1997). Then the chamber was placed again on collar for ER measurement, covered with opaque cloth and same procedure was repeated. The Infra-Red Gas Analyzer (IRGA) uses the chamber volume and plot area to calculate the gas mixing ratio from linear or near-linear change in headspace CO₂ concentration over the measurements period (Alm *et al.* 1999). GEP was later calculated by summing ER with the NEE (GEP=NEE+ER).

Measurements of Sphagnum growth

Sphagnum growth and production was measured in order to compare it with *Sphagnum* gas exchange measurements. Vertical growth of *Sphagnum* was measured by installing 48 cranked wires (Clymo 1970) per plot (864 total) on 30th of May,

2010. Wires were measured again on October 15th, 2010 to quantify vertical growth during the growing season. Ten bulk density samples were collected for each five *Sphagnum* species present at plots, samples were oven dried at 70°C for 48 hours and weighed. Vertical growth of each *Sphagnum* species was correlated with bulk density samples of *Sphagnum* biomass to calculate the biomass increment (NPP) in g m².

Data analysis

Uptake of CO₂ by plants was analyzed using three-way ANOVAs with treatment, species and topography set as independent variables. A separate two-way ANOVA was run for sedge and leather leaf with topography and treatment set as independent variables. To measure treatment effect for *Sphagnum* growth, one-way ANOVA was used. All analyses were carried out using Systat statistical software (Systat Software, Inc., Chicago, IL).

Results

The summer of 2010 had lower than average precipitation during July and August. This resulted in continuous water table drawdown through the season until the beginning of September (Figure 7). Photosynthetic uptake of vascular plants dropped by the middle of September while *Sphagnum* moss remained photosynthetically active until October (data not shown). IR-lamps raised the average soil temperature at 5 cm depth in 2010 summer months by more than 1.4°C and also increased canopy temperatures compared to control plots. OTC's had similar soil temperatures compared to control plots but experienced small cooling effect on mid-days (Chris Johnson, unpublished data).

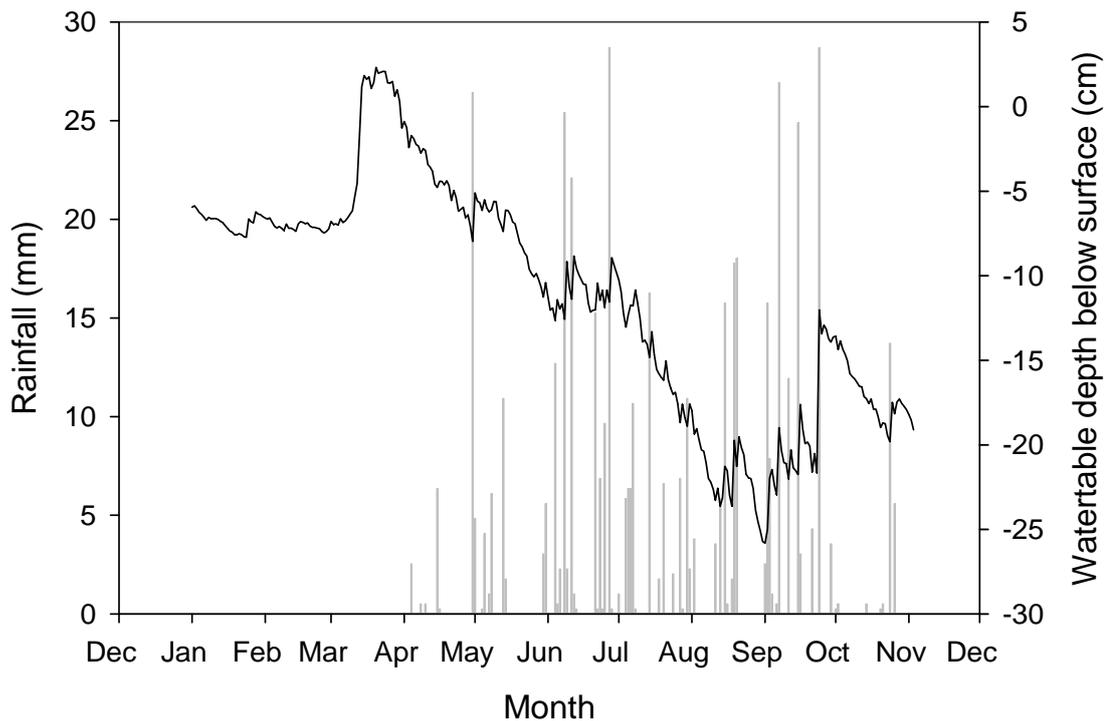


Figure 7. Water table depth and precipitation amounts (study period only) at Pequaming during 2010. Water table depth marked as solid black line and precipitation as gray bars.

Vascular plants

Average CO₂ uptake of leatherleaf was not significantly different (Table 2) between the hummocks and lawns, averaging 9.8 μmol of CO₂ m⁻² s⁻¹ (Figure 8). The control plots had the highest average rate of CO₂ uptake over the growing season (9.58 μmol of CO₂ m⁻² s⁻¹) (Figure 8). Warming was found to significantly lower CO₂ uptake (P=0.049, Figure 8), averaging 8.20 μmol of CO₂ m⁻² s⁻¹ under OTC treatment and 7.78 μmol of CO₂ m⁻² s⁻¹ with the lamp treatment. Water table depth was correlated with leatherleaf stomatal conductance (Figure 9), and CO₂ uptake by leatherleaf (Figure 10). Stomatal conductance of leatherleaf in lawns tended to be lower with warming, but not significantly (P=0.2, Figure 11).

