Peatland carbon cycle responses to hydrological change at time scales from years to centuries: Impacts on model simulations and regional carbon budgets

By

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Abstract

Peatlands cover large areas in boreal and subarctic regions. Due to the long-term storage of carbon in peat, these ecosystems contain a significant fraction of the global terrestrial carbon pool. Carbon cycling in peatlands depends on plant communities, hydrology, and climate in complex ways, and the responses of the terrestrial carbon cycle to climate change in these regions cannot be fully understood without including wetland processes. This research combines measurements and model simulations to identify key complexities in peatland responses to hydrological change at multiple time scales, and provides targeted recommendations for integrating these complexities into model simulations of carbon cycling in peatland-rich regions.

I investigated responses of peatland CO_2 fluxes to interannual variations in hydrology using CO_2 flux measurements from six peatland sites in Canada and the northern United States. The sites include both bog and fen wetlands, and the results suggest that declines in water table increase both ecosystem respiration and productivity in fens, but decrease these fluxes in bogs. I then evaluated the ability of commonly used ecosystem models to simulate these peatland processes. I accomplished this by analyzing results from an intercomparison study including seven computational models and three peatland field sites (two fens and one bog). CO_2 flux residuals (simulated $-$ observed) were positively correlated with observed water table depth, and models produced more accurate simulated fluxes at fen sites compared to the bog site. Models systematically overestimated peatland productivity and respiration. These results suggest that inability to simulate peatland processes can lead to significant bias in large-scale carbon cycle studies using these types of models. This section concludes with a review of important peatland processes, and recommendations for model changes to improve the accuracy of simulations in peatland-rich regions.

Ecosystem responses over time scales of decades or centuries can contrast with responses over shorter time scales. I used the LANDIS-II landscape succession model to

investigate ecological changes over these time scales for scenarios of long-term water table decline. For 100 cm water table declines, increases in plant growth led to substantial biomass accumulation and increases in total carbon over the first 100 years. However, over longer time scales of $200 - 400$ years, peatlands had a negative carbon balance due to continued soil carbon loss. For 40 cm declines, peatland carbon balance was dominated by soil carbon loss, and the results was a continued net loss of total carbon. At the landscape scale, water table declines led to net increases in total carbon over the first 100 years, followed by steady total carbon as a result of compensating gains in mineral wetlands and losses in peatlands. These results suggest that climatic changes leading to regional drought in wetland-rich areas could result in negative feedbacks to climate change over century time scales. However, a large part of that response is likely transient, and could come at the expense of other important ecosystem services. Therefore, considerations of wetland responses to hydrological changes should include long time scales and multiple ecosystem services.

Overall, the major contributions of this research were:

1. Highlighting the role of peatland plant communities in controlling couplings between carbon and hydrological cycles: Peatland community type determines the direction of the response to interannual hydrological changes, and peatland community succession is the primary driver of carbon cycle responses to long-term drying.
2. Identifying sources of bias in peatland modeling studies: Models overestimate peatland productivity and respiration, and miss hydrology-driven variability.
3. Showing the contrasts between short- and long-term peatland responses to hydrological change: Peatland carbon uptake response to drying can be neutral over inter-annual time scales, higher uptake over century time scales, and loss over longer time scales.

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A large portion of my research used results from the North American Carbon Program site-level interim synthesis, and I would like to express my appreciation to all of the scientists who contributed model output, field measurements, data products, and organizational support in order to make the synthesis possible. My work would not have been possible without their contributions. My research also depended on the LANDIS-II model, and I thank David Mladenoff, Robert Scheller, and all the other contributors to the development and testing of the model.

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Chapter 1

Background

1.1 The terrestrial biosphere in the climate system

Feedbacks in the terrestrial biosphere represent one of the primary sources of uncertainty in predictions of future climate [*Friedlingstein et al.*, 2006; *Meehl et al.*, 2007; *Booth et al.*, 2012]. Terrestrial ecosystems contain enormous pools of carbon, and process vast amounts each year. The diversity of ecosystems, complexity of internal processes, and potential for nonlinear responses to climatic forcings make understanding of ecosystem dynamics and sensitivities a difficult but essential component of modeling the climate system.

Carbon uptake and release by the terrestrial biosphere has been estimated at approximately 120 GtC/yr [*Denman et al.*, 2007; *Beer et al.*, 2010], a massive annual exchange compared to anthropogenic CO_2 emissions of 4-8 GtC/yr [*Forster et al.*, 2007]. However, natural sources and sinks of carbon approximately balance, leaving a net carbon sink of a few GtC per year [*Sundquist*, 1993]. Based on the difference between anthropogenic CO_2 emissions and the annual increase in atmospheric CO_2 concentration, approximately half of anthropogenic emissions remain in the atmosphere in the average year, while the other half are absorbed by the ocean and terrestrial biosphere [*Denman et al.*, 2007]. Based on inverse modeling, land inventories, and isotope techniques, the global carbon sink is split roughly evenly between the land and ocean [*Battle et al.*, 2000; *Schimel et al.*, 2001]. Therefore, ecosystem net CO_2 uptake is responsible for reducing the amount of anthropogenic CO_2 that remains in the atmosphere by an average of 25% annually. Studies have suggested that the northern hemisphere extratropics have a primary role in the terrestrial carbon sink [*Tans et al.*, 1990; *Schimel et al.*, 2001]. Interannual variability of global carbon uptake is dominated by the terrestrial biosphere rather than the oceans, and is quite high [*Bousquet et al.*, 2000; *Schimel et al.*, 2001]. These variations are driven by interannual changes in temperature, precipitation, and disturbances such as fire [*Braswell et al.*, 1997; *Houghton*, 2000; *Yang and Wang*, 2000; *Jones et al.*, 2001; *Amiro et al.*, 2001; *Meyn et al.*, 2009]. Due to the sensitivity of terrestrial CO_2 uptake to these drivers, the future of the global carbon sink is quite uncertain. In a comparison of ecosystem models driven by climate change scenarios, *Friedlingstein et al.* [2006] found a wide range in the magnitude of simulated responses, although there was general agreement that terrestrial uptake would decline in response to climate change. *Booth et al.* [2012] found that parameter uncertainty in terrestrial carbon cycle processes contributes approximately the same amount of uncertainty as parameter uncertainty in dynamical processes to total uncertainty in climate simulations. The important role of terrestrial ecosystems in the carbon cycle necessitates a better understanding of the processes that will drive future responses to climate change. The terrestrial carbon cycle is composed of a wide range of ecosystems, including forests, grasslands, deserts, and peatlands. The contributions and vulnerabilities of all of these ecosystems must be understood in order to build a complete picture of terrestrial biosphere feedbacks within the earth's climate system.

1.2 Wetlands and peatlands

This dissertation focuses specifically on northern wetland and peatland components of the terrestrial carbon cycle. Wetlands are defined by shallow water tables and the presence of plants adapted to survive in wet conditions. Saturated soil conditions permit the buildup of deep organic soil layers, or peat. The term "peatlands" refers to ecosystems with substantial layers of peat. Although peatlands cover a relatively small fraction of terrestrial land area, they are an important component of the terrestrial carbon cycle due to long-term carbon accumulation in peat and the resulting large carbon pools. Peatland biogeochemistry is governed by a complex interplay of climate, hydrology, and biological adaptations that pose problems for carbon cycle models originally developed for upland forests, grasslands, or crops.

1.2.1 Soil carbon accumulation and storage

Long-term changes in soil carbon are driven by imbalances between carbon inputs and decomposition. In typical ecosystems, total ecosystem respiration (ER) and photosynthesis are roughly balanced, with a net difference approximately one order of magnitude smaller that comprises the net ecosystem exchange (NEE) with the atmosphere [e.g. *Humphreys et al.*, 2006; *Desai et al.*, 2008b; *Luyssaert et al.*, 2010]. Decomposition rates of organic matter depend on a number of factors, including temperature, moisture, and the chemical characteristics of the organic matter. Soil decomposition models typically divide organic matter into "fast" or "active" and "slow" or "passive" decomposition pools with turnover times of years to decades and centuries to millennia, respectively [*Parton et al.*, 1988; *Schimel et al.*, 1994]. These distinctions are justified using differences in chemical or physical properties [*Schlesinger*, 1977], but these underpinnings have recently been called into question [*Trumbore*, 2006; *Schmidt et al.*, 2011].

The major external factors affecting organic matter decomposition rates are temperature and moisture. It is well established that decomposition rates increase with increasing temperatures. A variety of models are used to represent the specific temperature dependence, although these may miss important complexities of soil pools and decomposition processes [*Davidson et al.*, 2006]. The magnitude of the temperature dependence can vary significantly by latitude and ecosystem type [*Zhou et al.*, 2009].

Soil organic matter decomposition can be suppressed under both low moisture and high moisture conditions. Under very dry conditions, microbial growth and the accessibility of soil carbon is limited, leading to lower decomposition rates [*Orchard and Cook*, 1983; *Parton et al.*, 1987; *Borken et al.*, 2006]. Under very wet conditions, soil pores become saturated and decomposition is limited by oxygen availability. Oxygen diffuses much slower through water than through air, leading to oxygen depletion in wet soils [*Clymo*, 1984]. Since oxygen is the primary electron receptor in carbon mineralization, this severely inhibits decomposition. Decomposition continues using other terminal electron receptors such as sulfur, nitrogen, and carbon compounds, but these produce much less energy than aerobic decomposition and as a result proceed more slowly [*Keller and Bridgham*, 2007; *Limpens et al.*, 2008].

In northern wetlands, a combination of cool temperatures and saturated soils can lead to very low organic matter decomposition rates. Due to the suppressed rate of decomposition, carbon inputs from plant growth are greater than losses from decomposition, driving long-term carbon accumulation. Peatlands can continue to accumulate carbon over thousands of years without reaching a steady state relative to CO_2 fluxes [*Clymo*, 1984]. Typical peatland mean long term accumulation rates have been estimated at 29 g/m^2/year in a global inventory [*Gorham*, 1991], and at 18.5 g/m^2/year in a more recent inventory in Finland [*Turunen et al.*, 2002]. *Bridgham et al.* [2006] estimated a mean carbon accumulation rate of 71 g/m^2/year for peatlands in the coterminous United States. Over thousands of years, this accumulation produces peat layers that can be several meters thick and contain over

200 kg/m^2 of carbon [*Gorham*, 1991; *Frolking et al.*, 2001; *Buffam et al.*, 2010].

Globally, wetlands cover 4-6% of the earth's land area [*Mitra et al.*, 2005], with the highest concentration in a band between 50° and 70°N [*Matthews and Fung*, 1987]. Estimates of global peat carbon stores are fairly uncertain, varying from 120 to more than 500 GtC. For comparison, the estimated carbon pool in the atmosphere is 720 GtC [*Mitra et al.*, 2005]. *Gorham* [1991], a commonly cited global inventory, estimated a mean boreal and subarctic peat depth of 2.3 m, and a peat carbon pool equivalent to one third of global soil carbon. In a more recent inventory in Finland, *Turunen et al.* [2002] estimated a mean peat depth of 1.1 m and a pool of between 270 and 370 GtC. *Yu et al.* [2010] used radiocarbon dating of peat soil cores to estimate initiation dates and a time series of accumulation, and estimated a current northern peatland carbon pool of 547 GtC.

At regional scales, peatlands can contain large fractions of the total carbon pool. For example, *Buffam et al.* [2011] found that peatlands and lake sediments together contained more than 80% of the carbon in Wisconsin's Northern Highlands Lake District, despite covering only about one third of the land area. In an inventory in Minnesota, *Weishampel et al.* [2009] found that peatlands contained almost 50% of the landscape carbon pool while covering 13% of the area.

1.2.2 Methane emissions from peatlands

While the long-term accumulation of carbon in peat soils cools climate by removing CO_2 from the atmosphere, peatlands are large sources of methane at global scales, which complicates their net climate impact. *Matthews and Fung* [1987] estimated the global methane flux from wetlands to be 110 Tg/year, and *Petrescu et al.* [2010] estimated total methane flux from boreal and subarctic peatlands at 78 Tg/year. In a radiocarbon-based study of long-term peatland development, *Yu et al.* [2010] suggested that northern peatland methane emissions played a dominant role in the global methane budget during the early Holocene due to rapid expansion of peatland area. Over the life of a peatland, carbon sequestration and methane production have competing effects on climate. In a modeling study, *Frolking et al.* [2006] found that the methane and CO_2 effects lead to net warming over several hundred to several thousand years (depending on carbon sequestration rates), followed by long-term cooling as the peatland continues to remove carbon from the atmosphere.

Peatland methane fluxes are highly variable over small spatial and temporal scales. Methane emissions in northern Minnesota peatlands measured by *Harriss et al.* [1985] varied by three orders of magnitude between sites. *Waddington and Roulet* [1996] found that methane emissions varied by a factor of 40 between hummock and hollow microsites ($<$50 cm), by factors of 8 to 50 over mesotopographic scales (several meters), and by factors of 2 to 7 over macrotopogaphic scales (tens of meters). *Baird and Belyea* [2009] found that ignoring these topographical variations when upscaling peatland methane fluxes could result in substantial underestimates of total methane production.

Methane production in peatland soils is highly dependent on both temperature and hydrology. Methane is produced under anaerobic conditions below the water table, and can be consumed before reaching the atmosphere if it moves through dry soil layers. Multiple studies have observed suppression of CH_4 emissions connected with lower water tables [e.g. *Moore and Knowles*, 1989; *Freeman et al.*, 1992; *Roulet et al.*, 1993; *Strack et al.*, 2004; *Turetsky et al.*, 2008]. Methane emissions increase with warming temperatures, due to increased microbial activity and decomposition rates [e.g. *Dise et al.*, 1993; *Bubier et al.*, 1995; *Turetsky et al.*, 2008]. A modeling study by *Gedney et al.* [2004] found that peatland methane emissions could increase substantially due to climate warming, resulting in a positive feedback.

While methane emissions are an important component of the peatland carbon budget, the research presented in this dissertation focuses on CO_2, due to limitations in data and model development resources. However, it is important to include methane when interpreting the results of this research, in order to place them in the context of the full peatland greenhouse gas budget.

1.2.3 Peatland types and plant communities

Saturated soils pose challenges for plant growth. Oxygen depletion under saturated conditions is detrimental to roots, which require oxygen for growth and maintenance. Chemical reactions and decomposition processes in saturated soils can lead to high acidity and buildup of toxic compounds [*Pezeshki*, 2001]. Peatland soils can also pose physical challenges for woody plants, such as rapid changes in soil height connected with changes in hydrology [*Minkkinen and Laine*, 1998a; *Dise*, 2009]. As a result, peatlands are dominated by species specifically adapted to wet conditions, and are typically less productive and accumulate less biomass than upland ecosystems.

Within a peatland, different plant communities often develop in topographically different areas. Sedges, grasses, and mosses typically dominate wetter low-lying areas, or hollows, while woody plants dominate drier, higher hummocks. Differences in plant communities and height above the water table can lead to very different responses to changes in hydrology or temperature between microforms [*Waddington and Roulet*, 1996; *Strack et al.*, 2006; *Dimitrov et al.*, 2010, 2011; *Pelletier et al.*, 2011].

There are several distinct types of northern peatlands, distinguished by soil properties and plant communities [*Wheeler and Proctor*, 2000]. **Fens**, also classified as rich or minerotrophic wetlands, are wetlands with a water source provided by groundwater or surface water, which provides substantial nutrient inputs. These ecosystems generally develop productive communities of shrubs and sedges, depending on the hydrology. **Bogs**, classified as as poor or ombrotrophic wetlands, are fed exclusively or almost exclusively by rainwater. Lacking substantial nutrient inputs from water inflow, they are very poor in nitrogen, usually highly acidic, and generally develop groundcover dominated by *Sphagnum* moss species, along with stunted trees and shrubs in drier areas. Bogs are less productive than fens due to nutrient limitation and soil chemistry, but can still accumulate very thick peat layers. Litter produced by mosses has different physical properties and is generally slower to decompose than litter from vascular species, leading to substantially different peat characteristics between the two peatland types.

Tundra is an important additional northern peatland type. Tundra ecosystems are defined by perpetually frozen soils, or permafrost, and develop large carbon pools as cold conditions preserve carbon in frozen soils. While the large carbon pools and high vulnerability to warming make tundra ecosystems an important part of the boreal carbon cycle, this document focuses on boreal and subarctic wet peatlands. Our data and field sites were concentrated in mid-latitudes, well south of tundra-dominated areas. Furthermore, tundra ecosystems have different primary drivers and ecosystem dynamics due to the importance of perennially frozen ground, making direct comparison with wetland ecosystems and inclusion in a wetland modeling framework difficult.

1.2.4 Hydrology and temperature effects

Peatland plant communities, soils, and carbon fluxes can be highly sensitive to temperature and water table. Water table refers to the depth at which soil is saturated with groundwater. High water tables tend to inhibit both soil decomposition and productivity, so gradual drying can result in increases in both CO_2 uptake by plants and CO_2 emissions from decomposition [*Sulman et al.*, 2009; *Flanagan and Syed*, 2011]. Over long time scales, increased growth by woody plants can lead to plant community changes and substantial carbon accumulation following drying in some peatlands [*Talbot et al.*, 2010; *Laine et al.*, 1995; *Minkkinen and Laine*, 1998b]. However, more severe, short-term drying can lead to large decreases in productivity, leading to net carbon loss during droughts [*Schreader et al.*, 1998; *Alm et al.*, 1999; *Sonnentag et al.*, 2009].

Decomposition rates in peatlands are sensitive to both temperature and hydrology. Higher temperatures are correlated with higher CO_2 emission rates, due to increased microbial activity and decomposition [e.g. *Silvola et al.*, 1996; *Bubier et al.*, 1998; *Updegraff et al.*, 2001; *Lafleur et al.*, 2005b].

Changes in hydrology can drive changes in CO_2 emissions due to changes in oxygen availability in peat. Studies of peatland CO_2 responses to changes in water table have found conflicting results, with some measuring increased emissions driven by water table decline [*Moore and Knowles*, 1989; *Silvola et al.*, 1996; *Oechel et al.*, 1998; *Sulman et al.*, 2009; *Olivas et al.*, 2010], and others finding little sensitivity [*Lafleur et al.*, 2005b; *Parmentier et al.*, 2009; *Muhr et al.*, 2011]. These differences could be related to mean water table height, with soil respiration less sensitive to water table fluctuations at lower depths [*Lafleur et al.*, 2005b; *Sulman et al.*, 2009].

1.2.5 Threats and vulnerabilities

Climate change

Studies using general circulation models (GCMs) predict globally averaged surface warming of 1-2°C by 2050 and up to 3°C by 2100, depending on the future evolution of anthropogenic CO_2 emissions. Northern areas where large areas of boreal peatlands are situated are predicted to warm up to 4°C by mid-century and up to 6°C by 2100, and the incidence of very hot periods and severe droughts is expected to increase. In addition to direct effects on photosynthesis and soil decomposition rates, increased temperatures will lead to greater rates of evapotranspiration, potentially causing soil drying and drops in water table [*Meehl et al.*, 2007; *Erwin*, 2008]. Besides increases in temperature, climate models predict increases in precipitation in northern areas, which would increase water inputs [*Christensen et al.*, 2007]. While the net effect of changes in precipitation and evapotranspiration is uncertain, shifts in water balance could have profound impacts on peatlands, potentially resulting in positive feedbacks to climate change [*Ise et al.*, 2008].

Anthropogenic disturbance and development

Peatlands are often subject human disturbance. Examples include forestry [*Makiranta et al.*, 2010; *Minkkinen and Laine*, 1998b], agriculture [*Lloyd*, 2006; *Nieveen et al.*, 2005], and drainage resulting from construction and urban development. In tropical regions, a key threat to peatlands is destruction for palm oil production [*Tan et al.*, 2009; *Miettinen et al.*, 2011]. Wetland creation has also recently become an important category of land-use change [*Roulet*, 2000]. Human population growth, economic development, and increasing exploitation of remote regions for energy resources will likely impact peatland area and C storage in the future, both in northern [*Roulet*, 2000] and tropical regions [*Page et al.*, 2008, 2011].

1.3 Overview of dissertation research

The major theme of this dissertation research is the response of peatland carbon cycling to changes in water table depth over time scales from years to centuries. Both vegetation and soil responses have been integrated throughout, in order to build a complete picture of carbon cycle responses. The major questions addressed were:

- How do peatland carbon fluxes respond to variations in water table over **interannual** time scales?
- How well do existing models represent peatland responses to hydrological change over **interannual** time scales?
- How do peatland carbon pools respond to changes in water table over **multi-century** time scales?

- How can understanding responses at **multiple time scales** improve our ability to predict carbon cycle feedbacks?

This dissertation has been divided into three main chapters that address the goals identified above. Two of the chapters have been previously published in peer-reviewed journals, and are reproduced here with permission. I am the first author on both, and was responsible for both the central analysis and writing.

In Chapter 2, I address the question: **Are peatland responses to inter-annual water table fluctuations consistent between sites and ecosystem types?** This was accomplished by comparing CO_2 fluxes measured using the eddy covariance method at six different northern peatland sites, representing both fens and bogs. Inter-annual variations in CO_2 fluxes were tested as a function of inter-annual variations in water table depth in order to measure the sensitivity to hydrological change, and differences in responses between sites and ecosystem types were evaluated. This comparison illuminated contrasts between the sensitivities of different peatland ecosystem types to hydrological change that had not been previously shown.

Chapter 3 addresses the question: **How faithfully do ecosystem models simulate CO_2 fluxes and hydrology at peatlands, and what are the key limitations and areas for improvement?** The body of this research was an analysis of results from the North American Carbon Program (NACP) site synthesis activity. This synthesis combined eddy covariance measurements and ecosystem model simulations conducted for specific field sites across North America. Three peatland sites were included, and seven ecosystem models were run at all three sites. Model simulations were tested against observations to evaluate bias at both annual and diurnal time scales. Model simulations of hydrology were investigated, and bias was evaluated as a function of site hydrology in order to gauge the effects of wetland-specific hydrological processes on model bias. Finally, model structures and included processes were evaluated against key wetland hydrological and biological processes and avenues for improving model representations of wetland ecosystems were identified. This research produced important evaluations of commonly used ecosystem models, and had important implications for modeling studies that include peatland-rich regions. In-depth evaluations of ecosystem model performance at peatlands against observed fluxes had not previously been presented. The standardized framework of the NACP synthesis meant that the model results were directly comparable, making the analysis especially valuable.

Chapter 4 addresses the question: **What is the net impact of hydrological change on wetland carbon cycles over multiple-century time scales?** My main tool for this research was the LANDIS-II landscape succession model. This model was originally developed for simulating forest succession, and includes processes for growth, seed dispersal, tree cohort establishment, biomass accumulation, and mortality. I modified the model to add below-ground carbon cycling, and developed a framework for simulating soil and plant community responses to hydrological change. Soil changes were modeled using a simplified version of the peat development and decomposition model of *Frolking et al.* [2001]. Plant community responses were modeled by changing species establishment and growth parameters using a fractional area framework based on water table depth and topographical variation. I then investigated modeled responses to long-term declines in water table for a wetland-rich region in northern Wisconsin, USA, including both soil decomposition and plant community responses. Previous studies of peatland responses to long-term changes in hydrology had generally focused on historical observations [e.g. *Minkkinen and Laine*, 1998b] or chronosequences [e.g. *Laiho et al.*, 2003; *Talbot et al.*, 2010]. Previous peatland modeling studies over these time scales have focused on soil responses, and did not include changes in plant communities [e.g. *Ise et al.*, 2008]. This study also advances the field by placing the wetland carbon cycle changes in the context of the regional carbon budget.

Finally, Chapter 5 synthesizes the results and addresses the questions: **What are the key time scales of peatland responses to hydrological change, and how can under-**

standing responses at multiple time scales improve our ability to predict carbon cycle feedbacks? I compare the implications of short- and long-term studies, and highlight the potential for error in using the results of short-term studies to predict long-term carbon cycle responses. I also discuss the trade-off between carbon uptake and carbon storage services of ecosystems, and the importance of including multiple time scales, spatial scales, and ecosystem services in discussions of wetland ecosystem management and responses to climate change.

Chapter 2

CO_2 fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table[1]

Abstract

This study compares eddy-covariance measurements of carbon dioxide fluxes at six northern temperate and boreal peatland sites in Canada and the northern United States of America, representing both bogs and fens. The two peatland types had opposite responses of gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) to inter-annual fluctuations in water table level. At fens, wetter conditions were correlated with lower GEP and ER, while at bogs wetter conditions were correlated

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[1] A version of this chapter was previously published in a peer-reviewed journal: Sulman, B. N., A. R. Desai, N. Z. Saliendra, P. M. Lafleur, L. B. Flanagan, O. Sonnentag, D. S. Mackay, A. G. Barr, and G. van der Kamp (2010): CO_2 fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table, *Geophysical Research Letters*, 37(19), L19702, doi: 10.1029/2010GL044018. Copyright 2010 American Geophysical Union. Reproduced by permission of American Geophysical Union.

with higher GEP and ER. We hypothesize that these contrasting responses are due to differences in the relative contributions of vascular plants and mosses. The coherence of our results between sites representing a range of average environmental conditions indicates ecosystem-scale differences in resilience to hydrological changes that should be taken into account when considering the future of peatland ecosystem services such as carbon sequestration under changing environmental conditions.

2.1 Introduction

Northern peatlands are recognized as an important component of the terrestrial carbon cycle due to their large carbon stores [*Gorham*, 1991; *Turunen et al.*, 2002]. Short-term changes in hydrology are expected to affect ecosystem respiration (ER) in peatlands by changing the proportion of organic soil that is exposed to oxygen [*Clymo*, 1984], and this effect has been observed in both laboratory and field studies [*Moore and Knowles*, 1989; *Silvola et al.*, 1996; *Sulman et al.*, 2009]. Short-term changes in hydrology are also associated with changes in gross ecosystem photosynthesis (GEP) as growing conditions for plants change [*Sulman et al.*, 2009; *Strack and Waddington*, 2007]. Over longer time periods, hydrological changes can drive succession through shifts in vegetation composition and ecosystem structure, with substantial long-term changes in carbon cycling [*Minkkinen and Laine*, 1998b; *Talbot et al.*, 2010].

