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SOIL HYDROCLIMATE, VEGETATION, AND SUBSTRATE CONTROLS ON CARBON FLUX IN AN ALASKAN FEN

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ABSTRACT

SOIL HYDROCLIMATE, VEGETATION, AND SUBSTRATE CONTROLS ON CARBON FLUX IN AN ALASKAN FEN

By

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Peatlands store 30% of the world's terrestrial soil carbon and are located primarily at northern latitudes, where they are expected to experience severe climate warming. The goal of my thesis was to determine the effect of experimental soil climate manipulations on carbon (C) fluxes in an Alaskan rich fen and to assess the indirect influence of substrate quality on C mineralization rates in peat. I monitored growing season CO_2 fluxes across a factorial design of *in situ* water table and soil warming treatments. The lowered water table treatment did not alter ecosystem respiration (ER) of CO_2, but lowered gross primary production (GPP), making this plot more of an atmospheric source relative to the control. Relative to the control, the raised water table treatment had more positive NEE values in 2005, but was a greater C sink in 2006 due to increased early season GPP. To investigate the effect of the manipulations on carbon mineralization through changes in soil organic matter (SOM) quality, I measured CO_2 and CH_4 production from incubations at standard laboratory conditions. While CH_4 production rates were not affected by the manipulations, peat taken from the warmed subplots and lowered water table plot had the lowest CO_2 production rates, indicating a decrease in SOM quality induced by these climate treatments. My results suggest that climate change will impact peatland C fluxes to reduce ecosystem C storage under drought and to increase ecosystem C storage with flooding conditions.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1 Climate change and projections for high latitudes

Since the industrial revolution in the 1700's; human activities, including deforestation and the burning of oil, coal, and gas, have increased greenhouse gas (carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O)) concentrations in the atmosphere by 36%, 150%, and 15%, respectively (National Research Council 2001). Because greenhouse gases absorb and emit heat, their rising atmospheric concentrations have a warming effect on the Earth. This warming is expected to be greatest in northern high latitudes due to feedbacks from snow and sea ice, the stability of the lower troposphere, and thawing of permafrost (Houghton et al. 1992, Ramaswamy et al. 2001, Serreze et al. 2000).

Climate models project that the North American boreal forest will experience more warming than any other terrestrial forest biome, with the greatest warming occurring in the continental interiors (National Research Council 2001). Northern soils in boreal and subarctic regions store large amounts of C that has slowly accumulated since the last deglaciation (Harden et al. 1992). Boreal regions contain approximately 27% of the world's vegetation C (McGuire et al. 1997) and 25 - 30% of the world's soil C (estimated between 397-455 Pg or 10^{15} g C; Gorham 1991; Zoltai & Martikainen 1996, Moore et al. 1998). Multiple impacts of climate change including degrading permafrost (Romanovsky & Osterkamp 1997), reduced snow cover (Magnuson et al. 2000), and longer growing seasons (Serreze et al. 2000) are likely to impact plant and soil processes, which will impact C cycling in boreal regions.

Many regions are classified as "boreal" and grouped together for research purposes. However, boreal regions cover a wide area (18.5 million km^2; McGuire et al. 1995) and represent a large range in climate and topography. While many boreal regions are characterized by large, flat glacial lake plains, interior Alaska is bordered on the north and south by the Alaska Range and the Brooks Range, which successfully block coastal air masses resulting in a continental climate with cold winters (extremes of -50°C in January) and warm, relatively dry summers (highs over +33°C in July). Due to its high latitude, Alaska is characterized by drastic seasonal fluctuation in day length (more than 21 hours on June 21 and less than 4 hours on December 21; Hinzman et al. 2006). Additionally, interior Alaska has a short growing season (135 days or less from early May to mid-September) and minimal precipitation due to a montane rain shadow (the average annual precipitation is only 269 mm in Fairbanks, 30% of which falls as snow; Slaughter and Viereck 1986). Because of these differences in climate and topography, ecosystems in Alaska, likely will respond differently to climate change than ecosystems in Canada or Russian boreal regions.

Interior Alaskan soils have warmed rapidly over the past 30 years due to near-surface atmospheric warming of approximately 1° C per decade on average (Osterkamp and Romanovsky 1999). Global climate models predict temperature increases of 2.5 to 6° C and precipitation changes ranging from -10% to 30% for the Fairbanks, Alaska region by 2050 (Canadian Centre for Climate Modelling and Analysis 2003, Hinzman et al. 2005). Remote sensing work in Alaska shows that open water bodies in major wetland regions in Alaska are losing surface area (Riordan et al. 2006), which could be associated with increased summer water deficits due to increased evapotranspiration with climate warming (Hinzman et al. 2005). However, wetlands at the margins of continents may become wetter (Oquist and Svensson 1995) due to thermokarst and permafrost melting (Romanovsky & Osterkamp 1997). In some areas of Alaska, wetlands are becoming more saturated due to permafrost thaw and increased runoff from surrounding uplands, such as the expansion of open water in the Tanana Flats region of interior Alaska (Osterkamp et al. 2000). Thus, while some wetlands in Alaska are drying, others currently are becoming wetter, suggesting that future changes in wetland hydrology could include either drying or inundation due to increased runoff, permafrost thaw, changes in precipitation, and increased evapotranspiration.

1.2 Introduction to boreal peatlands

Peatlands and their distribution in northern regions

Peat, or partially carbonized vegetation, accumulates where C fixation through net primary production (NPP) at the surface exceeds losses from decomposition, leaching, and/or disturbance. Peatlands are defined as any wetland with 40 cm or more of accumulated peat. Approximately 80% of the world's peatlands are in high latitudes. Peatlands globally cover 24% of the circumboreal land area (Wieder et al. 2006) where they cover major portions of Alaska, Canada, Russia, the Baltic Republics, and Fennoscandia (Clymo 1983, Gorham 1991, Vitt 2006). The largest expanse of peatlands is in the boreal regions of Canada, Russia (Siberia), and Alaska (350 x 106 ha; Gorham 1991, Botch et al. 1995).

Five primary factors affect the function of a peatland, including hydrology, climate, substrate, chemistry, and vegetation (Vitt 2006). These "state factors" have been used to classify peatlands into three main types: bogs, rich fens, and poor fens. In bogs, peat is often built up above regional water tables to such an extent that the living vegetation is raised above sources of surrounding surface water or underlying groundwater. These peatlands are ombrotrophic, meaning that they receive water and nutrients solely from precipitation or dry fall. As such, bogs are usually the most nutrient poor and highly acidic type of peatland. Acidity comes from organic acid production with decay and from *Sphagnum* cation exchange capacity. *Sphagnum*, or peat moss, is typically the dominant vegetation type, and because *Sphagnum* species are strong competitors, bogs tend to have low species diversity. Fens are minerotrophic and receive some water and nutrients from ground- or surface- runoff in addition to precipitation. Fens vary from nutrient rich, emergent vascular or brown moss dominated ecosystems with a high species diversity (rich fens), to nutrient poor, *Sphagnum* dominated ecosystems with low species diversity (poor fens). The fundamental differences in hydrology and species composition among these peatland types influence rates of decomposition and productivity, and ultimately peat accumulation rates. For example, studies have found that bogs generally have lower rates decomposition and productivity relative to fens (Frolking et al. 1998, Thormann and Bayley 1997). Even though rich fens represent the most common peatland type in western boreal North America, most boreal peatland research has focused on *Sphagnum* dominated bogs or poor fens (Vitt 2006). Thus, while the peatland research community has some understanding of the response of bog (Alm et al. 1997, Moore et al. 2002, Lafleur et al. 2005) and poor fen (Silvola et al.

1996, Bubier et al. 2003) peat to climatic flux, less is known about rich fens and their vulnerability to climate change. Rich fens will likely differ in their response to climate change relative to these *Sphagnum*-dominated systems, given that brown moss and emergent vegetation respond differently than *Sphagnum* to warming and altered moisture (Weltzin et al. 2005) and systems with high nutrient availability respond differently to climate change than when nitrogen (N) is limited (warming increases net N mineralization rates; Rustad et al. 2000).

In Alaska, about 20% of the landscape is covered by poorly drained ecosystems (Harden et al. 2003). Wetland abundance in interior Alaska is largely influenced by landscape topography (responding to runoff from surrounding areas and permafrost degradation), and thus peatlands tend to form in valley bottoms. Interior Alaskan wetlands also are often found in floodplains that form large wetland complexes, such as the Minto and Yukon Flats. These large wetland complexes often are dominated by tussock marshes or sparsely treed wetlands underlain by permafrost. Areas that are protected from river erosion (i.e., old oxbows) or fire often accumulate peat to form peatlands

Studies of Alaskan peatlands to date largely have focused on southeastern Alaska (Ugolini and Mann 1979, Klinger et al. 1990, Concannon 1995, Hartshorn et al. 2003) or northern tundra ecosystems (Billings 1987, Oberbauer et al. 1992, Klinger 1996). Despite the documented changes in wetland hydrology in interior Alaska (Riordan et al. 2006), few studies have focused on interior Alaskan peatlands and their response to climate change.

Peatland carbon storage and fluxes

Peatlands globally cover only 3-5% of the Earth's terrestrial land base, but contain 30% of the world's terrestrial soil C (between 270 - 370 Pg C; Vasander and Kettunen 2006). Historically, peatlands have acted as a net sink for global atmospheric C, sequestering an estimated 29 g C m^{-2} annually from the atmosphere on a millennial time scale (Gorham 1991, Bartlett and Harriss 1993, Zoltai and Martikainen 1996). In general, peatlands began accumulating peat about 8-10 k years ago in Canada and Siberia and about 4-6 k years ago in Alaska. While estimates are not well constrained, Alaska peatlands today store approximately 41.7 ± 50% Pg of C (Bridgham et al. 2000).

A peat accumulation model developed by Clymo (1992) divides the peat profile into two sections based on the location of the water table. Fast aerobic decomposition pathways dominate the surface acrotelm (unsaturated oxic zone), while slower, anaerobic decomposition occurs in the catotelm (saturated deeper anoxic zone). 80-90% of the C that passes through the acrotelm is lost through decomposition. Therefore, long-term peat accumulation depends on the rate of C transfer to the slowly decomposing catotelm. The input of C to this anoxic zone is typically 10-20% of total vegetation litter production.

In general, peat accumulation occurs because cool, wet conditions in peatlands limit decomposition. Because of their dependence on soil climate, peatlands and their extensive C reservoirs are likely to be altered by climate change (Gorham 1994). Peatlands are strongly controlled by climate, and recent work shows that individual peatlands can switch from net CO_2 sinks to sources between wet and dry years (Shurpali et al. 1995, Alm et al. 1999, Bubier et al. 2003).

Peatlands play a key role in global C cycling by both sequestering and emitting atmospheric CO_2 and by emitting CH_4 to the atmosphere (Moore 1996). Peatlands currently act as a net sink for atmospheric CO_2, sequestering approximately 150 Gt yr^{-1} of C from the atmosphere (Gorham 1991, Gorham 1994). The net ecosystem exchange (NEE) of C is a direct measure of the net CO_2 exchange between ecosystems and the atmosphere. Net ecosystem exchange is the balance between gross primary production (GPP), which is plant C uptake, and ecosystem respiration (ER), which is the sum of heterotrophic and plant respiration. Rates of NEE provide an indication of whether the ecosystem is serving as a net sink or source of atmospheric CO_2. Rates of GPP are zero in the dark, so in dark conditions NEE is also a measure of ER. Root respiration and decomposition are the primary mechanisms contributing to CO_2 emissions from peat (Moore and Knowles 1987). Air and soil temperature, water table level, plant and microbial activity, and the quality of organic substrates are the main controls on CO_2 production in peatlands (Figure 1-1; Moore et al. 1998, Updegraff et al. 1995). Plant uptake of CO_2 depends principally on photosynthetically active radiation (PAR), air temperature, and plant community structure and composition (Figure 1-1; Moore et al. 1998).

While serving as a net sink for atmospheric CO_2, peatlands simultaneously serve as a net source of methane (CH_4; Gorham 1991, Gorham 1994), releasing an estimated 30 to 50 Tg CH_4 yr^{-1} (Chen and Prinn 2006). Over a 100-year time span, a sustained emission of CH_4 has approximately 25 times more global temperature change potential than CO_2 (Shine et al. 2005), so small emissions can contribute significantly to the total budget of radiatively active gases (Whalen 2005). Both CO_2 and CH_4 fluxes are mediated by temperature and moisture in peatlands (Figure 2-1), but CH_4 is produced in the absence of O_2. Therefore, the primary controls on CH_4 emissions in peatlands are water table level, soil temperature, and substrate quality (Moore and Knowles 1989, Moore et al. 1998, Bellisario 1999).

A major uncertainty in the face of climate change is whether peatlands will continue to act as a net sink for atmospheric CO_2, or whether changes in climate will release peatland C pools back to the atmosphere. Atmospheric C concentrations will likely be influenced by peatland responses to climate change and will be determined by either positive feedbacks that occur with enhanced CO_2 and/or CH_4 emissions from peatlands or negative feedbacks with increased GPP and enhanced C sinks (McGuire and Hobbie 1997, McGuire et al. 2000, Chapin et al. 2000, Matthews and Keith 2007).

1.3 Experimental manipulations to study peatland response to climate change

Predicting ecosystem responses to climate change requires a detailed and mechanistic understanding of climate-ecosystem interactions over long time scales. Many studies have used natural temporal or spatial gradients to investigate climatic controls on peatland C cycling (see Updegraff et al. 1995, Silvola et al. 1996, Alm et al. 1999, Bubier et al. 1998, Lafleur et al. 2005). Natural gradients are useful for acquiring large scale understanding of ecosystem responses to climate change. The value of predictions from gradient analyses depends on the assumption that ecosystems will track changing climate over time in the same way that ecosystems now vary with climate over space (Dunne et al. 1996). Long-term adaptation to local climate conditions, fine-scale environmental heterogeneity, co-varying abiotic factors, and differences in time constants may confound the use of gradients to predict responses to global warming (Vitousek 1994, Root and Schneider 1995).

Compared with gradient studies, experiments provide a more controlled, mechanistic approach to predicting ecosystem responses to climate change, and can identify the most important factors that influence those responses. Given that soil environments in northern ecosystems are predicted to change beyond their normal range of variability, model predictions of ecosystem function under future climate change often must rely on extrapolations beyond current data or on results from experiments that simulate climatic regimes outside of contemporary variability. Researchers who utilize the experimental approach must simulate the desired change in climate while minimizing confounding changes in other variables. Results from manipulation experiments are limited by a variety of issues including the difficulty in establishing good controls and the expense and time needed for large scale manipulations and replication (Marion et al. 1997). The short duration of most experiments also lead to dangers of false understanding of the response and/or predictions; as initial ecosystem responses to experimental change may differ from responses observed when the manipulation is sustained over longer periods (Rosswall et al. 1988, Dunne et al. 1996).

In this thesis, I investigate direct and indirect soil hydroclimate (water table position, soil temperature) controls on C fluxes in an Alaskan fen. Water table level and soil temperature have been identified as primary controls on CO_2 production; however I investigated the indirect effects of soil hydroclimate on C fluxes through vegetation and

C quality. Chapter 2 of my thesis describes the response of field CO_2 fluxes (NEE, ER, GPP) to a water table and soil temperature manipulation. These manipulations were guided by future climate predictions for interior Alaska, and thus will provide information beyond the scope of contemporary soil climate variation that will be useful for modeling the future C balance of poorly drained ecosystems in this region. This design gave me the opportunity to investigate water table position (3 treatments: control, soil drying, soil wetting), surface soil warming, and the interactions between water table and warming on vegetation and CO_2 dynamics.

Water table level and soil temperature have the potential to indirectly affect decomposition through changes in soil organic matter quality. Chapter 3 describes a laboratory experiment designed to isolate soil organic matter quality differences among peat collected across the experimental field treatments (Chapter 2). I measured aerobic and anaerobic CO_2 and anaerobic CH_4 production rates under constant moisture and temperature to understand whether the field manipulations affected soil organic matter quality and C mineralization rates. Detailed hypotheses and predictions for these two studies are described in sections 2.1 and 3.1 of this thesis. This study represents some of the most detailed C flux dataset from a boreal rich fen as well as from an interior Alaskan wetland. Given that the response of peatland C fluxes to a changing climate remains uncertain, this study will improve estimates of future C emissions from this landscape.

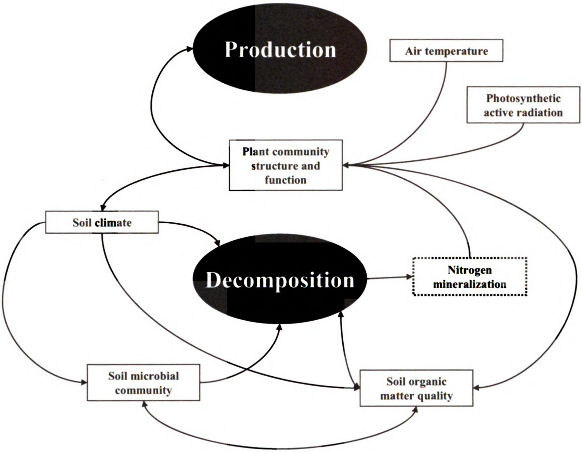

Figure 1-1. The net ecosystem exchange of CO_2 between ecosystems and the atmosphere is the balance between production (plant uptake of CO_2) and ecosystem respiration of CO_2 through autotrophic and heterotrophic respiration (decomposition). Interactions between soil organisms, soil microclimate, and organic matter quality influence decomposition processes in peatlands. Air and soil microclimate, photosynthetic active radiation, and organic matter quality control vegetation community structure and function. In peatlands, vegetation can have a strong influence on both soil climate and quality by altering inputs to the soil.

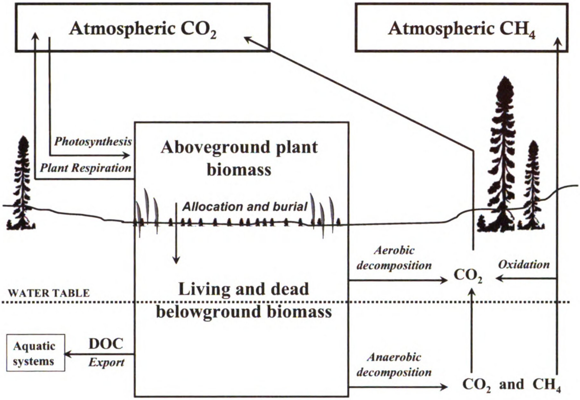

Figure 1-2. The peatland carbon cycle. Vegetation fixes atmospheric CO_2 through primary production and a portion of this carbon is transferred to belowground biomass (peat). Aerobic and anaerobic decomposition transforms solid and dissolved organic carbon into CO_2 and CH_4 that diffuse to the atmosphere.

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CHAPTER 2

Carbon dioxide (CO_2) Fluxes in an Alaskan Fen: Response to Experimental Manipulation of Water Table and Soil Temperature

2.1 INTRODUCTION

2.1.1 Peatlands as long term carbon sinks

Peatlands cover 15% of the boreal region (McGuire et al. 1995) and store up to 30% of the world's terrestrial soil carbon (C) (estimated between 397-455 Pg C; Gorham 1991, Zoltai & Martikainen 1996, Moore et al. 1998). The majority (98%) of North American soil C is stored in wetland soils and 83% of this C is contained in peatlands (Bridgham et al. 2006). Currently, peatlands are thought to function globally as a net sink for atmospheric carbon dioxide (CO_2), sequestering approximately 76 Tg (10^{12} g) C yr^{-1} (Zoltai & Martikainen 1996). However, recent work has shown that individual peatlands can switch from net CO_2 sinks to sources between wet and dry years (Shurpali et al. 1995, Alm et al. 1999). Such temporal trends indicate strong climatic controls on wetland C balance in northern regions.

Peat accumulates where C fixation through net primary production (NPP) at the surface exceeds losses from decomposition, leaching, and/or disturbance. Long term rates of C accumulation in peatlands (29 g C m^{-2} yr^{-1} averaged over millennia; Gorham 1991) are approximately 10 times larger than long term soil C accumulation rates for upland ecosystem soils (Schlesinger 1990). For long term C accumulation to occur in boreal peatlands, some proportion of plant production must be transferred to the catotelm (Clymo 1983). Generally, 80-90% of the C that passes through the acrotelm is lost to decomposition. Therefore, 10-20% of total vegetation production is transferred to the catotelm, where it generally is protected from fluctuating atmospheric conditions (Clymo 1992).

2.1.2 Climate change in Alaska and potential consequences for wetland CO_2 fluxes

Alaska's ecosystems are expected to experience earlier and more drastic climate changes compared to lower latitude systems (Keyser et al. 2000). A large amount of the global peatland C pool is stored in Alaskan peatlands (41.7 ± 50% Pg C; Bridgham et al. 2006), but the vulnerability of this C stock to C cycling in unknown. In upland ecosystems, Alaskan soils have undergone rapid warming over the past 30 years due to near-surface atmospheric warming of approximately 1° C per decade on average (Osterkamp and Romanovsky 1999, Serreze et al. 2000). These large changes in climate will not only warm peatland soils, but also will alter the hydrologic cycle in Alaska. Multiple impacts of climate change, including the degradation of permafrost (Romanovsky & Osterkamp 1997), reduced snow cover (Magnuson et al. 2000), and longer growing seasons (Serreze et al. 2000), are likely to impact plant and soil processes, which will have large implications for CO_2 dynamics and C storage in Alaskan peatlands.

Recent remote sensing work in Alaska shows changing hydrologic conditions in wetland complexes (Riordan et al. 2006). In several regions across interior Alaska, open water bodies are shrinking, often accompanied by the encroachment of drier terrestrial vegetation (Riordan et al. 2006). Wetland contraction is associated with increased summer water deficits due to increased evapotranspiration and/or decreased precipitation (Oechel et al. 2000, Hinzman et al. 2005). In other areas, however, wetlands are becoming more saturated due to permafrost thaw and increased upwelling of melt water. Few studies have explored such hydroclimate changes to wetland soil environments and how they are likely to influence C storage and emissions in Alaska.