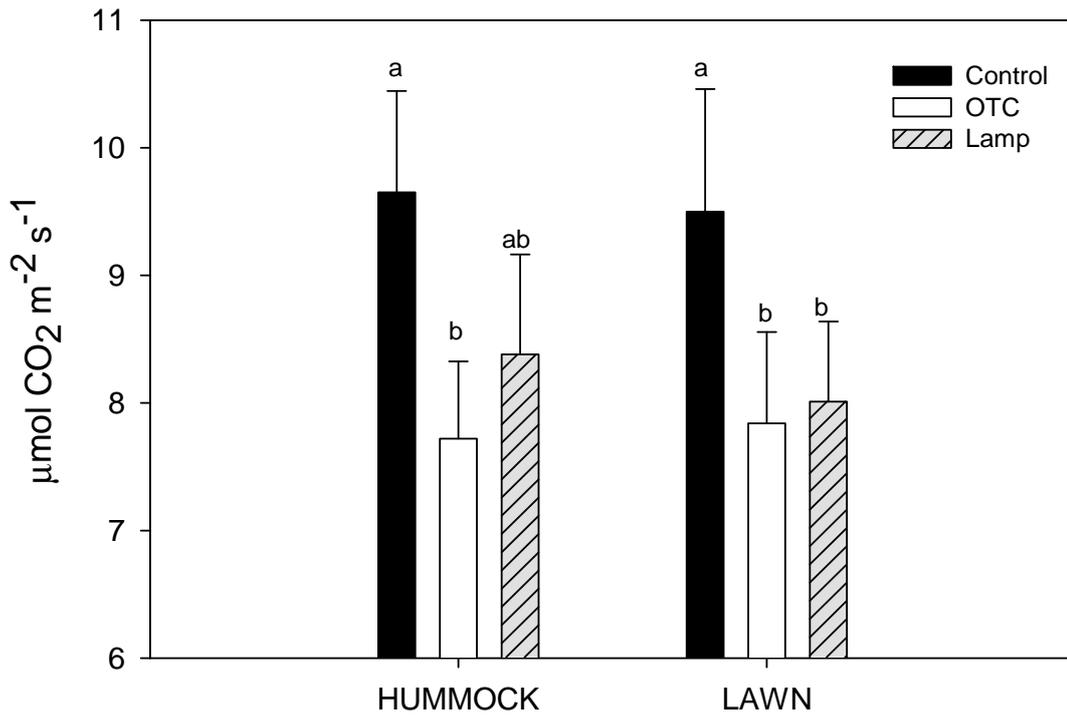


Figure 8. Average (se) CO₂ uptake of Leatherleaf (*Chamaedaphne calyculata*) in two different microtopography features and two different warming treatments. Positive values indicate CO₂ uptake by leatherleaf.

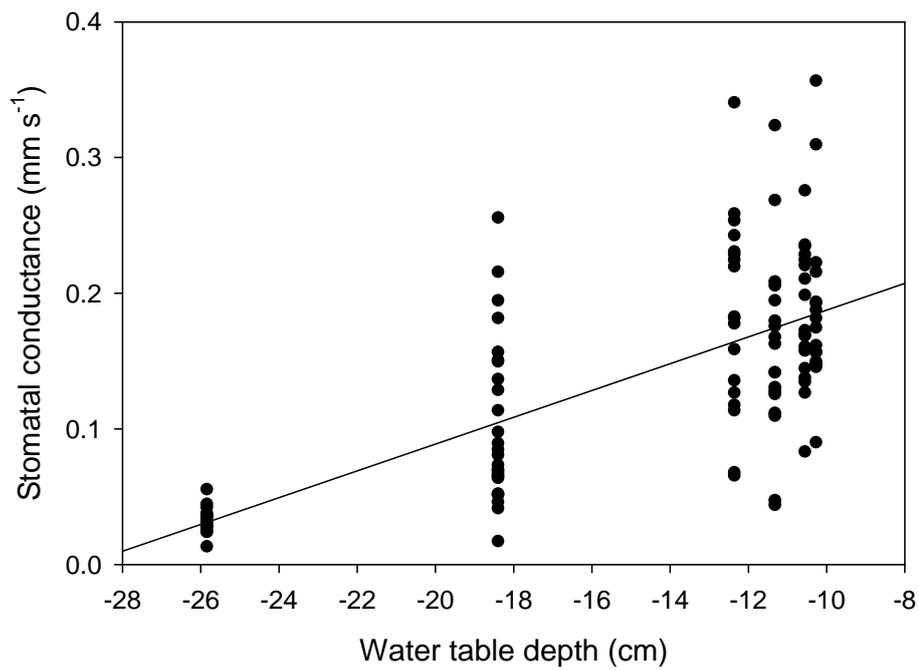


Figure 9. Correlation between water table depth (cm) and leatherleaf stomatal conductance. Larger values of stomatal conductance indicate the openness of stomata.

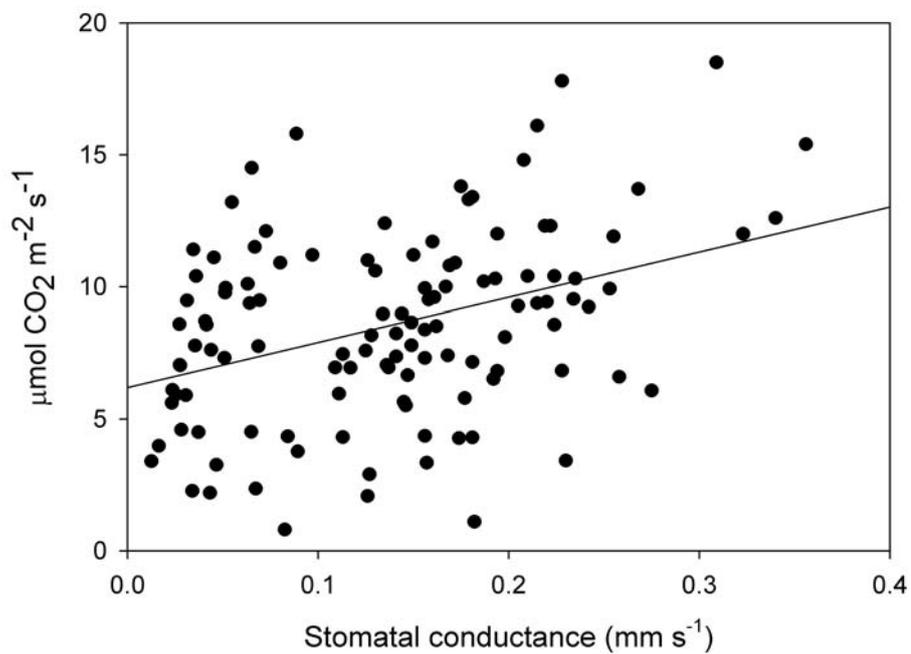


Figure 10. Correlation between leatherleaf stomatal conductance and CO₂ uptake.