In boreal regions, two dominant peatland types are fens and bogs. Fens are typically fed by groundwater in addition to precipitation and have substantial nutrient inputs, whereas bogs are primarily precipitation-fed and nutrient-poor [*Wheeler and Proctor*, 2000]. These differences lead to contrasting dominant plant communities and peat and hydrological properties, with potentially different responses of carbon dioxide (CO_2) fluxes to changes in hydrology. To assess these differences, we compared the relationships between water table levels and fluxes of carbon dioxide at fen and bog sites in Canada and the northern United

States.

2.2 Methods and sites

2.2.1 Site notes

We calculated fluxes of carbon dioxide based on eddy-covariance measurements from six sites in northern North America, representing four fens and two bogs. A map of site locations is shown in Fig. 2.1. Important data about the sites are compiled in Table 2.1. For site descriptions, see the citations for each site. US-Los-fen, US-WFL-fen, and US-SFK-bog are located close to each other in northern Wisconsin, USA. Ca-Mer-bog is located in southeastern Ontario, Canada; Ca-WP1-fen is located in eastern central Alberta, Canada; and Ca-SDH-fen is located in central Saskatchewan, Canada.

Two sites, Wilson Flowage (US-WFL-fen) and South Fork (US-SFK-bog), have not been previously published and are described below. These two sites were part of a regional study wherein two portable open-path eddy-covariance systems (LI-7500 gas analyzer and CSAT3 3-D sonic anemometer) were periodically moved among four sites (two wetlands and two clearcuts). A wetland and a clearcut were simultaneously measured, and eddy-fluxes were continuously recorded at each site during the measurement period. This approach allowed us to measure eddy-fluxes at multiple sites using limited equipment, but resulted in time series with large gaps. *Peichl et al.* [2010] used a similar rotating flux tower measurement approach. For the purposes of the present study, we only present the results from the wetland sites.

Lost Creek

The Lost Creek site (US-Los-fen) is located in a shrub wetland in the Northern Highlands State Forest in north-central Wisconsin, USA (46° 4.9’ N, 89° 58.7’ W), elevation approxi-

Figure 2.1: Study site locations.

mately 480 m above sea level. It is part of the Ameriflux network, and is associated with the Chequamegon Ecosystem Atmosphere Study (ChEAS; http://cheas.psu.edu/) along with South Fork and Wilson Flowage. The vegetation around the flux tower is primarily alder (*Alnus incana* ssp. *rugosa*) and willow (*Salix* sp.), with an understory dominated by sedges (*Carex* sp.). The site was established in September, 2000, and eddy covariance measurements are available for the years 2001–2006. Annual average temperature over the study period was 5.2 °C, and annual average precipitation was 900 mm. For a complete description, see *Sulman et al.* [2009].

Western Peatland

The Western Peatland site (Ca-WP1-fen) is a treed, moderately rich fen located in central Alberta, Canada (54.95384° N, 112.46698° W). Eddy covariance data were available for the years 2004–2007. Vegetation is dominated by stunted trees of *Picea mariana* and *Larix laricina* with a high abundance of a shrub, *Betula pumila*, and a range of moss species. The mean annual temperature was 2.1 °C, and annual average precipitation was 504 mm. For a complete site description, see *Syed et al.* [2006].

Wilson Flowage

US-WFL-fen is a wet meadow/marsh fen, dominated by sedges and marsh grasses with small patches of labrador tea (*Ledum groenlandicum*) and leather-leaf (*Chamaedaphne calyculata*). It is located in the Chequamegon-Nicolet National Forest, Medford-Park Falls District in North-Central Wisconsin, USA.

South Fork

US-SFK-bog is a *Sphagnum* bog with significant labrador tea and leather-leaf, and some black spruce (*Picea mariana*). US-SFK-bog is located in the Chequamegon-Nicolet National Forest, Medford-Park Falls District in North-Central Wisconsin, USA.

Mer Bleue

The Mer Bleue bog site (Ca-Mer-bog) is located on the Mer Bleue peatland, located in the Ottawa Valley-St. Lawrence Lowland of Canada (45 ° 24'N, 75° 30'W). The ecosystem is a raised ombrotrophic bog, dominated by mosses (*Sphagnum angustifolium*, *S. rubellum*, *S. magellanicum*); sedges (*Eriophorum vaginatum*); and shrubs (*Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia angustifolia*, and *Vaccinium myrtillodes*). A small fraction of the bog ($< 2\%$) is covered with trees (*Larix laricina*, *Betula papyrifera*, and *Picea glauca*).

Table 2.1: Site descriptions. T is mean summer (June-July-August) temperature over the study period, and Precip is mean total yearly precipitation (mm). WT is mean growing-season water table level over the study period, expressed in cm above hummock height at each site. Water table measurements have an uncertainty of a few cm due to spatial variability in topography within sites. NEE, ER, and GEP are net ecosystem CO_2 exchange, ecosystem respiration, and gross ecosystem photosynthesis (gC-m^{-2}-day^{-1}), respectively, all averaged for June-July-August over the time series of available data for each site. Averages for Ca-SDH-fen exclude the 2003 season due to atypical conditions.

Site name	Identifier	Lat	Lon	T (°C)	Precip	WT	NEE	ER	GEP	Citation
Lost Creek	US-Los-fen	46.082	89.978	15.7	900	-24	-2.2	4.8	6.9	*Sulman et al.* [2009]
Western Peatland	Ca-WP1-fen	54.954	112.467	13.6	504	-32	-2.3	4.5	6.8	*Syed et al.* [2006]
Wilson Flowage	US-WFL-fen	45.817	90.172	15.2	900	-4	-1.0	4.2	5.1	NA
Sandhill Fen	Ca-SDH-fen	53.80	104.62	15.6	467	-3.5	-2.1	1.8	3.9	*Sonnentag et al.* [2009]
South Fork	US-SFK-bog	45.925	90.13	14.0	900	-19	-0.18	3.7	3.8	NA
Mer Bleue	Ca-Mer-bog	45.40	75.50	19.2	910	-39	-0.96	3.3	4.3	*Roulet et al.* [2007]

Mean annual temperature is 5.8 °C, and mean annual precipitation is 910 mm. For a complete site description, see *Lafleur et al.* [2001].

2.2.2 Measurements and flux processing

Fluxes of carbon dioxide (CO_2) and water vapor were measured at each site using the eddy covariance method [*Baldocchi*, 2003]. Fluxes were screened for low turbulence conditions based on a u^* threshold assigned individually for each site. Gaps in CO_2 fluxes were filled and estimates of GEP and ER were produced using nonlinear least squares fits in a moving window. For Ca-SDH-fen, US-WFL-fen, US-SFK-bog, and US-Los-fen, the method of *Desai et al.* [2005] was used. For Ca-Mer-bog and Ca-WP1-fen, the similar Fluxnet-Canada method was used [*Barr et al.*, 2004]. In both methods, night-time NEE was fit to a function of temperature to determine ER, and GEP was estimated by subtracting modeled ER from daytime NEE and fitting the residual to a function of photosynthetically active radiation (PAR). Recent studies have shown that these highly constrained flux partitioning and gap-filling methods are consistent in estimates of GEP and ER [*Desai et al.*, 2008b; *Moffat et al.*, 2007]. Flux estimates were produced using both methods at US-Los-fen, with comparable results.

We estimated the effect of the large gaps at US-WFL-fen and US-SFK-bog by artificially introducing repeated one-week gaps into the US-Los-fen dataset, gap-filling, and comparing the result with the complete gap-filled record for US-Los-fen. To estimate the uncertainty due to random variability at those sites, we repeated the gap-filling procedure 1000 times with artificially added random noise. Random uncertainty estimates at Ca-Mer-bog, US-Los-fen, and Ca-WP1-fen were calculated using the method of *Richardson and Hollinger* [2007], and uncertainty resulting from the friction velocity (u^*) threshold for these sites was estimated using a bootstrapping procedure. Uncertainty estimates for Ca-SDH-fen were generated using the method described by *Sonnentag et al.* [2009].

In the following analysis, ER and GEP are presented as positive numbers, and NEE is GEP subtracted from ER so that negative NEE represents ecosystem uptake of CO_2.

Water table height (WT) was measured using pressure transducer systems at US-Los-fen, US-WFL-fen, and US-SFK-bog [*Sulman et al.*, 2009]; with a float and weight system at Ca-WP1-fen [*Syed et al.*, 2006]; with a float and weight system [*Roulet et al.*, 2007] at Ca-Mer-bog; and calculated as the difference between continuous measurements of ground surface elevation and hydraulic head at Ca-SDH-fen [*Sonnentag et al.*, 2009]. WT at US-Los-fen and Ca-WP1-fen was corrected for peat subsidence using the method described by *Sulman et al.* [2009]. No significant changes in peat surface level were observed at US-WFL-fen, US-SFK-bog, or Ca-Mer-bog. In the present paper, WT is referenced to the mean hummock surface. Negative values indicate a water table below hummock surfaces. WT levels and anomalies have an uncertainty on the order of a few cm due to spatial variations in site topography. We were not able to determine this uncertainty with greater precision because we did not have access to appropriate microtopographical survey information.

The relationships presented in this study were calculated using June-July-August flux anomaly and growing season WT anomaly for each site, because it was a portion of the growing season when flux magnitudes were greatest and flux and WT measurements were available for all sites [*Lafleur et al.*, 2001; *Sonnentag et al.*, 2009; *Sulman et al.*, 2009]. For WT calculations, growing season is defined as the portion of the year when daily average soil temperature is above 0 °C. We focused on anomalies rather than flux magnitude and absolute WT because differences in topography and ecosystem characteristics between sites made direct comparisons of measured WT and flux magnitudes problematic. Anomalies were calculated for each site by subtracting the mean growing season value of the measurement over the study period (time series of measurements for each site) from the growing season average value for each year, where growing season is June-July-August for carbon fluxes and the soil temperature criterion described above for WT. Longer periods were used for WT averages to capture the potential effects of spring hydrology on summer growth. Data from the 2003 season at Ca-SDH-fen were excluded from the anomaly calculation because of atypical hydrological conditions (described below).

2.3 Results

The first year of the flux record at Ca-SDH-fen (2003) was unusually warm and dry for the site, resulting in an anomalously low WT. Plant growth in that year was suppressed due to the drought stress [*Sonnentag et al.*, 2009]. Because the conditions were atypical compared to the rest of the study period, data from 2003 at Ca-SDH-fen were excluded from the statistical analyses in this study, although the data point for that year is retained in the plots in Figure 2.2.

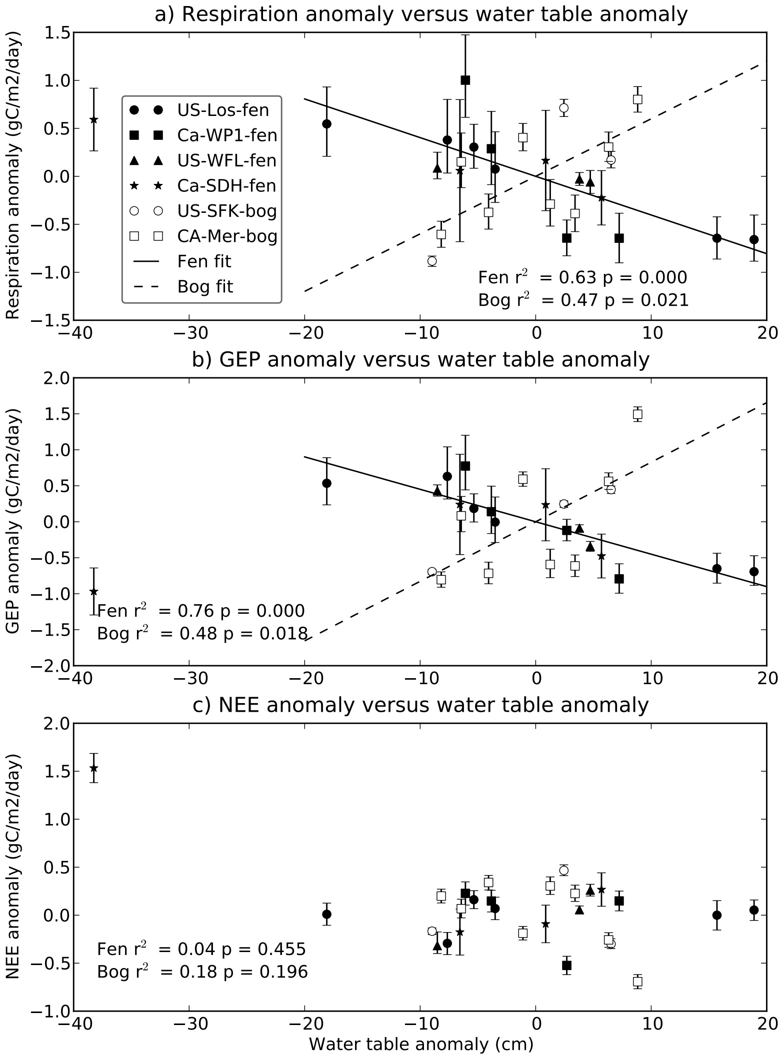

Figure 2.2: June-July-August average CO_2 flux anomaly at fen and bog sites as a function of growing season average water table (WT) anomaly. Fen sites are marked with black symbols, and bog sites with white symbols. Vertical error bars represent 95% confidence intervals. WT measurements have an uncertainty on the order of a few cm, but horizontal error bars are omitted in order to preserve clarity of the plots. The 2003 site-year at Ca-SDH-fen (stars) is shown, but was excluded from calculations. Ecosystem respiration anomaly was negatively correlated with WT anomaly at fen sites and positively correlated with WT anomaly at bog sites (a). Gross ecosystem photosynthesis anomaly was also negatively correlated with WT anomaly at fens and positively correlated with WT anomaly at bogs (b). Net ecosystem exchange anomaly was not significantly correlated with WT anomaly at fens or bogs (c).

Table 2.2: Relationships between June-July-August CO_2 flux anomaly and growing-season water table anomaly at each site. Slopes were calculated using linear regression, and are expressed in gC m^{-2} day^{-1} per cm of water table change. Standard error of the estimate is indicated in parentheses.

Site	ER slope		GEP slope		NEE slope	
US-Los-fen	−0.036	(0.003)	−0.037	(0.006)	0.0019	(0.005)
Ca-WP1-fen	−0.122	(0.034)	−0.102	(0.023)	−0.021	(0.038)
US-WFL-fen	−0.010	(0.0015)	−0.051	(0.014)	0.038	(0.011)
Ca-SDH-fen	−0.020	(0.026)	−0.054	(0.040)	0.034	(0.017)
US-SFK-bog	0.084	(0.057)	0.076	(0.007)	0.0052	(0.051)
Ca-Mer-bog	0.048	(0.026)	0.086	(0.043)	−0.038	(0.018)
All fens	−0.040	(0.008)	−0.045	(0.005)	0.0048	(0.006)
All bogs	0.060	(0.021)	0.083	(0.029)	−0.024	(0.017)

ER anomaly at fen sites (Fig. 2.2a) was negatively correlated with WT anomaly ($r^2 = 0.63; p < 0.001$) while ER anomaly at bog sites was positively correlated with WT anomaly ($r^2 = 0.47; p = 0.02$). GEP anomaly (Fig. 2.2b) at fen sites was also negatively correlated with WT anomaly ($r^2 = 0.76; p < 0.001$), while GEP anomaly at bog sites had a significant positive correlation with WT anomaly ($r^2 = 0.48; p = 0.018$). Each individual site had the same direction of correlation, although not all were significant (Table 2.2). NEE anomaly had no significant correlation with WT anomaly at either fen or bog sites (Fig. 2.2c). CO_2 flux anomalies were not significantly correlated with summer soil temperature anomaly (not shown), with the exception of ER at fen sites, which had a significant correlation with temperature that was substantially smaller than the correlation with WT ($r^2 = 0.30; p = 0.027$).

2.4 Discussion and Conclusions

The contrasting correlations of GEP with WT at fens and bogs may result from differences in the contribution of vascular plants to total GEP between sites. The species listings in

Table 2.3 show that the fen sites included in this study had substantially more shrub and sedge biomass than the bog sites, which had larger populations of mosses. These species differences can lead to contrasting responses to environmental perturbations as well as differences in peat properties [*Limpens et al.*, 2008]. Many vascular species can tolerate wet conditions, but grow faster during dry periods, causing an increase in GEP since generalist herbs and woody plants typically have higher maximum productivity than mosses. Such increased growth was evident at US-Los-fen, where shrub biomass increased during a multi-year decline in WT [*Sulman et al.*, 2009]. *Weltzin et al.* [2003] observed similar shifts in species composition in response to WT and temperature manipulations in mesocosms, and *Ewers et al.* [2007] observed distinct adaptations to flooding between different tree species in a study in northern Wisconsin using sap flux data. In contrast, the mosses that make up a large proportion of live biomass at the bog sites are more sensitive to fluctuations in hydrology [*Laitinen et al.*, 2008; *Talbot et al.*, 2010].

Table 2.3: Summary of plant species present at each site. Aboveground biomass estimates (g dry biomass/m^2) are included where data were available, and marked N/A where not available. Only NPP measurements were available for *Sphagnum spp* at US-SFK-bog.

Site	Species present	Comments	Aboveground biomass (g(dry)/m^2)
US-Los-fen	*Alnus incana*	Dominant	
	Salix spp	Dominant	Shrub total 828
	Carex spp	Scattered understory [*Sulman et al.*, 2009]	158
Ca-SDH-fen	*Larix laricina*	< 10 m high, dominant tree	N/A
	Andromeda polifolia	< 0.5 m evergreen shrub cover	N/A
	Betula glandulosa	< 0.5 m deciduous shrub cover	N/A
	Carex spp	Dominating sedges	N/A
	Eriphorum spp	Dominating sedges	N/A
	Brown mosses	Groundcover	N/A
	Menyanthes tridoliata	Present in swales	N/A

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		[*Sonnentag et al.*, 2009; *Suyker et al.*, 1997]	
Ca-WP1-fen	*Picea mariana*	Stunted trees dominate vegetation	467
	Larix laricina	Stunted trees dominate vegetation	208
	Betula pumila	Abundant shrub	77
	Salix spp		4.3
	Ledum groenlandicum		39
	Andromeda polifolia		25.6
	Carex spp		21.7
	Vaccinium vitisidaea		29
	Sphagnum spp	Biomass is capitulum only	185
		[*Syed et al.*, 2006]	Vascular total = 895
US-WFL-fen	Graminoids	Includes sedges and grasses. Biomass measurements were not further divided	83.1
	Forbs	Biomass measurements not further divided	2.5
	Woody shrubs	Biomass measurements not further divided	297
		[*Peter Weishampel*, unpublished data]	
US-SFK-bog	*Sphagnum spp*	Dominant; only NPP was measured	NPP = 297 g/m^2/year
	Picea mariana	Some scattered	0.3
	Ledum groenlandicum	Significant occurance	17.2
	Chamaedaphne calyculata	Significant occurance	146.7
	Kalmia polifolia		12.6
	Vaccinium oxycoccos		9.8
	Andromeda glaucophylla		9.7
	Vaccinium myrtilloides		5.2
		[*Peter Weishampel*, unpublished data]	
Ca-Mer-bog	*Sphagnum spp* (capitulum)	Cover hummocks and hollows; biomass is capitulum only	144
	Chamaedaphne calyculata	Dominant evergreen shrub; biomass values include leaves and shoots	124
	Ledum groenlandicum	Dominant evergreen shrub	50

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	Kalmia angustifolia	Dominant evergreen shrub	93
	Vaccinium myrtilloides	Dominant deciduous shrub	29
	Eriophorum vaginatum	Sparse cover	8
	Other vascular species		39
	Larix laricina	Few small trees on hummocks	N/A
	Betula populifolia	Few small trees on hummocks	N/A
		[*Moore et al.*, 2002]	Vascular total = 343

The presence of significant live *Sphagnum* biomass at Ca-WP1-fen and shrub biomass at Ca-Mer-bog expose potential weaknesses in this hypothesis, although *Sphagnum* capitulum makes up a smaller percentage of total aboveground biomass at the fen compared to the bog (17% and 29%, respectively). The presence of shrubs at Ca-Mer-bog may contribute to the high variability and lower sensitivity of the bog to WT fluctuations.

The decrease in ER with higher WT at fen sites is consistent with expectations and previous studies [*Freeman et al.*, 1992; *Bubier et al.*, 1998]. At bogs, however, there was a significant positive correlation between WT and ER. A possible explanation is that the upper layers of moss-derived bog peat dry out quickly during low-WT periods, limiting decomposition. In lower layers, increased oxygen availability could increase decomposition rates, leading to contrasting responses that could contribute to the high observed variability at Ca-Mer-bog. Labile carbon production resulting from higher photosynthesis rates at bogs under wet conditions could also contribute to the observed correlation. The positive correlation between WT and ER at bogs contrasts with *Lafleur et al.* [2003], which presented the first four years of the Ca-Mer-bog measurements and found higher ER rates during drier summers. Given the high inter-annual variability in the bog data, it is not surprising that extending the data set by several years could reveal additional patterns.

The observed fluxes from 2003 at Ca-SDH-fen are an exception to the relationships described above. During this exceptionally dry year, early senescence and dieback of drought-intolerant sedges occurred, and GEP was lower than in other years [*Sonnentag et al.*, 2009].

This suggests that the advantage of certain wetland species in drier conditions breaks down when the fluctuations exceed a threshold. Similar effects have been observed during anomalously dry years in both fens and bogs [*Alm et al.*, 1999; *Schreader et al.*, 1998; *Shurpali et al.*, 1995; *Arneth et al.*, 2002]. Such results, however, do not apply to long-term changes, which could drive succession [*Laine et al.*, 1995; *Talbot et al.*, 2010] or cause changes in peat surface height that counteract the effects of declining WT [*Dise*, 2009].

The observed contrast between bog and fen CO_2 fluxes is consistent with the high inter-site variability observed in a comparison of CO_2 fluxes from several Canadian peatland sites by *Humphreys et al.* [2006]. That study included measurements from Ca-Mer-bog, Ca-SDH-fen, and Ca-WP1-fen. *Lund et al.* [2009] identified significant correlations between annual CO_2 fluxes and pH at a range of peatland sites including bogs, fens, and tundra sites, but did not discuss interactive effects of nutrient status and WT on CO_2 fluxes. That study also included data from Ca-Mer-bog and Ca-WP1-fen. Similarly, *Bubier et al.* [1998] observed a difference in relationships between CO_2 fluxes and WT at fen and bog areas within a single peatland complex over the course of one year.

Because the results presented here include only fluxes of CO_2, and omit other carbon fluxes such as methane and dissolved carbon, they do not represent a complete peatland carbon budget. At Ca-Mer-bog, methane and dissolved carbon losses were significant portions of the total carbon balance, but on average were smaller in magnitude than NEE [*Roulet et al.*, 2007]. Measurements of methane emissions at US-Los-fen, US-WFL-fen and US-SFK-bog suggested that carbon losses through methane emissions at these sites were small compared to NEE [*B. Cook, unpublished data*]. Measurements of carbon fluxes other than CO_2 were not available at the other sites.

Although this study uses correlation analysis, and the results therefore cannot prove a causative relationship, the remarkable level of coherence in ecosystem-scale patterns between the different sites is striking, especially given the range of geographical locations, average temperature and WT, and species composition among sites. While differences in ecosystem function between fens and bogs have been previously observed, our study presents observational evidence of the effects of these differences on ecosystem-scale resilience of CO_2 fluxes to fluctuations in hydrological conditions. These differences go beyond local biological effects to impact ecosystem services (e.g. carbon sequestration) and ecosystem-level interactions with the atmosphere, and must be taken into account when considering the impacts of climate change, land management, and ecological change in the context of northern peatland carbon cycling and feedbacks.

Chapter 3

Impact of hydrological variations on modeling of peatland CO_2 fluxes: results from the North American Carbon Program site synthesis[1]

Abstract

Northern peatlands are likely to be important in future carbon cycle-climate feedbacks due to their large carbon pools and vulnerability to hydrological change. Use of non-peatland-specific models could lead to bias in modeling studies of peatland-rich regions. Here, seven ecosystem models were used to simulate CO_2 fluxes at three wetland sites in Canada and the northern United States, including two nutrient-rich fens and

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[1] A version of this chapter was previously published in a peer-reviewed journal: Sulman, B. N., A. R. Desai, N. M. Schroeder, D. Ricciuto, A. Barr, A. D. Richardson, L. B. Flanagan, P. M. Lafleur, H. Tian, G. Chen, R. F. Grant, B. Poulter, H. Verbeeck, P. Ciais, B. Ringeval, I. T. Baker, K. Schaefer, Y. Luo, and E. Weng (2012): Impact of hydrological variations on modeling of peatland CO_2 fluxes: results from the North American Carbon Program site synthesis, *Journal of Geophysical Research*, 117, G01031, doi: 10.1029/2011JG001862. Copyright 2012 American Geophysical Union. Reproduced by permission of American Geophysical Union.

one nutrient-poor, sphagnum-dominated bog, over periods between 1999-2007. Models consistently overestimated mean annual gross ecosystem production (GEP) and ecosystem respiration (ER) at all three sites. Monthly flux residuals (simulated observed) were correlated with measured water table for GEP and ER at the two fen sites, but were not consistently correlated with water table at the bog site. Models that inhibited soil respiration under saturated conditions had less mean bias than models that did not. Modeled diurnal cycles agreed well with eddy covariance measurements at fen sites, but overestimated fluxes at the bog site. Eddy covariance GEP and ER at fens were higher during dry periods than during wet periods, while models predicted either the opposite relationship or no significant difference. At the bog site, eddy covariance GEP did not depend on water table, while simulated GEP was higher during wet periods. Carbon cycle modeling in peatland-rich regions could be improved by incorporating wetland-specific hydrology and by inhibiting GEP and ER under saturated conditions. Bogs and fens likely require distinct plant and soil parameterizations in ecosystem models due to differences in nutrients, peat properties, and plant communities.