Air and soil temperature, water table level, photosynthetically active radiation (PAR), plant community structure and function, microbial community, and the quality of organic substrates have been identified as the main controls on CO_2 net ecosystem exchange (NEE) from peatlands (Figure 1-1; Updegraff et al. 1995, Waddington and Roulet 1996, Alm et al. 1997, Lafleur et al. 1997). Climate change has the potential to directly and indirectly influence CO_2 fluxes by modifying these primary controls. Warmer air and soil temperatures generally stimulate microbial activity resulting in high ecosystem respiration (ER) of CO_2 (Billings et al. 1982, Crill et al. 1988, Moore and Dalva 1993, Frolking and Crill 1994, Silvola et al. 1996, Updegraff et al. 1998, Bergman et al. 1999, Christensen et al. 1999) and increased gross primary production (GPP) due to greater nutrient availability (Arft et al. 1999). For example, field warming experiments conducted in arctic regions of Alaska at Toolik Lake (Hobbie and Chapin 1998, Grogan and Chapin 2000, Van Wijk et al. 2004), stimulated decomposition and ER (Grogan and Chapin 2000), increased GPP, and altered plant community structure (Hobbie and Chapin 1998).

Many studies have explored water table controls on peatland CO_2 fluxes from a variety of spatial scales, from controlled laboratory microcosm experiments, to larger mesocosms, and field settings. Small-scale laboratory microcosm incubations have examined soil moisture controls on peat decomposition rates (CO_2 production). Generally, CO_2 production rates increased with lower soil moisture due to greater aerobic mineralization (Hogg et al. 1992, Moore and Dalva 1997), but studies also have found a positive relationship between CO_2 production and soil moisture (Orchard et al. 1992, Waddington et al. 2001), likely due to an optimum soil moisture content for CO_2 production (Silvola and Ahlholm 1989). While these microcosm experiments provide valuable insight into general controls on decomposition, they do not consider the role of vegetation in impacting NEE (either through GPP or ER). The use of larger, mesocosm incubations of peat columns allows for a controlled experiment to manipulate water table level, while maintaining vegetation to understand controls on NEE. Generally, lowering the water table in these studies resulted in higher ER rates (Moore and Knowles 1989, Moore and Dalva 1993, Blodau et al. 2004) and decreased GPP (Williams et al. 1999, Blodau et al. 2004), while raising the water table resulted in decreased ER likely due to limited oxygen diffusion for aerobic mineralization (Moore and Knowles 1989, Moore and Dalva 1993, Aerts and Ludwig 1997, Chimner and Cooper 2003, Blodau et al. 2004, Corstanje and Reddy 2004). Mesocosms provide an ideal setting to manipulate water table while isolating and quantifying C flux responses, but do not accurately portray the true response of peatlands to climate change because of the lack of in-site variability in climate, vegetation community, geology, and hydrology. Field water table drawdown experiments have documented large responses of peatland CO_2 fluxes post drawdown, including increased ER from aerobic decomposition as the water table drops (Nykanen et al. 1995, Laiho 2006). Complex responses of vegetation community and productivity to water table drawdown experiments also have important consequences for NEE, including increased vascular vegetation (Strack and Waddington 2007) and decreased cover of *Sphagnum* mosses (Weltzin et al. 2001), which will alter GPP rates. Few studies have explored interactions between water table and warming in the field (but see mesocosm studies by Lafleur et al. 2005 and Updegraff et al. 1995) and how these abiotic factors might impact biotic controls on CO_2 fluxes (vegetation community and productivity) within peatlands. Experiments designed to understand these interactions found that temperature was a greater control on ER than water table level in both a temperate bog (Lafleur et al. 2005) and a patterned sedge fen (Updegraff et al. 1995) and also documented significant shifts in plant C allocation, plant community, and biomass production in response to water table and warming treatments, with few interactions between the two (Weltzin et al. 2000).

2.1.3 Study hypotheses and objectives

The objective of this study is to use an *in situ* factorial manipulation of water table and soil temperature to investigate controls on Alaskan peatland CO_2 flux and to understand the impact soil climate has on ecological controls of CO_2 fluxes over time. The experiment included a factorial design of water table position (three treatments including a control, a lowered or drying treatment, and a raised or flooded treatment) and surface soil temperature (two treatments including a control or no warming treatment, and surface soil warming via open top chambers) manipulations.

I hypothesize and that CO_2 fluxes will respond to manipulation of both water table position and soil temperature at the Alaskan fen; such that:

H_1: Early responses to both water table and soil warming manipulations (first 2.5 years) will be driven primarily by changes in decomposition rates. Changes in vegetation will become more substantial over time, especially changes in community structure.

- I predict that lowering water table position will increase acrotelm thickness, stimulating the aerobic mineralization (ER) of newly exposed labile C substrates followed by the turnover of older soil organic matter, which will results in greater ER of CO_2.

- Drier soils will decrease GPP due to vegetative drought stress, which will cause a shift from more negative (atmospheric sink) to more positive (atmospheric source) NEE values.

- Because inundation by higher water table levels will favor vascular and moss productivity, I predict that the raised water table treatment will decrease aerobic mineralization (ER), and increase GPP.

H_2: Warming will stimulate mineralization and ER at the fen. Rates of GPP will also increase in response to greater nitrogen (N) mineralization and availability.

H_3: Modified water table position and temperature will alter the balance between ER and GPP, thereby impacting NEE at the Alaskan fen.

This chapter describes the first two years of the large-scale manipulation of soil hydroclimate variables and the response of CO_2 flux components NEE, ER, and GPP and vegetation (% cover, vascular leaf area index (LAI)). Besides testing the hypotheses listed above, using these first two years of data, I also investigated whether the experimental manipulations of soil climate affected CO_2 fluxes while maintaining the same fundamental relationship between ambient water table position and temperature and CO_2 flux, or whether the experimental manipulations 'pressed' the system across a threshold yielding new relationships between ambient water table position, temperature and CO_2 fluxes (Figure 2-1). Significant interactions between experimental treatments and soil hydroclimate variables would provide evidence of such threshold changes.

2.2 METHODS

2.2.1 Study site

This study was conducted at the Alaska Peatland Experiment (APEX) site, which is just outside the Bonanza Creek Experimental Forest and within the Tanana River floodplain, approximately 35 km southeast of Fairbanks, Alaska, USA (64.82°N, 147.87° W). The APEX site is a moderately rich fen (surface water pH 5.2-5.4), which is one of the most common peatland types in western North America (Vitt et al. 2000). The mean annual temperature of the area is -2.9° C with mean annual precipitation of 269 mm (Hinzman et al. 2006). This site lacks trees and is dominated by brown moss, *Sphagnum,* and emergent vascular species (*Equisetum*, *Carex, Potentilla*). There is no obvious microtopography across the site and the peat depth is approximately 1 meter at the center of the site. Seasonal ice is present until late August and there is no surface permafrost (i.e., in the top 40 cm of organic soil) at the APEX fen. During early spring of 2005 we established a factorial design of water table position (control, raised water table, and lowered water table) and soil warming (control, or no warming, and passive soil warming) treatments (Figure 2-2), which are explained in more detail below.

2.2.2 Experimental manipulation of water table

We established three 120 m^2 plots and assigned each to one of three water table treatments (raised or flooded, lowered or drought, and control or no change) based on water flow. In March 2005, while soils were still frozen, we used a small excavator to dig drainage channels to divert water from the lowered water table plot to a small holding trench down slope. The goal of this manipulation was to lower water table position inside the lowered water table plot by about 15-20 cm relative to the control plot, reflecting the level of drying predicted for many boreal wetlands under a double CO_2 concentration atmosphere (Roulet et al. 1992). Boardwalks were constructed around each water table plot during trench construction. In May and June 2005, solar powered bilge pumps were installed to pump water into the raised water table plot from a surface well located about 20 m down slope of the plot (Figure 2-2). Water was added to the raised plot at a rate of approximately 10 cm of water/day, resulting in a 9-11 cm increase on average in the raised water table plot. The chemistry of water additions was similar to ambient pore water in the raised water table plot (no significant differences in pH, electrical conductivity, DOC, anion/cation or organic acid concentrations; data not shown). While the raised water table treatment does not involve a dilution of pore water DOC concentrations as would be expected with increased precipitation, this treatment does not lead to major changes in pore water chemistry in the raised plot and is probably a reasonable simulation of flooding involved in wetland thermokarst formation in this region.

The goal of the experiment was to maintain both a lowered (drought) and raised (flooded) water table treatment, without minimizing the considerable ambient variability in water table position that occurs naturally at this site. A Campbell datalogger communication system facilitated pumping and drainage across the raised and lowered water table plot based on natural fluctuations in water table levels in the control plot (by turning pumps on and off). In general, water levels in the raised and lowered water table plots tracked control plot water table changes in response to precipitation and seasonal drying trends.

2.2.3 Experimental manipulation of temperature

Within each water table plot, we established six 3 m^2 subplots, which were randomly assigned to one of two warming treatments; including no warming (control) and seasonal warming (Figure 2-3). Warming treatments were thus replicated in triplicate within each water table plot. We manipulated air and surface soil temperatures within the warming treatment subplots using open top chambers (OTCs) during the snow-free period following Walker et al. (2006). The OTCs were constructed out of 0.16 cm thick Lexan, with base dimensions of 0.8 m^2. Throughout the growing season of 2005 and 2006, OTCs passively warmed surface soil (2 cm beneath moss) and air temperatures by about 1 °C (0.5 °C and 0.7 °C, respectively). Relative humidity and temperature was recorded in each gas flux collar during the CO_2 flux campaigns (data not shown).

2.2.4 Environmental variables

Beginning in June 2005, mean hourly water table level, photosynthetically active radiation (PAR), and air and soil temperature were logged continuously with Campbell Scientific dataloggers in each subplot over two growing seasons. Air temperature and a depth array of soil temperatures (above moss surface and 2, 10, 25, and 50 cm beneath moss surface) were measured within each subplot using thermistors (Yoshikawa et al. 2004) (6 arrays per water table plot, 18 total). Water table levels were measured using one transducer (Campbell Scientific, Logan, UT) installed at the bottom of 5 cm diameter, 1 m long PVC wells in each water table plot (1 per water table plot, 3 total), and were calibrated against manual measurements from the same well. The spatial variability in water table position inside each water table plot was determined with weekly manual measurements of water table position collected from shallow wells within each subplot during the 2005 and 2006 growing seasons.

In 2006 I experienced datalogger malfunction, which impacted the lowered and control plot water table data. Weekly manual water table measurements, the continuous raised water table plot data, and calculations of peat storativity were used to model continuous water table position in the lowered (July 23 – September 2006) and control (July 14 – September 20, 2006) water table plots.

Photosynthetically active radiation (PAR) was measured at each gas flux collar using a Li-COR (Lincoln, Nebraska) quantum light sensor (μmol m^2 s^{-1}). These variables were logged every 5 seconds and hourly averages were recorded at each water table plot using Campbell Scientific CR10X dataloggers (Logan, Utah). Hourly averaged tipping bucket precipitation was measured at a meteorological station located within the Tanana River Floodplain.

2.2.5 Carbon dioxide exchange measurements

Net ecosystem CO_2 exchange (NEE) was measured using conventional chamber techniques following Carroll and Crill (1997). Immediately following snowmelt in 2005, I installed permanent replicate clear Lexan chamber bases, or gas flux collars, in all 18 subplots. The gas flux collars were inserted approximately 10 cm into the soil, taking care not to damage roots, and allowed to equilibrate for one week before taking the first flux measurement. A clear plexiglass chamber constructed out of 0.3 cm thick Lexan (area = 0.362 m^2 and volume = 0.227 m^3) was placed and sealed over the collars using foam tape around the chamber base during each flux campaign. An internal fan system maintained ambient temperature and humidity conditions within the chamber.

Carbon dioxide (CO_2) exchange measurements were conducted weekly throughout the growing season from late May - early October during 2005 and 2006. Carbon dioxide concentration inside the chamber was determined every 1.6 seconds for 2-3 minutes using a PP Systems EGM-4 portable infrared gas analyzer (IRGA; Amesbury, Massachusetts). The IRGA was calibrated before each gas flux campaign. In 2006, temperature, relative humidity, and PAR were logged continuously within the chamber during each flux measurement with a PP Systems TRP-1 sensor attached to the inside of the chamber (Amesbury, Massachusetts). I attempted to randomize time of day and weather conditions among all measurements to capture full variations of light and temperature for each collar. The CO_2 flux rate (μmol CO_2 m^{-2} sec^{-1}) was calculated as the slope of the linear relationship between headspace CO_2 concentration and time with r^2 > 0.8. By using this goodness of fit criterion I excluded all fluxes that did not exhibit linear change from the flux data set (<3% of the data). Immediately following the NEE measurements, the area above my gas flux collars was vented by opening the chamber for ~ one minute. Immediately after this venting, I measured total ecosystem respiration (ER) using a dark shroud that blocked all PAR from entering the gas flux chambers. I also used a series of opaque shrouds placed over the chamber to quantify NEE as a function of light intensity (Bubier et al. 1998). This included a shroud made of 1.2 mm^2 polyester mesh netting that blocked ~ 50% of PAR, as well as a shroud made of 0.5 mm^2 polyester mesh netting that blocked ~ 75% of incoming PAR. Gross primary production was determined as the difference between NEE and ER values from each gas flux collar during the same sampling period. Negative flux values represent net CO_2 uptake from the atmosphere.

2.2.6 Vegetation surveys

The percent cover of vascular and bryophyte species was visually estimated within each subplot in July and August 2006. Dominant vascular species included *Carex atherodes, Carex canescens, Potentilla palustris,* and *Equisetum fluviatile*. Dominant bryophyte species at the site include *Sphagnum* (*Sphagnum obtusum, Sphagnum platyphyllum*) and brown moss (*Hamatocaulis vernicosus, Drepanocladus aduncus*) species.

In 2007, vascular LAI was measured by counting all vascular plant leaves within five 8 x 8 cm subplots systematically distributed throughout each gas flux collar each month (Wilson et al. 2007). Total leaf numbers within the CO_2 gas flux collars were extrapolated from these subplots. Individuals of each species were selected outside of the flux collars at each site and their leaf area was measured biweekly using a calyper. An average biweekly surface area of leaves was computed and multiplied by leaf numbers to determine vascular LAI.

2.2.7 Data analysis

Treatment and hydroclimate controls on CO_2 fluxes

The main goal of my project was to understand controls on CO_2 fluxes (NEE, ER, GPP) within the water table and soil warming manipulation experiment in interior, Alaska. To investigate whether the experimental treatments impacted fluxes, I used a repeated measures analysis of variance (ANOVA) and Tukey *post hoc* analysis of means tests (Proc Mixed) in SAS 8.1 (SAS Institute Inc., Cary, NC, USA) to determine the effects of water table treatment, soil warming treatment, year, and all interactions among these fixed effects on all three CO_2 flux components (NEE, ER, and GPP).

The results from the repeated measures ANOVA models provide insight into how the treatments impacted fluxes, but do not provide insight into principal controls on CO_2 fluxes such as water table position and soil temperature. To understand basic soil hydroclimate controls on ER and GPP as well as whether the experiment induced threshold changes between hydroclimate and CO_2 flux, I used two general linear models

(Proc GLM) in SAS 8.1 to predict fluxes: (1) a continuous soil climate variables model, which included year, season, and the continuous soil climate variables (water table position, air temperature, and peat temperature at 2 cm and 25 cm depth) and (2) a treatment + continuous soil climate variables model, which included year, season, experimental treatments (control, lowered, raised water table treatments; warmed and un-warmed treatments), and continuous soil climate variables (water table position, air temperature, and peat temperature at 2 cm and 25 cm depth). These two models were compared using AIC to estimate goodness of fit and the model with the smaller AIC value was selected. The selection of Model 2 and the presence of significant interactions between treatment (water table or soil warming treatments) and continuous soil climate variables was used as evidence that the hydroclimate manipulations 'pressed' the system in a way that created new relationships between soil hydroclimate variables (water table and temperature) and CO_2 fluxes (Figure 2-1).

Light and vegetation controls on CO_2 fluxes

Simultaneous measurements of NEE and PAR were used to generate light-response curves. The relationship between NEE and PAR is often represented by a rectangular hyperbola (Thornley and Johnson 1990), where there is a near-linear increase in productivity at low light levels and an asymptotic approach at high light levels. Parameter estimation for the rectangular hyperbola to characterize NEE as a function of PAR was accomplished using nonlinear regression (PROC NLIN in SAS 8.1). I fit a rectangular hyperbola to the CO_2 flux data, estimating three parameters: the maximum gross photosynthetic CO_2 capture at high PAR, >1000 μmol m^{-2} sec^{-1} (GP_{max}, μmol CO_2

m^{-2} sec^{-1}), the photosynthetic quantum efficiency (α, µmol CO_2 m^{-2} sec^{-1} per µmol PAR m^{-2} sec^{-1}), and dark respiration at PAR = 0 (R, µmol CO_2 m^{-2} sec^{-1}).

$$NEE = \frac{GPmax * \alpha * PAR)}{(PAR * \alpha) + GPmax} - R$$

This equation has been used successfully to model the relationship between NEE and PAR in peatlands and other ecosystems (Frolking et al. 1998, Ruimy et al. 1996, Waddington and Roulet 1996, Whiting et al. 1992). I used a general linear model (Proc Mixed) in SAS 8.1 to describe light response curve model parameters (GP_{max}, α) using a combination of experimental treatments (control, lowered, raised water table plots; warmed and un-warmed subplots), cumulative vascular LAI (forbs, grass functional groups), and % vegetative cover of mosses (*Sphagnum,* brown moss) for each gas flux collar.

2.3 RESULTS

2.3.1 Soil climate

Interannual variation in temperature and precipitation at the Bonanza Creek LTER Tanana River floodplain site, which is close to the APEX fen, showed warmer and wetter conditions in 2005 than in 2006. Mean daily air temperatures (May 1 – September 30) on average were warmer in 2005 (13.4 ± 0.1 °C) than in 2006 (12.3 ± 0.1 °C; $F_{1, 7337} = 53.06$, $p < 0.0001$). The site was also wetter in 2005 than in 2006, likely due to more precipitation received as snowfall (snow water equivalent = 120 mm in 2005; 73 mm in

2006). Mean annual growing season precipitation, however, did not vary between years ($F_{1, 304} = 1.61$, $p > 0.10$).

The water table and soil temperature manipulations caused both the experimental water table and soil temperature treatments to differ from the controls. Manipulations in the raised water table plot raised water table levels by 9 cm and 11 cm on average relative to the control water table plot in 2005 and 2006, respectively. The lowered water table manipulation lowered water table levels by 5 cm and 8 cm on average relative to the control water table plot in 2005 and 2006, respectively (Figure 2-4).

During the growing seasons of 2005 and 2006, OTCs passively warmed surface soil (2 cm beneath moss) at the site by an average of 0.7, 0.9, and 0.6 °C in the control, lowered, and raised plots, respectively. However, surface peat temperatures varied more across water table treatments than between warming treatments or across sampling years. Most notably, both surface peat (2 cm beneath the moss surface) and deeper peat (25 cm beneath the moss surface) temperatures were consistently higher in the raised water table plot than in the lowered or control plots (Figure 2-5). In 2005, growing season peat temperatures (from July 14 – September 30) at 2 cm depth averaged 12.5 ± 0.1 °C, 12.5 ± 0.1 °C, 16.9 ± 0.0 °C in the control, lowered, and raised water table plots, respectively. These peat temperatures were slightly lower in 2006 (data not shown).

2.3.2 Species composition and leaf area index

Percent species cover of the dominant vascular and bryophyte plant species within each gas flux collar did not vary across the experimental treatments in 2005 (Turetsky unpublished data), and showed no significant shifts in species composition between 2005 and 2006 (canonical discriminate analysis, comparison of species composition in 2005 vs. 2006 across treatments; Table 2-1). However, upon visual observation, the abundance of brown mosses declined in the lowered water table plot and *Sphagnum* cover increased from 19% to 51% in the raised water table plot from 2005 to 2006 (Table 2-1). Vascular LAI measurements in 2007 showed the greatest cumulative vascular LAI in the control water table plot and the lowest in the lowered water table plot (Figure 2-6) throughout the growing season. Average vascular LAI was greatest in the middle of the growing season around Julian day (JD) 205 in 2007 (Figure 2-6).

2.3.3 Carbon dioxide fluxes

Net ecosystem exchange of CO_2 across the experimental treatments ranged from -5.02 to 6.91 μmol CO_2 m^{-2} sec^{-1} (control water table plot), -3.64 to 4.578 μmol CO_2 m^{-2} sec^{-1} (lowered water table plot), -8.05 to 4.65 μmol CO_2 m^{-2} sec^{-1} (raised water table plot) (negative values represent net CO_2 uptake from the atmosphere, positive values represent net emission to the atmosphere). There were no pronounced seasonal trends in NEE in any of the three water table plots (Figure 2-9). The control water table plot in 2005 and the raised water table plot in 2006 showed the greatest variability in seasonal NEE. The lowered water table plot showed the smallest variability in NEE across the season in both 2005 and 2006.

Repeated measures ANOVA models show that NEE varied by a water table treatment (control, lowered, raised) x year (2005, 2006) interaction (Table 2-2, Figure 2-11) with no other higher level interactions. The control water table plot showed a slight tendency toward more positive NEE values in 2006, but remained an overall sink of CO_2

in both years during flux measurement periods. The lowered water table plot switched from negative NEE values in 2005 to positive NEE values in 2006. The raised water table plot in 2006 generally had more negative NEE values. There was no significant warming treatment effect or higher level interactions involving warming on NEE.