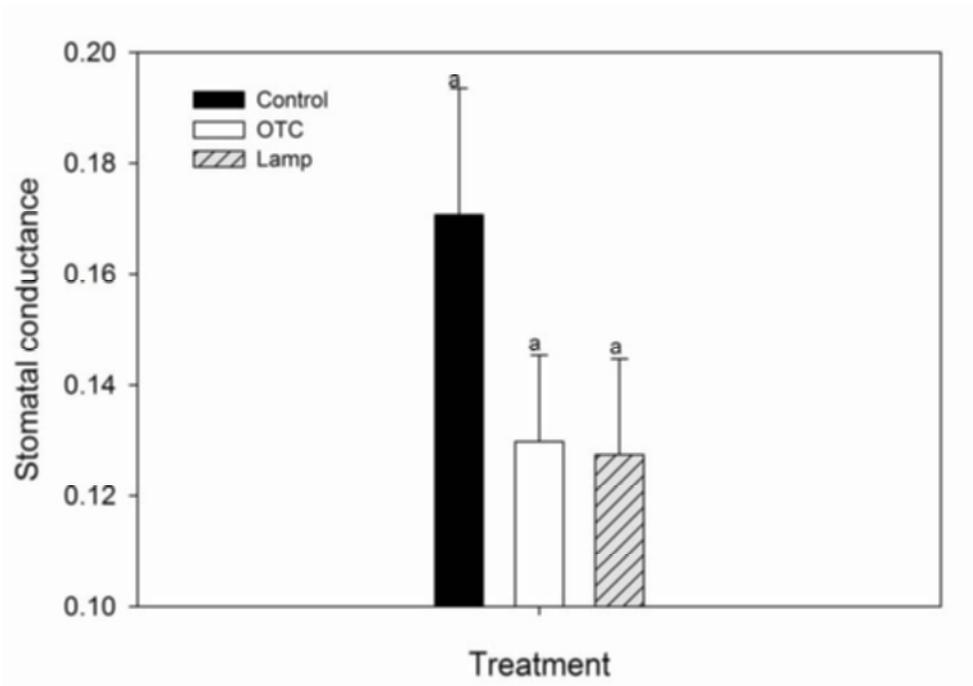


Figure 11. Average (se) warming treatment effect on stomatal conductance (mmol s^{-1}) of leatherleaf in lawns. Larger values of stomatal conductance indicate openness of stomata.

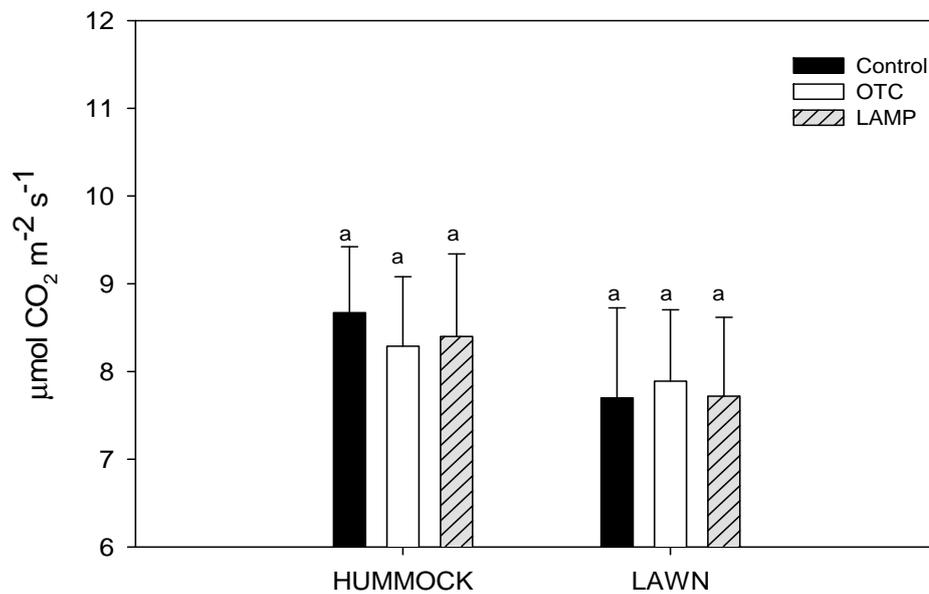


Figure 12. Average (se) CO₂ uptake of Sedge (*Carex utriculata*) in two different microtopography features and two different warming treatments. Positive values indicate CO₂ uptake by sedge.

Average CO₂ uptake of the sedge in the control plots (8 μmol) was found to be slightly lower than the leatherleaf control plots (Figure 12). Average CO₂ uptake was slightly greater in the hummocks than lawns, but the difference was not significant. There were also no significant differences found in CO₂ uptake with warming, nor a warming x microtopography interaction (Table 3).

Sphagnum moss

GEP of *Sphagnum* was not significantly different between lawns and hummocks (Figure 13). Pooled across microtopography, GEP was significantly greater under the lamps compared to the unwarmed control. In fact, GEP was almost 3 times as large. However, there was no significant difference between the OTC's and controls (Figure 13).

Similar to GEP, ER was significantly greater under lamps compared to the controls (Table 5), 5.6 and 2.8 μmol of CO₂ m⁻² s⁻¹, respectively. There was also no significant ER differences between the OTC's and control plots (P<0.18, Figure 13).

Average net ecosystem exchange (NEE) varied significantly between the warming treatments (Table 4). OTC's and control had similar average rates of NEE (2.33 and 2.83 58 μmol of CO₂ m⁻² s⁻¹, respectively), while the lamps had significantly greater NEE (P<0.001, Table 4) rates (8.42 μmol of CO₂ m⁻² s⁻¹). Microtopography was not a significant factor, but there was a near significant affect with the interaction of microtopography and warming (Table 4, P=0.07).

In sharp contrast to chamber based gas flux measurements, *Sphagnum* biomass production was greatest in control plots and decreased significantly with both warming treatments (Figure 14 & Table 6). This was mostly caused by decreased biomass production in the hummocks (Figure 15). In the lawns there was no significant difference with warming, but the biomass accumulation was lower compared to the hummocks (Figure 16).

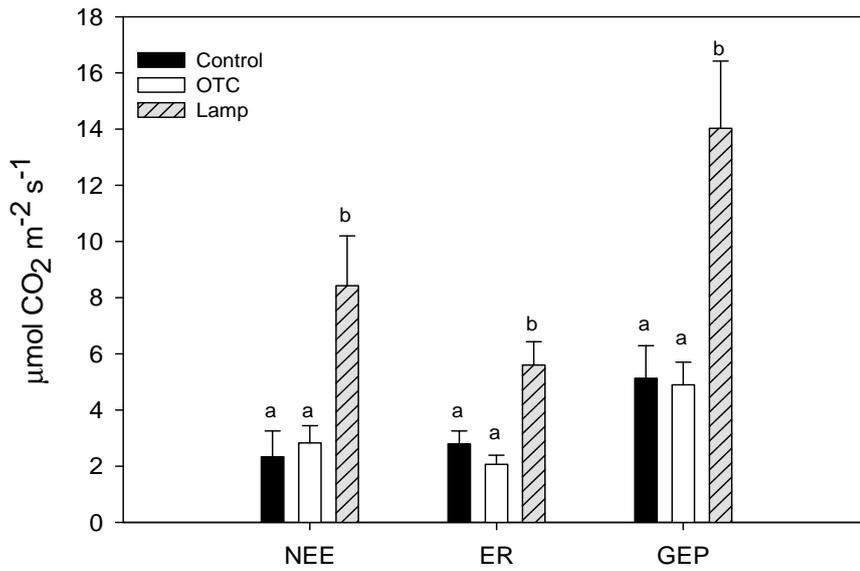


Figure 13. Average (se) CO₂ exchange by *Sphagnum* moss over two different microtopography features and two different warming treatments. Positive values of NEE indicate the amount of CO₂ taken up from the atmosphere and positive values of ER the amount of CO₂ released to the atmosphere by *Sphagnum*.