3.1 Introduction

Northern peatlands are an important component of the global carbon cycle due to large carbon pools resulting from the long-term accumulation of organic matter in peat soils [*Gorham*, 1991; *Turunen et al.*, 2002]. These carbon pools are vulnerable to changes in hydrology, which could cause climate feedbacks. Because ecosystem respiration and productivity can have opposite responses to hydrological change, the direction of the net carbon flux response can be unclear. Lowering of the water table exposes peat soils to oxygen, resulting in higher rates of ecosystem respiration (ER) and an increase in CO_2 emissions, along with decreases in CH_4 emissions [*Clymo*, 1984]. This effect has been observed in both laboratory and field studies [*Freeman et al.*, 1992; *Junkunst and Fiedler*, 2007; *Moore and*

Knowles, 1989; *Silvola et al.*, 1996; *Sulman et al.*, 2009]. However, very dry conditions can be associated with lower rates of ER due to drying of substrates [*Parton et al.*, 1987]. In wetlands with complex topography, different water tables in different microforms can lead to offsetting responses [*Dimitrov et al.*, 2010].

Sensitivity of gross ecosystem production (GEP) to changes in hydrology has also been observed in northern peatlands [*Strack and Waddington*, 2007; *Strack et al.*, 2006; *Flanagan and Syed*, 2011; *Sulman et al.*, 2009]. Under high water table conditions, saturation of soils tends to suppress productivity due to limitation of oxygen and nutrient availability in the root zone, leading to increased productivity during drier periods. However, very dry conditions can also be associated with lower productivity due to moisture stress. As a result, moderately wet conditions lead to higher productivity than either very dry or very wet conditions.

Fens and bogs are two dominant wetland ecosystem types in boreal regions. Fens, or minerotrophic wetlands, are fed by surface or groundwater flows in addition to precipitation, and have significant nutrient inputs, while bogs (ombrotrophic wetlands) are fed primarily by precipitation, and have lower nutrient levels and higher acidity. Plant communities in bogs tend to be dominated by shrubs, herbs, and non-vascular Sphagnum mosses, while shrubs, sedges, or flood-tolerant trees dominate typical fen plant communities [*Wheeler and Proctor*, 2000]. Mosses are less productive than typical wetland vascular plants, and produce litter that is more resistant to decomposition. Peat derived from vascular plants also has different structure and hydraulic conductivity than peat derived from Sphagnum mosses [*Limpens et al.*, 2008]. Previous studies have suggested that CO_2 fluxes at rich fens are more sensitive to hydrological change than fluxes at bogs, and that ER and GEP at the two wetland types may have opposite responses to hydrological change [*Syed and Flanagan*, 2011; *Sulman et al.*, 2010]. These distinctions are therefore important for understanding wetland contributions to the carbon cycle and responses to climatic changes.

Modeling studies incorporating hydrological effects on peatlands have predicted a substantial positive climate feedback due to future drying that cannot be ignored in studies of the evolution of the global carbon cycle under climate change [*Limpens et al.*, 2008; *Ise et al.*, 2008]. However, global-scale carbon cycle models do not have fine enough spatial resolution to accurately simulate conditions at peatlands, which can depend on local topography at scales from kilometers down to meters [*Baird and Belyea*, 2009; *Dimitrov et al.*, 2010; *Strack et al.*, 2006; *Waddington and Roulet*, 1996]. Further, some ecosystem models used in global-scale simulations may lack specific and accurate parameterizations for the various peatland types contained in their simulated regions, or may not contain wetland land cover types and plant functional types at all. Finally, land cover maps used to set up large-scale modeling studies may be based on remote sensing products or inventories that do not accurately identify peatland areas, or that cannot distinguish between peatland ecosystem types with contrasting plant communities or different sensitivities to environmental drivers [*Krankina et al.*, 2008]. Understanding the limitations of ecosystem model simulations of different types of peatland ecosystems is thus integral to interpreting the results of large-scale ecosystem model simulations in peatland-rich regions.

In this study, we compared eddy covariance CO_2 fluxes with simulated fluxes from a group of ecosystem models for three peatlands (two in Canada and one in the northern United States). The goal was to identify potential pitfalls and areas for improvement in simulating peatland CO_2 fluxes using, in general, non peatland-specific models with limited driver data, in an analog to the likely conditions for global-scale modeling studies in peatland-rich regions. We compared model output to measured fluxes to examine the accuracy of models and explore differences between models with different architectures. We tested three central hypotheses:

1. Differences between simulated and observed CO_2 fluxes will be correlated with observed hydrological conditions, since these conditions drive ecosystem responses that are not

included in general ecosystem models that lack peatland-specific processes.

2. Models with more soil layers and explicit connections between hydrology and soil respiration will be better able to simulate hydrology-driven ecosystem processes, resulting in closer matches between modeled and observed fluxes.
3. Models will perform better at the fen sites than at the bog site, due to the prevalence of nonvascular plants and the low nutrient availability in bogs. These factors make bogs more different from the plant communities for which general ecosystem models have been well parameterized.

3.2 Methods

3.2.1 Field sites

The three peatland sites used in this study are part of the Fluxnet-Canada and Ameriflux networks, respectively. Site characteristics are summarized in Table 3.1.

Table 3.1: Site characteristics. Temperature (T), precipitation (precip), and CO_2 fluxes are annual means over the study period for each site, with summer (June-July-August) average in parentheses. Water table is summer average. Annual and summer CO_2 fluxes are in g/m^2/year, and g/m^2/summer, respectively.

Site name	Mean T (C)	Mean precip (mm/year)	Mean water table (cm)	Mean GEP	Mean ER	Mean NEE	Peatland type	Years
Lost Creek	3.8 (16.5)	666 (225.9)	-33	849 (659)	771 (464)	-77.9 (-195.5)	Shrub fen	2001-2006
Western Peatland	1.7 (14.7)	465 (212)	-30	869 (624)	674 (414)	-195.5 (-210.2)	Treed fen	2004-2007
Mer Bleue	6.2 (19.0)	779 (249)	-43	617 (391)	548 (304)	-68.6 (-87.0)	*Sphagnum* bog	1999-2006

The Lost Creek flux tower is located in a shrub fen in northern Wisconsin, USA (46° 4.9' N, 89° 58.7' W). The creek and associated floodplain provide a consistent water and nutrient source. Seasonal average water table levels were significantly correlated with precipitation, and were also affected by downstream beaver (*Castor canadensis*) dam-building activity

[*Sulman et al.*, 2009]. Vegetation at the site is primarily alder (*Alnus incana ssp. Rugosa*) and willow (*Salix spp.*), with an understory dominated by sedges (*Carex spp*). The site experienced a decline in yearly average water table level of approximately 30 cm over a period from 2002 to 2006 [*Sulman et al.*, 2009].

The Western Peatland flux tower is located in a moderately rich, treed fen in Alberta, Canada (54.95°N, 112.47°W). Vegetation is dominated by stunted trees of Picea mariana and Larix laricina, along with an abundance of a shrub, Betula pumila. The understory is dominated by various moss species [*Syed et al.*, 2006]. The site experienced a decline in growing-season water table of approximately 25 cm over a period from 2004 to 2007 [*Flanagan and Syed*, 2011].

The Mer Bleue field station is located in a domed, ombrotrophic bog near Ottawa, Canada (45.41°N, 75.48°W). The peatland has an overstory of low stature, woody shrubs, both evergreen (*Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia angustifolia*) and deciduous (*Vaccinium myrtilloides*). The understory is dominated by *Sphagnum* mosses, with some sedges (*Eriphorum vaginatum*) [*Moore et al.*, 2002]. For additional details, see *Moore et al.* [2002] and *Roulet et al.* [2007].

3.2.2 Measurements and gap-filling

CO_2 fluxes were measured at all three sites using the eddy covariance technique [*Baldocchi*, 2003]. In this manuscript, gross ecosystem production (GEP) is defined as negative, and ecosystem respiration (ER) is presented as positive. Net ecosystem exchange of CO_2 (NEE) is defined as ER + GEP, so that negative values of NEE indicate uptake of CO_2 by the ecosystem. Eddy covariance NEE was supplied by investigators at each field site, and then gap-filled and decomposed into GEP and ER using a standardized process as part of the North American Carbon Program (NACP) Site Level Interim Synthesis (http://www.nacarbon.org/nacp; *Schwalm et al.* [2010]). The partitioning and gap-filling procedure is described in detail by

Barr et al. [2004]. Gaps resulted from equipment failure and from screening of data for outliers and periods of low turbulence. Simple empirical models were fit to screened eddy covariance observations at an annual time scale, and an additional time-varying scale parameter was applied using a moving window to account for variability within the year. ER was determined by fitting a function of soil temperature to nighttime NEE. GEP was then calculated by subtracting ER from daytime NEE and fitting the residual to a function of photosynthetically active radiation (PAR). The ER and GEP values presented in this study are therefore not strictly measured values, but result from the assumptions of the gap-filling procedure. However, since the gap-filling procedure involved fitting the simple empirical models to observed data in a short moving window, variations in these values over time do reflect real changes in the observed quantities [*Desai et al.*, 2008b].

Uncertainties in eddy covariance values were estimated based on a combination of random uncertainty, uncertainty due to the friction velocity (u*) threshold, gap filling algorithm uncertainty, and GEP partitioning uncertainty. These errors were assumed to be independent and summed in quadrature to determine total measurement uncertainty. Random uncertainty was estimated using the method of *Richardson and Hollinger* [2007]. Gap filling uncertainty was based on the standard deviation of multiple algorithms [*Moffat et al.*, 2007]. Partitioning uncertainty was based on the standard deviation of multiple partitioning algorithms [*Desai et al.*, 2008b].

Models were driven by meteorological data collected for each site and gap-filled according to the procedures described by *Schwalm et al.* [2010] and the NACP site synthesis protocol (http://nacp.ornl.gov/docs/Site_Synthesis_Protocol_v7.pdf). Briefly, tower measurements from each site were used where available. Periods with missing site data were filled using data from nearby weather stations included in the National Climate Data Center (NCDC) Global Surface Summary of Day dataset. Periods when both site and NCDC meteorology were unavailable were filled using output from the DAYMET model [*Thorn-*

ton et al., 1997]. Table 3.2 shows the meteorology data sets and the percentage of original tower measurements for each site. Additional site data were also available for model forcing, including soil properties and carbon and nutrient content, vegetation type, and biomass. Data were collected independently for each site, according to the Ameriflux biological data collection protocols [*Law et al.*, 2008].

Table 3.2: Site meteorological data coverage. Numbers are percentage of original site data used. The remainder for each variable was gap-filled, as described in Section 3.2.2. Psurf is surface atmospheric pressure; LWdown and SWdown are longwave and shortwave downwelling radiation, respectively; Qair is specific humidity; Tair is air temperature; and Precip is precipitation rate.

Site	Psurf	LWdown	Wind	SWdown	Qair	Tair	Precip
Lost Creek	96.3	58.5	78.8	80.8	0.0	81.2	99.9
Western Peatland	0.0	87.7	88.3	84.9	86.0	88.2	79.2
Mer Bleue	97.9	42.6	99.6	95.8	98.1	98.4	77.1

This analysis incorporates hydrological measurements from each site in addition to the standardized meteorology data sets. These data sets were not available for model parameterization. Water table was measured at Lost Creek using a pressure transducer system [*Sulman et al.*, 2009] and at Mer Bleue and Western Peatland using float and weight systems [*Roulet et al.*, 2007; *Syed et al.*, 2006]. In this manuscript, water table is referenced to the mean hummock surface. Negative values indicate water table below the hummock surface and positive values indicate water table above this level. Topographical relief between hummocks and hollows was on the order of 25 cm at Mer Bleue [*Lafleur et al.*, 2005a]. Detailed topographical information was not available for Lost Creek and Western Peatland. Water table values have uncertainties on the order of a few cm due to spatial variations in site topography. Multiyear declines in water table at Lost Creek and Western Peatland resulted in subsidence of the peat surface, which was subtracted from water table measurements using the method described by *Sulman et al.* [2009], so that water table values reflect the position relative to the peat surface over the observed time period for each site. No significant changes in peat level were observed at Mer Bleue during the study period.

In addition to water table, volumetric soil water content was measured at the Mer Bleue and Western Peatland sites. Measurement depths at Western Peatland were 7.5, 10, and 12.5 cm below the peat surface, and measurement depths at Mer Bleue were 5 and 20 cm below the surface. Fraction of saturation rather than volumetric soil moisture content was used for comparison purposes, since some of the included models reported soil moisture only in units of fraction of saturation. A fraction of saturation of 0.0 indicates completely dry soil, and a fraction of 1.0 indicates soil with pores completely filled with water. Mer Bleue soil water content was converted to fraction of saturation by dividing by an estimated peat porosity of 0.9 [*P. M. Lafleur*, personal communication], and Western Peatland soil water content was divided by the maximum value observed during periods of inundation. No soil water content measurements were available at Lost Creek.

3.2.3 Ecosystem models

This study used model results from the NACP Site Level Interim Synthesis. Seven process-based models were run at all three peatland sites, representing different simulation strategies, temporal resolutions, and levels of complexity, but sharing in common the site-level meteorological driver data and investigator-provided site initial conditions described above. A summary of model characteristics is shown in Table 3.3. Important differences in model structure included number of soil layers and carbon pools, representations of hydrology, and calculation of the light environment for photosynthesis.

Four of the models simulated soil moisture values up to saturation, while the other three models partitioned soil water above field capacity directly to runoff and subsurface drainage, making them incapable of simulating saturated soil conditions. Of the models included in this study, only *ecosys* produced simulations of water table level. SiB and SiBCASA shared a soil moisture redistribution submodel based on the Richards equation. TECO included

Table 3.3: Model characteristics. Soil layers is the number of soil layers used in model hydrology; Veg. C pools is the number of vegetation carbon pools; Psyn calculation is the model strategy for calculating photosynthesis; N cycle indicates whether the model included nitrogen cycling; Phenology indicates whether model leaf phenology was driven by internal model calculations or external satellite observations; Max soil moisture indicates whether the model was able to calculate saturated soil conditions or whether soil moisture above field capacity was directly partitioned to runoff.

Model name	Temporal resolution	Soil layers	Soil C pools	Veg. C pools	Photosynth calculation	N cycle	Phenology	Max soil moisture	Citation
DLEM	Daily	2	3	6	Stomatal conductance	Yes	Satellite	Saturation	*Tian et al.* [2010]
ecosys	Hourly	8 (Water table calculated)	9	9	Enzyme kinetic	Yes	Calculated	Saturation	*Grant et al.* [2009]
LPJ	Daily	2	2	3	Stomatal conductance	No	Calculated	Field capacity	*Gerten et al.* [2004]; *Sitch et al.* [2003]
ORCHIDEE	30-minute	2	8	8	Enzyme kinetic	No	Calculated	Field capacity	*Krinner et al.* [2005]
SiB	30-minute	10	None	None	Enzyme kinetic	No	Satellite	Saturation	*Baker et al.* [2008]
SiBCASA	30-minute	25	9	4	Stomatal conductance	No	Satellite	Saturation	*Schaefer et al.* [2008]
TECO	30-minute	10	5	3	Stomatal conductance	No	Calculated	Field capacity	*Weng and Luo* [2008]

multiple soil layers, with water infiltrating from an upper to a lower layer when soil water in the upper layer was above field capacity. *Ecosys* explicitly calculated matric, osmotic, and gravimetric components of water potential and was the only model to include vertical variations in peat hydrological properties through the soil profile. *Ecosys* was also the only model to include a representation of hummock and hollow topography. The model was run for one hummock and one hollow grid point, and the results were combined in a weighted average based on observed area fractions for the sites. LPJ, DLEM, and ORCHIDEE used two-layer soil models and therefore did not produce estimates of soil moisture at defined soil depths.

Model formulations of the light environment could be divided based on whether models included multiple canopy layers and explicitly calculated light extinction and the properties of sun and shade leaves, or used a single layer big leaf model for photosynthesis. *Ecosys* explicitly calculated carboxylation rates for leaf surfaces defined by height, inclination, and exposure to light. DLEM and TECO used a two layer approach that included sunlit and shaded leaves. SiBCASA parameterized differences between sunlit and shaded leaves using an effective leaf mass calculation that weighted leaf mass based on expected nitrogen content for sunlit and shaded leaves. SiB, ORCHIDEE, and LPJ used the single layer big leaf approach, without considering sunlit and shaded leaves separately.

Since hydrology is an important driver of peatland ecosystem processes, the model processes that connect soil respiration and photosynthesis to soil moisture are another important basis of comparison. Figure 3.1 shows the functions that relate photosynthesis and soil respiration to soil moisture fraction for six of the models. Soil moisture is represented as a fraction of saturation, where a value of 1.0 indicates that pore spaces are full and the soil cannot accommodate additional water. In order to include the models that do not simulate soil water fractions above field capacity, soil moisture values for those models were normalized by a field capacity fraction of 0.7. All of the models included in the photosynthesis plot have similar moisture limitation functions, with photosynthesis suppressed at low soil moisture and reaching a plateau at high soil moisture. LPJ and *ecosys* were not included in the photosynthesis plot, because their calculations of moisture-related photosynthesis limitation could not be reduced to simple functions of soil moisture. LPJ calculates water stress on photosynthesis by first calculating non-water-stressed photosynthesis rate, and then optimizing canopy conductance based on water-limited evapotranspiration [*Sitch et al.*, 2003]. Photosynthesis in LPJ is not limited by high-moisture conditions. *Ecosys* explicitly calculates water potentials and flows between soil, roots, plant tissues, and leaves, and allows for reduction of productivity as a result of saturated soils, through reductions in water and nutrient uptake by roots. *Ecosys* was the only model included in this study to include a process that suppresses photosynthesis at high soil moisture.

Of the models included in the respiration plot, only SiB, SiBCASA, and DLEM suppress respiration under wet conditions. Heterotrophic respiration in *ecosys* involves growth and respiration of microbial communities that are limited by the availability of substrates, nutrients, and oxygen. This process could not be reduced to a simple function of soil moisture, but heterotrophic respiration rates are limited under both dry and saturated conditions [*Grant et al.*, 2009].

Models were initialized with a spinup period intended to reach steady state conditions. According to the NACP synthesis activity protocol, steady state for the carbon cycle is reached when annual NEE is approximately zero when averaged over the last five years of model spinup. Since peatlands are defined by long-term carbon accumulation and since the sites included in this study are all presently net carbon sinks of between 68 and 105 gC/m2/year (Table 3.1), this steady state condition likely contributed to underestimation of CO_2 uptake by models. Because peatlands contain large soil carbon pools relative to aboveground biomass pools and because northern peatland carbon accumulation is driven by low rates of soil decomposition, this bias was most likely manifested as an overestimate

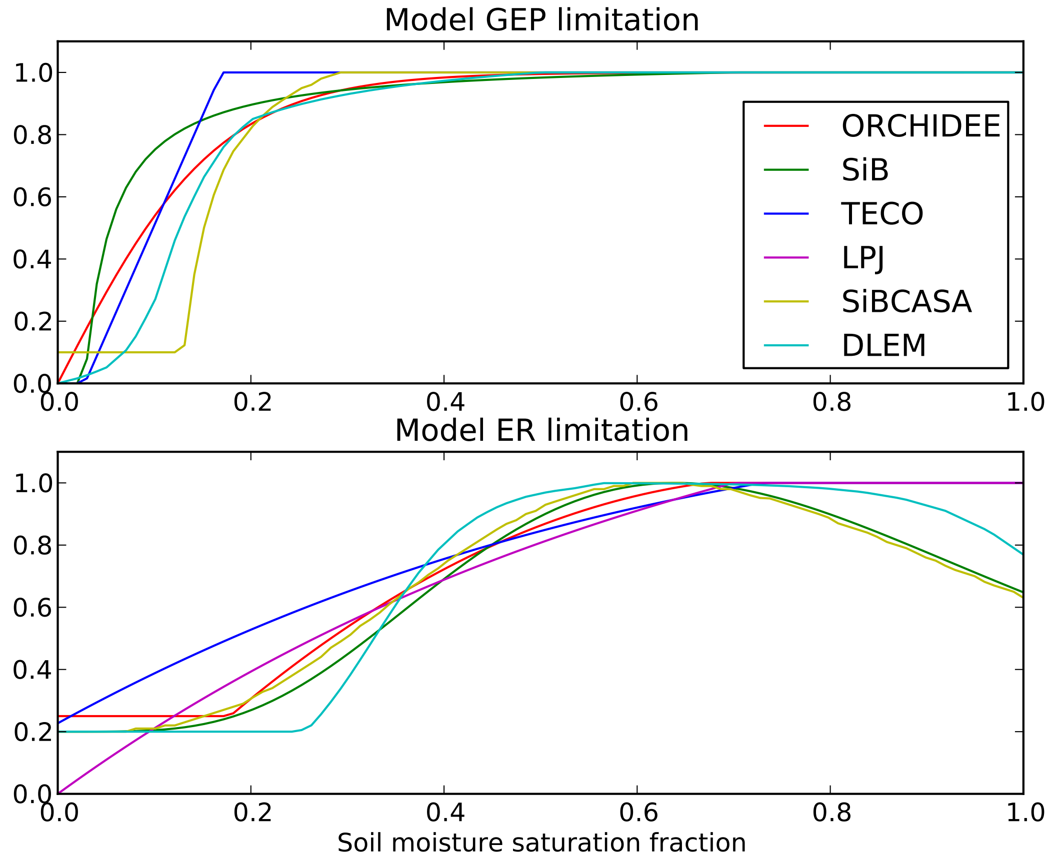

Figure 3.1: Model photosynthesis and respiration limitation functions. Plots show fractional limitation of photosynthesis (upper plot) and soil respiration (lower plot) as functions of soil moisture saturation fraction. Curves are based on internal model equations. Limitations on stomatal conductance and direct limitations on photosynthesis rate are taken to be equivalent. LPJ is not included in GEP, and ecosys is not included in either plot, because these models use more complex limitation schemes that cannot be easily expressed as functions of soil moisture.

of soil respiration relative to photosynthesis. To estimate the magnitude of this bias, annual average GEP/ER ratios were calculated for observed and modeled fluxes and ER was multiplied by the ratio of these factors to produce an adjusted ER that matched the annual GEP/ER ratio of eddy covariance measurements. Adjusted NEE was then calculated by subtracting GEP from adjusted ER. The majority of this analysis used the original ER and NEE, and adjusted values are identified as such when they appear.

3.2.4 Statistical analysis

Residuals in this study were defined as simulated minus observed time series, so that positive residuals indicate an over-estimate of the time series by a model. Confidence levels for correlation coefficients were calculated using a two-tailed t test. In diurnal variation plots, error bars indicate the 95% confidence limits on the mean of each time period, based on a two-tailed t test.

For diurnal plots (Figures 3.8-3.13), eddy covariance fluxes were divided into wet and dry periods on a weekly basis, with observations from weeks in the top 30th percentile of water table shown in blue and observations from weeks in the bottom 30th percentile of water table shown in red. Simulated NEE values from each model were similarly divided, based on weeks in the top (green) and bottom (orange) 30th percentiles of simulated soil moisture in the model layer closest to 20 cm below the surface. For models with only two soil layers, the reported root zone soil moisture was used. NEE plots were calculated using only non-gap-filled eddy covariance data, and only model data points corresponding to the included eddy covariance points. ER and GEP diurnal plots were calculated using all gap-filled eddy covariance data and all model data. LPJ and DLEM produced output with daily resolution and were not included in diurnal plots.

3.3 Results

3.3.1 Model simulations of hydrology

Figure 3.2 shows representative ranges of simulated and observed summer soil moisture saturation fractions, as well as representative ranges of water table observations and water table simulated by the *ecosys* model. Ranges are bounded by the 10th and 90th percentiles of the soil moisture values for each soil layer. As in Figure 3.1, models with an upper soil moisture limit of field capacity were normalized by a field capacity of 0.7. The upper plots show vertical profiles for observations and models that included soil layers with explicit depths. The lower plots show the upper and lower soil layers of LPJ and the mean root zone soil moisture of ORCHIDEE, for which soil moisture in multiple layers was not available. DLEM did not provide soil moisture data for this comparison. In general, ecosys predicted wetter conditions than the other models, but with a moderate range of temporal variability. TECO predicted a wider range of soil moisture variability at each site than the other models. SiB, SiBCASA, ORCHIDEE, and LPJ predicted small ranges of variability. SiB predicted almost constantly saturated conditions at Mer Bleue, but was closely matched with SiBCASA at the other sites. Observations indicated very low soil moisture and low variability at Mer Bleue, where only LPJ predicted a similar range in the upper soil layer. Measured soil moisture at Western Peatland had a large range of variability, including very wet conditions. All models except LPJ overlapped with this range in their upper soil layers.

If models are capturing the hydrological conditions at a site, they should simulate saturated soil moisture below the water table. *Ecosys* was the only model to predict saturated soil moisture below the observed water table level at any of the sites. Water table ranges predicted by *ecosys* (black arrows) were well matched to observations (white arrows) at Lost Creek and Mer Bleue, but predicted higher water table than observations at Western Peatland.