Ecosystem respiration of CO_2 (ER) ranged from 0.23 to 8.8 μmol CO_2 m^{-2} sec^{-1} (control water table plot), 0.15 to 10.79 μmol CO_2 m^{-2} sec^{-1} (lowered water table plot), 0.35 to 12.32 μmol CO_2 m^{-2} sec^{-1} (raised water table plot). In 2005 in the control water table plot, ER was generally greatest at the beginning of the growing season with declining values over time (Figure 2-7). In 2006, ER in the control water table plot was lowest at the beginning and end of the season, with the greatest flux in the middle of the season (~JD 163). The lowered water table plot responded similarly to the control water table plot in both years, with ER gradually declining throughout the season in 2005 and showing a general parabolic trend in 2006. In both 2005 and 2006, ER fluxes in the raised water table plot were lowest at the beginning and end of the season, with the greatest flux in the middle of the season (~JD 200-208).

Similar to the trends in NEE, repeated measures ANOVA models show that ecosystem respiration (ER) varied by a water table treatment x year interaction (Table 2-2, Figure 2-11). In 2005, ER did not vary among water table treatments but was highest in the control water table plot. In 2006, the raised water table plot averaged higher ER fluxes than either the control or lowered water table treatment plots.

The warming treatment significantly increased ER ($F_{1,5}$=14.18; p = 0.0131) with no higher level interactions involving warming. The mean ER flux was 3.99 ± 0.13 and 3.46 ± 0.12 μmol CO_2 m^{-2} sec^{-1} within the warmed and un-warmed subplots, respectively (data not shown). Gross primary production across the treatments ranged from -13.44 to -0.46 μmol CO_2 m^{-2} sec^{-1} (control water table plot), -11.29 to -0.44 μmol CO_2 m^{-2} sec^{-1} (lowered water table plot), -17.35 to -0.17 μmol CO_2 m^{-2} sec^{-1} (raised water table plot; negative values represent net CO_2 uptake from the atmosphere). In 2005, GPP fluxes in the control water table plot were generally constant until JD 208 after which they steadily declined to the end of the growing season (Figure 2-8). In 2006, GPP fluxes in the control plot were greatest in the early to middle of the growing season (JD 164-196) and declined late in the season. Rates of GPP in the lowered water table plot were similar between years, although fluxes were lower at the beginning of the season during 2006. Rates of GPP were highest in the middle of the growing season (JD 174-208) in the lowered water table plot. In the raised water table plot, there was greater overall variability in GPP in 2006 than in 2005. Fluxes in the raised water table plot were greatest in the middle of the season (JD 200-207), with the lowest fluxes occurring during the early and late seasons.

Similar to NEE and ER, the repeated measures ANOVA model showed that GPP varied by a water table x year interaction (Table 2-2, Figure 2-11). The control and lowered water table plots both had lower GPP fluxes (less CO_2 taken up from the atmosphere) in 2006 than in 2005. The raised water table plot showed higher GPP (more CO_2 taken up) in 2006 than 2005. Gross primary production showed more interannual variation in the raised water table plot than in the control and lowered water table plots.

Also similar to ER, GPP fluxes were significantly higher in the warmed subplots than the un-warmed subplots ($F_{1, 5}$=27.77; p = 0.0033) with no interactions among warming, year, and/or water table plot. Mean GPP fluxes were -4.31 ± 0.13 and -5.08 ± 0.13 μmol CO_2 m^{-2} sec^{-1} within the warmed and un-warmed subplots, respectively.

To understand how the balance between ER and GPP is contributing to changes in NEE, I plotted ER versus GPP (uptake of CO_2) against a 1:1 line (Figure 2-12). In 2005, points from each water table plot cluster together near the 1:1 line, with little variability among water table treatments. However, the control water table plot had the most points falling below the 1:1 line, indicating an overall net uptake of CO_2 from the atmosphere. In 2006, most data collected from the lowered water table plot tends to fall above the 1:1 line, while data points from the raised water table plot tend to fall below the 1:1 line. The lowered water table plot had positive NEE of CO_2 on average in 2006 and the 1:1 plot shows that this is likely due to low GPP (plant uptake) in the lowered plot (Figure 2-11, Figure 2-11). In the raised water table plot, there was an increase in GPP and a slight increase in ER, which resulted in more positive NEE (Figure 2-11). The 1:1 plot suggests an increase in GPP, not a decrease in ER, is responsible for this shift because there are more moles of CO_2 taken up by plants for each mole respired (Figure 2-12). From these 1:1 ER versus GPP relationships and from the repeated measures ANOVA model results, GPP appears to be driving the differences in NEE during 2006.

To explore the effects of seasonality on these trends, I also divided these data into early (JD 140-179), mid (JD 180-219), and late (JD 220-277) season 1:1 plots (Figure 2-13). While the whole season 1:1 plots (Figure 2-12) suggest that GPP largely causes differences in NEE during 2006, this trend appears to be driven by responses occurring in the early season (Figure 2-13). The raised water table plot was much more productive (points fall below 1:1 line) during the early season of 2006, than during the early season of 2005, while mid and late seasons do not show marked differences between years (data not shown).

Measurements of NEE at the site (across the treatments during one diurnal experiment) ranged from -5.908 to 11.797 μmol CO_2 m^{-2} sec^{-1} (Figure 2-10). Night time ER (measured between 2100 and 0200) ranged from 1.67 – 8.83 μmol CO_2 m^{-2} sec^{-1}. This falls within the seasonal range of ER. Because the diurnal range of both NEE and ER fell within (or very close to) the seasonal ranges, I believe I captured a full range in the environmental parameters (light, soil temperature, water table position) at the APEX fen during my CO_2 flux measurement campaigns.

2.3.4 Soil hydroclimate controls on CO_2 fluxes

For ecosystem respiration (ER), the model containing year, season, and continuous soil climate variables (Model 1) was a better-fit model using AIC than the model also containing treatment effects (Model 2). This model explained almost 50% of the variability in log-transformed daily ER fluxes (Table 2-3). In general, temperature variables (air and peat temperature at 2 cm and 25 cm) were important predictors of ER and all temperature variables were positively related to ER. Peat temperature (2 cm depth) was the most important predictor, explaining 25% of the variation in ER. The model also contained significant season x year, season x air temperature, and year x peat temperature (25 cm depth) interactions. Air temperature (explained 21% of the variability in ER) exhibited a stronger positive correlation with ER in the early season than in the mid and late seasons. Peat temperature (25 cm depth) overall was not a very important predictor of ER, but was a stronger predictor in 2006 (explained 14% of the variance) than in 2005 (explained 10% of the variance). Surprisingly, mean daily water table level was not a significant predictor of ER.

Similar to ER, the model including year, season, and continuous environmental variables (Model 1), was the best model explaining log-transformed daily GPP using AIC. This model explained almost 50% of the variability in GPP (Table 2-4). Peat temperature (2 cm depth) explained 16% of the variation in GPP. Season x year, season x air temperature, year x peat temperature (25 cm depth), and year x mean daily water table position were significant predictors of GPP. Rates of GPP did not vary substantially across seasonal periods in 2005, but GPP fluxes were highest in the mid-season and lowest in the late-season in 2006. Air temperature, which overall was the most important predictor of GPP explaining 21% of the variation, was a stronger predictor of GPP in the early season than in the mid and late seasons. Increased air temperature generally corresponded to increased GPP. Peat temperature at 25 cm depth was a stronger predictor of GPP in 2006 (explained 19% of the variance) than in 2005 (explained 5% of the variation). Mean daily water table was a stronger predictor of GPP in 2005 (explaining 17% of the variation) than in 2006 (explaining 5% of the variation). Increased water table in general corresponded to increased GPP, with more plant uptake of CO_2.

2.3.5 Light and vegetation controls on CO_2 fluxes

Light response curves show that there was little variability in rates of CO_2 exchange among individual gas flux collars within the water table plots (Table 2-5). GP_{max} ranged from 3.1 in the lowered water table plot to 11.7 in the raised water table plot. α ranged from 0.009 to 0.058. I used a general linear model to describe light response curve model parameters (GP_{max}, α) using a combination of experimental treatments (control, lowered, raised water table plots; warmed and un-warmed subplots), cumulative vascular LAI (forbs, grass functional groups), and % vegetative cover of mosses (*Sphagnum,* brown moss) for each gas flux collar. A model containing water table treatment and % brown moss cover explained 77% of the variability in GP_{max} values (Table 2-6). The raised water table plot had the greatest GP_{max}, while the lowered water table plot had the lowest values. GP_{max} values increased with % brown moss cover across all water table plots. Generally, drier gas flux collars tend to have lower % brown moss cover than wetter gas flux collars. The lowered water table plot had the lowest % brown moss cover while the control water table plot had the highest cover of these mosses (Table 2-1).

A model containing water table treatment (control, raised, lowered water table plots), warming treatment (warmed and un-warmed subplots), cumulative vascular LAI (forbs), and water table treatment x forb interaction explained 65% of the variability in α values (the maximum rate of increase of NEE versus PAR; Table 2-6). Warmed subplots had significantly higher α values than un-warmed subplots. Forb leaf area was negatively related to α values in the lowered water table plot (accounted for 44% of the variability in α), but showed no relationship with α in the control and raised water table plots. The lowered water table plot (31.9 m^2 m^{-2}) had lower cumulative forb LAI than either the control or raised water table plots (66.7, 50.7 m^2 m^{-2}, respectively).

When averaged across gas flux collars within a water table plot, the light response curves showed that the raised water table plot had larger parameter estimates (GP_{max}, α,

R) than the control and lowered water table plots (Figure 2-13). The raised water table plot had a higher GP_{max} (9.83 ± 0.93) than the lowered plot (4.51 ± 0.57).

2.4 DISCUSSION

2.4.1 Characterizing CO_2 fluxes in an Alaskan fen

The ranges in CO_2 fluxes (NEE, ER, GPP) measured at the control water table plot agree well with other studies that have used static chambers to quantify CO_2 flux from northern peatlands. Across studies, NEE generally has ranged from -3.95 to 7.1 μmol CO_2 m^{-2} sec^{-1}, while GPP has ranged from -12 to -5 μmol CO_2 m^{-2} sec^{-1} (Silvola et al. 1996, Alm et al. 1997, Alm et al. 1999, Moore et al. 2002, Strack et al. 2006, Wickland et al. 2006). Thus, NEE (-5.02 to 6.91 μmol CO_2 m^{-2} sec^{-1}) and GPP (-13.44 to -0.46 μmol CO_2 m^{-2} sec^{-1}) ranges from the APEX rich fen control water table plot were within the range of other published work, although GPP rates in this study were slightly higher, which led to slightly more negative NEE relative to other studies. This is not surprising given that few studies have investigated CO_2 fluxes from rich fens, which could be more productive than other peatland types due to minerotrophic conditions and more neutral pH than *Sphagnum* dominated bogs and poor fens. Also, the high latitude and the open nature (i.e., no trees) of my site contributes to high growing season light levels, which likely leads to high growing season GPP. Rates of ER in the control plot ranged from 0.12 to 12 μmol CO_2 m^{-2} sec^{-1} (Figure 9). This generally agrees with published values. For example, ER in an Alaskan forested peatland ranged from 0.28 to

4.72 μmol CO_2 m^{-2} sec^{-1} (Wickland et al. 2006), in a sub-boreal poor fen ER ranged from 5 to 12 μmol CO_2 m^{-2} sec^{-1} (Bubier et al. 2003), in a Finnish poor fen ER ranged from 0.5 to 5.0 μmol CO_2 m^{-2} sec^{-1} (Silvola et al. 1996), and in an ombrotrophic temperate bog ER ranged from 0.46 to 4.05 μmol CO_2 m^{-2} sec^{-1} (Blodau et al. 2007).

While CO_2 flux values in the control plot generally seem to agree with measurements collected from other northern peatlands, the range in CO_2 fluxes measured in the raised water table plot showed greater ER and GPP than other studies. Despite being located further north than most previously published work, these results suggest that Alaskan rich fens, when provided ample water, are very productive ecosystem types. Similarly, peak photosynthesis in an interior Alaskan permafrost collapse bog (Wickland et al. 2006) was greater than peak photosynthesis in a sub-boreal collapse bog (Bubier et al. 1998).

Generally, the NEE-PAR relationships developed for the APEX fen have similar attributes to those in other peatlands (Frolking et al. 1998, Bellisario et al. 1998). The model components of the light response curves (α, GP_{max}, and R) in this study fall within a similar range as those found in other studies. For example, studies spanning bogs and fens have found that α ranged from 0.001 to 0.025, GP_{max} ranged from 2.8 to 15.1, and R ranged from -6.1 to -1.98 (Frolking et al. 1998, Bellisario et al. 1998, Bubier et al. 2003, McNeil and Waddington 2003; Strack et al. 2006). While the α and GP_{max} components observed in this study were slightly lower than those from a poor fen in New Hampshire (where α: 0.012 to 0.019, GP_{max}: 10.1 to 13.8, and R: -6.1 to -2.1; Bubier et al. 2003), they agreed well with values from a poor fen in Ontario measured by static chambers (where α: 0.01 to 0.023, GP_{max}: 4.0 to 15.1, and R: -2.39 to -1.98; Frolking et al. 1998) and eddy covariance (where α: 0.025±0.002, GP_{max}: 11.5±0.29, and R: -2.39±0.1; Frolking et al. 1998).

2.4.2 Drought effects on CO_2 fluxes

Changes in precipitation, evaporation, and drainage already have caused water bodies in some wetland regions in interior Alaska to dry (Riordan et al. 2006) and many northern peatlands are predicted to become drier under future climate change scenarios (Roulet et al. 1992). Water table level is thought to serve as one of the most important controls on CO_2 fluxes from peatlands (Updegraff et al. 1995), as it determines plant community structure and function as well as the transition between oxic acrotelm and anoxic catotelm peat. Generally, the lowering of water table levels increases ER in peatlands due to increased oxygen diffusion into soils, which stimulates aerobic decomposition (Moore and Knowles 1989, Moore and Dalva 1993, Silvola et al. 1996, Nykanen et al. 1997). However, drought, or lowered water table position, has had differential impacts on GPP depending on the plant community. Several studies have investigated differences in NEE between wet and dry years to predict the response of peatland C cycling to potential drought. In most cases, these studies have concluded that under drier conditions, peatland GPP (CO_2 uptake) will be reduced due to reduced rates of photosynthesis (Alm et al. 1999, Griffis et al. 2000) and that peatlands will become sources of atmospheric CO_2 because of enhanced ER (Moore and Dalva 1993, Bellisario et al. 1998, Christensen et al. 1998, Bubier et al. 2003, Strack et al. 2006). Similar to my results, experimental manipulations of water table using both bog and fen mesocosms also found no significant difference in ER due to water table (Updegraff et al. 2001), but GPP did vary with water table level (Figure 2-11; Weltzin et al. 2000), likely due to drought stress (Alm et al. 1999, Bubier et al. 2003, Lafleur et al. 2003).

In addition to the experimental drought treatment, my sampling characterized CO_2 fluxes across two years representing very different climates in interior Alaska (Figure 2-4). 2006 was a drier year than 2005 due to a shallow snow pack and lower snow water equivalent in the winter of 2005-2006, which likely led to less runoff and lower water table positions at the fen (Figure 2-4). Differences in soil hydroclimate between sampling years had large consequences for daily CO_2 fluxes, resulting in significant water table treatment by year interactions (Figure 2-11, Table 2-2) for NEE, ER, and GPP. The large interannual variability observed in this study is typical of other wetland complexes (Bubier et al. 1998, Bubier et al. 2003, Lafleur et al. 2003, Myers-Smith 2007) where differences in CO_2 fluxes typically are driven by large fluctuations in water table level between years, which lead to dramatic changes in both respiration and photosynthesis. In general, the trends observed in the control plot between 2005 and 2006 (lower ER and GPP in the drier year) agree with the trends between the control and lowered water table plots (lower ER and GPP in the lowered water table plot; Figure 2-6).

The lowered water table plot switched from average negative NEE to average positive NEE in 2006 (Figure 2-11). Similarly, Bubier et al. (2003) observed significant differences in NEE in bogs and fens between wet and dry years, with smaller uptake of CO_2 during the dry summer and some sites switching from a net sink to a source of CO_2 between wet and dry years. In my study, mean daily NEE fluxes were 89% and 200%

more positive (source of CO_2) in the lowered water table plot than the control water table plot in 2005 and 2006, respectively (Figure 2-11). The lowered water table treatment did not significantly impact ER fluxes compared to the control water table plot. Averaged across the warming treatments, mean daily ER fluxes were 10% lower and 3% higher in the lowered water table plot from the control water table plot in 2005 and 2006, respectively (Figure 2-11). This is surprising given that Silvola et al. (1996) predict a 50-100% increase in respiration with a 14 - 22 cm drop in water table. The lack of ER response to drought could be because lowering the water table at this site exposed peat layers that were not readily decomposable. Alternatively, microbial populations in the surface peat layers of the lowered water table plot may have been drought stressed. Because ER did not differ between the lowered and control water table plots (Figure 2-11), the observed changes in NEE were due primarily to decreases in GPP in the lowered water table plot (Figure 2-12).

In both years, GPP was significantly lower (reduced plant CO_2 uptake) in the lowered water table treatment than the control water table treatment. Averaged across the warming treatments, mean daily GPP fluxes were 24% and 21% lower in the lowered water table plot than the control water table plot in 2005 and 2006, respectively (Figure 2-11). Low rates of GPP (Figure 2-11), low vascular LAI (Figure 2-6), low GP_{max} values (Figure 2-13), and low % brown moss cover (Table 2-1) in the lowered water table plot relative to the control water table plot indicate that dry conditions reduced photosynthesis and productivity, likely due to drought stress. This result contrasts with studies predicting that lowered water table levels tend to favor vascular woody vegetation (Gorham 1991, Thormann and Bayley 1997, Weltzin et al. 2000). Like the vascular vegetation, it is likely that the photosynthetic capacity of bryophytes was reduced because of mosses' strong dependence on tissue water content (Titus and Wagner 1984, Silvola 1990). Strack et al. (2006) and Weltzin et al. (2000) found a decrease in bryophytes (including *Sphagnum* and brown mosses) within drained sites other studies have documented a decrease in photosynthetic capacity of *Sphagnum* exposed to drought, where photosynthesis did not recover until 20 days of saturation (Moore 1989, Tuba et al. 1996, Alm et al. 1999, McNeil and Waddington 2003). It is likely that my data is dominated by early vegetation responses to these changes in water table level. Over time, I would expect to find increased success of vascular species in the lowered water table plot, which will have an important influence of GPP, ER, and substrate quality.

2.4.3 Flooding effects on CO_2 fluxes

In many areas of Alaska, peatlands are becoming more saturated due to permafrost thaw and increased runoff from surrounding uplands (Osterkamp et al. 2000). Flooding saturates surface soils, which limits the diffusion of oxygen into the peat, thereby limiting microbial activity and decomposition rates, and usually decreasing CO_2 emissions to the atmosphere (Clymo 1983). Few studies have examined the effects of raised water table positions or flooding on CO_2 fluxes in the field, but mesocosm studies that experimentally manipulate water table levels have shown variable responses of NEE, ER, and GPP. Chimner and Cooper (2003) raised water table position by approximately 5 cm and measured a 42% decrease in ER in a subalpine fen, while Updegraff et al. (2001) found no affect of flooding on ER in bog or fen mesocosms. Research on permafrost thaw in Canadian peatlands show that flooding due to thermokarst was associated with a 1.6 fold increase in ER (Turetsky et al. 2002), yet organic matter accumulation increased by 60% following permafrost thaw (Turetsky et al. 2000), probably due to increased GPP of *Sphagnum* and *Carex* in these newly disturbed and saturated ecosystems. Thus, flooding can reduce ER by minimizing acrotelm thickness, or can increase GPP and possibly ER through changes in plant community composition and substrate quality.

In my study, immediately following the onset of water additions in 2005, the raised water table treatment had 89% more positive NEE values compared to the control water table plot (Figure 2-11). In 2005, the raised water table plot had lower ER and GPP fluxes than the control water table plot, causing the site to be less of a CO_2 sink (more positive NEE values). This trend is driven by a 31% reduction in GPP (Figure 2-11), which is likely due to initial vascular vegetation displacement or stress following the start of the flooding treatment (raised water table plot vascular LAI was lower than vascular LAI in the control water table plot; Figure 2-6). However, the raised water table plot in 2006 had 200% more negative NEE values (i.e., more of a net CO_2 sink) compared to the control water table plot. In 2006, the raised water table plot had greater ER and GPP fluxes than the control water table plot (by 28% and 62%, respectively; Figure 2-11), which resulted in more negative NEE values (i.e., greater sink capacity). This trend, as well as the high GP_{max} values observed in the raised water table plot (Figure 2-13, Table 2-5), suggests that the vegetation community in the raised water table plot responded positively to higher water table levels, with increased productivity and plant uptake in 2006. This is similar to other studies where the maximum GP_{max} at wet sites was 2.5 times greater than the maximum GP_{max} at drier sites (McNeil and Waddington 2003).

Given that GP_{max} was correlated with % brown moss, increased GPP in the raised water table plot likely was dominated by changes in bryophyte cover (Table 2-1). Also, the interannual difference in GPP at the raised plot largely was driven by early season responses, as GPP in mid- and late-seasons did not vary between 2005 and 2006 (Figure 2-13). The fact that the change among years is driven by early season differences also highlights the importance of moss productivity to GPP in the raised water table plot, given that mosses begin to photosynthesize much earlier than vascular plants in these wetlands. This increase in GPP (in 2006) occurred despite a thinner snow pack, less runoff, and drier soil conditions than in 2005 (Figure 2-4), which likely led to reduced soil insulation and lower soil temperatures during early spring 2006. While reduced soil temperatures would likely inhibit early season productivity across plots, the greater % moss cover in the raised water table plot (Table 2-1) likely buffered the plot from climate by insulating the soils in the raised plots over the winter and early spring.