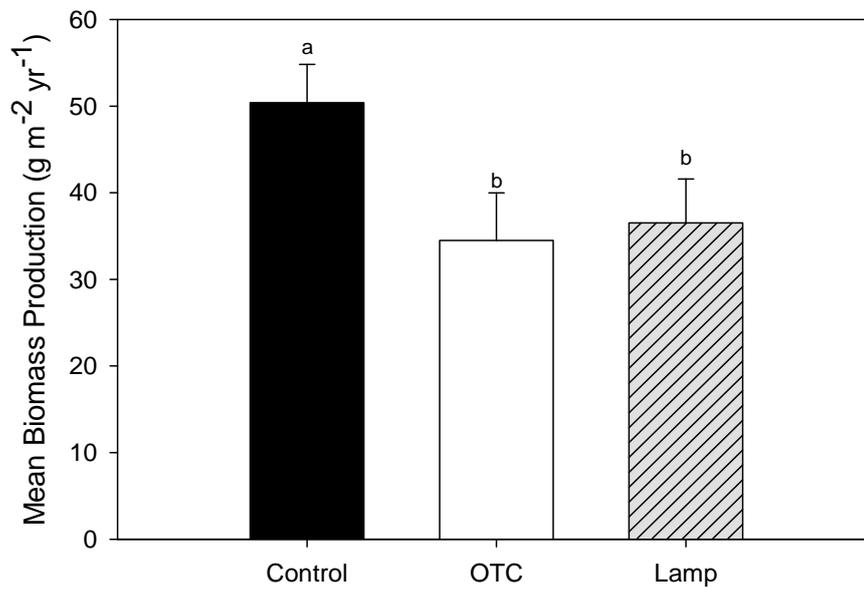


Figure 14. Mean (se) *Sphagnum* biomass accumulation from 30th of May to 15th of October 2010.

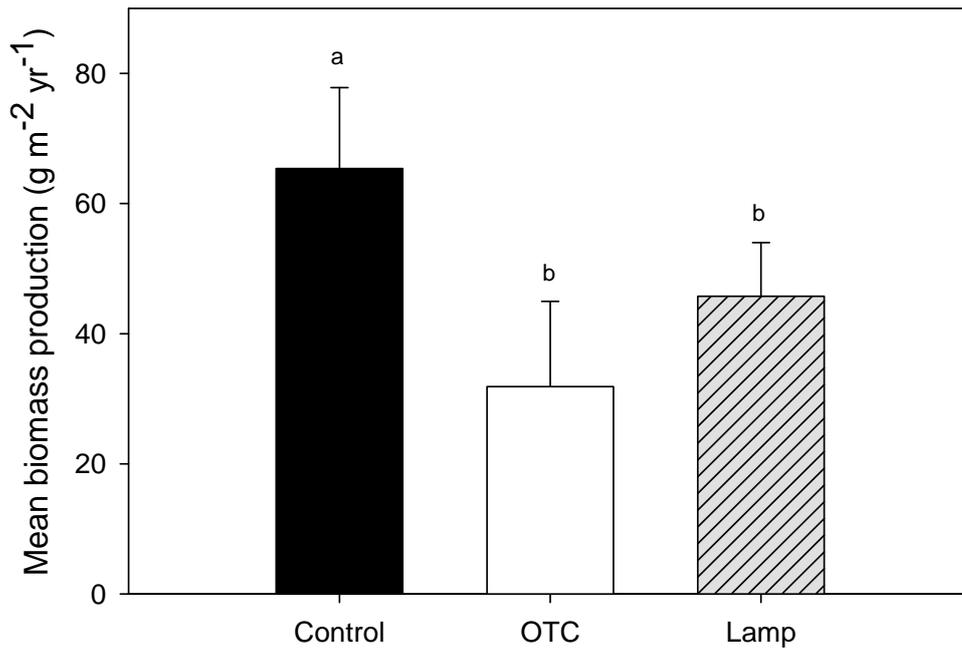


Figure 15. Mean (se) biomass production of *Sphagnum* moss on hummocks.

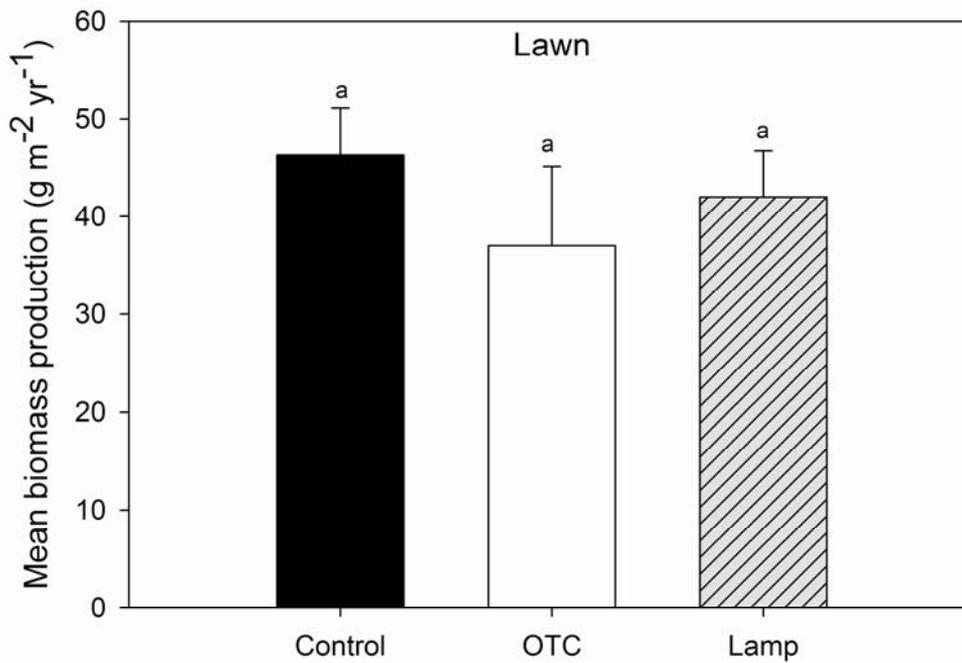


Figure 16. Mean (se) biomass production of *Sphagnum* moss on lawns.

Volumetric water content at 12 cm depth was lower in hummocks than in lawns indicating the importance of the water table depth on *Sphagnum* moss photosynthesis (Figure 17 & 18). Water content was related to *Sphagnum* NEE in lawns (Figure 19). Warming did not have an effect on *Sphagnum* moss moisture content. Highest vapor pressure deficit of the leaf (VpdL) occurred at August, early September (Figure 20). Simultaneously with high VpdL and low amount of precipitation, *Sphagnum* NEE ceased in most study plots and was especially visible in hummocks (Figure 21).