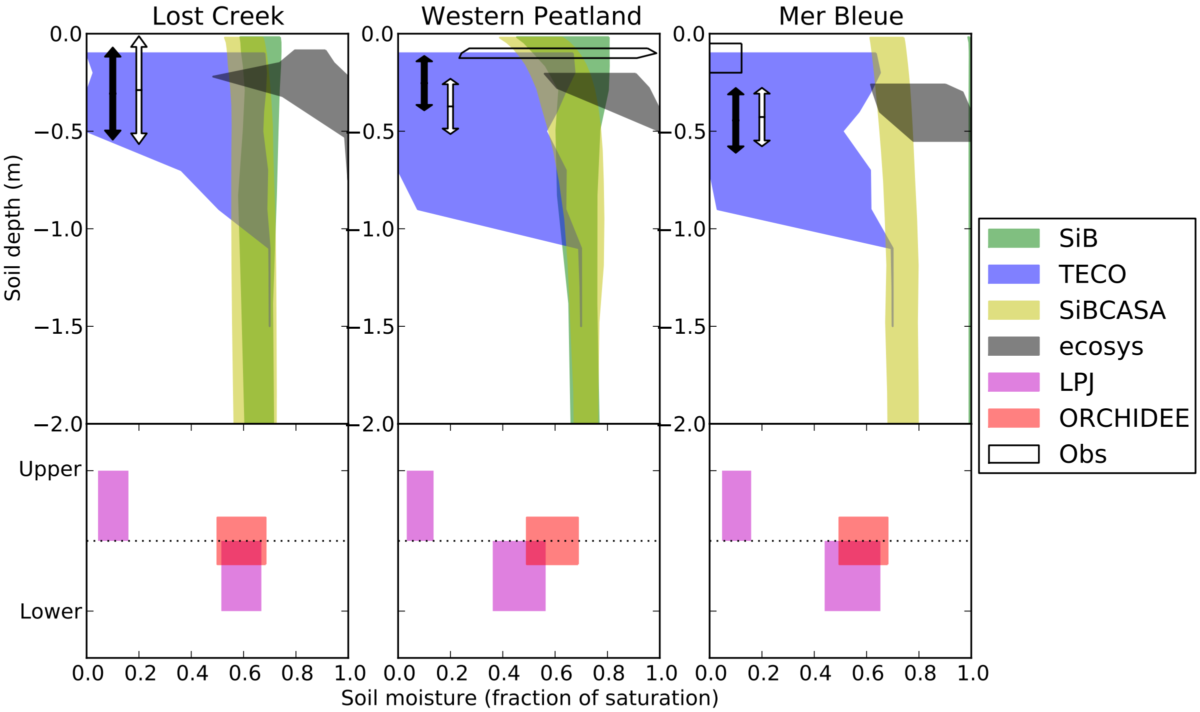

Figure 3.2: Ranges of summer soil moisture over the soil depth profile for each site. All ranges are bounded by the 10th and 90th percentiles. The upper plots include models with multiple soil layers at defined depths. Ranges of measured soil moisture (Obs) at Western Peatland and Mer Bleue are shown in un-shaded shapes. Soil moisture measurements were not available from Lost Creek. White arrows indicate the 10th-90th percentile range of observed water table depth for each site, and black arrows show the range of water table simulated by the *ecosys* model. In the lower plots, ranges are shown for the upper and lower soil layers of LPJ, and for mean root zone soil moisture reported by ORCHIDEE.

3.3.2 GEP to ER ratios

Comparing the ratio of GEP/ER for simulated and eddy covariance fluxes can help to assess the impact of the steady state assumption used in model setup. Models running in steady state should have annual ratios of approximately 1.0, while sites that are CO_2 sinks should have ratios greater than one. Annual and summer ratios for eddy covariance fluxes and simulated fluxes for all models are shown in Table 3.4. SiB, TECO, and SiBCASA had annual ratios of approximately 1.0 for all three sites, indicating that they maintained steady state for CO_2 fluxes. The other models all predicted a CO_2 sink at Lost Creek and Mer Bleue, and all except ORCHIDEE predicted an annual sink at Western Peatland as well. While the synthesis protocol required models to reach a steady state of zero net CO_2 flux during the spinup process, NEE was not necessarily zero following spinup due to differences in environmental drivers between spinup and subsequent simulations. Results were mixed for summer fluxes, with no consistent bias of GEP/ER ratio relative to eddy covariance data between models. LPJ predicted a ratio slightly above 1.0 for all sites, underestimating the growing season CO_2 sink. There was no consistent pattern of bias in summer ratios relative to eddy covariance ratios for the other models.

Table 3.4: Ratios of GEP/ER for each site. Ratio in eddy covariance data (EC) and values for each model are shown. Annual ratios include all months of the year, and summer ratios include the months of June, July, and August. 95% confidence limits on observed ratios are shown in parentheses.

Site		EC	SiB	TECO	LPJ	DLEM	ORCHIDEE	*ecosys*	SiBCASA
Lost Creek	annual	1.10 (0.03)	0.99	0.99	1.04	1.08	1.22	1.14	1.00
	summer	1.42 (0.05)	1.42	1.42	1.05	1.26	1.45	1.55	1.36
Western Peatland	annual	1.29 (0.05)	0.99	0.99	1.02	0.99	0.90	1.09	0.99
	summer	1.51 (0.09)	1.21	1.40	1.04	1.30	1.18	1.94	1.24
Mer Bleue	annual	1.12 (0.03)	0.99	0.99	1.03	1.02	1.09	1.04	1.00
	summer	1.29 (0.04)	1.30	1.35	1.04	1.15	1.56	1.56	1.34

3.3.3 Mean model bias

Figure 3.3 shows mean model residuals for flux components at the three sites, as well as adjusted ER and NEE. Annual average simulated GEP and ER at all three sites were significantly higher than eddy covariance values for all models. All models significantly overestimated annual NEE at Western Peatland and Mer Bleue, while three of the seven models had a significant positive bias of NEE at Lost Creek. Since negative NEE corresponds to CO_2 uptake, this positive bias indicates an underestimate of the CO_2 sink, which was expected as a result of the steady state assumption.

Summer-only bias showed similar patterns to annual bias, but was somewhat less consistent between sites. All models significantly overestimated summer ER at Western Peatland and Mer Bleue. All models also overestimated summer GEP at Mer Bleue, as did the majority of models at Western Peatland. At Lost Creek, there was a larger range in model bias of summer fluxes, with some models overestimating and some models underestimating all three fluxes relative to eddy covariance values.

The effect of steady state assumptions on ER and NEE can be estimated by comparing original values with values adjusted to match the observed ratio of GEP to ER. For the majority of models, this adjustment reduced ER, with the largest differences occurring at Western Peatland. However, some models predicted higher GER/ER ratios than eddy covariance, so that adjusted ER was higher than original modeled ER. Applying GEP/ER adjustments to modeled NEE resulted in substantial reductions in NEE residuals, changing residuals from positive to negative for many models. These results suggest that steady state model assumptions contributed significantly to model bias in NEE predictions.

Figure 3.4 shows mean bias for subsets of models divided according to important differences in model structure. The most consistent difference was between models that included functions to limit soil respiration in wet conditions and those that did not. Models that included this functionality (SiB, SiBCASA, DLEM, and ecosys) had significantly lower bias

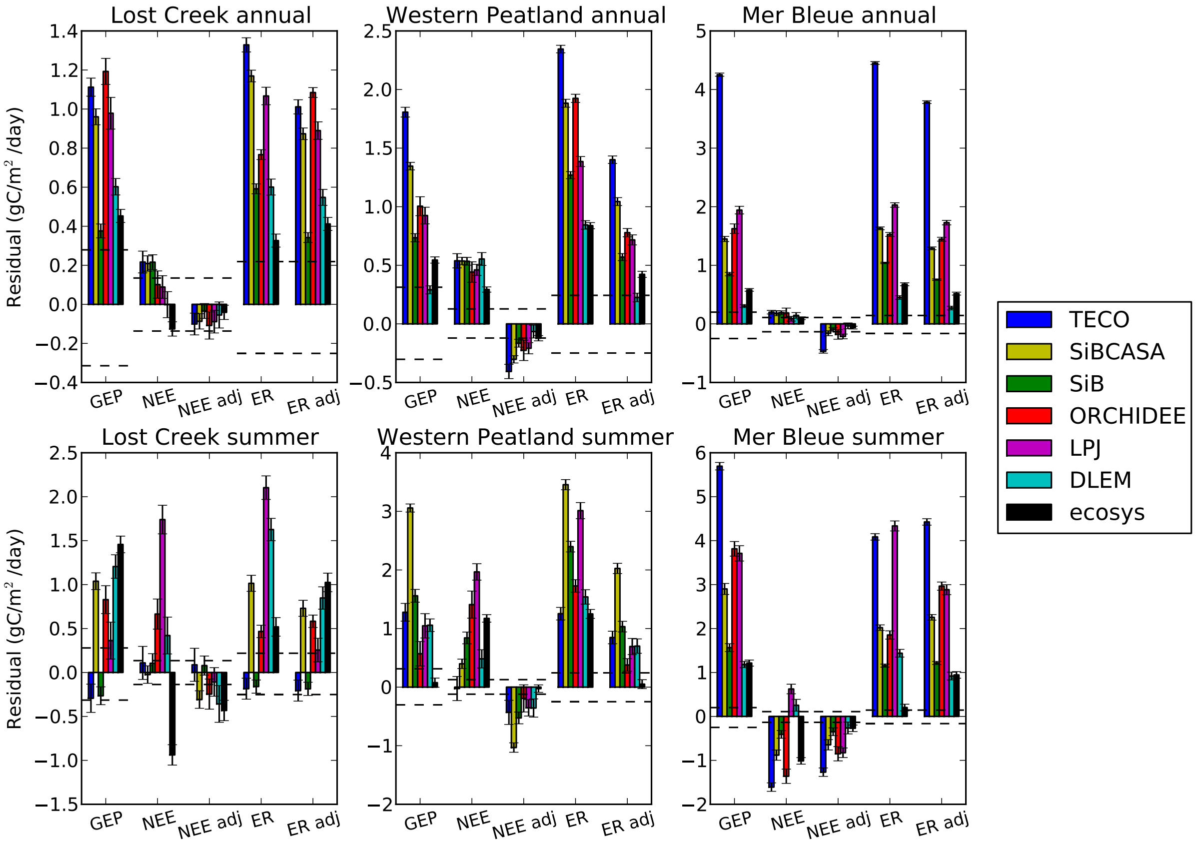

Figure 3.3: Mean annual and summer model CO_2 flux residuals. Dashed lines represent observation uncertainty (95% confidence interval) for each flux component, and error bars represent 95% confidence interval for model means. GEP, NEE, and ER bars show mean residuals, while NEE adj and ER adj bars show residuals adjusted to account for the effects of steady state model assumptions.

of annual ER at all three sites. However, the same subset also showed decreased bias in annual GEP at all sites, suggesting that this functionality was also associated with other model differences that lead to overall improvements in performance. Models with more than two soil layers (TECO, SiBCASA, SiB, and ecosys) had significantly less bias in both annual GEP and ER at Lost Creek and Mer Bleue compared to models with two soil layers, but multiple-layer models had higher bias at Western Peatland. Big leaf models (LPJ, SiB, SiB-CASA, and ORCHIDEE) had slightly higher bias in GEP at Lost Creek compared to models including sunlit and shade leaves, but showed slightly lower bias at Mer Bleue. Differences in mean summer bias between model subsets did not show consistent patterns between sites.

3.3.4 Simulated CO_2 flux residual relationships with observed water table

Figure 3.5 shows monthly mean June, July, and August model residuals for the three sites, plotted as a function of monthly mean observed water table. Figure 3.6 shows the correlation coefficient (upper plots) and linear regression slope (lower plots) describing the relationships between flux residuals and water table for each individual model as well as the mean of all models.

At Lost Creek and Western Peatland, the two fen sites, residuals for GEP and ER were both positively correlated with water table for all models individually as well as the mean of all models, indicating that models overestimated both ER and GEP under high water table conditions relative to drier conditions. ER relationships were significant at the 95% level for all models at both fen sites. GEP relationships were significant for all models except DLEM at Western Peatland, and for three models as well as the model mean at Lost Creek. The slopes of the relationships were higher at Western Peatland than at Lost Creek, and slopes were consistent between models for GEP and ER for both sites. Correlations of NEE

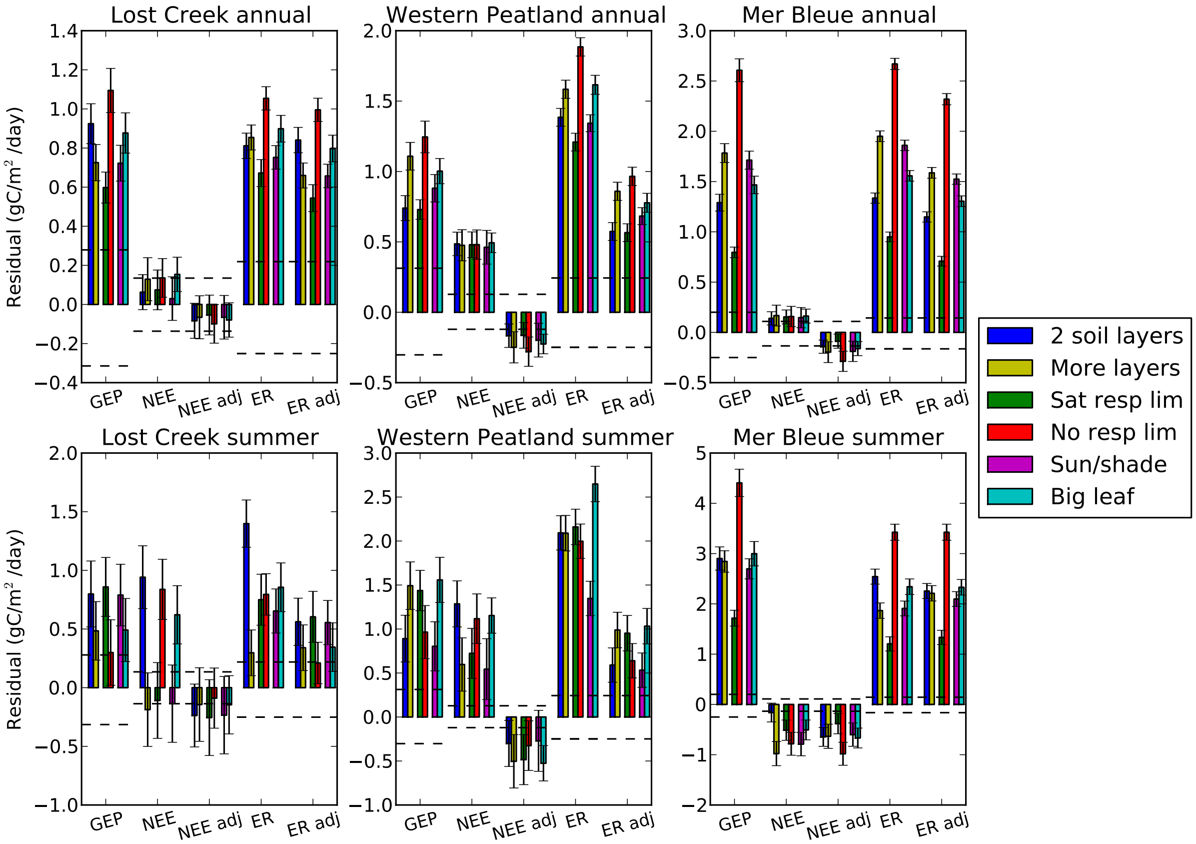

Figure 3.4: Mean annual and summer residuals for model subsets. “2 Soil layers” and “More Layers” divide models based on the number of soil layers. “Sat resp lim” and “No resp lim” divide models based on whether the models soil respiration function included a decline in soil respiration at high values of soil moisture. “Sun/Shade” and “Big Leaf” divide models based on whether the light environment included separate treatment of sunlit and shaded leaves or used a one-layer leaf model.

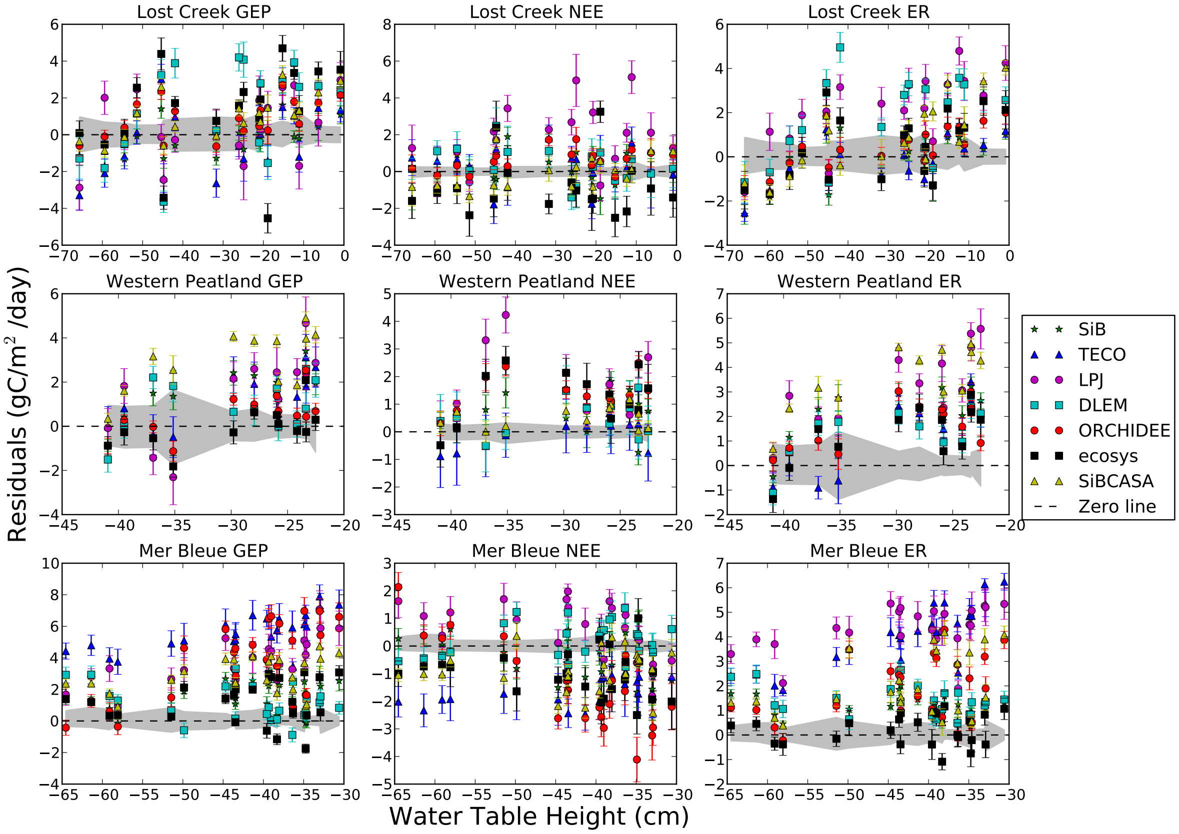

Figure 3.5: Model residuals for summer months. Residuals are shown for months of June, July, and August, plotted as a function of monthly mean observed water table level for each site. Residuals are defined as simulated minus observed fluxes. Left column is gross ecosystem production (GEP), middle column is net ecosystem exchange (NEE), and right column is ecosystem respiration (ER). Error bars on points indicate 95% confidence interval of monthly model mean. Gray region indicates 95% confidence interval of monthly mean observed fluxes.

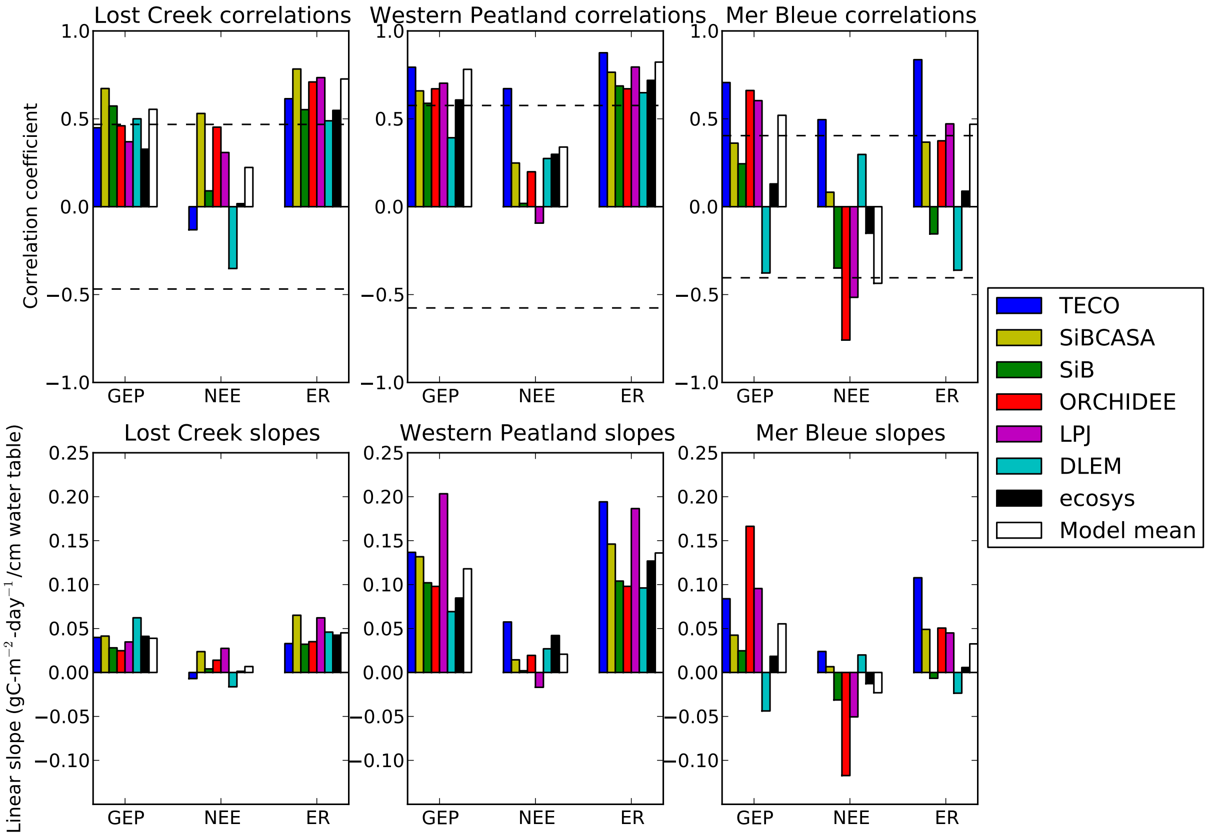

Figure 3.6: Correlation and slope between summer model residuals and observed water table. Upper row of plots is correlation coefficient (r), and lower row of plots is slope of a linear least squares fit. Each colored bar represents the statistic for an individual model, and the white bar represents the relationship for the mean of all models. Dashed lines indicate the 95% confidence level for correlation coefficients.

residuals with observed water table at the fen sites were positive for most, but not all, of the models, and were not significant at the 95% level for most models, indicating weaker relationships between observed water table and model-measurement mismatch in net CO_2 flux. This suggests that errors in GEP and ER cancelled each other.

At Mer Bleue, the bog site, the majority of models also had positive correlations between GEP and ER residuals and observed water table while four of the models as well as the model mean showed negative relationships between NEE residuals and water table. Most of the relationships at Mer Bleue were not statistically significant at the 95% confidence level, although the mean of all models was significantly correlated with water table for ER, GEP, and NEE.

Figure 3.7 shows correlation coefficient and slope between observed water table and monthly residuals for model subsets, divided as described above. The only site where model subsets were associated with significant differences in correlation coefficient was Mer Bleue, where models that included high soil moisture limitation of soil respiration and models with multilayer leaf functions were both associated with lower correlations between GEP residuals and water table compared to models without those attributes. The same pattern was evident for the water table-residual slopes.

3.3.5 Simulated and observed diurnal cycles of NEE

The diurnal cycle of NEE can illuminate features of both GEP and ER, and can be produced without including gap-filled values. Mean summer diurnal cycles of measured and simulated NEE at Lost Creek, Western Peatland, and Mer Bleue are shown in Figures 3.8, 3.9, and 3.10, respectively, divided into dry and wet modeled and observed periods as described above. Only data from non-gap-filled periods was included in these plots. At Lost Creek, measured daytime net CO_2 uptake was slightly higher during dry periods than wet periods, while nighttime CO_2 emissions were higher during dry periods than wet periods. Measurements

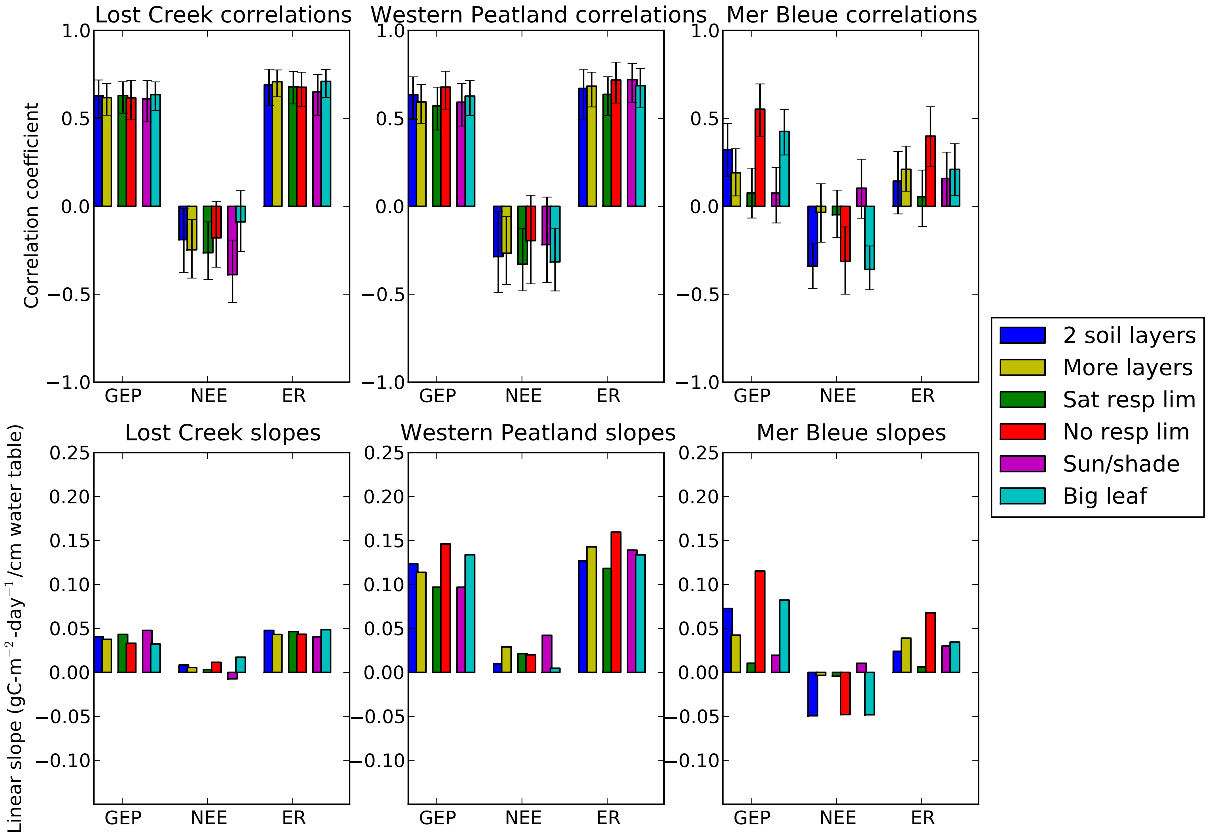

Figure 3.7: Correlation and slope between summer model residuals and observed water table for model subsets, divided as in Figure 3.6.

at Western Peatland also showed higher nighttime CO_2 emissions during dry periods, but did not show a significant difference in daytime CO_2 uptake between wet periods and dry periods. Measurements at Mer Bleue showed higher daytime CO_2 uptake during wet periods than dry periods, and no difference in nighttime emissions between wet and dry periods.