Increased ER in the raised water table plot could be due to a variety of processes, including 1) an increase in autotrophic respiration (ER often scales positively with GPP), 2) increased microbial activity in the warm conditions present in the raised water table plot (Figure 2-5). In the model predicting ER, peat temperature at 2 cm depth explained 25% of the variation in ER (Table 2-2). Given that temperature was the most important predictor of ER, high ER in the raised water table plot is probably due primarily to warm conditions at the raised plot (Bubier et al. 1998, Lafleur et al. 2005), or 3) faster rates of anaerobic CO_2 production (Figure 3-9). For example, Aerts and Ludwig (1997) used mesocosms to document high anaerobic CO_2 production and consequently high ER from peat under a high water table treatment compared to a lowered water table treatment. More detail on anaerobic C mineralization is provided in Chapter 3.

2.4.4 Warming effects on CO_2 fluxes

Temperature is often shown to be a major control on CO_2 fluxes in boreal systems (Bridgham and Richardson 1992, Moore et al. 1998, Lafleur et al. 2005). Warmer air and soil temperatures stimulate microbial activity resulting in increased ER (Crill et al. 1988, Frolking and Crill 1994, Silvola et al. 1996) and increased GPP (Hobbie and Chapin 1998, Arft et al. 1999). A meta-analysis of terrestrial warming experiments found that 2-11 years of warming in the range of 0.3 – 6.0° C significantly increased soil respiration rates by 20%, net N mineralization rates by 46%, and plant productivity by 19% (Rustad et al. 2001). Indeed, in my study, warming increased ER and GPP consistently across all water table plots and years by 16% (mean ER flux was 3.99 ± 0.13 and 3.46 ± 0.12 μmol CO_2 m^{-2} sec^{-1} and mean GPP flux was

-4.31 ± 0.13 and -5.08 ± 0.13 μmol CO_2 m^{-2} sec^{-1} within the warmed and un-warmed subplots, respectively). While there was no warming x water table interaction (Figure 2-3), warming increased ER by 11% in the control water table plot, 18% in the lowered water table plot, and 17% in the raised water table plot. Therefore, the warming treatment had a more pronounced effect on ER in the lowered and raised water table plots than in the control water table plot. In the lowered water table plot, drier surface moss and soils have less insulation, which could have led to greater increase in ER than the control water table plot. In the raised water table plot, which inherently had warmer soils independent of the warming treatment, the warm and wet conditions in the warmed subplots may have created ideal conditions for both plant and microbial activity, thereby increasing ER through both autotrophic and heterotrophic pathways.

Because the warming treatment increased both ER and GPP, there was likely increased C mineralization and N mineralization in the warmed subplots. Given that N is often a key limiting nutrient in terrestrial ecosystems (Vitousek et al. 1997), increased N availability due to high mineralization rates could have stimulated plant growth. Similar soil warming experiments in arctic tundra sites also attributed increases in GPP to increased N availability (Hobbie and Chapin 1998). There was no significant warming treatment effect or higher level interactions involving warming on NEE, likely due to both increased GPP and ER rates within the OTC treatments, cancelling a net effect in either direction in NEE. These results are similar to other temperature manipulations across arctic tundra sites, the ITEX experiment, and peatland mesocosms (Hobbie and Chapin 1998, Arft et al. 1999, Updegraff et al. 2001), where there was an increase in both ER and GPP with warming, thereby with little influence on NEE. Surprisingly, neither GP_{max} values (Table 2-6) nor vascular LAI were affected by the warming treatment, but warming was positively correlated with α, or photosynthetic quantum efficiency (Table 2-6). This indicates that warming may be increasing vegetation production in a different way than the raised water table is increasing production—for example, possible differences in community response or C allocation to warming.

2.4.5 Modeling CO_2 fluxes and the potential for threshold changes

Climate change is expected to alter soil climate dynamics beyond the scope of contemporary variability. A key question is whether our current models will be able to accurately represent CO_2 fluxes under these changing climatic conditions, or whether ecosystems will undergo threshold changes that create new controls on and/or new trajectories of CO_2 fluxes that are not represented in current models. This experiment allowed me to determine whether this ecosystem showed evidence of such threshold changes to affect CO_2 fluxes in the first few years of experimentation (Figure 2-1). For ecosystem respiration (ER), the model containing year, season, and continuous soil climate variables (Model 1, Table 2-3) was a better fit model than the model that also contained treatment effects (water table or soil warming treatments). Temperature variables were important predictors of ER, with peat temperature at 2 cm depth explaining 25% of the variation in ER. Surprisingly, water table position was not a significant predictor of ER. However, water table position could still have indirect controls on CO_2 emissions via heat transfer. For example, the raised water table plot was significantly warmer than the control and lowered water table plots (Figure 2-5), likely a result of heat transfer from surface water to deeper peat layers. Thus, the strong CO_2 flux response to water table treatment may be more of a response to soil temperature than to water table position, although hydrological and thermal regimes in these ecosystems clearly are coupled.

The model containing treatment variables (Model 2) was not the best model according to AIC and contained no significant interactions between experimental treatment (water table, warming) and continuous variables (soil temperature or water table position). Model 1, or the model including year, season, and continuous environmental variables, also was the best model explaining GPP (Table 2-4). In general, temperature and mean daily water table position were both important controls on GPP in the model, and together explain 32% of the variation. Together, these modeling exercises suggest that the water table and warming treatments have simply extended the ambient relationship between temperature, water table position, and CO_2 fluxes at this site and did not create new relationships between soil hydroclimate and ER. However, processes operating at longer time scales, such as changes in plant community structure and soil organic matter quality may invoke such thresholds in future years of this experiment.

In this study, models of ER and GPP explained less than half the variation across the growing season (Table 2-3, Table 2-4). Similar peatland chamber studies attempting to model CO_2 fluxes also have had either low predictability (McNeil and Waddington 2003) or have built models that explained less than 25% of the variability in fluxes (Myers-Smith 2007). The lack of predictive power likely can be attributed to the interactive nature of plant responses to changes in temperature, moisture, and PAR, especially under drought stress. In contrast to ER and GPP models however, general linear models explained 77% of the variability in GP_{max} values (using water table treatment and % brown moss cover) and 65% of the variability in α values (with water table treatment, warming treatment, and cumulative forb leaf area; Table 2-6). The large amount of variability explained by the GP_{max} and α models relative to the poorer-fitting ER and GPP flux models indicates that while I decently characterized vegetation controls on CO_2 flux, I am not characterizing an important control on decomposition at my site. Further investigations of nutrient levels, reduction oxidation reactions, and microbial community structure in this ecosystem will improve our ability to effectively model C exchange in response to variations in climate.

2.4.6 Conclusions

Significant changes to growing season CO_2 fluxes were found following a 2.5 year ecosystem-scale manipulation of soil hydroclimate (water table position and surface soil temperature) in an Alaskan rich fen. The lowered water table treatment did not alter ER, but lowered GPP by 21-24%. Differences in GPP were attributed to decreased photosynthetic uptake of CO_2 by vascular vegetation and bryophytes due to drought stress. This resulted in increased NEE (trend toward increased atmospheric emissions) in the lowered water table plot relative to the control plot. The raised water table treatment was less of a CO_2 sink (more positive NEE values) in 2005, but a greater sink in 2006 compared to the control plot. This trend was driven primarily by interannual changes in GPP with greater GP_{max} values and % bryophyte cover in the raised water table plot relative to the control water table plot in 2006. Soil warming increased both ER and GPP by 16% resulting in no net effect of warming on NEE. Models of vegetation components at the APEX fen (GPP, GP_{max}, α) indicate that water table position and soil temperature are both important controls on plant uptake, while temperature was a stronger control than water table position on ER. There were no significant interactions with water table position and soil warming, indicating that responses to these processes across other Alaskan peatlands will be similar to my site, despite variations in hydrology or peat temperature.

Contrary to many hypotheses and model predictions in the literature, drought and lowered water table levels will not trigger a large increase of CO_2 to the atmosphere in this site, but will decrease productivity resulting in a loss of C uptake. Flooding and warming are both likely to increase mineralization rates, stimulating vegetation productivity and causing at least some peatlands to become a greater sink of atmospheric C. Together, my results show that studies investigating only climate change effects on decomposition rates (i.e., most lab incubation and mesocosm studies) will miss important vegetation controls on ecosystem-level C fluxes in the context of climate change, and will not capture the direction or magnitude of C flux changes in peatlands.

Table 2-1. Dominant vascular and bryophyte plant species at the Alaska Peatland Experiment (APEX) fen with average percent cover of each species ± one standard error in each water table plot (control, raised, lowered) in 2006.

FAMILY	GENUS SPECIES	2006 Average % Cover		
		Control	Lowered	Raised
Equisetaceae	*Equisetum fluviatile*	3% (0.03)	2% (0.00)	3% (0.03)
Cyperaceae	*Carex atherodes*	5% (0.04)	5% (0.01)	5% (0.04)
Rosaceae	*Potentilla palustris*	24% (0.19)	25% (0.03)	21% (0.06)
Rubiaceae	*Galium trifidum*	2% (0.02)	10% (0.04)	5% (0.04)
Poaceae	*Calamagrostis canadensis*	0% (0.00)	0% (0.00)	0% (0.00)
Sphagnaceae	*Sphagnum obtusum* *Sphagnum platyphyllum*	19% (0.19)	29% (0.17)	51% (0.42)
Amblystegiaceae	*Hamatocaulis vernicosus* *Drepanocladus aduncus*	59% (0.48)	2% (0.01)	12% (0.11)

Table 2-2. Results of a repeated measures analysis of variance analyzing net ecosystem exchange (NEE), ecosystem respiration (ER), and gross primary production (GPP) across the experimental treatments. Significant higher-level predictors are marked in bold ($p > 0.05$).

	df (numerator, denominator)	F	*p*
Net Ecosystem Exchange (NEE)			
Water table treatment	2, 8	44.73	**<.0001**
Warming treatment	1, 5	0.11	0.76
Year	1, 5	4.07	0.10
Water table treatment x warming treatment	2, 8	1.70	0.24
Water table treatment x year	2, 8	44.77	**<.0001**
Warming treatment x year	1, 5	3.98	0.10
Water table treatment x warming treatment x year	2, 8	0.76	0.50
Ecosystem Respiration (ER)			
Water table treatment	2, 8	0.41	0.68
Warming treatment	1, 5	14.18	**0.01**
Year	1, 5	0.71	0.44
Water table treatment x warming treatment	2, 8	1.59	0.26
Water table treatment x year	2, 8	8.85	**0.01**
Warming treatment x year	1, 5	0.67	0.45
Water table treatment x warming treatment x year	2, 8	0.71	0.52
Gross Primary Production (GPP)			
Water table treatment	2, 8	28.64	**0.0002**
Warming treatment	1, 5	12.65	**0.02**
Year	1, 5	17.48	**0.01**
Water table treatment x warming treatment	2, 8	0.53	0.61
Water table treatment x year	2, 8	60.75	**<.0001**
Warming treatment x year	1, 5	1.54	0.27
Water table treatment x warming treatment x year	2, 8	2.05	0.19

Table 2-3. Results of a general linear model using environmental parameters to predict log transformed ecosystem respiration (ER) of CO_2. The model explained 47% of the variation in ER of CO_2. Peat temperature (2 cm depth) was the most important predictor, explaining 25% of the variation in ER. Significant predictors ($p > 0.05$) are highlighted in bold.

	df	**Type III SS**	**F**	***p***
ER Model 1	15	57.45	18.14	**<0.0001**
Season	2	8.58	20.31	**<0.0001**
Year	1	1.99	9.47	**0.0023**
Air temperature	1	5.28	25.00	**<0.0001**
Peat temperature (2 cm)	1	0.77	3.63	**0.06**
Peat temperature (25 cm)	1	1.67	7.88	**0.01**
Mean daily water table position	1	0.57	2.71	0.10
Season x year	2	6.96	16.50	**<0.0001**
Season x air temperature	2	4.44	10.52	**<0.0001**
Year x air temperature	1	0.08	0.35	0.55
Year x peat temperature (2 cm)	1	0.04	0.19	0.67
Year x peat temperature (25 cm)	1	1.44	6.81	**0.01**
Year x mean daily water table position	1	0.08	0.35	0.55
Error	306	64.60		

Table 2-4. Results of a general linear model using environmental parameters to predict log transformed gross primary production (GPP) of CO_2. The model explained 48% of the variation in GPP of CO_2. Peat temperature (2 cm depth) alone was the most important predictor of GPP explaining 16% of the variation. Significant predictors (p > 0.05) are highlighted in bold.

	df	**Type III SS**	**F**	***p***
GPP Model 1	15	139.72	40.25	**<0.0001**
Season	2	11.20	24.20	**<0.0001**
Year	1	2.41	10.40	**0.0013**
Air temperature	1	14.27	61.64	**<0.0001**
Peat temperature (2 cm)	1	1.41	6.07	**0.01**
Peat temperature (25 cm)	1	2.22	9.61	**0.0020**
Mean daily water table position	1	8.03	34.71	**<0.0001**
Season x year	2	6.05	26.14	**<0.0001**
Season x air temperature	2	4.74	10.24	**<0.0001**
Year x air temperature	1	0.23	0.98	0.32
Year x peat temperature (2 cm)	1	0.08	0.36	0.55
Year x peat temperature (25 cm)	1	2.31	9.99	**0.0016**
Year x mean daily water table position	1	2.10	9.09	**0.0027**
Error	648	149.97		

Table 2-5. Non-linear NEE-PAR curve parameter estimates for 2006. Coefficients for the CO_2 exchange and light relationships were derived from equation 1 (± 1 standard error). α is the initial slope of NEE versus PAR (also called the apparent quantum yield), GP_{max} is the gross photosynthesis above light saturation, and R is the y (NEE) axis intercept, or dark respiration.

Water Table Treatment	Warming Treatment	α	GP_{max}	R
CONTROL	NON	0.0187 (0.007)	7.115 (1.106)	-3.659 (0.288)
	WARM	0.026 (0.013)	5.7046 (0.8162)	-3.807 (0.335)
LOWERED	NON	0.021 (0.014)	4.512 (0.863)	-3.792 (0.297)
	WARM	0.026 (0.016)	4.529 (0.788)	-4.025 (0.348)
RAISED	NON	0.028 (0.009)	9.958 (1.262)	-4.129 (0.357)
	WARM	0.034 (0.014)	9.942 (1.429)	-5.002 (0.433)

Table 2-6. Results of general linear models using vegetation indices and treatment parameters to predict GP_{max} and Alpha (α) for 2006. The two models explained 77% and 65% of the variation in GP_{max} and α, respectively. Significant predictors ($p > 0.05$) are highlighted in bold.

	df	Type III SS	F	*p*
GP$_{max}$				
Model	3	86.851	14.18	**0.0002**
Water table treatment	2	80.198	19.64	**0.0001**
% brown moss cover	1	8.798	4.31	**0.0583**
Error	13	26.542		
Alpha (α)				
Model	6	0.002	3.06	**0.0573**
Water table treatment	2	0.001	4.27	**0.0455**
Warming treatment	1	0.0008	6.34	**0.0305**
Cumulative leaf area index (forbs)	1	0.001	11.25	**0.0073**
Water table treatment x cumulative leaf area index (forbs)	2	0.001	4.61	**0.0380**
Error	10	0.003		

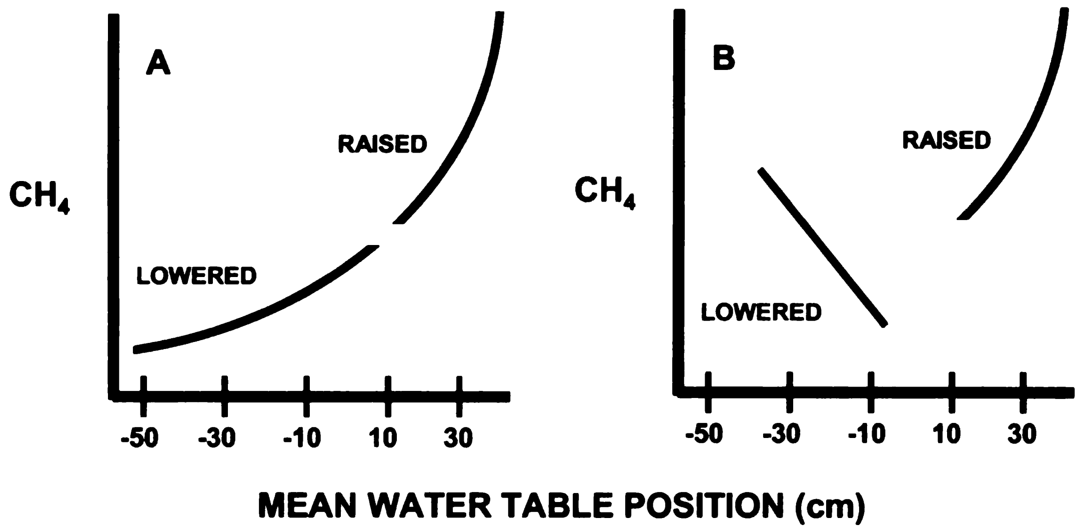

Figure 2-1. Schematic illustrating possible thresholds to ecosystem function induced by climate change. This example shows the effect of water table position on methane (CH_4) emissions in an experimental raised and lowered water table plot. Here, -50 represents a low water table position below the moss surface and 10 represents a high water table position above the moss surface. Figure A) As expected, an increase in mean water table position increases CH_4 flux to the atmosphere exponentially due to greater anaerobic mineralization. Thus, there is no interaction between ambient water table position and water table treatments governing CH_4 emissions. This indicates no threshold changes induced by the climate manipulation. Figure B) In this case, CH_4 emissions increased with water table position in the raised water table plot as expected. However, CH_4 emissions decreased with water table drawdown in the lowered water table plot, due to an increase in sedge production that led to more CH_4 transport through the acrotelm peat via aerenchyma tissue. This illustrates an interaction between water table position and water table plot, indicating that the experimental manipulation 'pressed' the system across a threshold creating a new relationship between water table position and CH_4 production.

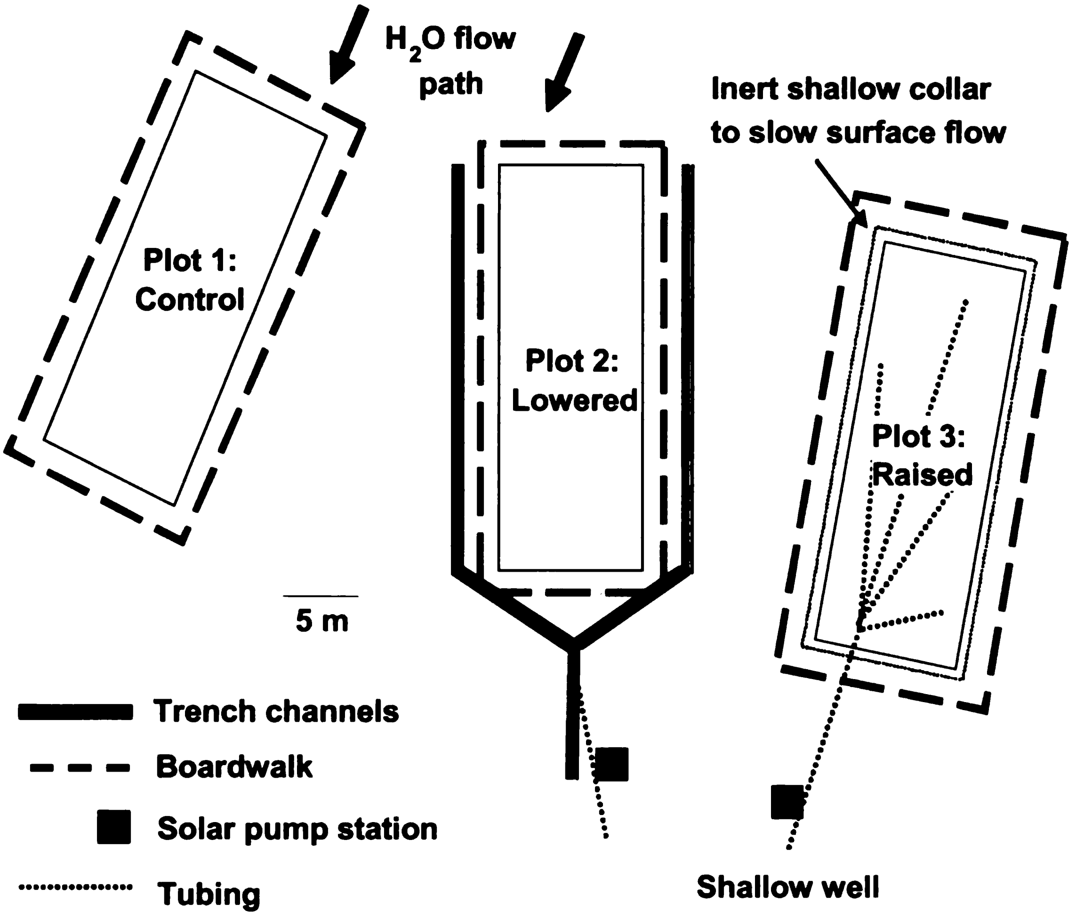

Figure 2-2. The Alaska Peatland Experiment (APEX) experimental design was initiated in March 2005. Trenches drain water from the lowered water table plot and solar powered pumps divert water from the shallow well to the raised water table plot.