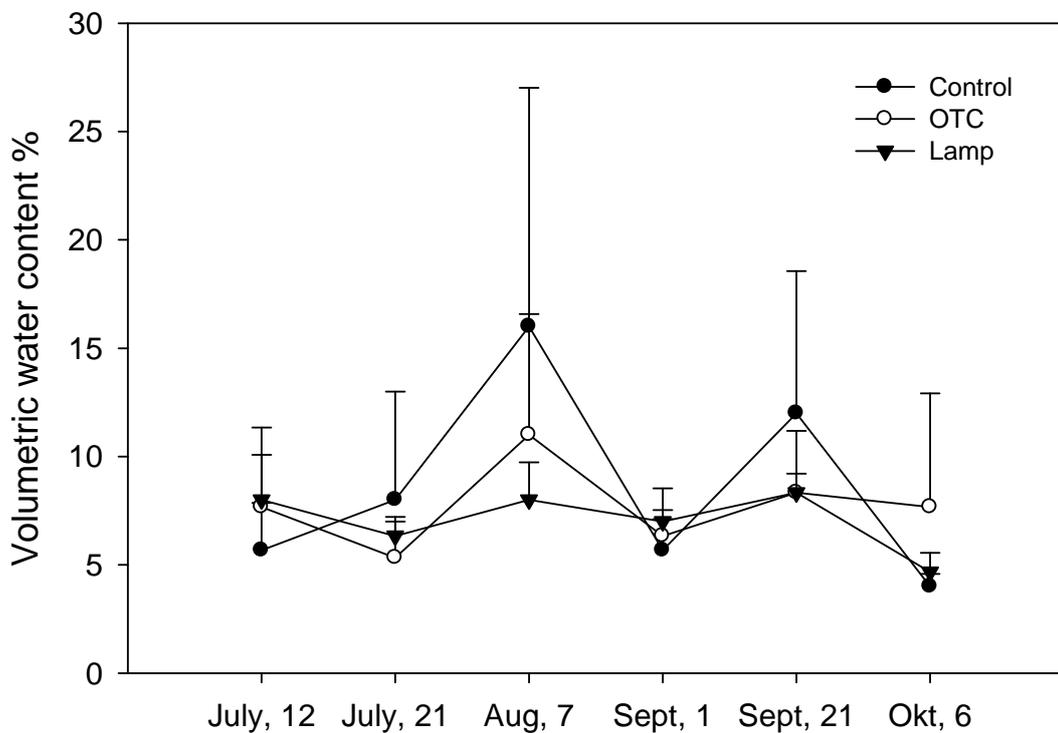


Figure 17. Average volumetric water content (se) of *Sphagnum* moss in hummocks, 12 cm beneath the surface. Lines help to clarify trends but do not indicate changes in volumetric water content between measurement days.

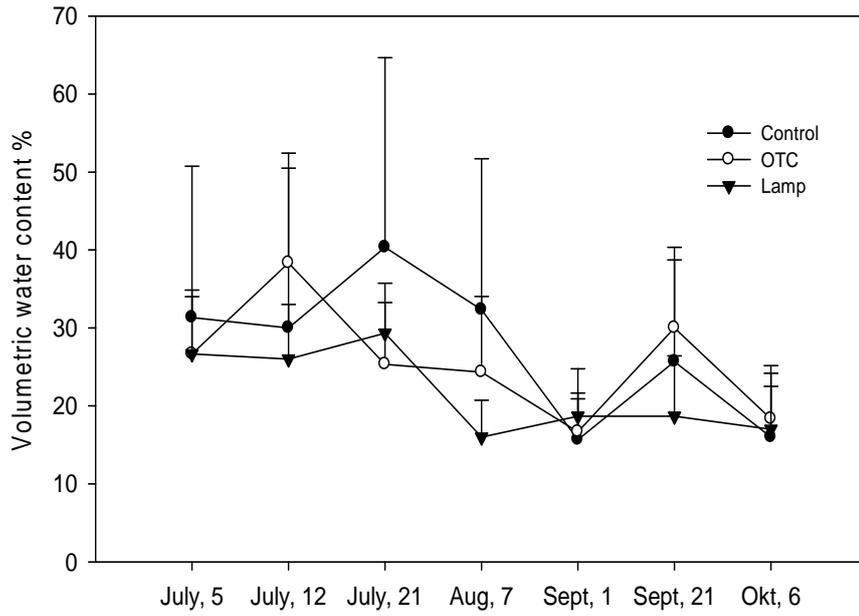


Figure 18. Average volumetric water content (se) of *Sphagnum* moss in lawns, 12 cm beneath the surface. Lines help to clarify trends but do not indicate changes in volumetric water content between measurement days.

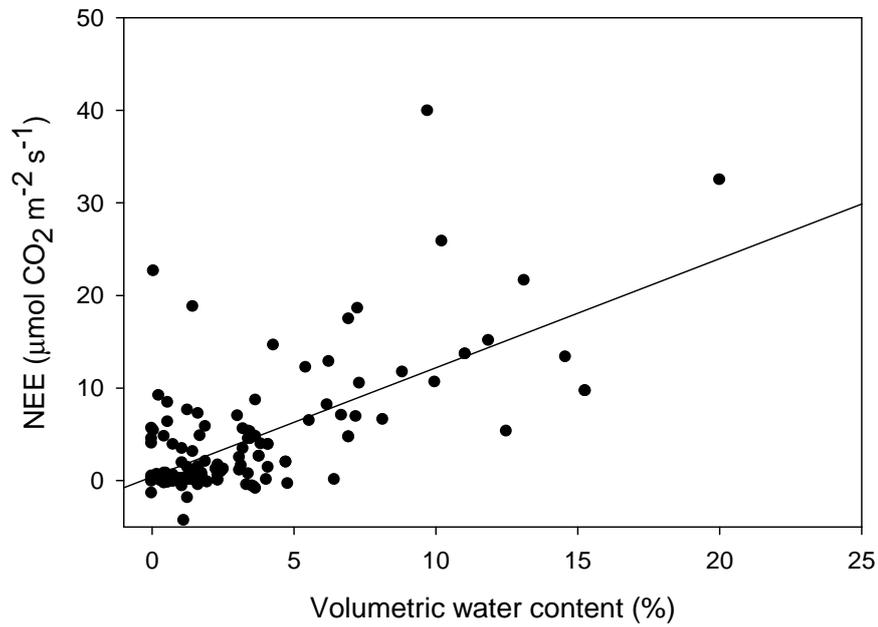


Figure 19. Correlation between volumetric water content 12 cm beneath the surface and *Sphagnum* NEE in lawns.