At the fen sites, most of the models slightly overestimated nighttime CO_2 emissions. TECO and *ecosys* overestimated peak daytime uptake at Lost Creek. *Ecosys* and ORCHIDEE underestimated peak daytime uptake at Western Peatland, while TECO overesti-

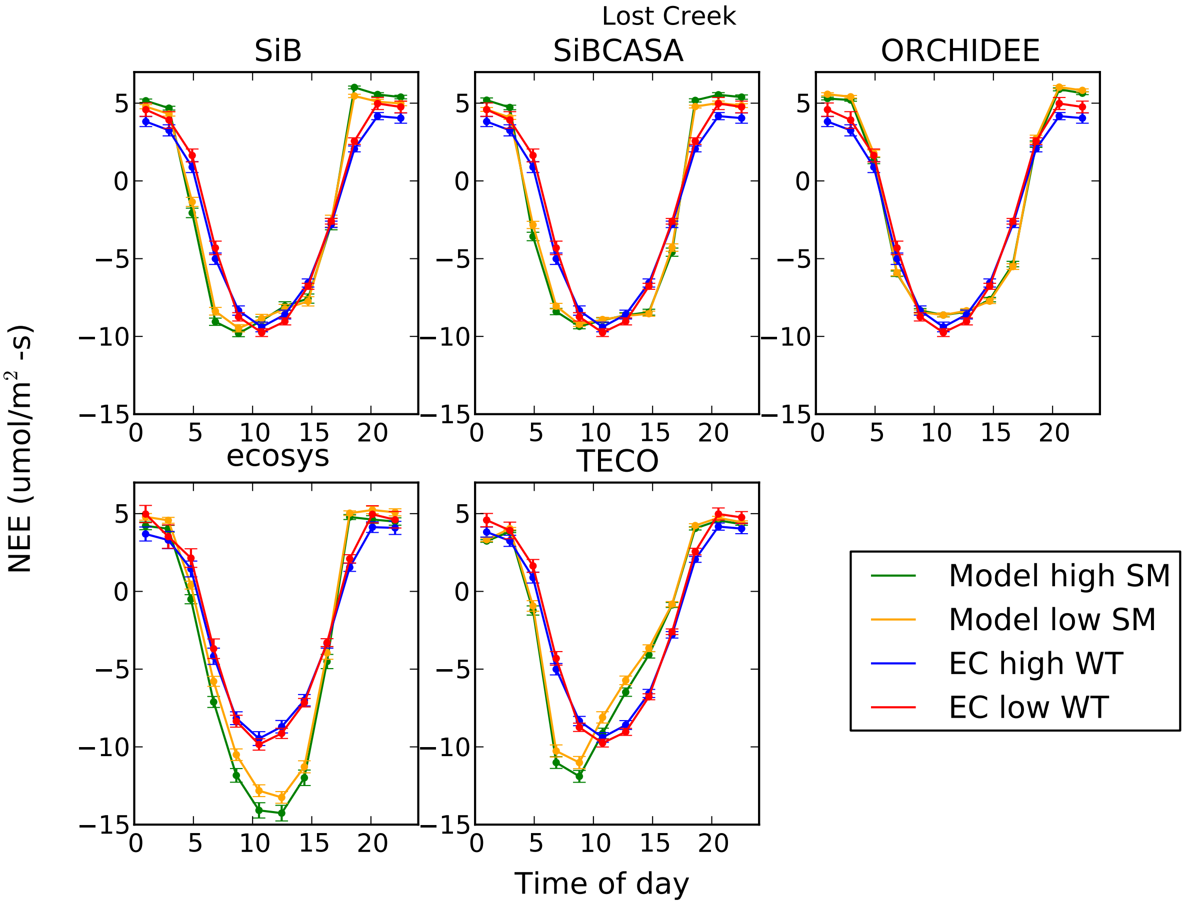

Figure 3.8: Mean summer diurnal cycle of net ecosystem CO_2 exchange (NEE) at Lost Creek shrub fen. Only non-gap-filled data are included. Error bars indicate 95% confidence intervals on the mean of each bin. Blue and red curves include eddy covariance data from weeks in the top and bottom 30th percentiles of water table height, respectively. Green and orange curves include modeled NEE from weeks in the top and bottom 30th percentile of modeled soil moisture, respectively.

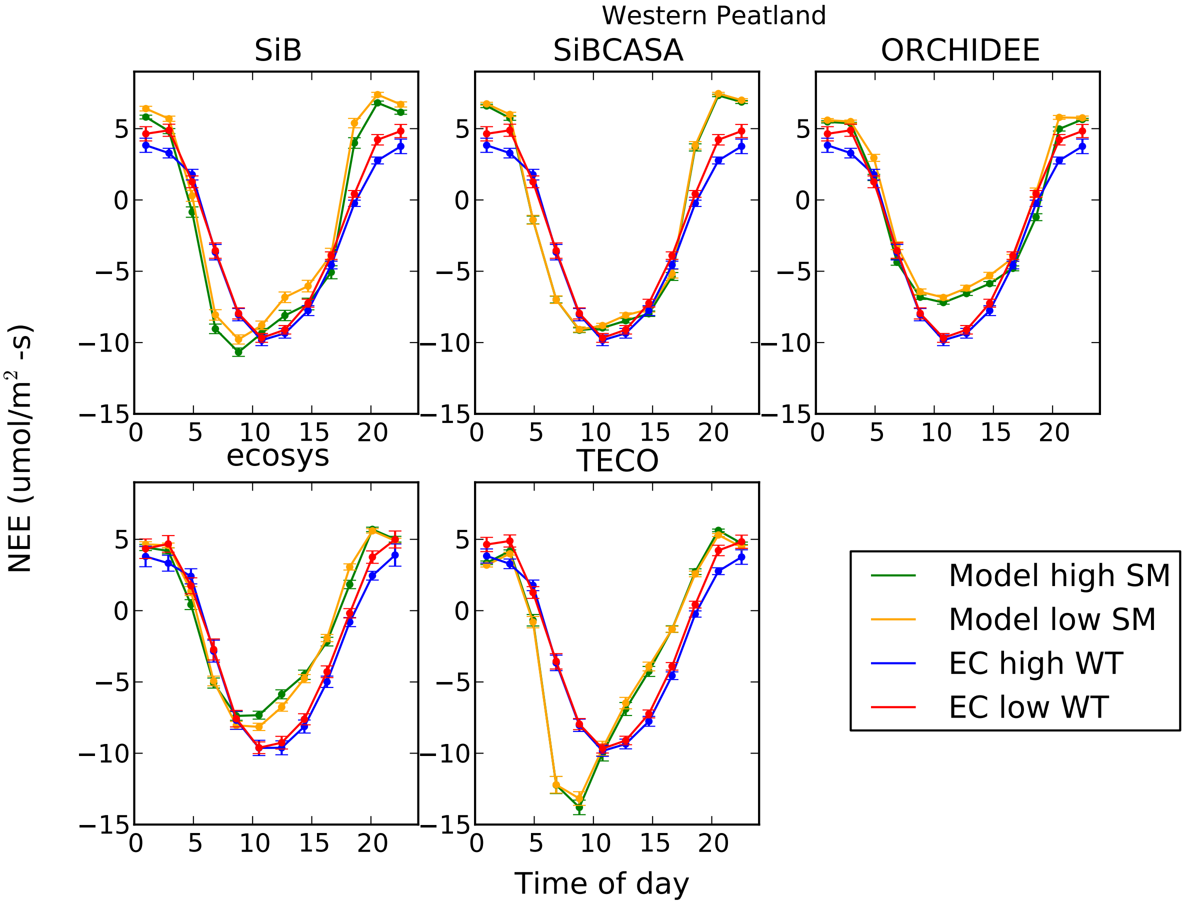

Figure 3.9: Mean summer diurnal cycle of net ecosystem CO_2 exchange (NEE) at Western Peatland treed fen. Details of calculation are the same as Figure 3.8.

mated daytime uptake. TECO predicted a sharp, early peak in uptake at all three sites. All models overestimated the magnitude of the diurnal cycle at the Mer Bleue bog site, and all but ecosys substantially overestimated nighttime CO_2 emissions there.

At Lost Creek, the dependence of modeled NEE on soil moisture was either weak or in the opposite direction from observations. SiB, TECO, and ecosys showed higher daytime update during wetter periods, and SiBCASA showed higher nighttime emissions during wetter periods. At Western Peatland, SiB predicted higher nighttime emissions during dry periods, in agreement with observations. ORCHIDEE and TECO predicted slightly higher

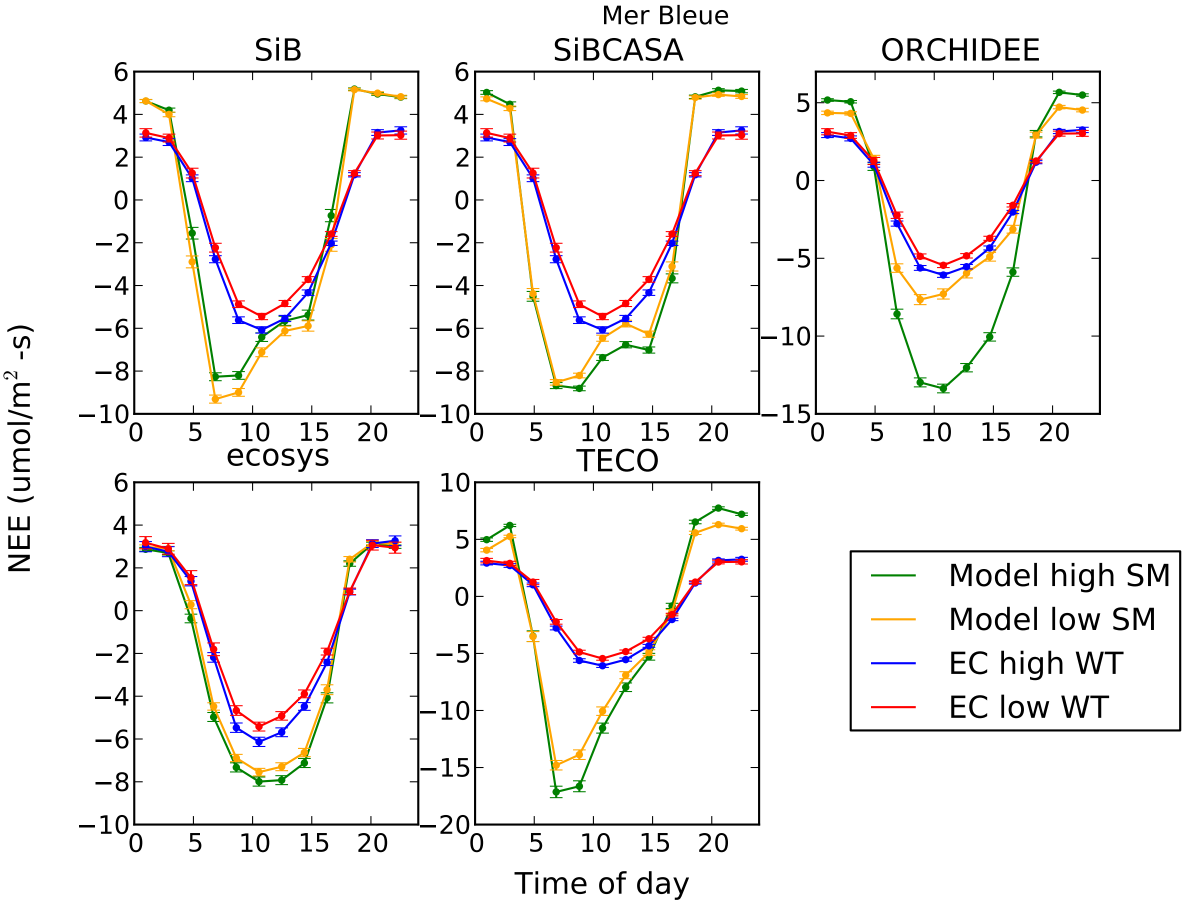

Figure 3.10: Mean summer diurnal cycle of net ecosystem CO_2 exchange (NEE) at Mer Bleue bog. Details of calculation are the same as Figure 3.8. Note that vertical scales are different for ORCHIDEE and TECO.

daytime uptake during wetter periods, while ecosys predicted lower daytime uptake during wetter periods. At Mer Bleue, ORCHIDEE predicted much higher daytime uptake during wet periods, and SiBCASA and TECO also predicted increased uptake during wet periods, but to a lesser degree. In the case of ORCHIDEE, the contrast in sensitivity is likely due to the fact that the two fen sites were modeled using a forest plant functional type, while Mer Bleue was modeled using a grassland plant functional type. ORCHIDEE and TECO predicted significantly higher nighttime emissions at Mer Bleue during wet periods as well.

3.3.6 Diurnal cycles of ER and GEP

The diurnal cycles of ER and GEP, the components of NEE, can further illuminate sources of model-observation mismatch. These are shown for Lost Creek, Western Peatland, and Mer Bleue in Figures 3.11, 3.12, and 3.13, respectively. Data were divided into wet and dry periods using the same process as in the NEE figures. ER values are positive, and are shown with solid lines. GEP values are negative, and are shown with dashed lines.

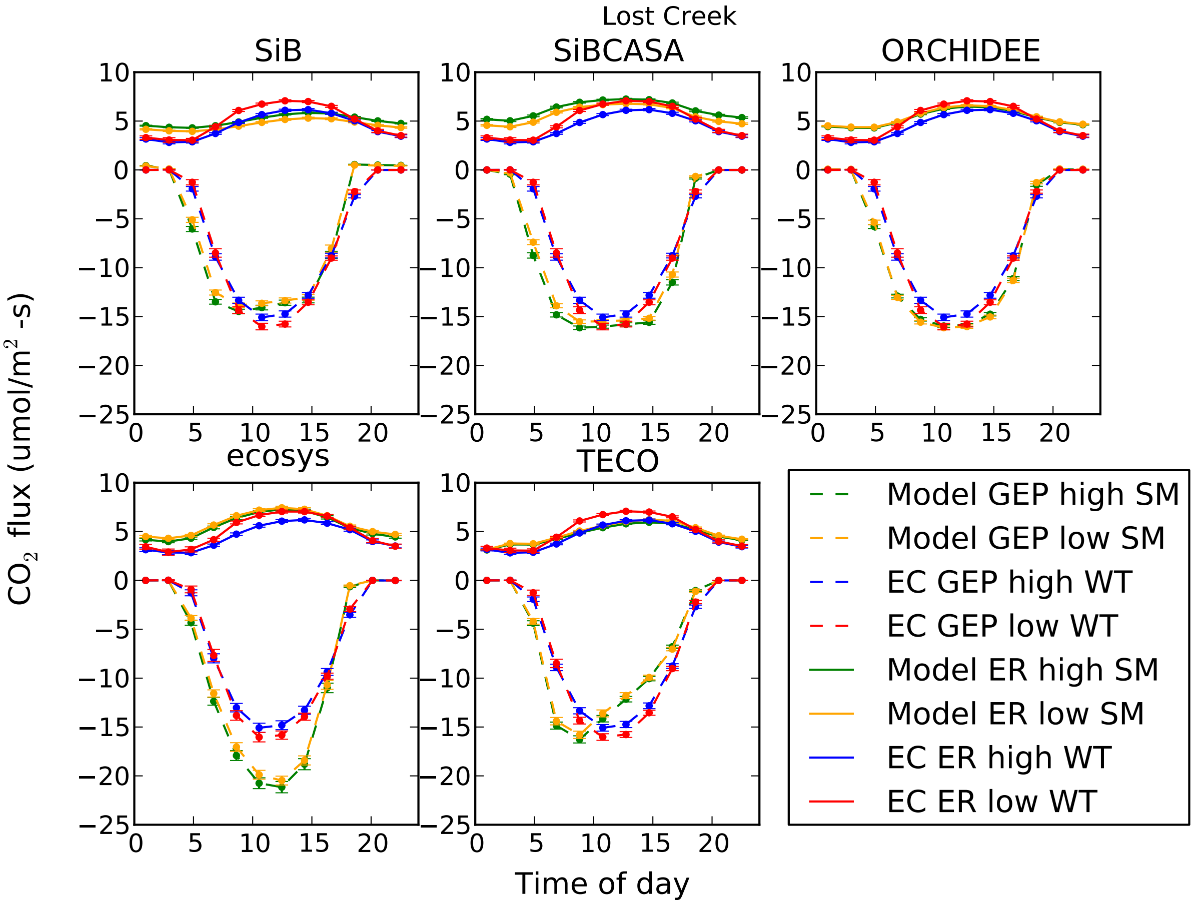

Figure 3.11: Mean summer diurnal cycles of ecosystem respiration (ER) and gross ecosystem production (GEP) at Lost Creek shrub fen. ER is positive, and shown with solid lines. GEP is negative, and shown with dashed lines. Calculation of error bars and separation of wet and dry periods were as in Figure 3.8.

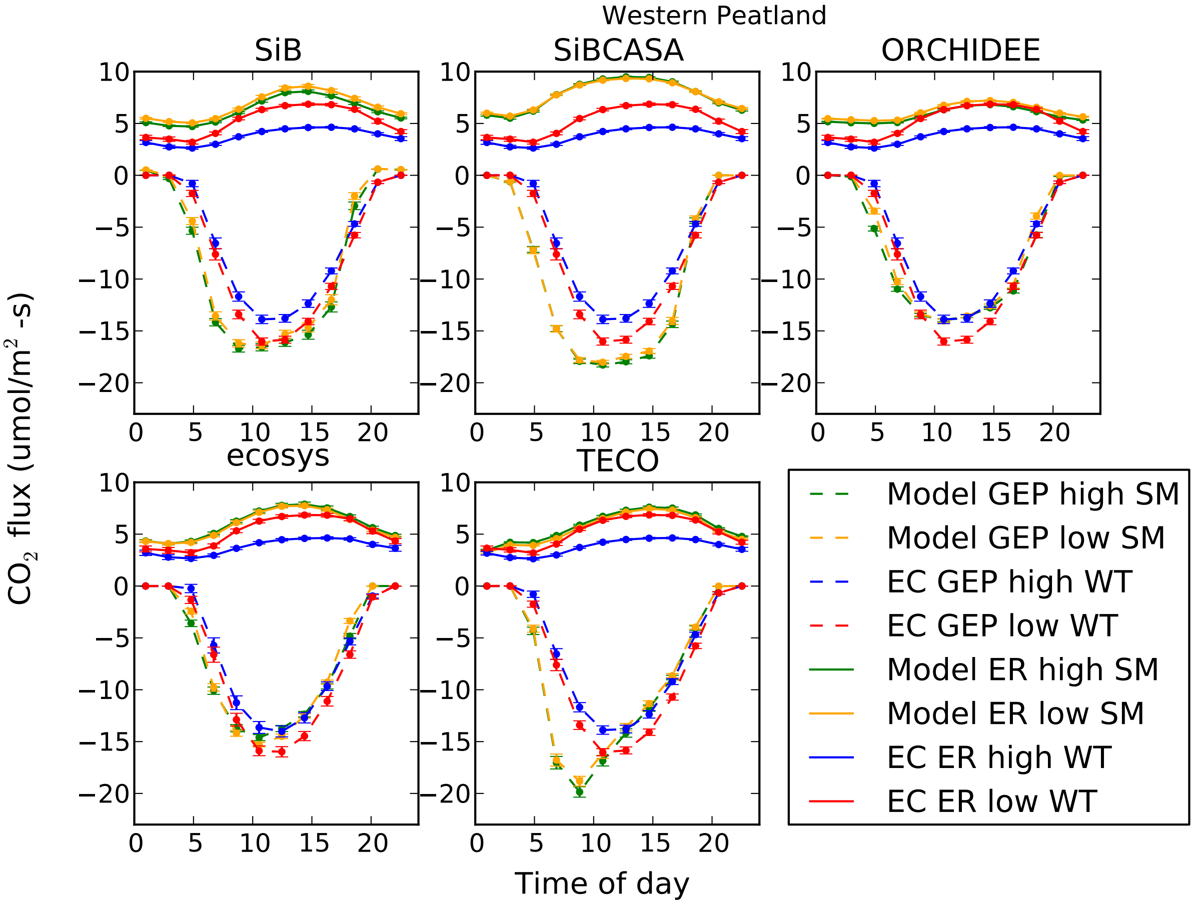

Figure 3.12: Mean summer diurnal cycles of ecosystem respiration (ER) and gross ecosystem production (GEP) at Western Peatland treed fen.

Eddy covariance ER and GEP were not strictly observed quantities, but were derived from observed NEE as described above. Patterns of model bias relative to eddy covariance values as well as differences between wet and dry periods were consistent with the patterns seen in the non-gap-filled NEE data, providing confidence that these results do reflect actual ecosystem processes rather than artifacts of the gap-filling process.

At Lost Creek and Western Peatland, eddy covariance values of both ER and GEP were higher during drier periods. These relationships offset, leading to smaller differences between wet and dry periods in the diurnal cycle of NEE at these sites. In contrast to the fen sites,

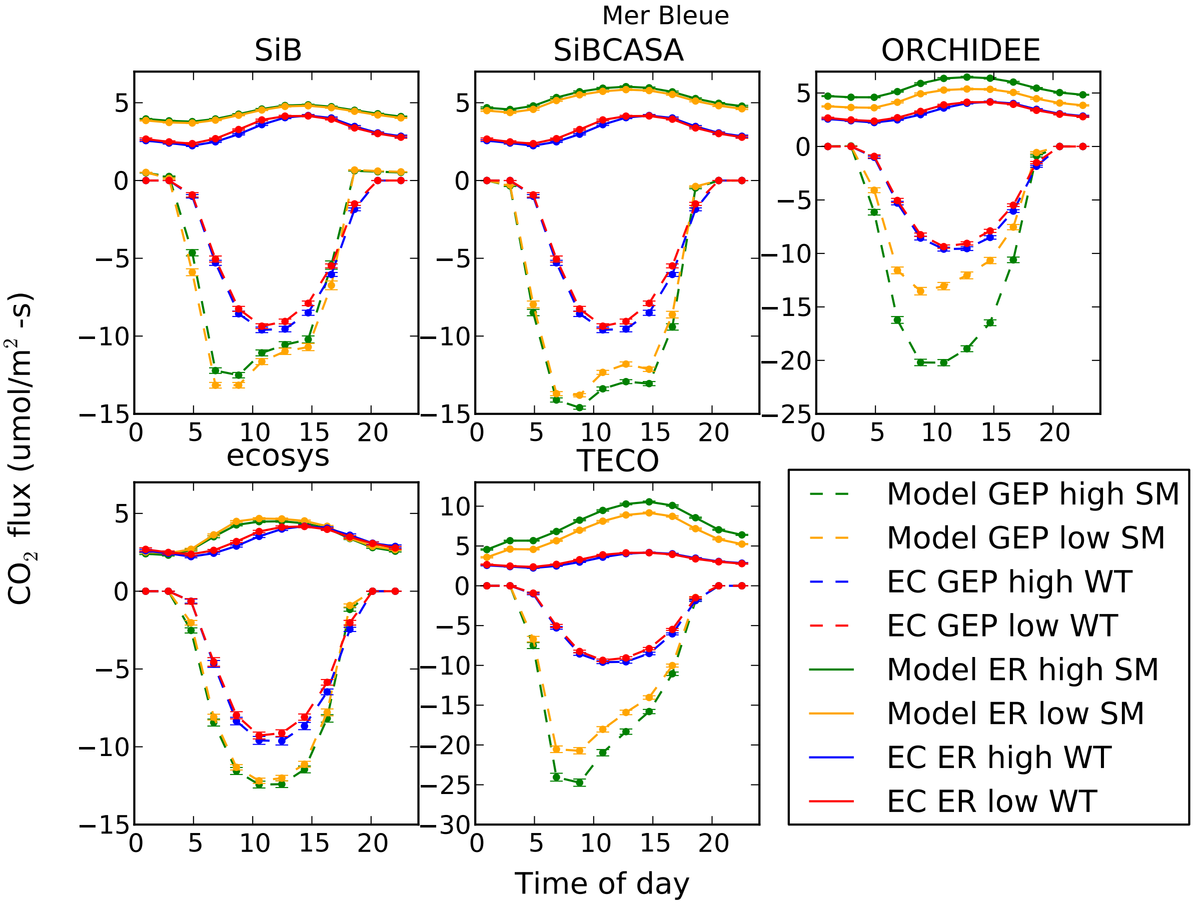

Figure 3.13: Mean summer diurnal cycles of ecosystem respiration (ER) and gross ecosystem production (GEP) at Mer Bleue bog. Note that vertical scales are different for ORCHIDEE and TECO.

eddy covariance ER at Mer Bleue was not significantly different between wet and dry periods, and GEP was slightly higher during wet periods.

As with NEE, the majority of ecosystem models simulated either no difference between wet and dry periods, or the opposite direction of change compared to eddy covariance results. At Lost Creek, ORCHIDEE showed no difference in GEP between dry and wet periods, while the other models simulated slightly higher GEP during wet periods. SiBCASA simulated higher ER during wet periods, while the other models showed no difference. At Western

Peatland, SiBCASA and TECO simulated higher GEP during wet periods. Ecosys showed higher GEP during dry periods, in agreement with eddy covariance results but with a smaller magnitude of difference. TECO and ecosys simulated higher ER during wet periods, while SiB simulated slightly higher ER during dry periods, in agreement with the direction of the relationship identified in eddy covariance data but with a smaller magnitude of difference. At Mer Bleue, ORCHIDEE and TECO predicted substantially higher ER and GEP during wet periods, and SiBCASA simulated slightly higher GEP during wet periods. The other models showed no difference between wet and dry periods, in agreement with eddy covariance results.