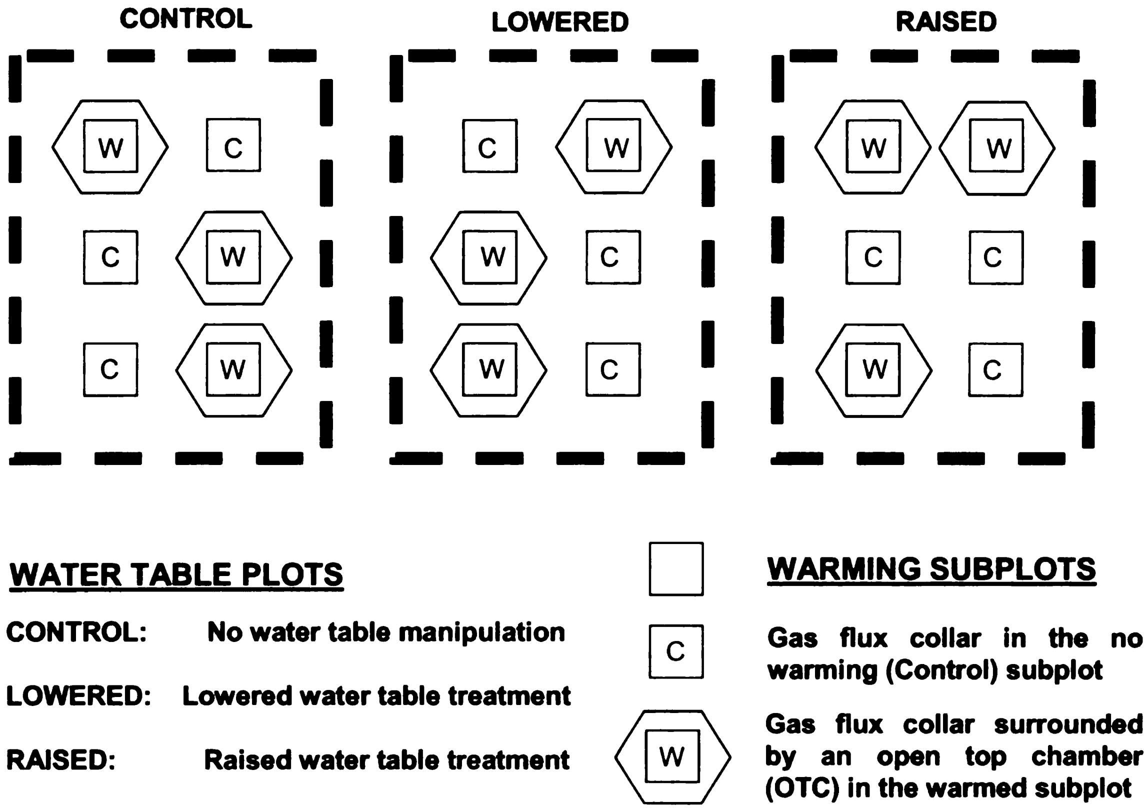

Figure 2-3. At the Alaska Peatland Experiment (APEX) rich fen, I established six 3 m^2 subplots within each water table plot (control, lowered, raised). The subplots were randomly assigned to one of two warming treatments, including warmed subplots (identified with a "W"; seasonally warmed using open top chambers (OTCs; octagon shapes)) and un-warmed subplots (identified with a "C"; control). Warming treatments were replicated in triplicate within each water table plot. Gas fluxes were taken at each subplot on a weekly basis.

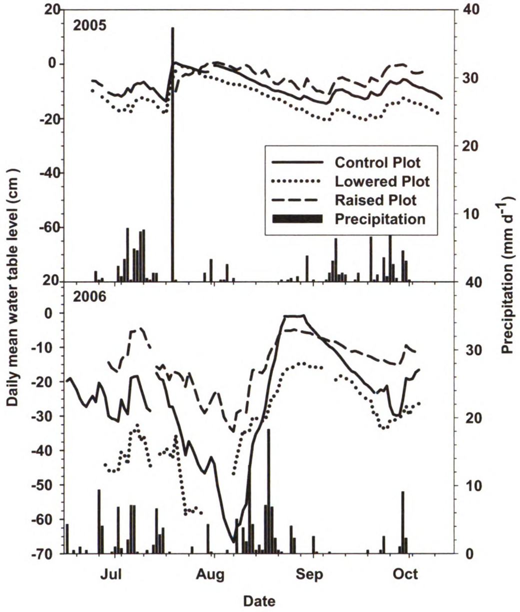

Figure 2-4. Water table levels and precipitation at the manipulation plots in 2005 and 2006. Positive values denote water table position above the peat surface (inundated). Bars represent precipitation events. Precipitation was not significantly different between the two study years (F=1.61, df=1, *p*=0.21).

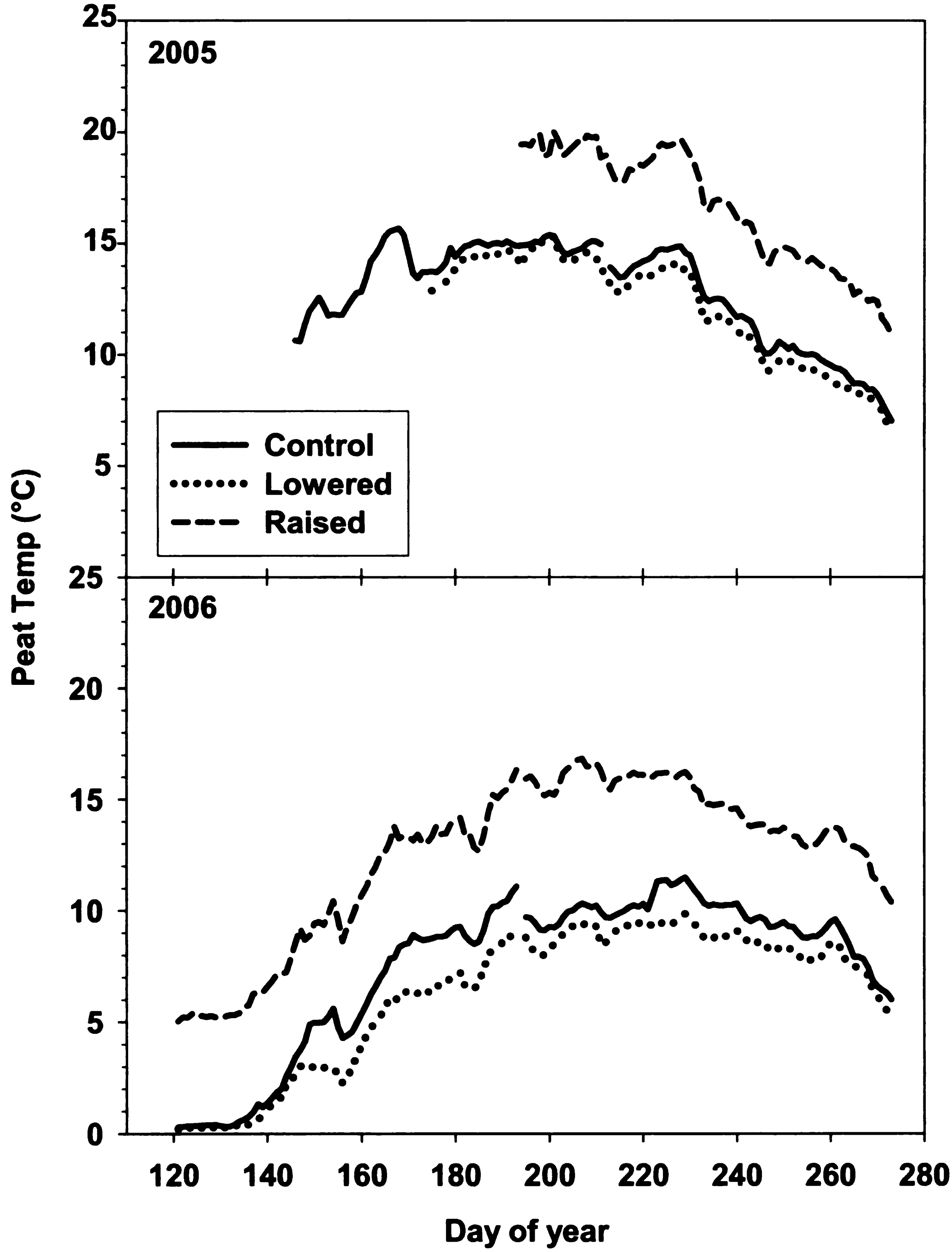

Figure 2-5. Mean peat temperatures at 25 cm beneath the moss surface in 2005 and 2006 across the three water table plots (corresponding to the control, lowered, raised water table plots).

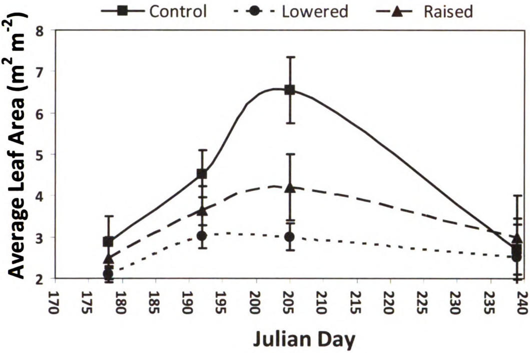

Figure 2-6. Average vascular leaf area index (m^2 m^{-2}) across our three water table plots (control, lowered, raised) throughout the 2007 growing season (June 19 – August 28, 2007). Each point represents average leaf area index (averaged across species) ± standard error.

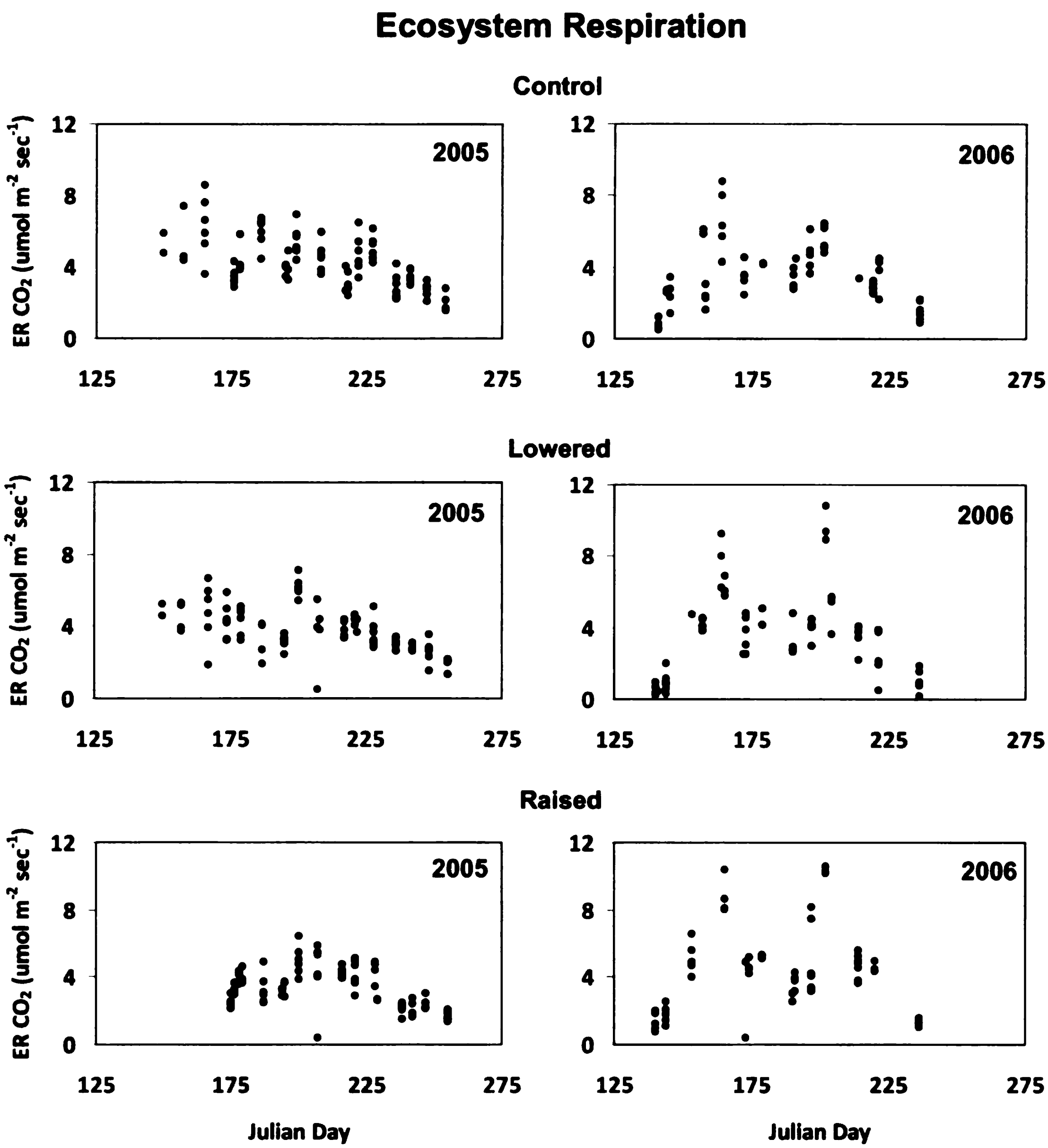

Figure 2-7. Growing season ecosystem respiration (ER) within each water table treatment (control, lowered, raised) and year (2005, 2006). Each point represents a specific measure of ER within each subplot.

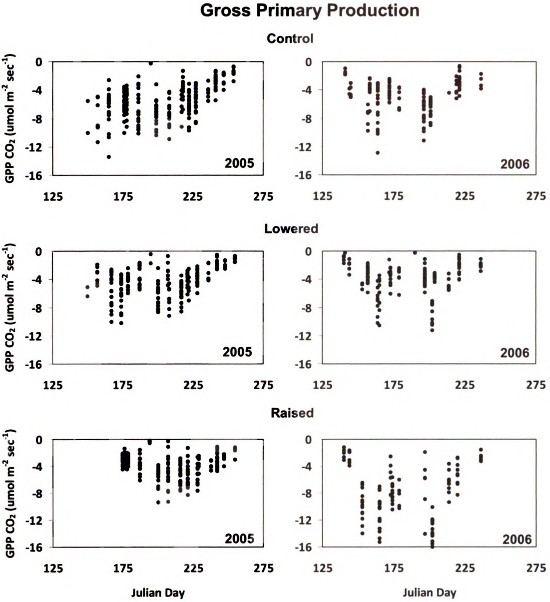

Figure 2-8. Growing season gross primary production (GPP) within each water table treatment (control, lowered, raised) and year (2005, 2006). Each point represents a specific measure of GPP within each subplot.

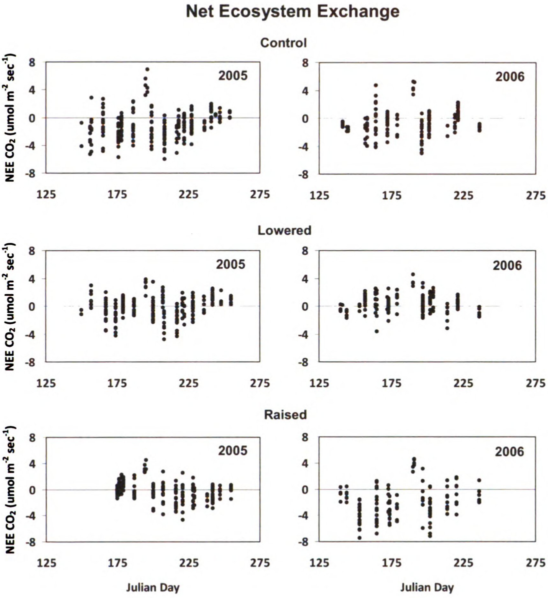

Figure 2-9. Growing season net ecosystem exchange (NEE) within each water table treatment (control, lowered, raised) and year (2005, 2006). Each point represents a specific measure of NEE within each subplot.

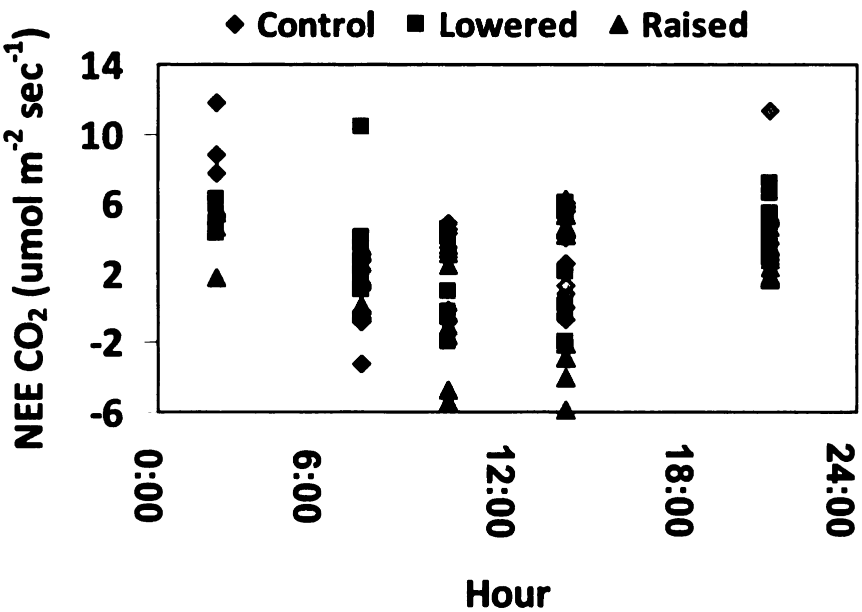

Figure 2-10. Diurnal net ecosystem exchange (NEE) of CO_2 within our water table treatment (control, lowered, raised) on August 2, 2007. Each point represents a single NEE flux measurement at a single gas flux collar.

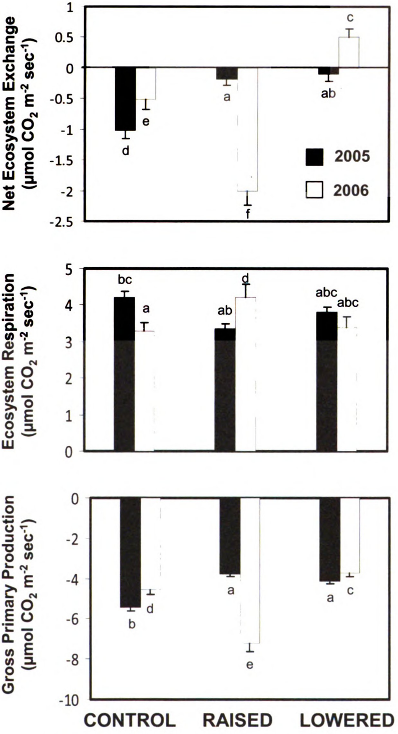

Figure 2-11. Results of a repeated measures analysis of variance model analyzing CO_2 flux components of net ecosystem exchange, ecosystem respiration, and gross primary production across water table treatments and years. Data are means ± one standard error (not adjusted for model comparisons). Same letter superscripts denote non-significant differences from *post hoc* comparison of means tests.

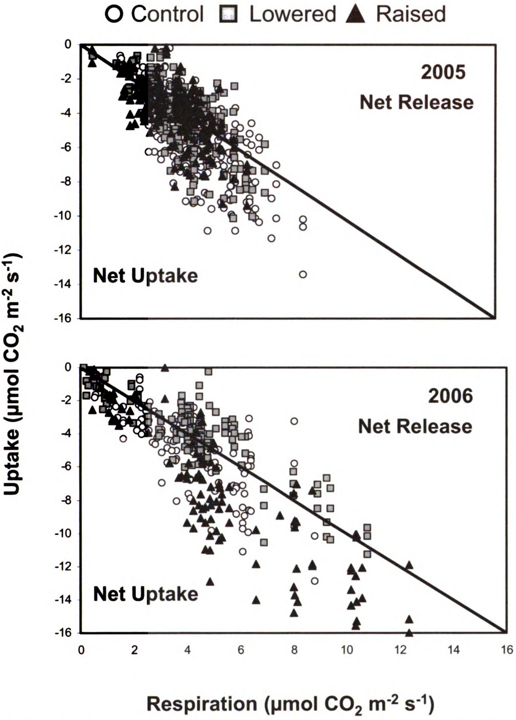

Figure 2-12. Ecosystem respiration (ER) versus gross primary production (GPP; uptake) plotted against a 1:1 line for 2005 and 2006. Each data point represents a specific measurement of CO_2 ER and GPP in a subplot on a particular day. Points falling above the line represent a net release of CO_2 to the atmosphere (less moles of CO_2 taken up by plants for each mole respired), points falling below the line represent net uptake of CO_2, while the 1:1 line represents no net uptake or release of CO_2.

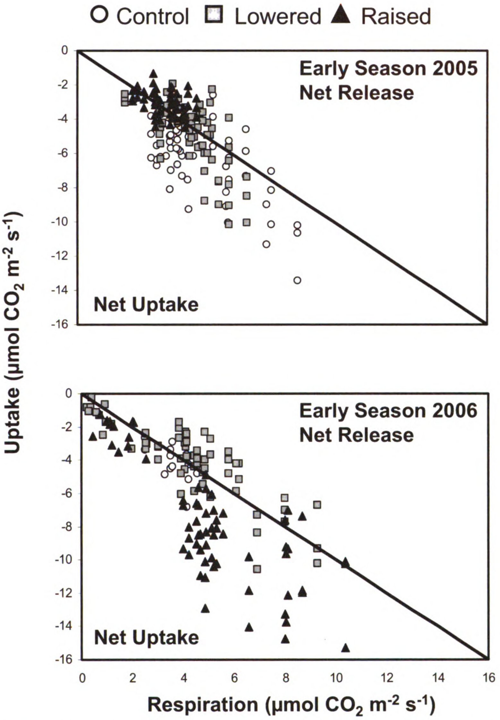

Figure 2-13. Early season (Julian Day 140 – 179) ecosystem respiration (ER) versus gross primary production (GPP) plotted against a 1:1 line for 2005 and 2006. Each data point represents a specific measurement of CO_2 ER and GPP in a subplot on a particular day. Points falling above the line represent a net release of CO_2 to the atmosphere falling below the line represent net uptake of CO_2, while the 1:1 line represents no net uptake or release of CO_2.