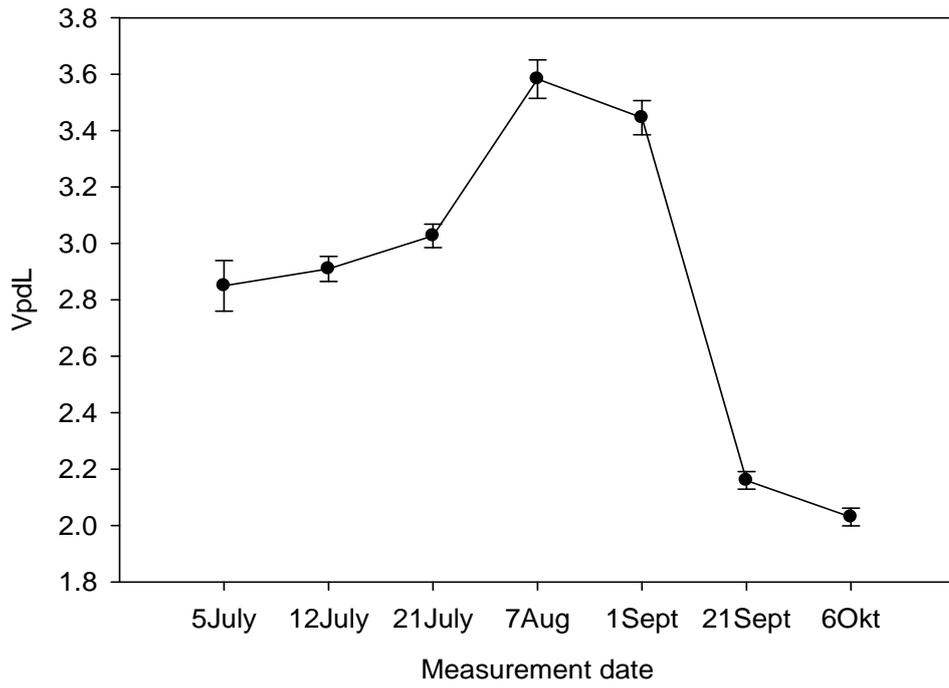


Figure 20. *Sphagnum* vapor pressure deficit (se) by date.

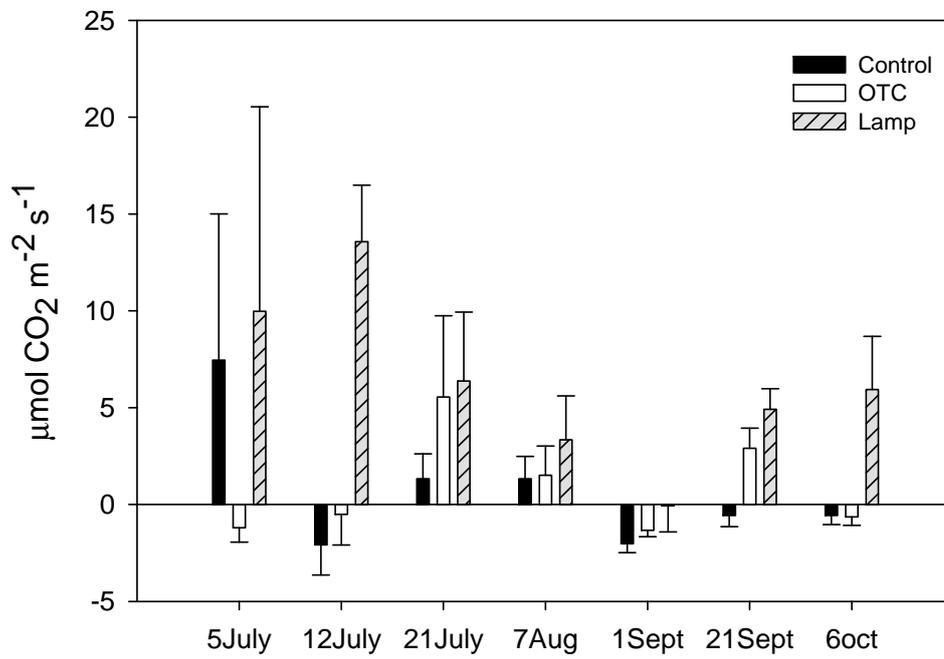


Figure 21. *Sphagnum* NEE (se) in hummocks by date.

Discussion

Vascular plants

The two vascular plants in our study responded differently to experimental warming. Our results were contradictory to our hypothesis that vascular plants should increase their CO₂ uptake. We found no difference in sedge CO₂ uptake between warmed and control treatments, while the rate of CO₂ uptake of leatherleaf dropped under both of our warming treatments independent of microtopography.

Our results are similar to those of (Weltzin *et al.* 2000), who found that *Carex limosa*, *C. lasiocarpa* and *C. livida* production was unaffected by IR warming in a fen mesocosm study in Minnesota, USA. Sullivan *et al.* (2008) also found that leaf length growth and CO₂ uptake of *Carex bigelowii* did not change with OTC warming in a high arctic sedge fen in Greenland. However, long-term (25 yrs.) study in the Arctic found that increased temperatures increased *Carex aquatilis* and *Carex membranacea* above- and belowground biomass (Hill and Henry 2011).

Contrary to our finding, bog monolith mesocosms treated with IR lamp warming showed no difference in leatherleaf aboveground NPP (Weltzin *et al.* 2000). In addition, OTC warming in the high arctic significantly increased stem growth of shrub *Salix arctica* in hummocks (Sullivan *et al.* 2008). Although most of the increased growth was invested above ground through a doubling of stem length growth and probably increased leaf area, increases in root growth was also measured (Sullivan *et al.* 2008). Simultaneous increase in shrub *Betula nana* height growth with increased *Sphagnum* growth has been observed in OTC warming treatments (Dorrepaal *et al.* 2006).

These studies indicate that the physiology of these sedge species was not affected by warming and at higher temperatures they may not take up more carbon. Since the Pequaming field site is a poor fen, there are relatively few sedges and the amount of available nutrients and competition pressure might have limited sedge response to warming. That might be the reason why our initial hypothesis proved to be incorrect. Similarly, *Carex oligosperma* aboveground primary productivity in bog

community did not respond to IR lamp warming (Weltzin *et al.* 2000). Sedges have been shown to have high growth rates and are influenced by nutrient addition (Aerts *et al.* 2006). Short-term warming manipulations do not increase nutrient availability since there is time lag of over 3 years between the initiation of a warming experiment and ecosystem response in nutrient availability (Chapin *et al.* 1995). An experiment in Alaskan sedge meadows showed that biomass production did not respond to short-term changes in temperature (Rydin and Jeglum 2006). However, a long-term (25 yrs.) warming study in Arctic measured an increase in *C. aquatilis* and *C. membranacea* above- and belowground biomass (Hill and Henry 2011). This increase probably was due to increased decomposition and mineralization in soil (Hill and Henry 2011). Because of the competition pressure and nutrient deficiency in our study, sedges may not have been able to take up more CO₂ even if the temperature increase would be beneficial for sedge growth.