The magnitude and shape of modeled diurnal cycles at the fen sites were generally in agreement with eddy covariance values, although ecosys and SiBCASA predicted somewhat higher GEP than eddy covariance values at Lost Creek and SiBCASA overestimated GEP and ER at Western Peatland. Modeled ER was closer to eddy covariance values for dry periods than for wet periods for most of the models at both fen sites. TECO predicted an earlier daytime peak GEP than eddy covariance values at both fen sites. Despite large differences in model complexity, simpler models such as SiB did not perform significantly better than models such as *ecosys*, which includes many soil layers and specific parameterizations for wetland hydrology.

At Mer Bleue, all models substantially overestimated GEP and daytime NEE relative to eddy covariance values, and all models except ecosys overestimated ER. SiB, SiBCASA, and TECO all predicted peak GEP early in the day, followed by suppressed GEP in the late morning and afternoon. This could be an indicator of simulated moisture stress within these models.

3.4 Discussion

3.4.1 Correlations between model residuals and hydrology

Hypothesis 1 stated that model residuals would be correlated with observed water table as a result of hydrology-driven peatland processes not included in the models. This hypothesis was confirmed at the fen sites by the positive correlation between model residuals of GEP and ER, suggesting that hydrological processes were important sources of model-data mismatch. At the bog site, the relationship was not consistent between all models but there was still a significant correlation for the mean of all models. The differences in eddy covariance CO_2 fluxes between high and low water table periods at the fen sites suggest that both GEP and ER are suppressed under wet conditions, which is consistent with previous peatland field studies [*Flanagan and Syed*, 2011; *Silvola et al.*, 1996; *Strack et al.*, 2006; *Sulman et al.*, 2009]. Of the seven models included in this study, four (SiB, SiBCASA, *ecosys*, and DLEM) include processes that suppress ER under saturated conditions, and only *ecosys* includes a process that suppresses GEP under saturated conditions. Although the majority of models were capable of simulating the observed sign of the relationship between ER and soil moisture, only one predicted increased ER during dry periods at any site. Models that included processes for suppressed ER at high soil moisture had significantly lower correlations between ER residuals and water table at Mer Bleue compared to models that did not include those processes, but there was no significant difference at other sites. This was most likely a consequence of models inability to accurately predict saturated conditions in peatland soils. Only ecosys consistently predicted saturated conditions below the water table at the three sites. Furthermore, three of the models partition moisture above the soils field capacity directly to runoff and subsurface drainage, making them incapable of simulating saturated soil conditions at all. If they cannot successfully simulate wetland hydrological conditions, even models that include responses of respiration and photosynthesis to saturated soil cannot successfully replicate the observed relationships with hydrology.

The fact that fens, by definition, are fed by incoming water flows makes accurately simulating hydrology in these ecosystems more difficult. For example, the Lost Creek site is fed by a stream, and the water table responds to changes in stream flow that can result from such factors as upstream precipitation, regional water management, and downstream beaver dam-building activity [*Sulman et al.*, 2009]. The difficulties presented by local water flows are consistent with the results of *Yurova et al.* [2007], a modeling study at a minerotrophic mire. That study found good agreement between measured and modeled water table during periods of the year dominated by precipitation events, but poor agreement when site hydrology was dominated by snowmelt. While snowmelt was not a focus of this study, it is an example of a hydrological process that integrates lateral flows and inputs from a larger spatial area, and can contribute significantly to variations in seasonal CO_2 fluxes in some ecosystems [*Aurela et al.*, 2004; *Hu et al.*, 2010].

Bond-Lamberty et al. [2007] addressed the issue of lateral inflow in a modeling study by including site-specific information about the modeled sites relationship with the surrounding watershed. *Pietsch et al.* [2003] used a similar approach, including explicit information about timing and magnitude of flood events. While these approaches do address some of the issues with modeling wetlands that are influenced by lateral inflows, they require fairly detailed information about regional hydrology. Including this local information in large-scale modeling studies would not be feasible, but a regional hydrological model combined with an accurate elevation map could be used to simulate redistribution of surface and groundwater over a region, providing a good alternative. Wetland location and fractional area could be predicted based on topographically low areas that collected water in hydrological simulations, and water table variations could be calculated based on modeled water flows. This information could then be incorporated into larger grid scales using a fractional area approach. Examples of global-scale models incorporating this type of sub-grid-scale peatland fractional area approach include *Gedney* [2003]; *Kleinen et al.* [2012], and *Ringeval et al.* [2011].

3.4.2 Effect of model structure on mean bias

Hypothesis 2 stated that models with more complex hydrology would produce more accurate simulations of peatland CO_2 fluxes. In fact, models with more than two soil layers did not consistently have less mean bias than models with more soil layers. Models that included processes for reducing soil respiration at high soil moisture did have less mean bias in both GEP and ER than models that did not include those processes. These results suggest that increased vertical resolution of soil processes is not sufficient for improving model performance at peatlands. More explicit connections between hydrology and carbon cycling are necessary.

3.4.3 Contrasting results between bogs and fens

Hypothesis 3 stated that models would perform better at fens than at the bog. This hypothesis was confirmed by the relative fidelity of modeled diurnal cycles at fens compared to the large overestimates of the magnitudes of diurnal cycles at the bog site. These differences suggest that fens and bogs should be considered separately in modeling studies that include peatlands. The successful results at fens suggest that extensive model changes such as the development of fen-specific plant functional types are not necessary, and that improving modeled hydrology and effects of saturated soils on respiration and photosynthesis would be sufficient.

Accurately representing bogs in general ecosystem models is likely more difficult. While GEP bias could be addressed by introducing bog-specific maximum photosynthesis rate parameters, the unique chemistry, nutrient levels, and plant communities of bog ecosystems require additional specific parameterizations to be added to general ecosystem models. Distinguishing between fen and bog wetlands could be problematic for large-scale studies, where spatial maps that distinguish bogs from other ecosystem types may not be available, and the spatial resolution of the model will be much larger than the scale of heterogeneity between peatland types. Fractional area approaches based either on digital elevation maps and topography-based classifications or on statistical predictions of peatland type areal coverage could provide a solution to this problem.

3.4.4 Aspects of peatlands not included in general ecosystem models

Heterogeneity at small spatial scales

Variations in site topography at small scales, in the form of hummock and hollow landforms with sizes on the order of 1 to 100 m, contribute significantly to site hydrology, plant community composition, and carbon fluxes [*Strack and Waddington*, 2007; *Waddington and Roulet*, 1996]. *Becker et al.* [2008] suggested that topographical variations on scales as small as 25 cm may be important for accurately calculating carbon fluxes in wetlands with hummock-hollow topography. *Sonnentag et al.* [2008], in a spatially explicit modeling study at Mer Bleue, successfully simulated water table responses to precipitation at the bog, but demonstrated that lateral flows within the bog contributed significantly to the overall variations in water table. *Govind et al.* [2009] also used a spatially explicit model to investigate CO_2 fluxes under different hydrological scenarios, and found significant differences in net CO_2 flux between scenarios that did or did not include topographically driven hydrological flows within the peatland ecosystem. However, in a recent study at Mer Bleue, *Wu et al.* [2011] found that differences in net CO_2 flux between hummocks and hollows could be successfully accounted for by using an average of parameters for each microsite, weighted by relative areas. Of the ecosystem models included in this study, only *ecosys* simulated hummock and hollow topography and internal lateral flows. Small-scale heterogeneity is further complicated by the formation of peatland macropores and pipes, which lead to preferential pathways for water and carbon flows that can be decoupled from the processes that drive near-surface flows [*Limpens et al.*, 2008].

Small-scale variations in topography lead to variations in vegetation. In this study, Western Peatland and Mer Bleue were examples of peatlands that support heterogeneous vegetation, including areas of sedges, shrubs, and small trees. This is problematic for computation of the light environment, as most of the models included in this study calculate light attenuation as a function of LAI or canopy depth, implicitly assuming a horizontally homogeneous canopy. In simulations of Mer Bleue, *Sonnentag et al.* [2008] determined that a multiple-layer canopy including separately mapped tree, shrub, and moss layers was necessary for an accurate simulation. Of the models included in this study, only *ecosys* incorporated this type of canopy heterogeneity, by separately modeling hummock and hollow areas. Failure to simulate the separate contributions of different vegetation layers likely contributed to model bias of GEP at Western Peatland and Mer Bleue.

Baird and Belyea [2009] suggested that sub-grid-scale peatland processes could be parameterized in low-resolution models through a multi-scale modeling method. Peatland landscapes within a grid cell would be identified using high-resolution remote sensing and elevation data. Representative samples of each peatland type would be simulated at high resolution, including lateral flows and topography within the peatland, and the results would be scaled up to the coarse resolution grid scale.

GEP under saturated soil conditions

Under the moisture limitation schemes used in the models included in Figure 3.1, GEP decreases under dry conditions when photosynthesis is limited by moisture stress, and moisture is not a limiting factor for GEP under wet conditions. In peatlands, high water tables can provide a consistent source of water that prevents moisture limitation except during exceptionally dry periods. During wet periods, saturated soil can cause plant stress due to reduced availability of oxygen and buildup of toxins in the root zone [*Pezeshki*, 2001; *Mitsch and Gosselink*, 2007]. Thus, ecosystem models used in peatland-rich areas could be improved by a moisture limitation parameterization that suppresses GEP under both very dry conditions and very wet conditions. Biological adaptations such as air spaces in the roots (aerenchyma) allow flood-tolerant plant species to transport oxygen below the water line, mitigating the impact of soil saturation on plant function. However, since these adaptations are limited to specific wetland plant species, including them in models would require calibration of plant functional types to match the other photosynthetic and physiological properties of wetland communities. The only model included in this study that included detrimental effects of saturated soils on plant function was *ecosys*, which simulated lower GEP and ER in hollows compared to hummocks. *Ecosys* did predict higher GEP under dry conditions at Western Peatland, but not at Lost Creek, possibly due to differences in simulated hydrology between the sites. A mechanism for including saturation stress was integrated into peatland plant functional types added to the LPJ model in a previous study [*Wania et al.*, 2009] , although they concluded that their modified model still over-estimated net primary production at peatlands.

Changes in productivity can directly impact ER by affecting autotrophic respiration. Most of the models included in this study calculated autotrophic respiration either as a fixed fraction of productivity, or as a function of temperature and living biomass. *Ecosys* explicitly included oxygen limitation of root respiration, but the other models did not. Eddy covariance data could not be partitioned into autotrophic and heterotrophic components of respiration, so model predictions of autotrophic respiration could not be evaluated against measurements. Few peatland carbon cycling studies have explicitly considered the sensitivity of autotrophic respiration to hydrology, and further research is needed in this area.

Further complicating the relationship between water table and GEP is the importance of time scale. Long term decline of water tables can cause changes in dominant plant communities from mosses and graminoids to shrubs and trees over time scales of five to ten years [*Flanagan and Syed*, 2011; *Strack and Waddington*, 2007; *Talbot et al.*, 2010; *Weltzin et al.*, 2003]. This suggests that model simulations of GEP could be improved by including dynamic plant communities that shift between grassy and woody dominance depending on water table elevation. Over shorter time scales, flooding can introduce additional nutrients to ecosystems without causing long-term anoxia in soils, potentially increasing productivity.

Steady state model conditions and non-CO_2 carbon fluxes

Analysis of GEP/ER ratios and adjusted ER and NEE showed that the steady state condition of model spinup used in this study led to overestimates of ER and underestimates of net ecosystem CO_2 uptake. The approach used here to estimate the amount of bias introduced depended on observed GEP/ER ratios, and thus could not be used for studies where direct observations of CO_2 fluxes are not available. Accurate simulations of NEE and ER may require parameterizations informed by ecological histories and independent estimates of peat carbon pools. Estimates of typical long-term peat accumulation rates based on peat cores could be used to develop alternative steady state conditions for model initialization. Models that include the hydrological processes necessary for peat accumulation could then be spun up using a condition of constant soil carbon accumulation rate rather than constant soil carbon pool size.

The importance of non-CO_2 fluxes such as methane and dissolved organic carbon (DOC) in peatland carbon balances further complicates the application of steady state model conditions to peatlands. For example, at Mer Bleue, *Roulet et al.* [2007] found that DOC and methane fluxes accounted for carbon losses equivalent to 37% and 9% of NEE, respectively, over a five year period, and that ignoring these fluxes could lead to substantial overestimates of net carbon uptake in some years, and to estimating a carbon sink instead of a source in other years. In a regional study in northern Wisconsin, USA, *Buffam et al.* [2011] estimated that DOC and methane fluxes accounted for 17% and 10% of peatland NEE, respectively. *Billett et al.* [2004] reported that C loss in drainage and downstream evasion was greater than or equal to CO_2 uptake at a peatland complex in Scotland, and *Hope et al.* [2001] estimated that downstream evasion of CO_2 and CH_4 accounted for 28-70% of the net peatland C accumulation rate when divided by the watershed area. *Clymo* [1984] suggested that for peat-accumulating wetlands, a steady state can only be reached when carbon inputs from NEE are balanced by losses of methane and DOC from submerged peat. Based on these results, a carbon budget or steady state assumption based only on CO_2 is not sufficient for characterizing the actual carbon balance of a peatland ecosystem.

These fluxes pose additional complications for including peatlands in general ecosystem models, but they can feasibly be included. Methane production has been included in models related to those included in this study. These include versions of ORCHIDEE [*Ringeval et al.*, 2011], DLEM, and *ecosys*. While the transport and evasion of dissolved carbon depends on detailed hydrology and surface flow, dissolved carbon could be included in the peatland carbon budget by assuming that all dissolved carbon will ultimately be released to the atmosphere over relatively short time scales compared to other carbon accumulation processes. In that case, dissolved carbon could simply be treated as an additional source of carbon to the atmosphere, and models would only need to include processes for dissolved carbon production, which could be parameterized as an additional form of anaerobic decomposition. *Ecosys* does include dissolved carbon production, but this process was not included in the other models in this study.

3.5 Conclusions

The consistent positive bias in model predictions of GEP and ER for all three sites suggests that ignoring peatlands could lead to systematic overestimates of productivity and respiration in modeling studies of peatland-rich regions. Therefore, it is important for modelers to consider the impact of peatland areas when designing large-scale modeling studies and interpreting their results.

Our results did show that non wetland-specific ecosystem models can produce fairly accurate simulations of NEE at fen wetlands, especially during relatively dry periods. Specific areas for improvement include:

1. Improved simulations of site hydrology are required for correctly simulating responses of ecosystem respiration to changes in hydrology for the majority of models included in this study. Coupling carbon cycle models with hydrological models that include regional flows and small-scale topographical variations could help with incorporating processes important to wetland hydrology, as could including explicit treatment of saturated soil conditions and a variable water table.
2. Suppression of both photosynthesis and respiration under saturated conditions should be included in models used at wetlands in order to match observed effects. Hydrology-related succession could also improve simulations.

Models substantially overestimated both photosynthesis and respiration at the bog site, suggesting that more effort is necessary in order to successfully model bogs using general ecosystem models. Additional measurements from other bog ecosystem sites that contrast with the relatively dry Mer Bleue site are needed in order to evaluate model performance in bog ecosystems representing a broader range of environmental conditions. It may be necessary to add bog-specific plant communities or plant functional types to models that will be used for these ecosystems. Furthermore, large-scale modeling projects need to develop strategies for distinguishing between fens and bogs, since these ecosystems are too different to be treated as a single wetland ecosystem type.

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Chapter 4

The role of plant community succession in wetland carbon cycle responses to hydrological change

Abstract

Northern peatlands contain a significant fraction of the global carbon pool, and are vulnerable to changes in hydrology driven by climatic change or human disturbance. We used the LANDIS-II forest landscape model combined with an external model of plant community and soil responses to water table changes to simulate regional carbon cycle responses to declining water table in northern Wisconsin, USA. This novel approach enabled the study of peatland succession using an ecosystem model that was originally developed for upland forests. Declines in water table increased soil decomposition rates, but also increased plant community biomass accumulation rates due to invasion by upland species and increases in habitat area for more productive woody plants. The net effect was an increase in landscape carbon during the first 150 years following drainage, followed by carbon loss over longer time scales. Water table declines of 100 cm led to greater increases in biomass as well as short-term increases in soil carbon, while declines of 40 cm led to continuous declines in soil carbon and smaller increases in biomass, with the net result being a loss of total carbon. The time scale of water table decline (10 years or 40 years) did not cause differences in long-term carbon cycle responses, but responses were quite different when considered over time scales of decades compared to centuries. We conclude that plant community responses are crucial to understanding the full impact of hydrological change on wetland carbon cycles, and that wetland carbon cycle responses measured over short time scales are not representative of long-term changes.

4.1 Introduction

Northern peatlands contain a significant fraction of the global terrestrial carbon pool, and the future evolution of peatland carbon reserves is an important factor in predicting carbon cycle feedbacks to climate change [*Gorham*, 1991; *Turunen et al.*, 2002; *Mitra et al.*, 2005]. Because peat accumulation and preservation depends on anaerobic soil conditions connected with high water tables, changes in water table affect CO_2 emissions and peat decomposition rates [*Moore and Knowles*, 1989; *Freeman et al.*, 1992; *Junkunst and Fiedler*, 2007; *Yurova et al.*, 2007; *Sulman et al.*, 2009; *Olivas et al.*, 2010; *Flanagan and Syed*, 2011]. Peatland modeling studies have identified significant positive feedbacks to climate warming due to increased peat decomposition [*Ise et al.*, 2008]. However, field and laboratory studies suggest that hydrological change leads to changes in plant communities [*Laine et al.*, 1995; *Weltzin et al.*, 2003; *Strack et al.*, 2006; *Talbot et al.*, 2010], which can significantly affect the net CO_2 budget over the short term [*Sulman et al.*, 2009; *Flanagan and Syed*, 2011]. Studies of long-term responses to drainage have highlighted the importance of above-ground carbon accumulation, which in some cases can outweigh the loss of carbon from increased peat decomposition [*Minkkinen and Laine*, 1998b; *Lohila et al.*, 2011].

Peatland sensitivity to changes in hydrology can be highly dependent on topography and plant communities. Typical peatlands have topographical variations at scales from centimeters to tens of meters, with elevation varying by 25-60 cm over short distances [*Lafleur et al.*, 2003; *Eppinga et al.*, 2008; *Sonnentag et al.*, 2008]. These topographic differences can lead to substantial differences in plant communities and sensitivity to hydrological changes [*Waddington and Roulet*, 1996; *Palmer*, 2005; *Strack et al.*, 2006]. A schematic of peatland microtopography is shown in Fig. 4.2.

Climate change may cause declines in wetland water tables. Studies using general circulation models (GCMs) predict globally averaged surface warming of 1-2°C by 2050 and up to 3°C by 2100, depending on the future evolution of anthropogenic CO_2 emissions. Northern areas where large areas of boreal peatlands are situated are predicted to warm up to 4°C by mid-century and up to 6°C by 2100, and the incidence of very hot periods and severe droughts is expected to increase [*Meehl et al.*, 2007]. In addition to direct effects on photosynthesis and soil decomposition rates, increased temperatures will lead to greater rates of evapotranspiration, potentially causing soil drying and drops in water table [*Manabe and Wetherald*, 1986; *Wetherald and Manabe*, 2002; *Erwin*, 2008]. Hydrology can vary coherently at regional scales, as shown by *Stow et al.* [2008]. In addition to climatic change, peatlands are often subject human disturbance. Examples include drainage for forestry [*Minkkinen and Laine*, 1998b; *Makiranta et al.*, 2010], agriculture [*Lloyd*, 2006; *Nieveen et al.*, 2005], or construction and urban development.

In northern temperate regions, wetlands can cover a large fraction of the area, contain significant portions of the carbon pool, and contribute significantly to the regional CO_2 budget. For example, *Weishampel et al.* [2009] found that peatlands in a Minnesota region contained 50% of the regional carbon pool despite occupying only 13% of the area. Similarly, *Buffam et al.* [2011] found that peatlands in a northern Wisconsin region contained 36% of the regional carbon pool while occupying 20% of the area. Lake sediments contained another 38% of the carbon pool, so the combination of wetlands and lakes accounted for 74% of the regional carbon pool. These results suggest that changes in peatland carbon cycling could have disproportionately strong effects on regional carbon budgets compared to their area.

In this study, we use a landscape modeling framework to evaluate the responses of peat decomposition and plant community succession to changes in mean water table. We attempt to place peatland responses in the context of regional carbon budgets, over multi-century time scales. Because of the relatively large spatial scales, long time periods, and inclusion of plant community responses, we chose to use the LANDIS-II landscape succession model. While the design of the LANDIS-II model makes it well suited for studying plant community dynamics at the scales of interest to our study, it does not include explicit hydrology or wetland biogeochemistry. While numerous peatland-specific ecosystem models exist, they are generally either too computationally intensive for long-term, large-scale studies [e.g. *Grant et al.*, 2001; *Frolking et al.*, 2002; *Govind et al.*, 2009], or do not include processes for simulating seed dispersal and long-term plant community changes related to hydrology [e.g. *Pietsch et al.*, 2003; *Belyea and Malmer*, 2004; *Bond-Lamberty et al.*, 2007; *St-Hilaire et al.*, 2010].

This research tests four hypotheses:

1. Over short time periods, wetland CO_2 flux responses to water table change are dominated by plant community changes
2. Over longer time periods, wetland CO_2 flux responses to water table change are dominated by changes in soil decomposition rates
3. Fast declines in water table lead to net decreases in wetland CO_2 uptake, while slow declines lead to net increases in CO_2 uptake
4. Wetland responses to hydrological change contribute significantly to the carbon budget of wetland-rich northern temperate regions

4.2 Methods

4.2.1 LANDIS-II model

Landscape succession was modeled using the biomass version of the LANDIS-II model [*Scheller and Mladenoff*, 2004; *Scheller et al.*, 2007]. A schematic of the model is shown in Fig. 4.1. Rather than simulating individual trees, the model uses cohorts divided by species and age class. For example, when using a 5 year time step red maple trees with ages between 20 and 25 years would be modeled as a single unit in competition with other cohorts. Aboveground biomass, net primary productivity (NPP), and seed dispersal are simulated for each cohort. The landscape is divided into ecoregions, and growth and establishment parameters are individually defined for each species in each ecoregion. Parameters can be updated over the course of the simulation in order to simulate environmental changes affecting species growth, such as changes in climate or hydrology.

Annual NPP for each cohort is based on a maximum NPP parameter, and modified by factors related to cohort age as a fraction of species maximum age, cohort biomass as a fraction of maximum biomass, and competition with other cohorts in the same grid cell. Seed dispersal occurs between grid cells, and is controlled by effective dispersal radius parameters for each species. Establishment of new cohorts in seeded areas is a function of grid cell shade class (based on total biomass), species shade tolerance, and ecoregion-specific establishment probability for each species. Plant growth, mortality, and soil decomposition are calculated at an annual time step. In our simulations, seed dispersal and reproduction were calculated at a 5-year time step, and carbon pool and flux values are presented at that temporal resolution.

Maximum NPP and establishment probability parameters for tree species were calculated using a version of the PnET model, as described by *Xu et al.* [2009], driven using temperature and precipitation measurements from a nearby National Climate Data Center

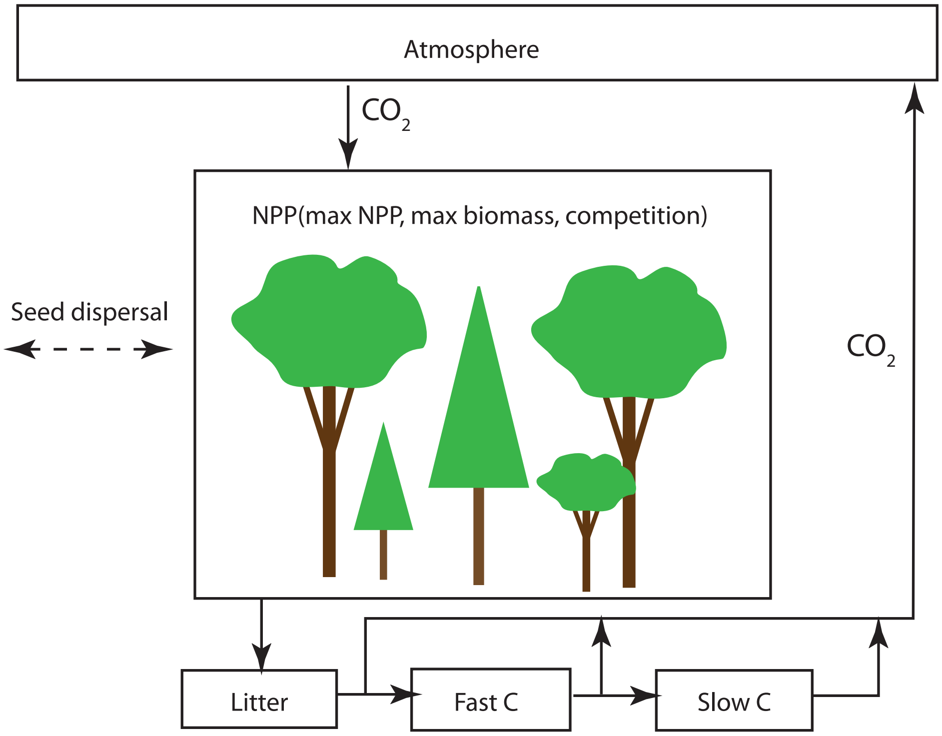

Figure 4.1: Schematic of the LANDIS-II biomass succession model.

(NCDC) station. Maximum NPP for wetland shrub and grass species were based on field measurements from sites in the area [*Sulman et al.*, 2009, 2010]. Maximum biomass for tree species was based on the values from *Thompson et al.* [2011]. Species parameters are shown in Table 4.1. Shrub and graminoid species were assigned shade tolerances of 4, because the wetland areas where they grow would generally have open canopies and not be shade limited compared to forests.