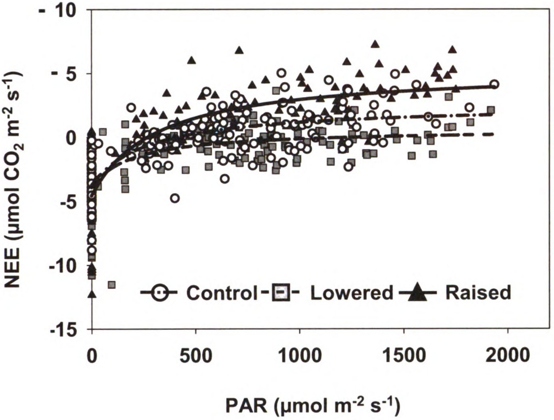

Figure 2-14. Relationship between net ecosystem exchange of CO_2 (NEE) and photosynthetic active radiation (PAR) across our three water table treatments (control, lowered, raised) during 2006. Lines are hyperbolical fits through the data. Model parameters were fit using PROC NLIN in SAS 8.1.

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CHAPTER 3

Effects of an Experimental Manipulation of Water Table and Soil Temperature on Soil Carbon Mineralization and Organic Matter Quality

3.1 INTRODUCTION

Peatlands store up to 30% of the world's terrestrial soil carbon (C) and are located primarily in areas expected to experience dramatic climate warming (Gorham 1991, Vitt 2006). Peat accumulates where C fixation through net primary production (NPP) at the surface is greater than losses of C from decomposition, leaching, and/or disturbance. Peat accumulation rates will be altered if the cold, wet conditions that maintain slow decomposition rates and promote C storage in peatlands are altered with climate change (Gignac et al. 2000). Given that responses of peatland C cycling to climatic change are likely to influence atmospheric C concentrations, how peatlands and their C fluxes will respond to C cycling remains an important issue.

Air and soil temperature, water table level, and soil quality are the main controls on carbon dioxide (CO_2) and methane (CH_4) emissions from peatlands (Figure 1-1; Updegraff et al. 1995). Many studies have shown that water table level (Nykanen et al. 1995, Moore and Dalva 1993, 1997, Strack and Waddington 2007) and temperature (Hobbie and Chapin 1998, Updegraff et al. 1995, Christensen et al. 1999, Grogan and Chapin 2000, Rustad 2001) strongly control C mineralization rates in peatlands. Because many northern peatlands are expected to experience warmer and drier conditions, future climate change likely will directly impact C mineralization rates in peatlands.

Besides direct soil hydroclimate controls on mineralization rates, indirect controls on mineralization processes such as substrate quality have also been shown to impact mineralization even on a short-term basis (Figure 1-1; Keller et al. 2004). Thus, changing climatic conditions could indirectly impact rates of C mineralization in peatlands through changes in soil organic matter quality (Moore and Dalva 1993, Keller et al. 2004) caused by changes in decomposition and/or vegetation structure and function.

Soil quality is a broad term that encompasses many properties of soil including the sizes of labile C pools, turnover rates of these pools, chemistry, nutrient concentrations, bulk density, and microbial community. In one study, soil organic matter quality was shown to be more important than temperature in controlling rates of mineralization in peatlands (Nadelhoffer et al. 1991). Generally, higher concentrations of labile organic matter can result in higher C mineralization rates while higher concentrations of recalcitrant C compounds decrease mineralization (Updegraff et al. 1995).

Shifts in vegetation productivity and community structure will impact the quality of litter into the soil, with potential positive or negative feedbacks to heterotrophic respiration (Hobbie and Chapin 1996, Madritch and Hunter 2003). For example, studies have documented increased bryophyte cover in peatlands exposed to higher water tables (Strack and Waddington 2007). An increase in bryophytes, especially *Sphagnum* mosses, could lead to more recalcitrant organic matter inputs due to the high concentrations of organochemical compounds such as phenolics and uronic acids in the tissue, which inhibit microbial activity (Verhoeven and Liefveld 1997, Turetsky 2003). Weltzin et al. (2000) raised soil temperature and documented an increase in woody vegetation abundance, which would influence lignin inputs to soil as well as vascular root biomass and root exudates. Overall, changes in vegetation structure toward emergent vegetation is likely to increase labile compounds in soils (Van Wijk et al. 2004) while increases in bryophyte or woody-dominated communities will increase the inputs of recalcitrant organic matter to soils, with negative feedbacks to heterotrophic respiration.

As fresh litter inputs begin to decompose, soil organic matter quality becomes more and more dominated by the signature of recalcitrant compounds. Moving down through a peat profile, concentrations of labile compounds decrease and concentrations of recalcitrant compounds generally increase (Turetsky et al. 2000). Changing soil hydroclimate conditions that are conducive to decomposition (warmer soils, water table drawdown) likely will accelerate the decomposition of labile compounds preferentially to recalcitrant materials in peat.

The goal of this chapter is to understand whether the field manipulation of water table and soil warming influenced soil organic matter quality and C mineralization rates. I measured anaerobic CH_4 production and anaerobic and aerobic CO_2 production rates from peat exposed to the soil climate manipulation treatments from Chapter 2. I incubated all samples at the same moisture content and temperature. Thus, differences in C mineralization rates (CO_2 and CH_4 production) among treatments likely are the result of changes in soil quality due to the experimental manipulations of soil warming and water table position (Chapter 2). I also quantified other soil quality properties such as % C, % nitrogen (N), and bulk density. The C/N ratio, or the ratio of energy to nutrients, is often used as a proxy for soil quality because it is a good indicator of the chemical resistance of organic material to break down (quality). Bulk density (g cm^{-3}) is also an important soil parameter for predicting C mineralization (Bridgham et al. 1998). Lowered water tables and subsidence as well as high rates of decomposition have both been shown to increase bulk density (Minkkinen and Laine 1998). I hypothesize and predict that C mineralization rates will respond to manipulation of both water table position and soil temperature at the Alaskan fen; such that:

H_1: Given that the field manipulation influenced vegetation structure, gross primary production (GPP), and ecosystem respiration (ER) (Chapter 2), my overall hypothesis is that relatively short-term (2.5 year) changes in soil temperature and water table level induced by the treatments will effect C mineralization (as CO_2 and CH_4 production) in peatlands through changes in soil quality or microbial community.

H_2: Soils exposed to the lowered water table and warming treatments will have poor soil quality, which will correspond to lower mineralization rates, because of previous exposure to drier, warmer conditions and greater decomposition of labile C relative to the control.

H_3: Given that higher water tables appeared to increase bryophyte cover, I hypothesized that the raised water table treatment will lead to more recalcitrant organic matter inputs to soils which will inhibit microbial activity and C mineralization rates.

3.2 METHODS

3.2.1 Study site and experimental design

The soil used for this incubation experiment was collected from the Alaska Peatland Experiment (APEX) site; a moderately rich fen located approximately 35 km southeast of Fairbanks, Alaska (64.82°N, 147.87° W). The APEX site is representative of other boreal peatlands because rich fens are one of the most common peatland types in western boreal North America (Vitt et al. 2000). The APEX site is described in detail in Chapter 2 (2.2.1) and Turetsky et al. (in press).

I examined laboratory C mineralization rates (as CO_2 and CH_4 production) in Alaskan fen peat samples that had undergone experimental water table and soil warming manipulations for approximately two years. Details of these experimental manipulations are provided in Chapter 2 (2.2.2 and 2.2.3). Briefly, the field experiment consists of a factorial design of water table position (three treatments including a control, a lowered or drained treatment, and a raised or flooded treatment) and surface soil temperature (two treatments including a control, or no warming, treatment and surface soil warming via open top chambers) that was initiated in the winter of 2005.

3.2.2 Soil sampling and processing

In September 2007 (approximately 2.5 years after initiation of the field manipulations), I removed one soil core (7 cm diameter, 25 cm long) from each subplot (2 temperature treatments x 3 water table treatments x 3 replicates=18 cores total). Because the experiment is designed as a long-term study, there is limited space inside the subplots for destructive sampling. However, to increase replication in the sampling of the water table treatments, I extracted 2 soil extra cores from each water table treatment (6 extra cores total) away from the established subplots (representing un-warmed soil). Thus, in total I sampled 24 cores, 8 per water table treatment). In the field, the cores were cut into 5 cm increments at depths of 0-5, 5-10, 10-15, 15-20, and 20-25 cm, where 0 cm was equivalent to the top of the moss surface. Each 5 cm section was sealed in a ziplock bag to retain moisture and frozen. Once frozen, the cores were placed in ice chests with ice packs and shipped overnight to Michigan State University where they were promptly placed in freezers. For this study, we used soil from the 5-10 cm depth increment (the surface-most increment with no green moss) and the 20-25 cm depth increment of each core. While frozen, each depth increment was subdivided into quarters. Bulk density and field volumetric moisture content were determined on one quarter (a sub sample) of peat. The dry mass of the subsample was measured by oven drying the sample at 55° C for 72 hours; dry mass values were used in bulk density calculations. After recording the dry weight, each subsample was ground using a cyclone sample mill (UDY Corporation; Fort Collins, CO) for homogenization, and run on an elemental combustion system (Costech ECS 4010, Valencia, CA) for % C and N (C/N) analysis. Peat from another quarter (separate subsample) was thawed at 2° C overnight, large roots and sticks (greater than 0.5 cm) were removed by hand, and the peat was homogenized gently by hand. Soils were equilibrated for 9 days at 2° C to allow for the C mineralization pulse from dieing roots to pass.

I placed approximately 10 g of wet soil (at field capacity) from each depth increment into a 250 mL incubation jar (Chromatographic Specialties, Inc.; Ontario, Canada). To create similar soil moisture conditions across all incubation samples, each incubation sample was brought to a similar moisture content (40-60% representing ideal non-limiting moisture) by adding an appropriate volume of distilled water given the bulk density of that particular sample (Skopp 1990). Jars assigned to the aerobic headspace treatment were flushed with ambient room air (~400 ppm CO_2) and sealed with lids fitted with septa. Jars assigned to the anaerobic headspace were flushed continuously with N gas (N_2) in an anaerobic glove box for 10 minutes during processing. The jars were then immediately sealed with lids fitted with septa and were purged with 60 mL of N gas followed by the removal of 60 mL of headspace; this process was repeated three times to ensure an anaerobic headspace. All jars (96 total; n = 3 for warming treatment, n = 8 for water table treatment, n = 3 for warming x water table treatment) were incubated in the dark at constant room temperature conditions (approximately 22° C) for the 6 week incubation experiment.

3.2.3 Carbon dioxide and methane production

Rates of CO_2 and CH_4 production were estimated during five 24-hour periods over the 40 day experiment. The five 24-hour periods began on days 1, 3, 10, 24, and 39 of the incubation. During each period, a 10 mL headspace gas sample was taken from each jar using syringes equipped with three way stopcocks immediately after jars were sealed (time=0), and then every 12 hours over the 24 hour period (3 headspace samples/24 hours). Prior to sampling, each jar was shaken by hand to mix the gases within peat pore spaces and to release trapped gas bubbles. After headspace samples were collected, jars were backfilled with 10 ml of N gas to ensure constant air volume/pressure. For jars assigned to the aerobic headspace treatment, after each 24 hour sampling period the lids were removed, samples were gently flushed with a stream of room air, and the jars were wrapped with plastic wrap to prevent moisture loss. Jars assigned to the anaerobic headspace treatment were flushed in the anaerobic glove box with N_2 at the end of each 24 hour experiment before being resealed. Anaerobic jars also were purged as described above prior to each 24 hour sampling period to ensure anaerobic conditions throughout the duration of the experiment.

Each headspace sample was analyzed for CH_4 and CO_2 concentrations. Five mL of each sample was analyzed for CH_4 concentrations using a Varian 3800 gas chromatograph (GC) equipped with a Haysep Q column (GC; Varian Inc., Palo Alto, California). The GC was calibrated using four CH_4 standard gases (0, 10.2, 100, 1000 ppm) before each sampling day and standardized by running a standard after approximately every 10 samples. The remaining 5 mL of each sample was analyzed for CO_2 concentrations using a PP-system EGM-4 infrared gas analyzer (IRGA). The IRGA was standardized using a CO_2 standard gas after every 10 samples.

Before assessing production rates, the measured concentrations were corrected for headspace dilution caused by backfilling with N gas, corrected for standard pressure and temperature, and multiplied by the corrected headspace volume. Overall gas production rates were calculated from the slope of the gas concentrations over incubation time and were divided by the dry peat weight (g) to report data on a mass basis (nmol CH_4 g^{-1} day^{-1}, µmol CO_2 g^{-1} day^{-1}) or were divided by sample bulk density (g cm^{-3}) to report data on a volume basis (nmol CH_4 cm^{-3} day^{-1}, µmol CO_2 cm^{-3} day^{-1}). Slopes with r^2 values less than 0.75 were discarded (representing less than 2% of the CO_2 data and 5% of the CH_4 data).

3.2.4 Statistical analysis

The first round of measurements (day 0) was excluded from all analysis due to possible disturbance. The overall goals of my statistical analyses were 1) to explore treatment (soil warming and water table treatments) effects on C mineralization rates, and 2) to assess the correlations between C mineralization and indices of organic matter quality (%C, %N, C/N, bulk density).

To investigate whether the manipulation experiment impacted CO_2 and CH_4 production rates, I used a repeated measures analysis of variance (ANOVA) and Tukey *post hoc* analysis of means tests (Proc Mixed) in SAS 8.1 (SAS Institute Inc., Cary, NC, USA) to determine the impact of water table treatment, soil warming treatment, depth, and all interactions among these fixed effects on CH_4 and CO_2 production rates

To understand basic organic matter quality controls on CH_4 and CO_2 production rates, I used a general linear model (Proc GLM) in SAS 8.1 to explain production rates. This model included %N, %C, C/N, bulk density, depth (10 cm, 25 cm), incubation treatment (aerobic, anaerobic) and experimental treatment (control, lowered, raised water table treatments; warmed and un-warmed treatments) and interactions among these factors as predictors of CO_2 or CH_4 production.

3.3 RESULTS

3.3.1 Carbon dioxide and methane production rates

Over the 40 day incubation experiment, there was no aerobic production of CH_4. Anaerobic CH_4 production from the incubations ranged from 0 to 47.79 nmol g^{-1} day^{-1} and 0 to 3.96 nmol cm^{-3} day^{-1} on a per mass and per volume basis, respectively. At both depths and across water table treatments, CH_4 production rates were either constant or increased slightly over the duration of the 40 day incubation experiment (Figure 3-1).

Repeated measures ANOVA models showed that anaerobic CH_4 production rates on a mass basis (nmol g^{-1} day^{-1}) varied by depth (Table 3-1). Rates of CH_4 production from the 5-10 cm depth increment were faster than the 20-25 cm depth increment (2.0 ± 0.1 and 1.6 ± 0.1 nmol g^{-1} day^{-1} in the 5-10 and 20-25 cm depth increments, respectively). On a volume basis (nmol cm^{-3} day^{-1}), there were no differences in CH_4 production rates across depths, warming, or water table treatments (Table 3-1). When data were analyzed as a cumulative production rate (i.e., nmol g^{-1} 40 day^{-1} or nmol cm^{-3} 40 day^{-1}), results were similar to those described above, with a depth effect for CH_4 production on a mass basis and no difference among treatments for CH_4 production on a volume basis.

Aerobic CO_2 production rates ranged from 0.93 to 26.66 µmol g^{-1} day^{-1} and 0.09 to 2.89 µmol cm^{-3} day^{-1} on a mass and volume basis, respectively. At both depths and across water table treatments, aerobic CO_2 production rates increased between day 2 and day 10, and then generally decreased over the duration of the 40 day incubation experiment (Figure 3-2). Anaerobic CO_2 production rates ranged from 0 to 71.61 μmol g^{-1} day^{-1} and 0 to 5.19 μmol cm^{-3} day^{-1} on a mass and volume basis, respectively. Anaerobic CO_2 production rates increased between day 2 and day 10, and then remained constant over the duration of the 40 day incubation experiment (Figure 3-2).

A repeated measures ANOVA model showed that CO_2 production on a mass basis (μmol g^{-1} day^{-1}) varied by an incubation treatment (aerobic, anaerobic) x depth interaction (Table 3-2). For both depths, anaerobic CO_2 production rates were significantly faster than aerobic production rates (Figure 3-3). The 5-10 cm depth increment had faster anaerobic CO_2 production rates than the 20-25 cm increment, while there was no difference between depths in aerobic CO_2 production rates (Figure 3-3).

A repeated measures ANOVA model showed that CO_2 production on a volume basis (μmol cm^{-3} day^{-1}) varied by treatment. Aerobic CO_2 production rates were slower than anaerobic production rates (means ± one standard error; 0.926 ± 0.049 and 1.089 ± 0.061 μmol cm^{-3} day^{-1} in the aerobic and anaerobic treatments, respectively; Table 3-2). Rates of CO_2 production on a volume basis also varied by a depth x soil warming treatment interaction (Table 3-2). For both depth increments, CO_2 production rates from peat collected within the soil warming subplots were significantly slower than from peat taken from the un-warmed subplots (Figure 3-4). In the warmed treatment, peat from the 5-10 cm depth increment had faster CO_2 production rates than deeper peat (20-25 cm depth increment), while there was no difference between depths in peat from the un-warmed subplots. Carbon dioxide production rates on a volume basis also varied by a water table treatment by depth interaction (Table 3-2). At 5-10 cm depth, peat collected from the lowered water table treatment had the slowest CO_2 production rates, while peat from the same depth interval collected from the control and raised water table treatments had the fastest. Conversely, for the 20-25 cm depth increment, the lowered water table treatment peat had the fastest CO_2 production rates, while peat taken from the control water table treatment had the slowest (Figure 3-5). Therefore, peat at the 5-10 cm depth increment corresponded to faster CO_2 production rates in the control and raised water table treatments than deeper peat, but showed the opposite pattern in the lowered water table treatment, with slower rates of CO_2 production in the 5-10 cm depth increment than in the 20-25 cm depth increment.

Across depths and treatments, the ratio of CO_2 to CH_4 production ranged from 297 to 6620. Ratios of CO_2 to CH_4 varied by a water table treatment x depth interaction ($F_{2, 72} = 4.25$, $p = 0.02$). Across water table treatments, ratios were always higher in the 5-10 cm increment than in the 20-25 cm increment. However, this was particularly true for the lowered water table plot where the 5-10 cm increment corresponded to very high ratios.

To investigate whether CO_2 inhibition caused greater anaerobic CO_2 production than aerobic CO_2 production, temporal development of aerobic CO_2 production rates was modeled using linear regression. In the aerobic jars, the CO_2 concentration at time zero explained 10% of the variation in relative CO_2 production rates, while day of incubation explained 13% of the variation. The residuals of this linear regression were examined and CO_2 concentration at time zero explained less than 13% of the variation in residuals for both aerobic and anaerobic CO_2 production rates. This suggests that CO_2 inhibition is not an important factor controlling differences in aerobic and anaerobic CO_2 production rates.

3.3.2 Soil physical and chemical variables

Across the incubation samples, bulk density ranged from 0.049 g cm^{-3} to 0.199 g cm^{-3}. Bulk density varied by a warming treatment x depth interaction (Table 3-3). Generally, peat from the 20-25 cm depth increment had a higher bulk density than peat from the 5-10 cm depth increment though this was less obvious in the warmed subplots in the lowered water table treatment than in the other treatments.

Carbon concentrations ranged from 35.1 to 45.7%. Percent (%) C data varied by a depth effect alone, and peat from the 20-25 cm depth increment had greater %C than from the 0-10 cm depth (Table 3-3). Nitrogen concentrations ranged from 1.2 to 3.1% across the field treatment and varied by a significant water table treatment x warming treatment x depth interaction (Table 3-3). This interaction is complex, but generally peat at the 5-10 cm depth increment taken from the raised water table treatment had the highest %N, while peat within the 20-25 cm depth increment taken from the un-warmed subplots in the control and lowered water table treatments had the lowest. C/N ratios ranged from 0.028 to 0.079 across the site and varied by a depth effect alone. C/N was significantly higher in the 20-25 cm depth increment than in the 5-10 cm depth increment (Table 3-3).

In general, neither CO_2 nor CH_4 production rates (μmol g^{-1} day^{-1} or μmol cm^{-3} day^{-1}) showed relationships with chemical variables (Figure 3-7). General linear models investigating controls on CO_2 production rates showed that soil chemical parameters (%C, %N, BD, C/N) and interactions between these soil chemical parameters and the water table or warming treatments were not significant controls on C production rates.

3.4 DISCUSSION

3.4.1 Characterizing carbon mineralization in an Alaskan rich fen

Rates of anaerobic CH_4 production measured in my incubation experiment, which averaged 0 to 47.79 nmol g^{-1} day^{-1} across all treatments, are on the low end but tend to fall within the range documented in other peatland incubation experiments (0-51,000 nmol g^{-1} day^{-1}; Yavitt et al. 1987, Magnusson 1993, Moore and Dalva 1997, Waddington et al. 2001, Keller et al. 2004, Glatzel et al. 2004, Turetsky and Ripley 2005; Table 3-3). Peat incubation studies generally report a wide range of production rates, likely due to different experimental methods (temperatures, duration), but also due to differences in microbial abundance, peat characteristics, and substrate quality (Table 3-4). Field CH_4 fluxes at the APEX site, where these soils were collected, also were low compared to other studies (Turetsky et al. in press). There are several possible explanations for why CH_4 production and emissions are low at the APEX site, including 1) high CH_4 oxidation rates in surface peat, 2) acidic conditions that inhibit methanogenesis (Bergman et al. 1998), 3) large water table fluctuations that cause short-duration anaerobic conditions, which lower methanogen abundance, 4) an inadequate supply of C substrates (Yavitt et al. 1997), and 5) redox conditions that favor alternate anaerobic mineralization pathways.

Since CH_4 production rates were low both in the field and laboratory incubations; these results are not likely a direct result of climate, but due to poor substrate quality or low methanogen abundance. However, it is likely that climate may indirectly impact CH_4 production by altering substrate quality and/or methanogen population. Also the fact that CH_4 production rates from the 5-10 cm depth increments (where C quality tends to be better due to proximity to fresh organic matter inputs) were faster than production rates from the 20-25 cm depths points to poor C quality as the most plausible cause for the overall low CH_4 production rates.