Our finding of a decline in leatherleaf CO₂ uptake could be related to drier than average growing season and low water table levels. Shrub aboveground NPP seems to be related to site wetness; bogs and poor fens have much higher shrub NPP than rich fens (Szumigalski and Bayley 1997). During the growing season, the water table gradually declined to 25 cm below the surface. Low water table resulted in lower stomatal conductance. Stomatal conductance is directly linked to the photosynthesis since plants need to keep the stomata open in order to photosynthesize (Lambers *et al.* 1998). At the same time, we did not find significant differences in stomatal conductivity nor Vpd of the leaf between the warming treatments. Therefore, we cannot confirm why CO₂ uptake decreased. One possible reason is that decreased N content in leaf due to decreased N availability in the soil. Leaf N content is vital for photosynthesis since more than 50% of the N in plant appears in leaf's photosynthetic apparatus, especially in enzyme Rubisco which drives photosynthesis (Lambers *et al.* 1998). Leatherleaf is probably not at the thermal limit in the region since it can be found in much southerly locations (Myneni *et al.* 1997).

Sphagnum gas exchange

The limited amount of studies focusing on CO₂ uptake of *Sphagnum* have generally been community scale responses to temperature where *Sphagnum* has been the dominant plant species (Silvola *et al.* 1996; Sullivan *et al.* 2008; Updegraff *et al.* 2001). We hypothesized that increased temperatures would reduce *Sphagnum* CO₂ uptake but the opposite was observed with IR lamps. OTC warming resulted in no change at *Sphagnum* CO₂ uptake compared to control plots, which means that our third hypothesis proved to be true. In our study, IR lamp warming increased NEE, ER and GEP of plots covered only by *Sphagnum* spp. Increase in NEE exhibits positive effect of temperature on *Sphagnum* photosynthesis. This might indicate that *Sphagnum* is not at its thermal limit and might be able to photosynthesize faster at higher temperatures. There was also a simultaneous increase in both ER and GEP. ER is dependent on water table position and temperature (Moore *et al.* 1998; Updegraff *et al.* 2001). In our case ER rose significantly under IR lamps, which had much higher soil warming than the OTC's. The IR lamps raised the average soil temperatures by 1.4°C while OTC's had similar soil temperatures compared to control plots (Chris Johnson, unpublished data). Similarly, Updegraff *et al.* (2001) observed an increase in ER in both bog and fen plant communities under IR lamp warming while the water table depth had no significant influence (Updegraff *et al.* 2001). In our study, the water table depth stayed in upper 25 cm for most of the growing season and IR lamp warming had positive effect on ER compared to control, which resulted in a 100% increase. Since we did not modify water table levels between treatments, we can conclude that IR lamp warming increased ER in our study.

In nutrient poor ecosystems, like boreal peatlands, warming has been found to enhance ER (Chapin 1983). Summarized findings from different ecosystems indicate exponential relationship between temperature and ER (Lloyd and Taylor 1994). Increase in ER indicates the increase either in plant biomass, and therefore plant respiration, or an increase in soil respiration (Sullivan *et al.* 2008). Both plant production and ER are positively influenced by temperature, but ER increases more in short time scale warming treatments (Woodwell 1995). CO₂ fluxes from soils were found to be influenced by temperature much more if the water table is 0-20 cm

beneath the surface compared to lower water tables (Q_{10} value of 4.9 and 1.3, respectively)(Weltzin *et al.* 2001). The same temperature effect for water table depths of 0-20 cm (Q_{10} value being 2.9) has been shown by (Silvola *et al.* 1996). Temperature and water table level play significant role in carbon cycling of boreal peatlands. CO_2 fluxes from boreal peatlands have shown to rise up to 10 times if you compare fluxes under $10^\circ C$ with high water table levels and summertime CO_2 fluxes with lowered water table (Silvola *et al.* 1996). Summer ER might be higher than CO_2 uptake of bog plant community, resulting in negative NEE (Alm *et al.* 1999; Moore *et al.* 2002). At present, peatlands can be sources for CO_2 at current summer temperatures (Burrows 2005). Drier than average summers resulted in water table level 15 cm below surface which resulted in increased ER which exceeded NPP in study by Alm *et al.* (1999). This all indicates that during the summer, when water table levels drop and peat is exposed to aeration, ER increases due to higher temperatures and could be even higher than CO_2 uptake by vegetation.

Sphagnum NPP

Our seasonal *Sphagnum* NPP measurements were contradictory to our daytime gas flux measurements. Increased CO_2 uptake by *Sphagnum* should increase seasonal NPP, but the opposite was observed. While this reduction was evident in both hummocks and lawns, it was significantly greater only in hummocks where *S. fuscum* was dominant. This indicates that while *Sphagnum* is able to take up more CO_2 at higher temperatures, it is vulnerable to moisture availability. Our results are contradictory to studies where summer warming increased *Sphagnum* growth (Dorrepaal *et al.* 2004; Dorrepaal *et al.* 2006; Sonesson *et al.* 2002). OTC warming in northern Sweden increased *S. fuscum* summer length increment by 62 and 42% in two consecutive years after the warming treatment was set up (Dorrepaal *et al.* 2004). Even though the warming also reduced bulk density of *Sphagnum*, the biomass accumulation increased. Also Sonesson *et al.* (2002) found increased *S. fuscum* length increment in warming treatments. When combined with additional precipitation of 1 mm per day, the length increment rose by 50% in spring and 33% in peak growing

season. However, IR lamp warming of boreal peatland mesocosms did not increase *Sphagnum* production in Minnesota (Weltzin *et al.* 2001).

Our observed reduction in *Sphagnum* NPP might be due to water stress since *Sphagnum* production is highly water dependent (Titus *et al.* 1983; Weltzin *et al.* 2001). Our observed reduction in NPP was greater in hummocks, which are even further away from the water table. The summer of 2010 had less than average amount of precipitation, especially in July and August. Vapor pressure deficit of the leaf was significantly higher in August and early September compared to July or October (Figure 20). During the growing season, the water table fell gradually, reaching a minimum of 25 cm below the lawn surface by the end of August. During measurement days in August, the *Sphagnum* photosynthesis was decreased at most study plots since the capitulum was dry and had a bleached color (Figure 21). Just before the next measurement (September 2010), there was a small precipitation event (2.5 mm) in the morning, which allowed photosynthesis to recover. Small precipitation events less than 5 mm have the same effect on capitulum moisture content as a rise in water table level of 20 cm, and has major implications on photosynthesis (Strack and Price 2009). These small events moisten the capitulum and therefore have big implications on photosynthesis since *Sphagnum* does not possess roots. Water is essential in maintaining photosynthetic capacity for *Sphagnum* and water lost in evaporation must be replaced from water table (Schipperges and Rydin 1998). Height of the water table determines the *Sphagnum* capitulum moisture content; moisture content decreases with decreasing water table levels (Titus *et al.* 1983). We found that NEE was influenced by the moisture content at 12 cm depth in lawns (Figure 19).