Belowground carbon cycling was added to the LANDIS-II biomass succession model for this study. In addition to woody and non-woody litter pools, a fast and a slow soil carbon pool were added. When decomposition occurs, carbon flows sequentially between pools (litter to fast to slow), with a fixed fraction respired as CO_2 in each step. This soil pool formulation follows *Parton et al.* [1988]. Decomposition rates in the litter pools are

Table 4.1: Species parameters used in LANDIS-II model. SEP is species establishment probability, shade tol is shade tolerance, and wetland tol is wetland tolerance. Shade tolerance is a number between 1 and 5, with 5 being the most tolerant of shade. Longevity is species maximum age in years. Max NPP is in gC/m^2/year, and Max biomass is in gC/m^2. In wetland areas, maximum NPP, maximum biomass, and SEP were multiplied by the vegetation area fraction for the species wetland tolerance (see Figures 4.2 and 4.7). "Upland" species were limited to "Upland" fractions, "mineral woody" species were limited to "Wet woody" fractions in mineral wetland ecoregions, "peat woody" species were limited to "Wet woody" fractions in peat wetland ecoregions, and "wet tolerant" species were allowed in both mineral wetland "Wet woody" areas and "Upland" areas. Graminoids were limited to peat "sedge" areas.

Species	Max NPP	Max biomass	SEP	Shade tol	Wetland tol	Longevity
Abies balsamea	565	4905	0.72	1	Mineral woody	200
Acer rubrum	615	9405	0.24	4	Wet tolerant	150
Acer saccharum	537	11205	0.62	5	Upland	300
Betula alleghaniensis	548	9360	0.92	4	Upland	300
Betula papyrifera	407	9585	0.92	2	Upland	100
Carya cordiformis	670	11250	0.83	2	Wet tolerant	200
Fagus grandifolia	329	11250	0.92	5	Upland	300
Fraxinus americana	495	11655	0.92	4	Upland	300
Fraxinus nigra	471	5000	0.92	2	Mineral woody	300
Fraxinus pennsylvanica	412	11250	0.92	3	Wet tolerant	300
Larix laricina	189	5500	0.76	1	Peat woody	200
Picea mariana	189	7000	0.72	3	Peat woody	300
Pinus banksiana	673	11250	0.85	1	Upland	100
Pinus resinosa	583	11250	0.86	2	Upland	200
Pinus strobus	411	14355	0.91	3	Upland	400
Populus deltoides	657	11250	0.87	1	Upland	250
Populus tremuloides	620	8370	0.89	1	Upland	120
Quercus rubra	644	10350	0.86	3	Upland	250
Thuja occidentalis	541	11250	0.74	2	Wet tolerant	400
Tilia americana	505	11250	0.93	4	Upland	250
Ulmus americana	582	11250	0.88	3	Upland	350
Shrubs	286	6000	0.92	4	Peat woody	40
Graminoids	300	2400	0.90	4	Peat sedge	10

determined by a species-specific coarse litter decomposition rate and foliar lignin content, respectively [*Scheller and Mladenoff*, 2004]. Decomposition rates in the fast and slow soil carbon pools are determined by a fixed turnover rate parameter, which can be specified for each ecoregion and time step. For these simulations, a fast soil pool turnover rate of 0.15 yr^{-1} was used for all ecoregions.

4.2.2 Wetland simulation strategy

Because the LANDIS-II model does not include explicit hydrology, hydrological scenarios were imposed by externally simulating hydrological effects on plant growth and soil decomposition for each ecoregion, and then applying the resulting changes to LANDIS-II plant and soil pool parameters over the course of the simulations. The ecoregion framework was used to distinguish between wetland classes. Each ecoregion was assigned a characteristic water table. Sub-grid-scale heterogeneity was modeled using a bimodal topography distribution [*Eppinga et al.*, 2008], with distribution parameters adjusted to match water table variations observed between two measurement points at the Lost Creek wetland field site [*Sulman et al.*, 2009]. This strategy made it possible to include hydrology-related carbon cycle changes without implementing a complete hydrological and biogeochemical model within LANDIS-II. The framework's level of detail matched well with our focus on bulk changes in carbon pools over long periods of time. While additional complexity would improve simulations of the detailed ecology of wetland succession, it would be beyond the scope of our analysis.

Plant communities

Plant community dependence on water table was modeled using a fractional area approach. Land surface area was divided into categories based on distance above the water table (Figure 4.2), and species were divided into categories based on flood tolerance and typical presence in wetlands as described by *Burns and Honkala* [1990] (Table 4.1). “Underwater” areas did not support vegetation. Areas very close to the water table were limited to grassy species (“Sedges”). Moderately wet areas were assigned wet-tolerant woody species (“Wet woody”), and areas well above the water table were assigned to upland species (“Upland”). In addition, wetland ecoregions were divided into wet mineral (higher productivity and lower soil carbon) and peatland (lower productivity and higher soil carbon) wetland types. Wetland woody species were designated as either “Peat woody” or “Mineral woody”, and limited to only those wetland areas. “Wet tolerant” species were allowed in both “Upland” and “Mineral woody” areas.

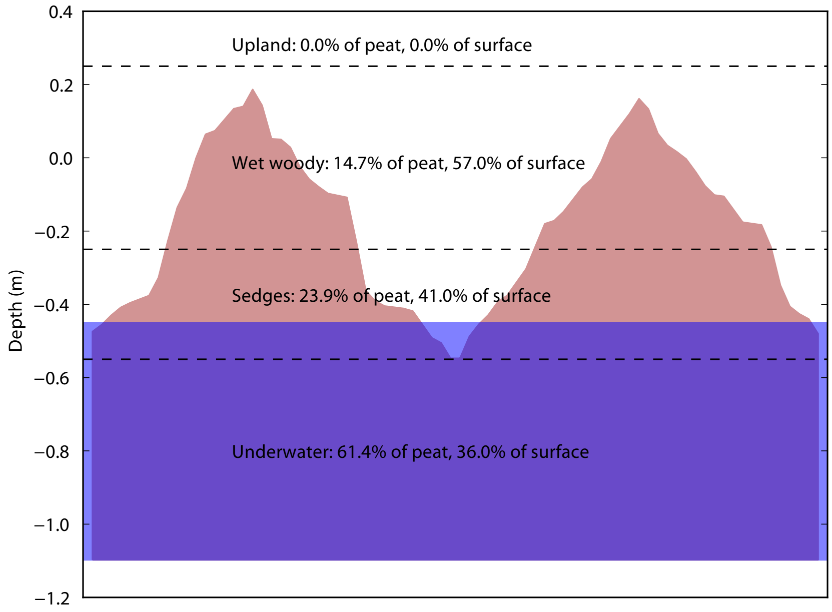

Figure 4.2: Wetland soil and land surface calculations. Topography shown is sampled from a bimodal hummock/hollow distribution. Percentages reflect the entire distribution, so they do not correspond exactly to the surface shown. Land surface categories are defined relative to water table, so declining water table would bring more surface into the drier categories. Area fraction of each land surface category was used to determine plant growth parameters in each ecoregion.

Maximum NPP, maximum biomass, and establishment probability for each species were multiplied by the area fraction representing habitat for that species within the grid cell, on an ecoregion-specific basis. As area fractions changed in response to changing water table, simulated plant communities responded through the modeled growth, reproduction, and mortality processes. For example, lowering the water table in a wetland area would allow the establishment of upland species through seed dispersal from nearby upland areas, while wetland species biomass and growth would decrease as a result of reduced maximum biomass and NPP parameters.

Soil decomposition

Turnover rates for the slow carbon pool in peatlands were calculated using a simplified version of the *Frolking et al.* [2001] peat decomposition model. The underlying model of organic matter decomposition is:

$$\frac{dm(t)}{dt} = -k_0 m_0 \left(\frac{m(t)}{m_0}\right)^{\alpha} \tag{4.1}$$

where $m(t)$ is soil pool mass, k_0 is an initial turnover rate (set to 0.2, following *Frolking et al.* [2001]), m_0 is initial mass, and α is a parameter describing the decline in organic matter decomposability with time. The general solution is

$$m(t) = \frac{m_0}{[1 + (\alpha - 1)k_0 t]^{1/(\alpha-1)}} \tag{4.2}$$

Using $\alpha = 2$ (following *Frolking et al.* [2001]), a turnover rate k can be specified as a function of age t:

$$k(t) = k_0 \frac{m(t)}{m_0} = \frac{k_0}{1 + k_0 t} \tag{4.3}$$

Rather than directly simulating peat age cohorts, an age profile was defined as a function of depth ($k_t(z)$), using the results of *Frolking et al.* [2001]. Peat age was limited to a

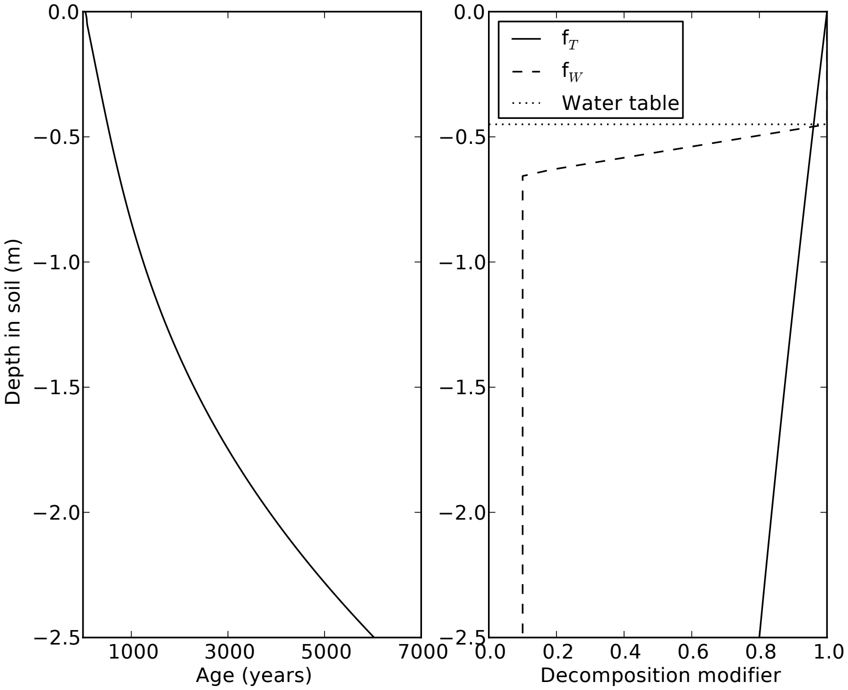

Figure 4.3: Left: Peat age profile. Right: Functions for the effects of soil temperature profile and water table on decomposition rate.

minimum of 50 years because additional litter and fast decomposition pools were included in the LANDIS-II model. The age profile is shown in Fig. 4.3. Due to the increasing age of carbon with depth, total decomposition was more sensitive to the upper peat layers than to the lower peat layers. Additions of young carbon to the soil pool over the course of simulations were decomposed using a 50 year turnover time as described below. These simplifications of the model were similar to those previously used by *St-Hilaire et al.* [2010]. In addition to the age profile, the depth profile of k depends on the effect of the vertical soil temperature profile ($f_T(z)$) and the effect of water table level ($f_W(z)$). f_W is defined relative to the water table level, allowing the soil decomposition parameter to capture the effect of changing water table. The depth profiles of these functions are show in Fig. 4.3.

The value of k at each soil depth was the product of these functions:

$$k(z) = k_t(z) f_T(z) f_W(z) \tag{4.4}$$

The turnover rate for an individual soil column was calculated by averaging k vertically over the soil profile. This calculation was conducted for 100 soil columns sampled from the soil height distribution (Fig. 4.2), and the mean value $\bar{k}$ was used as the slow carbon pool turnover rate for that ecoregion. The upland and wet forest ecoregions used a single characteristic soil age (50 years for upland and 60 years for wet forest) rather than an age profile, since those ecosystems do not develop thick peat layers over long time periods. Table 4.2 shows the important soil parameters for each ecoregion.

Table 4.2: Ecoregion parameters. WT_0 is water table level (m) at the start of simulation, relative to soil hummock height. Pool sizes are in kg/m^2, and soil depths are in meters. "Shallow" and "deep" refer to the shallow and deep peat scenarios. Area fraction refers to the fraction of active grid cells containing that ecoregion. Non-active grid cells include open water, crops, and developed areas.

Ecoregion	WT_0	Pool size (shallow)	Pool size (deep)	Soil depth (shallow)	Soil depth (deep)	Area fraction
Upland	−2.0	9.1	9.1	0.21	0.21	38%
Wet forest	−0.45	13.6	13.6	0.62	0.62	27%
Shrub peat	−0.30	18.5	100	0.47	2.53	29%
Gram peat	−0.15	18.4	100	0.47	2.53	5%

Annual decomposition for soil pools in the LANDIS-II model was calculated using an exponential dependence on $\bar{k}$:

$$\Delta m = m(1 - e^{-\bar{k}}) \tag{4.5}$$

Therefore the annual CO_2 production from soil decomposition for each ecoregion depended on a combination of soil pool size and $\bar{k}$. Two peat scenarios were used, as shown in Table 4.2. The shallow peat scenario used peat depths based on site measurements at Lost Creek, while the deep peat scenario used peat depths based on the results of inventories by *Buffam et al.* [2010] and *Weishampel et al.* [2009] (see section 4.2.3 for more details). Soil organic layer depth refers to the minimum soil layer thickness, so soil thickness under hummocks is greater than the soil depth parameter. Peat depth was calculated from peat mass using the bulk density profile from *Frolking et al.* [2001]. Wet forest and upland soil depths were calculated using the same function, but assumed one half the carbon density compared to peat, because these ecosystems had mineral soils with lower concentrations of organic matter. These soil depths represent the area where significant soil carbon is located, and are important for determining the vertical range where water table affects soil decomposition rate.

Simulation scenarios

We conducted several model simulations in order to test the hypotheses listed above. A diagram of the model simulations conducted for each peat depth scenario is shown in Fig. 4.4. Four water table decline scenarios were run: Two magnitudes of water table decline (40 cm and 100 cm), and two time periods over which the decline occurred (10 years and 40 years). Each water table scenario was initiated after 50 years of model time, in order to avoid transient effects related to model spinup. Four model runs were conducted for each scenario in order to separate soil and vegetation effects. "Control" simulations included no water table effects. "Veg" and "soil" simulations included only water table effects on plant communities or only water table effects on soil decomposition, respectively. The "both" simulation included both plant community and soil decomposition responses.

If there are substantial increases in carbon inputs to peatland soils, the age profile used to calculate $\bar{k}$ will no longer reflect the age profile of the soil, and the estimated soil decomposition rate will be too low. To correct for this, additional decomposition with a 50 year characteristic soil age was applied to simulated "new" soil carbon in "Veg" and "Both" scenarios. The size of the new soil carbon pool was determined by subtracting the control

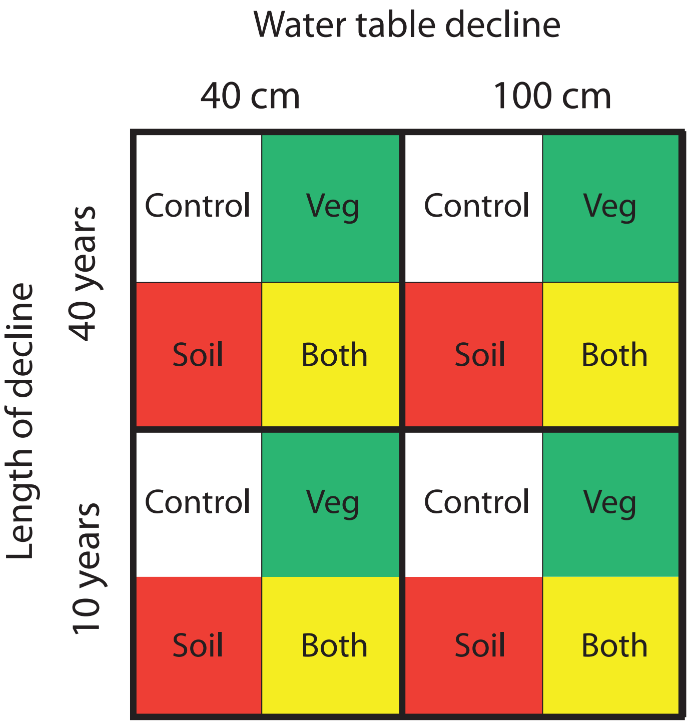

Figure 4.4: Simulations conducted for each peat depth scenario. Rows show scenarios in terms of water table decline, so negative numbers are increases in water table. Columns show the length of time over which the water table change occurred. "Control" is no water table effect, "Veg" is vegetation effect only, "Soil" is soil decomposition effect only, and "Both" included soil and vegetation effects.

simulation soil carbon pool from that of the vegetation effect simulation. Because plant community changes were the same in deep and shallow peat scenarios, equal levels of additional decomposition were applied to both.

4.2.3 Study region

The model was run for an area within Price and Oneida counties in northern Wisconsin, USA, with a spatial resolution of 100 m. This region was chosen because of the large areas of forests and wetlands, and relatively small areas of urbanization and agriculture. This region has also been subject to previous flux tower studies [*Cook et al.*, 2004; *Desai et al.*, 2005, 2008a; *Sulman et al.*, 2009, 2010] and regional carbon cycle studies [*Buffam et al.*, 2010, 2011; *Xiao et al.*, 2011], which provided data resources for model parameterization. The landscape was categorized into wetland and upland ecoregions based on a combination of National Landcover Database (NLCD) 2001 remote-sensing-based landcover classification map [*Homer et al.*, 2004], and the United State Geological Survey (USGS) Soil Survey Geographic Database (SSURGO) [*Natural Resources Conservation Service*, 2011]. NLCD maps were used to distinguish between forest, shrub, and graminoid areas, and SSURGO maps were used to locate areas with hydric or peat soils. Grid cells were categorized as upland, mineral wetland, shrub peatland, or graminoid peatland. A map of ecoregions is shown in Figure 4.5, and the fraction of the landscape occupied by each ecoregion is shown in Table 4.2. These fractions exclude areas that were not modeled, such as open water and built-up areas. Initial plant communities were assigned based on the NLCD map, with tree species fractions and ages determined based on area fraction estimates from the United States Department of Agriculture (USDA) Forest Inventory and Analysis (FIA) data set. The specific tree species shown in Table 4.1 were inferred based on forest community types from the FIA dataset. Because the analysis was focused on bulk carbon pools and ecosystem types, the results were not sensitive to the individual tree species that were included.

Soil pools for the upland ecoregion and the shallow peat scenario were determined using measurements from sites in the Chequamegon Ecosystem Atmosphere Study, a network of field sites in northern Wisconsin and the upper peninsula of Michigan. These sites included the Lost Creek shrub wetland [*Sulman et al.*, 2009], Willow Creek mature hardwood forest [*Cook et al.*, 2004], and Sylvania old-growth forest [*Desai et al.*, 2005]. Soil pools for the deep peat scenario were based on inventories from areas in Wisconsin [*Buffam et al.*, 2010] and Minnesota [*Weishampel et al.*, 2009]. The soil carbon pool size for wet forests was determined using estimates from *Bridgham et al.* [2006]. Soil pools for each ecoregion were further tuned from initial values in order to reach a steady state for initial soil carbon pools.

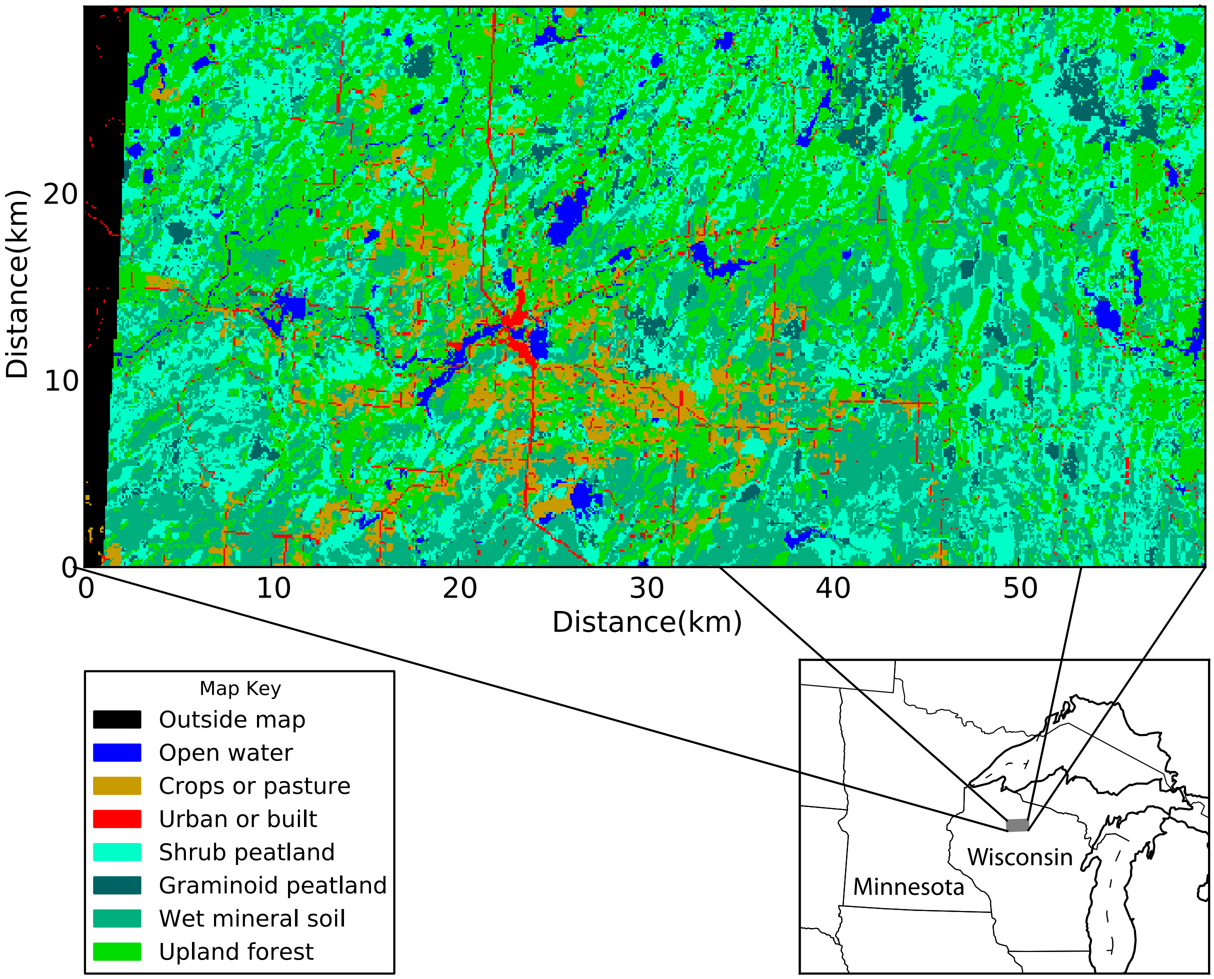

Figure 4.5: Ecoregion map used to drive simulations. The region was located in Price County in northern Wisconsin, USA. The gray rectangle in the regional map shows the location of the modeled area. The built up area near the center is Philips, WI.

4.3 Results

4.3.1 Modeled baseline carbon fluxes

Modeled net ecosystem production (NPP) and heterotrophic respiration from control simulations are shown in Figure 4.6. Fluxes in upland areas started with substantial carbon uptake, which declined over time until reaching approximate neutrality after 100 years of simulated time. Wet forests showed a similar pattern, but reached neutrality earlier and recovered from the decline in uptake and became a net carbon sink again at approximately 100 years. Shrub peatland areas were net carbon sinks for the duration of the simulation except for a short period. Graminoid peat areas were sinks of carbon in the shallow peat scenario, but the larger carbon pools and higher soil decomposition in the deep peat scenario led to net carbon loss over time. Overall, upland forest areas were the most productive and graminoid peatland areas were the least productive.

4.3.2 Effects of water table on soil decomposition and plant communities

The effect of water table level on soil decomposition rates is shown in the left panel of Fig. 4.7. Sensitivity was highest in the upper soil layers due to the increase in age and resulting decrease in maximum decomposition rate at lower depths. The shallow peat simulations were insensitive to water table levels below approximately 1 m, because water tables below this level were below the bottom of the peat layer. Deep peat simulations were sensitive to lower water table levels, leading to moderately higher decomposition rates at low water table, but the difference between simulated total emissions was minor due to the high age of peat at low levels in the soil profile.

Upland and wet mineral soil decomposition rates were both higher and more sensitive to

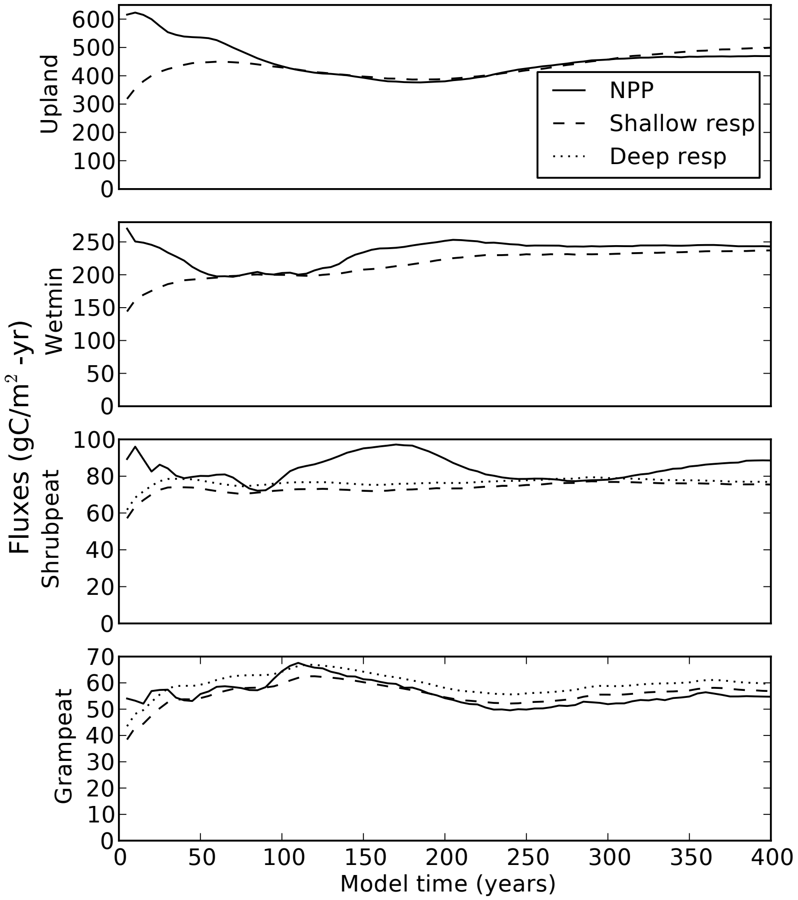

Figure 4.6: Modeled NPP and heterotrophic respiration for the four ecoregions. Control scenarios are shown. The ecosystem is gaining carbon when NPP is greater than respiration. Respiration in the deep peat scenarios was higher than in the shallow peat scenarios due to larger soil carbon pools.

water table level, because of lower soil age. However, simulated water tables in upland areas were always well below the soil depth, so upland soil decomposition did not vary between hydrological scenarios.