Generally, rates of aerobic CO_2 production from this study (0.93 to 26.66 μmol g^{-1} day^{-1}) coincide with other peat microcosm incubations (including bog and fen peat from an array of depths; Table 3-4). My anaerobic CO_2 production ranged from 0 to 71.61 μmol g^{-1} day^{-1}, which is substantially higher than most peat incubations (Table 3-4). Surprisingly, anaerobic CO_2 production was greater than aerobic production across all climate manipulation treatments (Figure 3-3). Aerobic : anaerobic CO_2 ratios ranged from 0.28:1 – 0.84:1, which are extremely low compared to other peatland studies. Most studies report aerobic: anaerobic CO_2 production ratios within the range of 2.5:1 to 4.3:1 (Bridgham and Richardson 1992, Johnson et al. 1990, Updegraff et al. 1995, Bergman et al. 1999, Waddington et al. 2001, Glatzel et al. 2004). Post-incubation leachates from this experiment were analyzed on a Dionex ICS 2000 and show lower NO_3 (mg L^{-1}) concentrations in the aerobic treatment compared to the anaerobic treatment (Figure 3-8). Therefore, the high anaerobic CO_2 production is likely a result of denitrification, or the mineralization of organic N, which reduces nitrate and produces CO_2. There was no difference in sulfate concentrations (SO_4, mg L^{-1}) in post-incubation leachates from the aerobic and anaerobic treatments; therefore, sulfate reduction is not likely the cause of high anaerobic CO_2 production.

Similar to other peat incubation experiments, CH_4 and CO_2 production rates generally decreased with depth (Figure 3-4 and Figure 3-5; Yavitt et al. 1987, Bridgham and Richardson 1992, Nadelhoffer et al. 1991, McKenzie et al. 1998, Waddington et al. 1998, Glatzel et al. 2004). Shallow (5-10 cm depth increment) anaerobic CH_4 production rates (nmol g^{-1} day^{-1}) and CO_2 production (μmol g^{-1} day^{-1}) were 23% and 28% greater than production rates from deeper peat (20-25 cm depth increment). This is likely because older soils found in deeper peat layers contain higher proportions of recalcitrant C than younger soils at the surface (Yavitt et al. 1987, Nadelhoffer et al. 1991, Hogg et al. 1992, Christensen et al. 1999). The decrease in production with depth can also be explained by the accumulation of compounds unfavorable to microbial activity such as lignin, phenolic, or humic substances (Hogg et al. 1992). Surprisingly, aerobic CO_2 production (μmol g^{-1} day^{-1}) did not significantly vary with depth (Figure 3-3), suggesting that microbial groups responsible for anaerobic mineralization are more responsive to changes in substrate quality and/or changes in soil hydroclimate occurring with depth compare to aerobic microbes.

The soil physical and chemical variables (bulk density, %C, %N, and C/N) did vary across the experimental treatments (Table 3-3), but did not exhibit any linear relationships with CO_2 or CH_4 production (Figure 3-7). This lack of correlation is surprising because many studies have found strong correlations between these indices and rates of C mineralization. For example, Bridgham et al. (1998) found a strong positive correlation between CO_2 production and bulk density (bulk density explained 75-80% of production). However, Moore and Dalva (1997) explained only 20-25% of the variation in CO_2 production using botanical origin of peat material, pH, depth, and water table position.

3.4.2 Soil hydroclimate effects on CH_4 and CO_2 production rates

All peat was incubated under uniform temperature and moisture conditions; therefore any differences in CH_4 or CO_2 production rates were the result of indirect effects of the manipulations (water table and soil temperature) on soil quality or microbial populations during the previous 2.5 years. There was no difference in CH_4 production in response to the water table or soil warming field manipulations. Contrary to my findings, Keller et al. (2004) found a 28% increase in CH_4 production rates from fen peat exposed to high water tables than from peat exposed to intermediate water tables. However, other studies have shown that CH_4 production rates were not altered by exposure to differing water tables in bogs or high soil temperatures in both bogs and fens (Glatzel et al. 2004, Keller et al. 2004). As discussed previously, CH_4 production was very low across all of my samples. Turetsky et al. (in press) found increased methanogen concentrations in the APEX fen warming and flooding treatments, with strong correlations between methanogen abundance and average CH_4 emissions. My data suggest that these trends in field emissions are not due to soil substrate quality conditions.

However, redox conditions not conducive to methanogens are the likely cause of low CH_4 production rates and lack of significant differences across treatments.

***Drought and CO_2 production*:** The lowered water table treatment impacted aerobic and anaerobic CO_2 production in the incubations (Figure 3-5). Compared to peat collected within the control water table treatment, peat taken from the lowered water table treatment had slower CO_2 production rates at shallow depths (5-10 cm increments) and faster CO_2 production rates deeper into the peat (decreased by 34% and increased by 36%, in the shallow and deep increments, respectively). Other studies have found no difference in CO_2 production rates from peat collected from lowered and control water table treatments (Keller et al. 2004, Glatzel et al. 2004). Given that I found no net effect of the lowered water table treatment on ER and a decrease in GPP in the field (Figure 2-10), it is possible that lowering the water table position increased heterotrophic respiration and decreased autotrophic respiration, resulting in no effect on total ER. If indeed there was an increase in heterotrophic respiration in the lowered water table treatment, my incubation results likely reflect a shift in soil quality with greater C mineralization towards more recalcitrant compounds. Another explanation for low surface mineralization rates from the lowered plot could be moisture limitation on the microbial community, which in other studies have resulted in low microbial abundance in the lab (Silvola and Ahlholm 1989). Faster CO_2 production rates in the 20-25 cm depth increment in the lowered water table could be due to either 1) increased fine root turnover due to vegetation shifting resources from above to belowground with drought stress or 2) more ideal moisture conditions at depth, which could result in greater microbial activity.

There were no obvious effects of the lowered water table treatment on %C, %N, C/N, or bulk density, with the exception of generally lower %N in surface peat samples from the lowered water table plot relative to the control and raised water table plots (Table 3-3). This coincides with low C mineralization rates measured from surface peat from the lowered water table plot and is likely due to reduced vegetation inputs because of drought stress (Figure 3-5).

***Flooding*:** The raised water table treatment did not have a consistent effect on CO_2 production rates (Figure 3-5). In surface peat (5-10 cm depth), there was no difference between CO_2 production rates from peat taken from the control and raised water table treatments (Figure 3-5). In deeper peat (20-25 cm depth), CO_2 production rates from the raised water table treatment were 23% greater than C production rates from control water table peat (Figure 3-5). This is similar to other studies where peat exposed to high water tables or taken from wetter sites had 10-52% greater CO_2 production compared to peat exposed to lower water tables (Waddington et al. 2001, Glatzel et al. 2004, Keller et al. 2004).

In the field, the raised water table plot had higher ER than the control water table plot (Figure 2-10), likely due to a combination of higher temperatures in the raised water table treatment increasing mineralization (Figure 2-4), high anaerobic CO_2 production, and increased autotrophic respiration (coinciding with high GPP in this plot). Increased bryophyte cover in the raised water table treatment (Weltzin et al. 2007) probably led to more recalcitrant organic matter inputs, which was expected to inhibit microbial activity at the surface. However, the warm conditions in the raised water table plot likely stimulated organic matter turnover of these relatively fresh inputs. Thus, the effects of the soil microclimate and vegetation inputs could have led to opposite influences on organic matter quality and laboratory C mineralization rates. In deeper peat collected from the raised water table treatment, CO_2 mineralization rates were faster relative to deep peat in the other treatments (Figure 3-5). This could be due to greater plant inputs to the deeper soil horizons via belowground NPP or root exudates in the flooding conditions.

Warming and CO_2 production: Temperature has been found to impact many biogeochemical processes such as soil respiration (Grogan and Chapin 2000, Updegraff et al. 2001, Chapter 1), litter decomposition (Meentemeyer 1978, Jansson and Burg 1985, Hobbie 1996), N mineralization (MacDonald et al. 1995), CH_4 emission (Crill 1991, Turetsky et al. in press), fine root dynamics (Gill and Jackson 2000), and plant productivity (Hobbie and Chapin 1998). Warming has been shown to affect mineralization rates in the field by stimulating microbial activity in soils, which increases organic matter breakdown and results in lower quality peat (Grogan and Chapin 2000). This would result in lower amounts of labile C substrates in the warmed subplots compared to un-warmed subplots resulting in lower CO_2 production. However, field soil temperature manipulation treatments similar to Chapter 2 found that warming modified soil quality (Keller et al. 2004), likely due to differences in plant productivity. A change in vegetation productivity and/or C allocation with warming could enhance the production of labile C substrates (moss DOC 'leakage' or root exudation). While this would likely stimulate C mineralization, the addition of labile C also can trigger a priming effect, stimulating the decomposition of more recalcitrant compounds in the field (Weltzin et al. 2000). Differential effects of warming on vegetation types could lead to an increase or decrease in select species (Weltzin et al. 2000) and potentially impact the quality of plant inputs into the soil. Hobbie (1996) also found that changes in plant community structure and composition in response to warming in tundra wetlands had important consequences on C mineralization, due to differences in litter decomposition rates.

The warmed subplots were associated with 26% and 45% lower CO_2 production rates compared to peat from the un-warmed subplots in shallow and deep peat, respectively (Figure 3-4). Therefore, it appears that the soil warming treatment lowered the substrate quality of peat, which resulted in lower aerobic and anaerobic CO_2 mineralization rates in the lab incubations. Despite greater inputs of fresh organic matter to surface soils with higher GPP with warming, faster organic matter turnover in the field likely reduced the organic matter quality signature in the warmed subplots, which then affected C mineralization rates. Generally, surface peat collected from the warmed subplots had higher bulk density than peat collected from un-warmed subplots (Table 3-3). This is similar to other studies that have found increased bulk density associated with high rates of mineralization rates and collapse of pore structure in the peat matrix (Minkinnen and Laine 1998).

3.4.3 Conclusions

To investigate the effects of the ecosystem-scale in-situ climate manipulations on C mineralization through changes in soil organic matter (SOM) quality, I collected peat from the experimental field treatments and incubated all samples under standard laboratory conditions. Rates of CH_4 production were not affected by the manipulations, suggesting that substrate quality or other aspects of redox reactions are limiting methanogenesis. Peat taken from the warmed subplots and surface peat from the lowered water table plot had the lowest CO_2 production rates, indicating a decrease in soil organic matter quality likely due to increased heterotrophic respiration in these climate treatments. This suggests that the changes in ER measured in Chapter 2 likely involve some component of changing heterotrophic respiration.

My results suggest that relatively short-term changes in climate can alter peatland C flux and result in potential feedbacks to climate change through altered soil organic matter quality. Water table position has complex affects on soil organic matter quality and microbial community. Because I found differential effect of the water table treatments on C mineralization at different depths, is likely that microbial metabolism is interacting with vegetation inputs across the manipulations to control soil quality at this site. For example, warming increased both ER and GPP (Chapter 2) while lowering the soil organic matter quality (Figure 2-11). Future monitoring of this experiment will be able to clarify whether poor substrate quality driven by faster organic matter turnover in the field eventually will serve as a negative feedback to decomposition and plant production (through decreased nutrient availability).

Table 3-1. Results of two repeated measures analysis of variance (ANOVA) models analyzing CH_4 production as nmol g^{-1} day^{-1} and nmol cm^{-1} day^{-1} across our experimental treatments. Significant higher-level effects are marked in bold ($p > 0.05$).

Model effects	**df (numerator, denominator)**	**F**	***p***
CH_4 Production (nmol g^{-1} day^{-1})			
Plot	2, 36	0.76	0.47
Warm	1, 36	0.07	0.79
Depth	1, 36	5.05	**0.03**
Plot x Warm	2, 36	0.60	0.55
Plot x Depth	2, 36	0.97	0.39
Depth x Warm	1, 36	0.00	0.98
Plot x Depth x Warm	2, 36	0.21	0.81
CH_4 Production (nmol cm^{-3} day^{-1})			
Plot	2, 36	0.78	0.47
Warm	1, 36	0.52	0.47
Depth	1, 36	0.08	0.78
Plot x Warm	2, 36	2.01	0.15
Plot x Depth	2, 36	0.49	0.62
Depth x Warm	1, 36	1.13	0.29
Plot x Depth x Warm	2, 36	0.50	0.61

Table 3-2. Results of two repeated measures analysis of variance (ANOVA) models analyzing CO_2 production as μmol g^{-1} day^{-1} and μmol cm^{-1} day^{-1} across our experimental treatments. Significant higher-level effects are marked in bold (p > 0.05).

Model effects	df (numerator, denominator)	F	*p*
CO_2 Production (μmol g^{-1} day^{-1})			
Plot	2, 72	2.52	**0.09**
Warm	1, 72	0.68	0.41
Depth	1, 72	188.18	**<.0001**
Treatment	1, 72	11.22	**0.0013**
Plot x Warm	2, 72	2.89	0.06
Plot x Depth	2, 72	1.95	0.15
Plot x Treatment	2, 72	1.70	0.19
Depth x Warm	1, 72	0.06	0.81
Depth x Treatment	1, 72	7.92	**0.01**
Treatment x Warm	1, 72	0.16	0.69
Plot x Depth x Warm	2, 72	0.90	0.41
Plot x Warm x Treatment	2, 72	0.41	0.67
Plot x Depth x Treatment	2, 72	0.71	0.49
Depth x Warm x Treatment	1, 72	0.01	0.93
Plot x Depth x Warm x Treatment	2, 72	0.27	0.76
CO_2 Production (μmol cm^{-3} day^{-1})			
Plot	2, 72	1.14	0.32
Warm	1, 72	0.01	0.92
Depth	1, 72	43.35	**<0.0001**
Treatment	1, 72	5.23	**0.03**
Plot x Warm	2, 72	0.09	0.91
Plot x Depth	2, 72	4.69	**0.01**
Plot x Treatment	2, 72	0.80	0.45
Depth x Warm	1, 72	4.45	**0.04**
Depth x Treatment	1, 72	2.76	0.10
Treatment x Warm	1, 72	0.35	0.56
Plot x Depth x Warm	2, 72	2.93	**0.06**
Plot x Warm x Treatment	2, 72	0.09	0.91
Plot x Depth x Treatment	2, 72	0.16	0.85
Depth x Warm x Treatment	1, 72	0.00	0.99
Plot x Depth x Warm x Treatment	2, 72	0.06	0.94

Table 3-3. Bulk density (g cm^{-3}), % nitrogen (N), % carbon (C), and C/N for peat collected across the water table and warming treatments at the APEX fen. Means with the same letter superscript do not differ significantly ($p < 0.05$). Data are means with one standard error in parentheses.

	Control Water Table				Lowered Water Table				Raised Water Table			
	Un-warmed		Warmed		Un-warmed		Warmed		Un-warmed		Warmed	
	10 cm	25 cm	10 cm	25 cm	10 cm	25 cm	10 cm	25 cm	10 cm	25 cm	10 cm	25 cm
Bulk Density (g cm^{-3})	0.089^{a} (0.01)	0.157^{c} (.013)	0.09^{ab} (.005)	0.107^{b} (.021)	0.089^{a} (.010)	0.146^{c} (.011)	0.11^{ab} (.031)	0.093^{b} (.014)	0.078^{a} (.009)	0.125^{c} (.022)	0.09^{ab} (.004)	0.139^{b} (.009)
% N	2.54^{a} (0.09)	2.93^{b} (0.06)	2.41^{a} (0.11)	3.01^{b} (0.02)	2.32^{a} (0.25)	2.57^{b} (0.29)	2.57^{a} (0.04)	2.50^{b} (0.52)	2.45^{a} (0.07)	2.87^{b} (0.07)	2.05^{a} (0.41)	2.81^{b} (0.04)
% C	40.99^{d} (0.24)	39.5^{ac} (0.49)	39.3^{ab} (0.66)	40.81^{b-d} (1.09)	42.0^{df} (0.59)	38.68^{a} (0.93)	41.3^{bd} (0.70)	40.75^{g} (1.02)	44.06^{g} (0.53)	43.1^{e-g} (0.93)	44.21^{g} (0.68)	41.1^{a-d} (1.66)
C/N	0.062^{a} (0.00)	0.074^{b} (.001)	0.062^{a} (.004)	0.074^{b} (.002)	0.055^{a} (.006)	0.067^{b} (.001)	0.062^{a} (.001)	0.062^{b} (.014)	0.055^{a} (.002)	0.067^{b} (.003)	0.047^{a} (.009)	0.068^{b} (.002)

Table 3-4. Synthesis of peatland microcosm incubation experiments examining CO_2 and CH_4 production. Data were converted to the same units ($\mu mol\ g^{-1}\ day^{-1}$ and $nmol\ g^{-1}\ day^{-1}$ for CO_2 and CH_4 production). Rates are reported as ranges and means ± std errors.

Reference	Peatland type and depth	Temperature / moisture	Duration (days)	CO_2 production Anaerobic	CO_2 production Aerobic	CH_4 prod. Anaerobic
Turetsky and Ripley 2005	Extreme rich fen; surface samples	Room temp / field moisture	60	-	48.29±1.36	359.5±138.7
Keller et al. 2004	Bog; 0-15 cm homogenized	15° C / field moisture	77	-	0.018±.03[1]	0.14±0.05[2]
Keller et al. 2004	Fen; 0-15 cm homogenized	15° C / field moisture	77	-	0.122±.01[1]	144.4±11.53[2]
Yavitt et al. 1987	*Sphagnum* dominated fen; Surface samples	19±2° C / slurries	10	2.62 – 16.53	-	105 – 15,600
Glatzel et al. 2004	Harvested and restored bogs; Surface samples	20° C / slurries	30	0.23 – 6.59	0.91-23.86	0 – 51,000 (1312.5)
Waddington et al. 2001	Harvested and restored bogs; 0, 5, 10, and 20 cm	Anaerobic: 4, 12, 20° C / slurries Aerobic: 12° C / slurries	2	0.21 – 4.87	0.37-15.69	-
Moore and Dalva 1997	Bog and fen; upper peat profile	15 or 20° C / field moisture	5	11.36	22.73	193.75
Magnusson 1993	*Sphagnum* dominated poor fen; 5, 20, and 50 cm	16° C / field moisture	182	1.06-1.13	8.56-14.02	0-49.5
This study	Moderately rich fen; 5-10 and 20-25 cm	22° C / 40-60% moisture	40	0 to 71.61	0.93 to 26.66	0 to 47.79

[1] $\mu mol\ cm^{-3}\ day^{-1}$, [2] $nmol\ cm^{-3}\ day^{-1}$

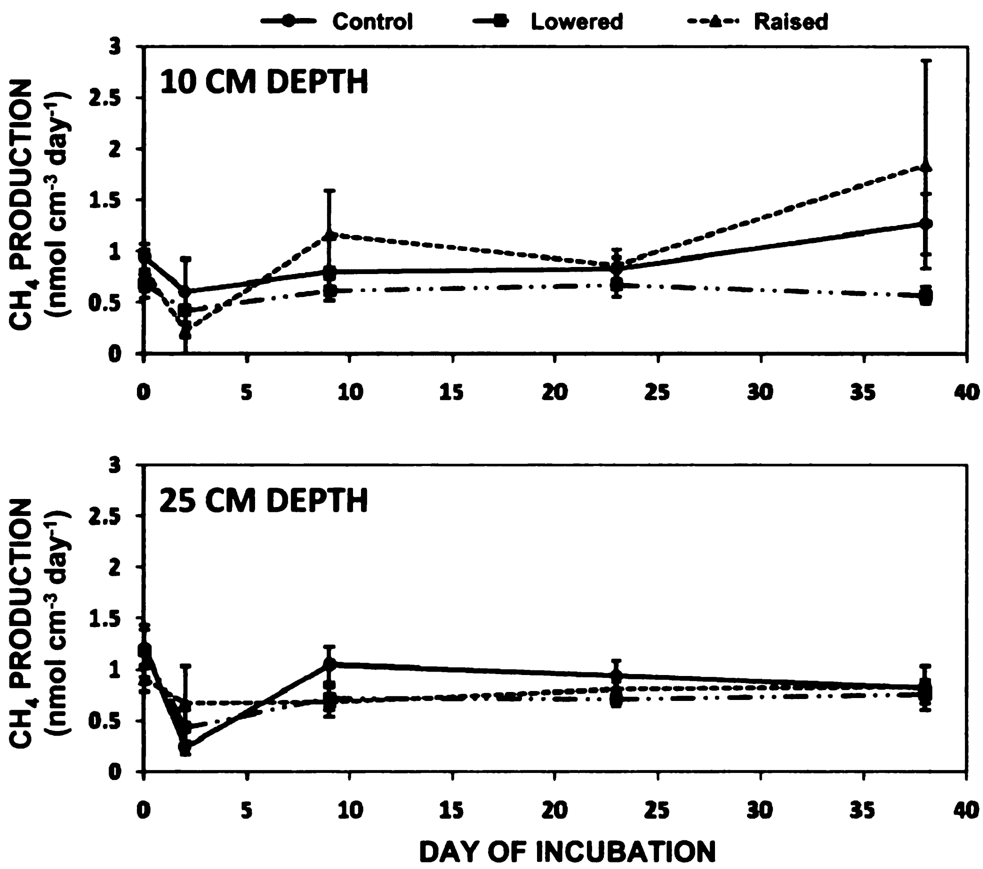


Figure 3-1. Mean anaerobic CH_4 production (nmol cm^{-3} day^{-1}) ± one standard error over the 40 day incubation experiment. Peat was taken from the 5-10 cm and 20-25 cm depth increments below the moss surface across three water table treatments (control, raised, and lowered water table plots, Chapter 2).