Volumetric water content in upper 10 cm of soil is dependent of the water table depth in upper 55 cm of peat (Strack and Price 2009). *Sphagnum* abundance has shown to decline if water table levels are lower than 50 cm beneath the surface (Moore *et al.* 2002). Lower water table resulted in 50-80% reduction of *Sphagnum* NPP between two years of measurements (Szumigalski and Bayley 1997). Additionally, *S. fuscum* growth has been shown to be highest when water table is 0-10 cm below the capitulum (Jauhiainen *et al.* 1997). In our study the water table level fell

as low as 25 cm beneath the surface while *Sphagnum fuscum*, the dominant *Sphagnum* species on hummocks where the reduction in NPP was significant, was elevated even further away from the water table. *Sphagnum* production seems to be correlated to the height of the water table since low microtopography has 100% higher NPP values than high microtopography (Weltzin *et al.* 2001). Similarly in the same study, warming did not increase *Sphagnum* production, instead it was more influenced by the water table. In Alaska, optimum water content for photosynthesis for *Sphagnum* mosses was 6-10 times the dry weight, below that the photosynthesis starts to decrease (Murray *et al.* 1989). If *Sphagnum* capitulum is dry for extended periods, growth has been found to be reduced (Schipperges and Rydin 1998). Desiccation experiments showed that *Sphagnum* is able to recover to some extent from short desiccation periods, but is not able to recover after 12 days of desiccation (Schipperges and Rydin 1998). Because of the low water table level and high VpdL from August to September, the reduction in NPP might have occurred between the measurement days. Both warming treatments might have increased canopy temperatures and therefore higher evapotranspiration compared to control plots making water even less available for photosynthesis.

Another aspect which could have influenced the reduction of *Sphagnum* NPP in our study is an increase in nighttime plant respiration. Like all biological processes, plant and soil respiration increases with higher temperatures (Woodwell and Whittaker 1968). During the nighttime when no photosynthesis occurs, it can result in greater CO₂ losses compared to nights with lower soil temperatures. Nighttime soil respiration has been linked to temperatures at 5 cm depth (Goulden and Crill 1997) and areas with greater plant cover have been shown to lose more CO₂ at night, indicating the role of root respiration in nighttime soil respiration (Billings 1987).

Conclusions

Neither of the vascular plants increased CO₂ uptake under warming, which is contrary to our hypothesis. We expected that short term warming would increase vascular plant photosynthesis, while long-term warming would cause nutrient

limitations and inhibit photosynthesis (Shaver *et al.* 2000). It is possible that the low nutrient status of our site might have influenced the non-responsiveness of sedges to warming. Leatherleaf decreased its CO₂ uptake at higher temperatures which again is against our hypothesis. Low water table level might play a role here since water table is able to influence stomatal conductance of leatherleaf. But we still could not find any evidence behind the drop in leatherleaf CO₂ uptake. Our hypothesis that *Sphagnum*'s CO₂ uptake will drop turned out to be disproven as *Sphagnum* was able to increase its CO₂ uptake under IR lamp warming, while this increase in CO₂ uptake seems to be dependent on moisture availability. However, *Sphagnum* NPP decreased. Current climatic predictions indicate that precipitation in northern latitudes will increase (IPCC 2007), however most of the precipitation increase will probably happen during the wintertime (Dorrepaal *et al.* 2004; Houghton 2005; Prentice *et al.* 1991). Our results indicate the importance of summer precipitation to *Sphagnum* biomass accumulation. *Sphagnum* has shown to gain competitive advantage over *Dicranum elongatum* in natural mixtures of these two species if both temperature and precipitation increase (Sonesson *et al.* 2002). Since higher temperatures are able to increase evapotranspiration (Gignac and Vitt 1994; Mitchell 1989), summertime water table height and precipitation events become even more important. Our study demonstrates that *Sphagnum* is not at its thermal limit in sub-boreal climatic zone but future summertime precipitation amounts and patterns will determine its vitality in this ecosystem.

Tables

Table 1.

Average percent (%) cover of plant species by treatment and microtopography. *Sphagnum* and vascular plants are divided into two vegetation layers, each summing up to 100%

Species	Hummock			Lawn		
	Control	OTC	Lamp	Control	OTC	Lamp
<i>Picea mariana</i>	32%	2%	7%			
<i>Chamaedaphne calyculata</i>	19%	27%	37%	6%	1%	22%
<i>Vaccinium oxycoccos</i>	19%	17%	24%	28%	31%	22%
<i>Carex exilis</i>	8%			21%	13%	20%
<i>Carex oligosperma</i>	4%		3%	17%	13%	18%
<i>Ledum groenlandicum</i>	4%	5%	6%			1%
<i>Kalmia polifolia</i>	4%	13%	8%	8%	19%	7%
<i>Andromeda polifolia</i>	3%	17%	4%	8%	10%	4%
<i>Myrica gale</i>	3%	12%		6%	3%	2%
<i>Sarracenia purpurea</i>	1%			2%		1%
<i>Drosera rotundifolia</i>	1%		4%		9%	2%
<i>Larix laricina</i>	1%	4%				
<i>Carex utriculata</i>	1%	3%	1%	4%	1%	1%
<i>Carex pauciflora</i>			6%			
<i>Sphagnum fuscum</i>	59%	30%	82%	1%		
<i>Sphagnum rubellum</i>	27%	7%	5%	63%	57%	62%
<i>Sphagnum magellanicum</i>	10%	60%	13%	1%		12%
<i>Sphagnum papillosum</i>	4%	1%		17%	43%	26%
<i>Sphagnum angustifolium</i>		1%		18%		
<i>Sphagnum capillifolium</i>		1%				

Table 2.
ANOVA results for Leatherleaf CO₂ uptake

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Topography	0.546	1	0.546	0.045	0.83
Warming	74.356	2	37.178	3.091	<0.05
Warming*Topography	1.250	2	0.625	0.052	0.95
Error	1443.365	120	12.028		

Table 3.
ANOVA results for Sedge CO₂ uptake

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Topography	13.212	1	13.212	0.899	0.35
Warming	0.339	2	0.169	0.012	0.99
Warming*Topography	1.697	2	0.849	0.058	0.94
Error	1602.174	109	14.699		

Table 4.
ANOVA results for *Sphagnum* net ecosystem exchange (NEE)

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Warming	961.047	2	480.524	12.630	<0.01
Topography	79.530	1	79.530	2.090	0.15
Warming*Topography	212.678	2	106.339	2.795	0.07
Error	4565.398	120	38.045		

Table 5.
ANOVA results for *Sphagnum* Ecosystem respiration (ER)

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Warming	292.101	2	146.051	12.065	<0.01
Topography	13.731	1	13.731	1.134	0.29
Warming*Topography	7.842	2	3.921	0.324	0.72
Error	1452.593	120	12.105		

Table 6.
ANOVA results for mean *Sphagnum* biomass accumulation

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Warming	129499.7	2	64749.877	34.549	<0.01
Microtopography	0.129	1	0.129	0.000	0.99
Warming*Topography	44124.5	2	22062.292	11.772	<0.01
Error	1892897	101	1874.156		

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