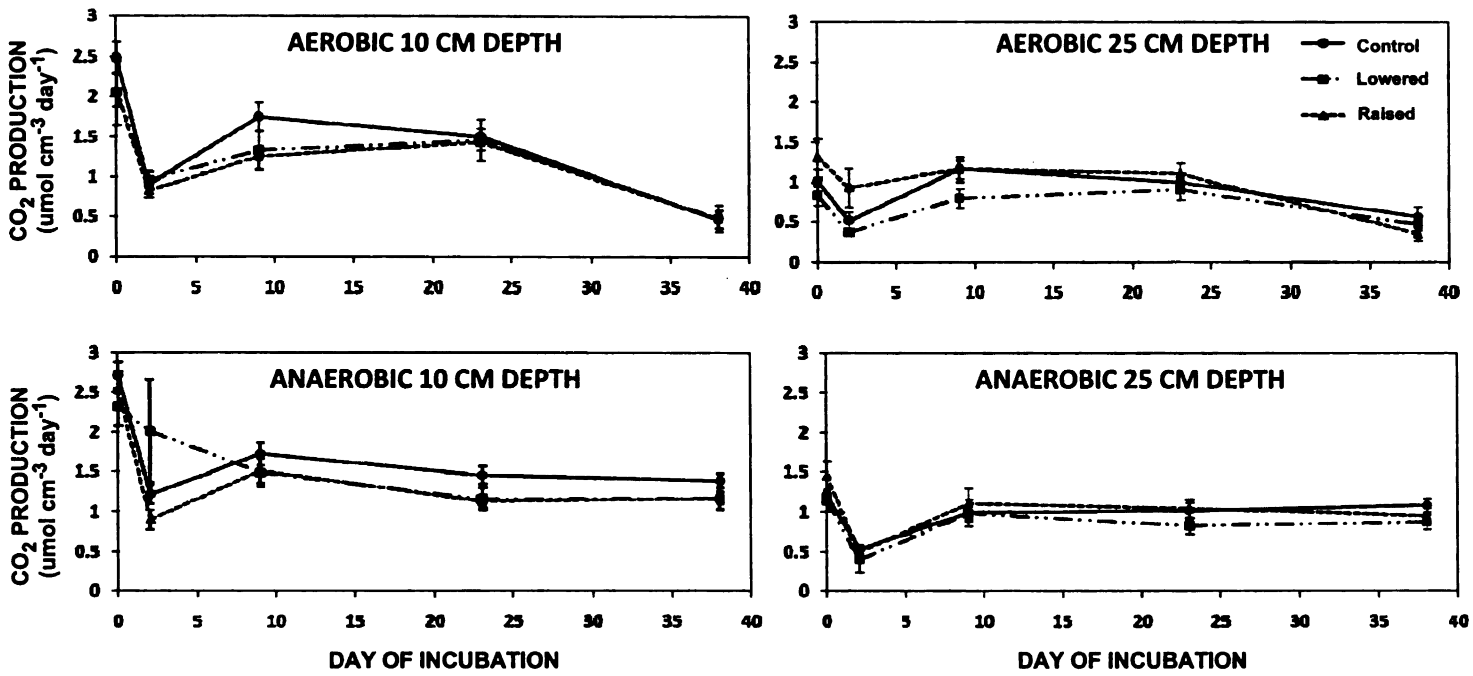


Figure 3-2. Mean CO_2 production (μmol cm^{-3} day^{-1}) ± one standard error over the 40 day aerobic and anaerobic incubation experiment. Peat was taken from the 5-10 cm and 20-25 cm depth increments below the moss surface across three water table treatments (control, raised, and lowered water table plots, Chapter 2).

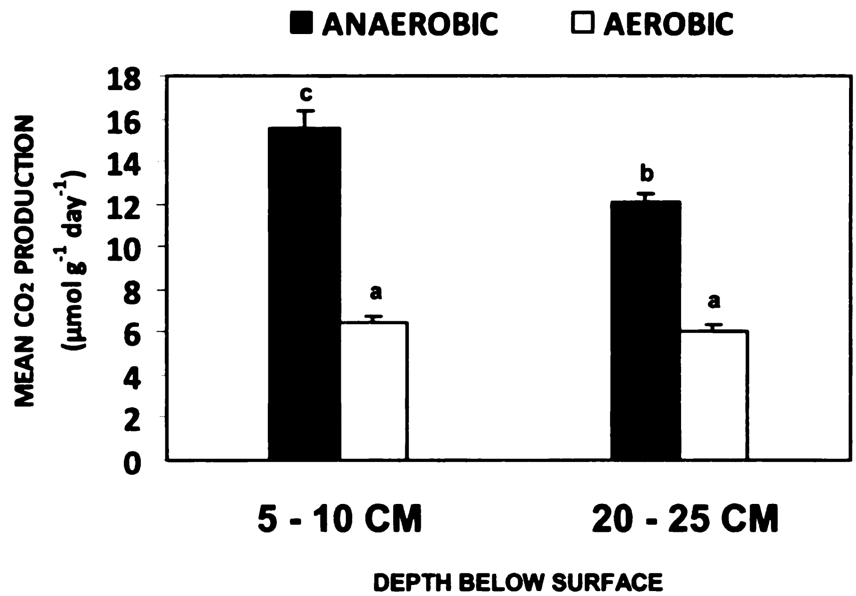


Figure 3-3. Results of an interaction between depth increment and headspace treatment (aerobic, anaerobic) on CO_2 production rates on a mass basis. Data are means ± one standard error (not adjusted for model comparisons). Same letter superscripts denote non-significant differences from Tukey *post hoc* comparison of means tests.

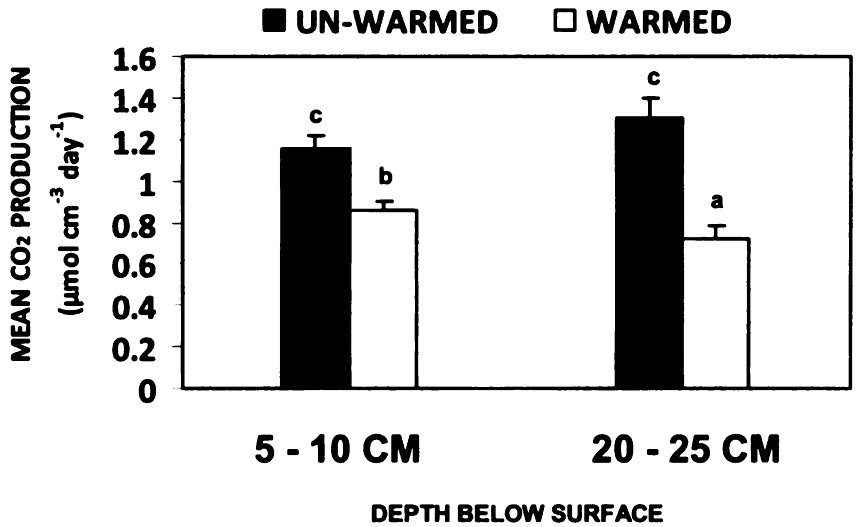


Figure 3-4. Results of an interaction between depth increment and warming treatment on CO_2 production rates on a volume basis. Data are means ± one standard error (not adjusted for model comparisons). Same letter superscripts denote non-significant differences from Tukey *post hoc* comparison of means tests.

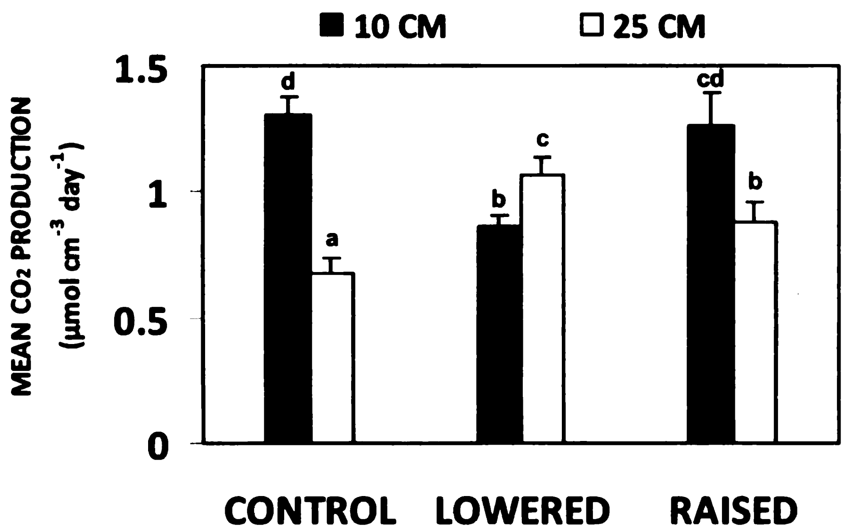


Figure 3-5. Results of an interaction between depth increment and water table plot on CO_2 production rates on a volume basis. Data are means ± one standard error (not adjusted for model comparisons). Same letter superscripts denote non-significant differences from Tukey *post hoc* comparison of means tests.

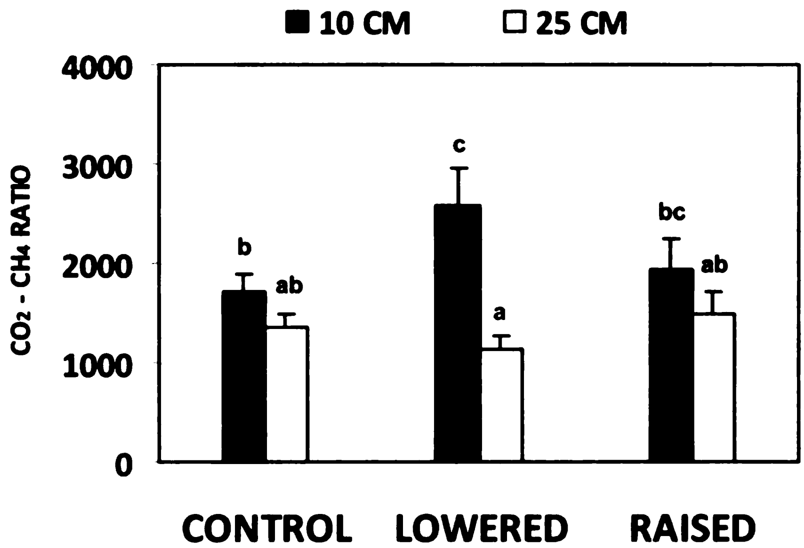
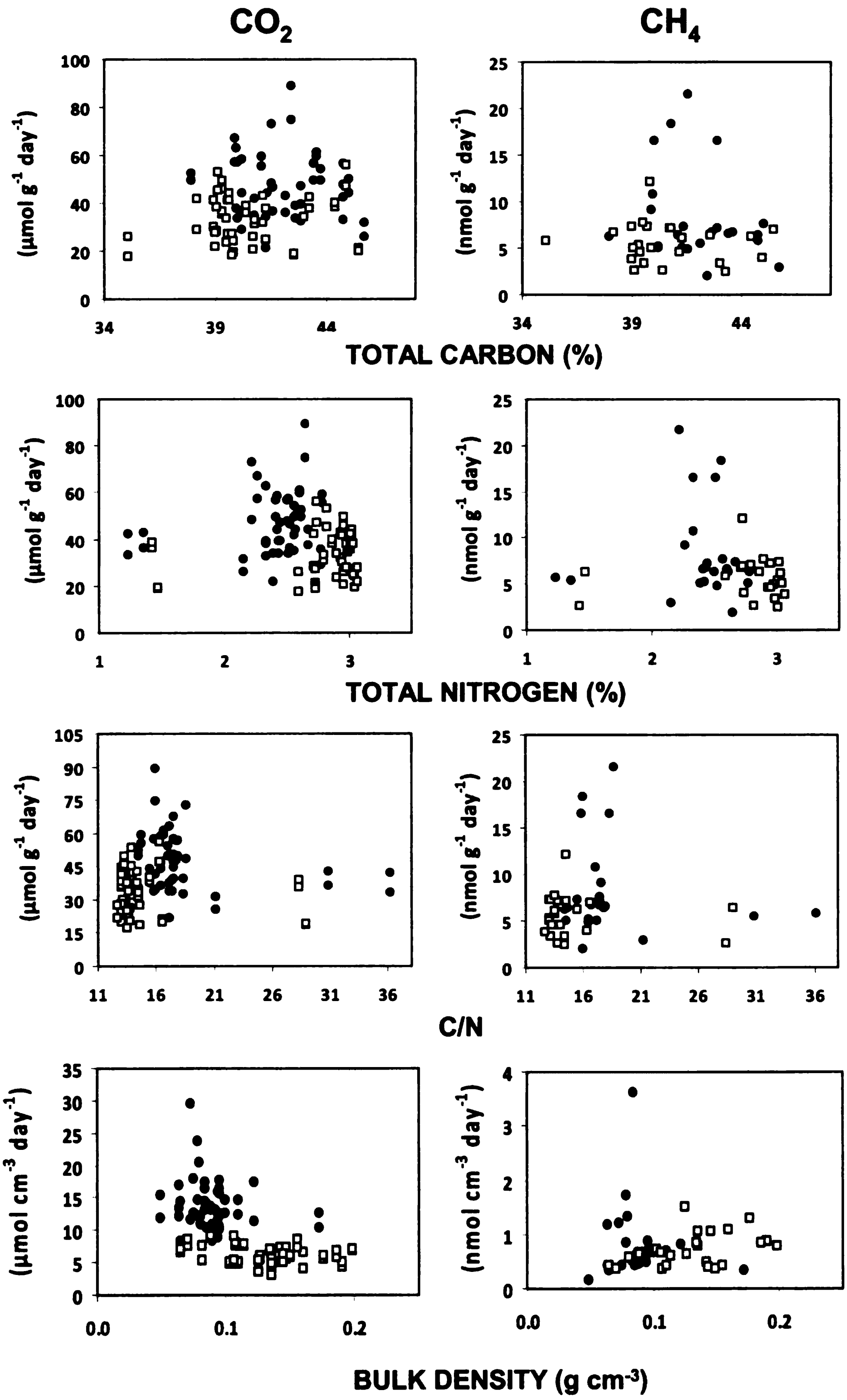


Figure 3-6. Results of an interaction between depth increment and water table plot on ratios of $CO_2 - CH_4$ production rates. Data are means ± one standard error (not adjusted for model comparisons). Same letter superscripts denote non-significant differences from Tukey *post hoc* comparison of means tests.

Figure 3-7. Relationship between CO_2 and CH_4 production rates from incubated peat and soil quality variables. Closed circles represent data from the 5-10 cm increment, while open squares represent the 20-25 cm increment. No relationships between gaseous carbon production rates were significant ($p>0.05$).



CO2
CH4
(µmol g-1 day-1)
(nmol g-1 day-1)
TOTAL CARBON (%)
TOTAL NITROGEN (%)
C/N
(µmol cm-3 day-1)
(nmol cm-3 day-1)
BULK DENSITY (g cm-3)

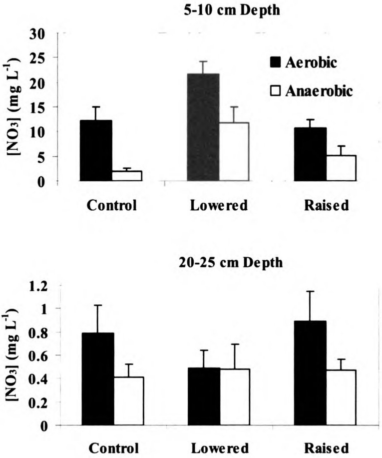


Figure 3-8. NO_3 (mg L^{-1}) concentrations from the aerobic and anaerobic post-incubation leachates across water table plot and depth.

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CHAPTER 4

CONCLUSION

Northern soils in boreal regions serve as an important reservoir for terrestrial soil carbon (C) that has accumulated since the last deglaciation (12,000 – 18,000 yr ago; Harden et al. 1992). Boreal forests contain approximately 27% of the world's vegetation C (McGuire et al. 1997) and between 25 – 30% of the world's soil C (Gorham 1991, McGuire et al. 1997). The majority of this boreal C stock is stored in peatlands, where cold soils, saturated conditions, and recalcitrant substrate quality limit decomposition and promote peat accumulation (Gorham 1991). Due to the controls, soil climate and its influence on C fluxes (respiration and net primary production) represents a major control on boreal C stocks (Harden et al. 1992, Bhatti et al. 2002). However, climate models generally predict warmer conditions for high latitudes (Raisanen 1997), an area where peatlands are an important component of the landscape. Thus, how peatland C stocks will respond to climate change remains an important issue with implications for atmospheric C concentrations.

The majority of peatland C studies have been conducted in *Sphagnum*-dominated poor fens and bogs in Canada and Fennoscandia. Relatively little is known about Alaskan peatlands, although Bridgham et al. (2006) estimate that Alaska wetlands store as much as 42 Pg of C. Alaskan peatlands are changing due to near-surface atmospheric warming of approximately 1° C per decade on average (Osterkamp and Romanovsky 1999, Serreze et al. 2000). These climatic changes have led to regional changes in surface hydrology and vegetation structure throughout interior Alaska (Riordan et al. 2006, Hinzman et al. 2005, Hinzman et al. 2006).

The goal of this thesis was to investigate direct and indirect soil hydroclimate (water table position, soil temperature) controls on C fluxes in an Alaskan fen. I investigated the response of field CO_2 fluxes (NEE, ER, GPP) to a water table and soil temperature manipulation. Water table level and soil temperature have the potential to indirectly affect decomposition through changes in soil organic matter quality. I designed a laboratory experiment to isolate soil organic matter quality differences among peat collected across the experimental field treatments. To understand whether the field manipulations affected soil organic matter quality and C mineralization rates, I measured aerobic and anaerobic CO_2 and anaerobic CH_4 production rates under constant moisture and temperature.

I had hypothesized that drought would increase decomposition rates, leading to an increase in ER and an increase in NEE (atmospheric emissions). Two years of field fluxes showed that the lowered water table treatment did not alter ER, but did lower GPP by 21-24% (Figure 2-11). I attribute this change in GPP to decreased photosynthetic uptake of CO_2 by vascular vegetation and bryophytes due to drought stress (Figure 2-6). The lowered water table plot generally had lower GP_{max} values than the other water table treatments, which supports this conclusion (Figure 2-13). Reductions in GPP resulted in increased NEE (trend toward increased atmospheric emissions) in the lowered water table plot relative to the control plot. So while drought affected NEE as hypothesized, the change in NEE was driven primarily by plant productivity rather than microbial activity. Surface peat from the lowered water table plot also had the slowest CO_2 production rates during a laboratory incubation experiment (Figure 3-5), indicating a decrease in soil organic matter quality either from reduced input of fresh organic matter by plants or accelerated turnover of organic matter in the field. Whether this organic matter quality signature has or will serve as a feedback to ecosystem fluxes could be determined by additional C flux monitoring at the site.

The raised water table treatment was less of a CO_2 sink (more positive NEE values) than the control water table plot in 2005, but was a greater sink in 2006. In 2006, this trend was driven primarily by interannual changes in GPP, with greater GP_{max} values and % bryophyte cover in the raised water table plot relative to the control (Figure 2-13, Table 2-1). I had hypothesized that increased water table level would decrease decomposition and lead to decreased ER. However, the raised water table treatment also had increased ER compared to the control water table plot; likely due to high autotrophic respiration and/or high rates anaerobic C mineralization. Additionally, temperature was the strongest control on ER, and warmer soils at the raised plot (Figure 2-5) and likely stimulated microbial activity. My laboratory experiment showed that in deeper peat, CO_2 production rates at the raised water table treatment were 23% greater than CO_2 production rates in control water table peat (Figure 3-5), likely due to high vegetation productivity under wet conditions that could have led to increased fine root turnover or root exudation.

Soil warming increased both ER and GPP by 16% relative to un-warmed subplots, resulting in no net effect of warming on NEE. Laboratory CO_2 production rates from peat taken from the warmed subplots were 26% and 45% lower than peat from the un-warmed subplots in shallow and deep peat (Figure 3-4). Despite greater inputs of fresh organic matter to surface soils with higher GPP, faster organic matter turnover in the field in the warming treatment seems to dominate the organic matter quality signature, thereby controlling potential C mineralization rates. Models of vegetation components at our site (GPP, GP_{max}, α) indicate that water table position and soil temperature are both important controls on plant C uptake, while temperature was a stronger control on ER than water table position.

Taken together, these results indicate that 2.5 years of soil warming and water table manipulations can significantly alter CO_2 fluxes in an Alaskan fen. While much of the literature has focused on how climate change will influence decomposition rates (and thus peat accumulation), my study clearly demonstrates the need to consider vegetation and substrate quality in addition to microbial activity when investigating ecosystem-level responses to water table levels.

My data do show that drought is likely to decrease soil C storage in Alaska peatlands, but primarily through reduced plant productivity. Future work at the APEX site should monitor GPP with species succession over time in the lowered water table plot to determine if the trends I observed are likely to change over long time scales (decades).

Peatland flooding has received less attention in the literature compared to drought, but my results suggest that inundation can have large effects on C fluxes and can decrease NEE, promoting C storage. The raised water table treatment increased GPP and ER, but overall caused a net decrease in NEE. This agrees well with C flux studies focusing on saturated peatlands post-permafrost (Turetsky et al. 2000, Turetsky et al. 2002, Wickland et al. 2006). Thus, as climate change progresses, causing more and more permafrost degradation, increased soil C storage in peatlands could serve as a negative feedback to climate change. However, Turetsky et al. (2007) showed that the response of peatlands post-thaw to sequester more C was temporary, lasting only ~100 years.

Warming might stimulate both GPP and ER in Alaska peatlands, so it seems likely that the direction of C flux changes will be driven mostly by changing hydrological conditions. However, this study demonstrates how soil hydrology and thermal regimes in peatland environments are coupled due to increased buffer capacity and heat transfer of saturated soil layers compared to dry soils. Peatland and boreal C models need to account for feedbacks between plant and microbial activity (i.e., through nutrient availability or substrate quality) as well as the interactions between physical peat properties, soil hydroclimate, and biological processes that regulate C fluxes and emissions.

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