The dependence of plant community area fractions on water table is shown in the right panel of Fig. 4.7. When water tables are close to the surface, a substantial fraction of landscape area is underwater and nonproductive, and the rest is dominated by sedge species.

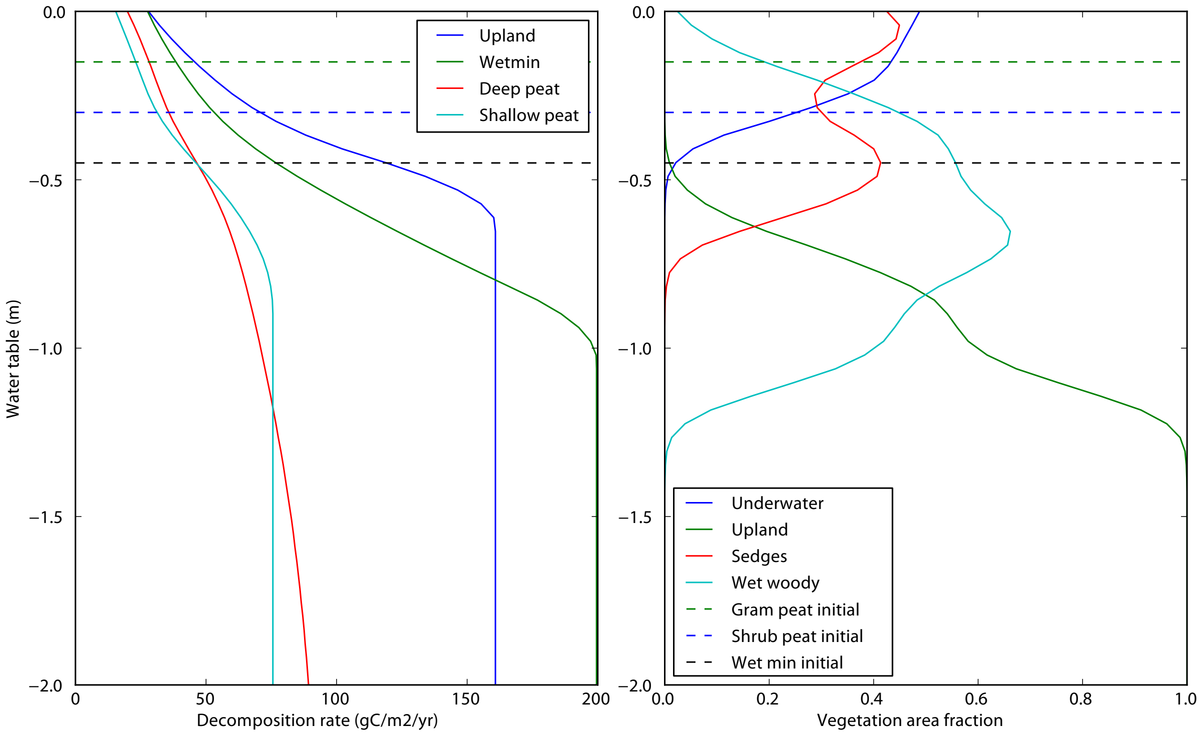

Figure 4.7: Effects of water table level on soil decomposition and vegetation fractions. Left panel shows annual CO_2 production from soil carbon pool decomposition for each ecoregion. Deep peat and shallow peat scenarios used different peat depths and carbon pools (see Table 4.2). Shrub and graminoid peat decomposition profiles were identical. Right panel shows the area fraction occupied by each vegetation type as a function of water table. Species growth and biomass parameters were multiplied by this area fraction at each time step. Dashed lines show the initial water table positions for the three wetland ecosystems.

With deeper water tables, wet-tolerant woody species occupy more area, and dry upland communities become well established when water table is below approximately 1 m. The effect of hummock and hollow topography can be seen clearly in the pattern of sedge area, as sedges occupy hummock or hollow areas at 10 cm and 45 cm water table depths, respectively. Dashed lines show the initial water table positions for each wetland ecoregion. Upland ecoregions had an initial water table of −2.0 m, placing them entirely in the upland species range.

4.3.3 Effects of water table decline on landscape carbon balance

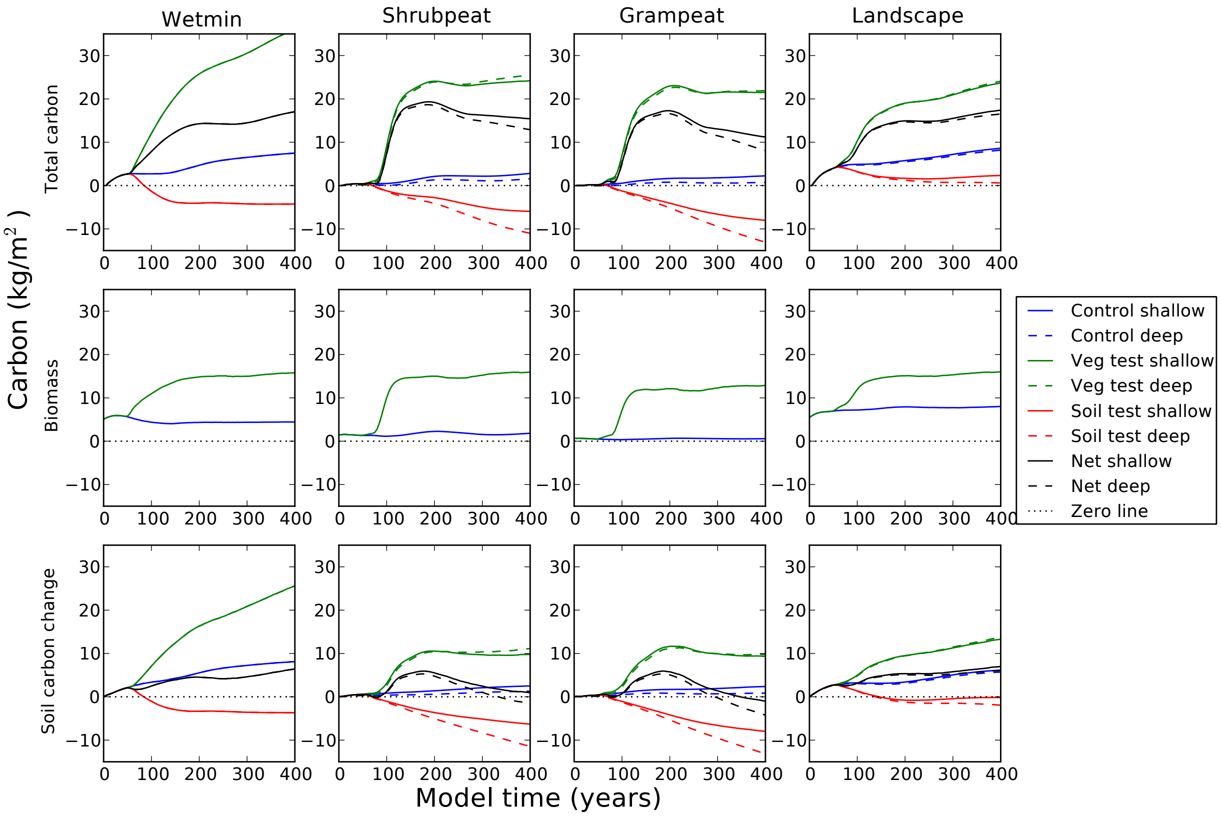

Figure 4.8: Effects of water table decline on ecosystem carbon balance for 100 cm water table decline over 40 years. Water table decline was initiated at the 50 year point. Control simulation (blue), separated effects of water table on vegetation (green) and soil (red), and the net effect (black) are shown. Solid lines show results from the shallow peat simulation and dashed lines show the deep peat scenario. Columns show results for the three included wetland ecosystem types (wet mineral soil forest, shrub peatland, and graminoid peatland), and the entire landscape, which also included upland regions. Results for the upland ecoregion are omitted because they did not vary between water table scenarios. Rows show total carbon, biomass, and soil carbon. Total carbon and soil carbon are plotted relative to their initial values.

Figure 4.8 shows simulated carbon pools from “Control”, “Veg”, “Soil,” and “Both” simulations for a 100 cm water table decline over 40 years. Biomass and total soil carbon are shown as well as the sum of these pools, representing the total ecosystem carbon pool.

Soil and total carbon are shown relative to their values at the start of the simulation to allow easier comparison between the shallow and deep peat scenarios. Water table decline led to immediate and continued loss of soil carbon in “Soil” simulations, relative to control simulations. All wetland ecosystems experienced large increases in biomass relative to control for approximately 100 years following water table decline. The net effect on soil carbon and total carbon was an increase in carbon over the first 100 years after water table decline, followed by a loss of carbon over the next 250 years in peatland ecoregions, and relatively constant carbon relative to control for wet mineral ecoregions. The difference between soil-only and net effect scenarios shows the importance of including vegetation effects in the carbon balance. Simulations that only included water table effects on soil decomposition predicted a net loss of carbon over the entire simulation, while simulations including vegetation effects predicted initial net carbon gain resulting from water table decline. At the end of the 400 year simulation, “Both” simulations had somewhat more total carbon than “Control” simulations, while “Soil” simulations had substantially less. The larger, deeper peat carbon pools in the deep peat scenarios led to increased carbon loss relative to shallow peat scenarios, but the temporal pattern of effects was similar. The total landscape simulations included upland areas, which were not sensitive to water table changes. However, the changes in carbon pools were still significant at the landscape scale.

Results for different water table decline scenarios are shown in Figure 4.9. Each plot shows the difference between the “Both” simulation and the “Control” simulation. Water table declines resulted in initial increases in aboveground biomass for the three wetland ecosystems. Biomass reached a maximum approximately 50-100 years following the water table decline, and remained relatively constant afterward. Declines of 100 cm led to much more biomass accumulation than declines of 40 cm. The time scale of decline caused differences in the initial rate of biomass accumulation, but there was little difference by about 50 years following water table decline.

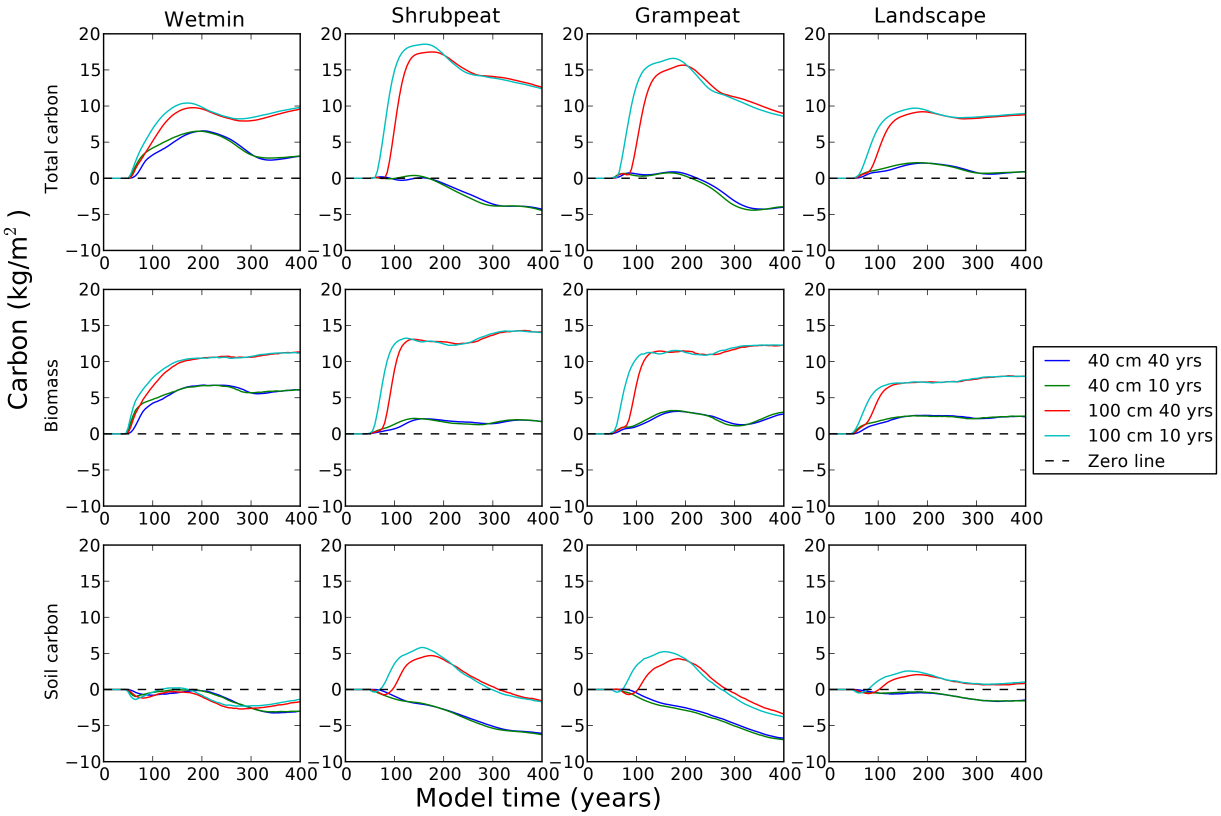

Figure 4.9: Effects of water table decline on ecosystem carbon balance. This plot shows results from the shallow peat scenarios. Each plot shows difference between scenario results and control run results. Water table decline was initiated at the 50 year point. Columns show results for the three wetland ecosystem types (wet mineral soil forest, shrub peatland, and graminoid peatland), and the entire landscape. Rows show total carbon, biomass, and soil carbon. Total and soil carbon are plotted relative to their initial values.

40 cm water table declines led to continuous net loss of soil carbon in the peatland ecosystems, but soil carbon in the wet mineral ecosystem showed little sensitivity to water table decline. 100 cm water table declines resulted in increases in soil carbon in peatlands over approximately 100 years following water table decline, because increased carbon inputs from vegetation growth outweighed losses from increased decomposition. However, after biomass accumulation leveled off after about 100 years, soil carbon began to decline, and by the end of the simulations soil carbon was at or below the control simulation. Additions of

new carbon from increased plant growth were largely transient, due to faster decomposition compared to old carbon in peat.

For 100 cm declines, the net effect of changes in biomass and soil carbon in peatland ecosystems was a substantial increase in total carbon for about 100 years after the water table decline, followed by a gradual loss of carbon over the remainder of the simulation. At the end of the simulations, all wetland ecosystems and the whole landscape retained additional carbon compared to control simulations, although peatland ecosystems were continuing to lose carbon. 40 cm declines led to net loss of peatland carbon, although the carbon balance was neutral for approximately 100 years after water table decline. Upland carbon cycles did not respond to decreases in water table, because initial water tables were already too low to affect vegetation or soil.

The changes in carbon pools resulting from water table decline were still significant when averaged over the entire landscape, confirming our initial hypothesis. Total carbon increased at the landscape scale in all scenarios, and total carbon appeared to be stable at the end of the simulations, due to cancellation between continuing losses in peatlands and gains in mineral wetlands.

4.4 Discussion

The peatland decomposition model used in this study predicted an increase in CO_2 emissions from soil decomposition of approximately 100% with a 40 cm decrease in water table level (Fig. 4.7). Sensitivity of the overall soil decomposition rate to water table declined at lower levels due to the effect of increasing carbon age in deeper peat. The magnitude of the soil respiration increase is consistent with the dependence observed in soil columns by *Moore and Knowles* [1989] and *Freeman et al.* [1992], and in field observations by *Oechel et al.* [1998] and *Silvola et al.* [1996]. The decline in water table effect on soil respiration at lower water table levels is consistent with the observations of *Silvola et al.* [1996], *Sulman et al.* [2009], and *Lafleur et al.* [2005b]. However, those studies observed a drop-off of water table dependence at 30 cm below the surface, a higher level than predicted by our model. This suggests that our model may have overestimated the increase in soil respiration resulting from lowering of the water table.

In peatlands, the magnitudes of soil and total carbon over the course of the simulations were somewhat dependent on the method used to correct for additions of new carbon to the soil profile, revealing a potential weakness of the model. However, because new carbon had an inherently faster turnover time than peat carbon, much of the additional soil carbon in "Both" simulations should decompose, and the total will eventually reach an equilibrium where soil carbon is equal to that of the "Soil" simulations plus the additional steady state inputs from continuing plant growth. As soil carbon continues to decline while biomass maintains a steady state, we expect that total carbon would eventually reach an equilibrium value lower than the initial value before drainage, representing a net loss of carbon.

The initial net gain in soil carbon modeled in the 100 cm water table decline scenarios contradicts the implications of short-term studies that focused on soil effects and found substantial losses of carbon following soil drying, such as *Moore and Knowles* [1989]; *Freeman et al.* [1992]; *Silvola et al.* [1996], and *Bubier et al.* [2003]. However, the steady state of total carbon for the first 100 years following drainage was consistent with *Sulman et al.* [2009] and *Flanagan and Syed* [2011], who observed no change in NEE following drainage of that magnitude in peatlands. In simulations that included only soil effects, the model did predict substantial losses of carbon, indicating that the major difference between our simulations and these studies was the inclusion of plant community changes. In addition, our simulations did show some net carbon loss in shrub peat ecoregions in the first few years following water table decline, except in the most extreme scenario (100 cm water table decline in 10 years). These results highlight the importance of plant community changes in the net carbon budget response of peatlands to hydrological change.

Increased plant growth resulting from declining water table has been observed in field studies over inter-annual time scales [*Sulman et al.*, 2009; *Flanagan and Syed*, 2011], although *Strack et al.* [2006] observed variations in the response between hummock, hollow, and lawn microforms. Wetland succession studies over decadal time scales have observed large increases in biomass as sedge, shrub, or moss-dominated wetland landscapes are converted to forest [*Laine et al.*, 1995; *Laiho et al.*, 2003]. *Minkkinen and Laine* [1998b] observed a net increase in wetland soil carbon after 60 years of drainage and afforestation. The results of our 100 cm decline simulations agreed well with these field studies, indicating that large declines in water table could cause a net increase in stored carbon in wetland-rich landscapes over time scales of about 100 years. However, the trajectory at the end of our simulations suggests that over time scales of several centuries to millenia, peatland drainage could eventually result in net carbon loss. This would be consistent with the results of *Ise et al.* [2008], who identified a large positive climate feedback from wetland drying, although their results did not include an initial increase in carbon following drainage. Since several decades were necessary for the net results to become clear in some scenarios, and since several centuries of simulation time were required to see the long-term trajectory, our results suggest that longer measurement periods are necessary to accurately represent wetland responses to hydrological change, and that short-term measurements should not be interpreted as predictive of the long-term carbon cycle response.

Our model of vegetation response to declining water table did not include nitrogen cycling, which could be a significant limiting factor to biomass increase in nutrient-poor peatlands. We can assess the additional nitrogen required using a simple mass balance. We use tree tissue nitrogen concentrations measured in northern lower Michigan of 0.5 g/kg in aboveground wood, 6.0 g/kg in fine roots, and 2.0 g/kg in belowground wood [*Nave et al.*, 2009] and leaf nitrogen concentrations of approximately 20 g/kg [*Reich et al.*, 1998].

Based on measurements by *Gough et al.* [2008], forest biomass is divided into approximately 74% aboveground wood, 18% belowground wood, 1.6% leaf, and 6% fine root. Assuming a biomass carbon content of 40%, this gives an overall nitrogen mass of 3.5 grams nitrogen per kilogram live carbon, and 4.6 grams total nitrogen per kilogram aboveground live carbon. The maximum increase in aboveground biomass predicted by our simulations was 10 kg/m^2, which would require 46 g/m^2 of additional nitrogen based on this estimate. *Nave et al.* [2009] identified nitrogen deposition of approximately 0.75 g-m^{-2}-year^{-1}, which would supply the required additional nitrogen over a period of 61 years, approximately the same time scale as the simulated growth. Additional nitrogen would probably also be available from increased soil decomposition. Therefore, the simulated increase in biomass would not be precluded by nitrogen requirements alone.

Peatland type and nutrient levels likely determine whether biomass accumulation following drainage would be nitrogen limited. A comparison of wetland plant community responses to drainage by *Laine et al.* [1995] found that forest development was much faster on nutrient-rich sites than on poorer sites, and that poorer sites gained less biomass overall. *Vasander* [1982] found little increase in biomass at all following drainage of an ombrotrophic bog, and *Talbot et al.* [2010] identified a shift in shrub species and only moderate increase in biomass related to declining water table at a dry bog. These findings suggest that the results of our simulation may not be applicable to very nutrient-poor peatlands. Our simulations also assume a conversion from peatland to forest. If drained peatlands were instead converted to cropland, pasture, or built areas, biomass accumulation would be much less, and the net change in landscape carbon would likely be negative rather than positive over century time scales.

Rather than declining, water tables could rise due to increased precipitation resulting from climate change [*Meehl et al.*, 2007] or due to wetland creation activities [*Roulet*, 2000]. Within the framework of our model, rising water tables would result in decreased productivity as productive upland and shrub species occupy less area. This seems like a plausible outcome for wetland-rich regions, where precipitation is not a major limiting factor to forest growth. Increased flooding could kill less flood-tolerant species in upland areas, and drive succession toward lower-biomass grassy species in wetlands. While higher water tables can reduce soil decomposition rates and begin to drive long-term peat accumulation, biomass and productivity loss would likely cause reduced carbon uptake or carbon loss over the short term. This is consistent with the results of *Frolking et al.* [2006], who found that wetland creation did not have a net climate cooling impact until hundreds of years after flooding occurred.

Our landscape simulations did not include any interaction between declining water tables and upland forest productivity. In actuality, declines in water table due to climatic change would likely be accompanied by drought stresses on tree growth, which could cause declines in forest productivity and reduce the carbon gains at the landscape scale. Alternatively, CO_2 fertilization and extension of the growing season could increase forest productivity [*Pastor and Post*, 1988]. *Falge et al.* [2002] estimated that extending growing season length would increase NPP by 5-8 g-m^{-2}-d^{-1} for temperate forests. Our simulations predicted increases in landscape mean NPP of around 200 g-m^{-2}-year^{-1} following a water table decline of 100 cm, equivalent to a growing season increase of 26-40 days according to these estimates. Landscape scale water table responses would therefore be important even in the context of increasing forest productivity.

Furthermore, these simulations did not include changes in temperature, which could increase soil decomposition rates and offset carbon gains [*Updegraff et al.*, 2001; *Dorrepaal et al.*, 2009]. *Christensen et al.* [2007] predict an average surface warming of 4-6°C in boreal regions. For a Q_{10} of 2.0, this is equivalent to an increase in respiration of 30-50%. Using a Q_{10} of 2.9, as measured by *Silvola et al.* [1996] for a peatland under high water table conditions, this is equivalent to an increase of 50-90%. These estimates place the effect of warming on soil decomposition in the same order of magnitude as the increase in respiration following a 40 cm decline in water table using our model.

Our simulations showed that wetland drainage could cause significant carbon cycle effects at the regional scale in wetland-rich landscapes, but would these effects be significant at global scales? A synthesis of several global peatland area estimates by *Mitra et al.* [2005] found a range of $2 - 4 \times 10^{12}$ m^2. Scaling up our results to this area can give a rough upper bound to the global consequences of wetland drainage. Our simulated post-drainage increases in wetland biomass of $5 - 10$ kgC/m^2 would mean $10 - 40$ PgC at the global scale, while simulated soil carbon losses of 5 kgC/m^2 translate to $10 - 20$ PgC globally. Simulated changes in total wetland carbon ranged from an increase of 15 kgC/m^2 (over 100 years) to a decrease of 5 kgC/m^2 (over 350 years), although carbon continued to decline at the end of the simulation. Scaling these numbers by global wetland area gives $30-60$ PgC and $10-20$ PgC, respectively. In terms of estimated anthropogenic CO$_2$ emissions of $4 - 8$ PgC/year [*Forster et al.*, 2007], an increase in global carbon pools of $30 - 60$ PgC is equivalent to a $4 - 15\%$ decrease in total emissions over a century. A loss of $10 - 20$ PgC would be equivalent to a $1 - 5\%$ increase in emissions over a century.

The soil model used in this study predicted that carbon contained in deep peat was stable due to its age, and would decompose slowly even when the water table was substantially lowered. However, soil carbon losses resulting from fires could be much more rapid. Fire can be an important factor in the net carbon balance of northern peatlands [*Kuhry*, 1994; *Pitkänen et al.*, 1999], and individual events can lead to large losses of soil carbon [*Mack et al.*, 2011]. Greater fire incidence is a likely consequence of climatic warming and wetland drying, and could be a crucial factor in future peatland carbon accumulation and retention rates [*Turetsky et al.*, 2010; *Grosse et al.*, 2011].

Another process omitted in our model was aquatic carbon cycling. In fact, lakes and inundated areas can contribute significantly to regional carbon cycles. *Buffam et al.* [2011]

found that lake sediments contained approximately 38% of the regional carbon pool in a northern Wisconsin carbon inventory, while lake and stream CO_2 evasion were equivalent to approximately 4% of regional carbon uptake. *Cardille et al.* [2009] estimated mean lake emissions in the same region at 44 $g/m^2/year$, with substantial variability depending on lake size, and found that lake emissions would be highly sensitive to regional hydrological change. This level of emissions is significant relative to the magnitude of modeled net ecosystem exchange, and therefore likely contributes significantly to the landscape carbon budget and responses to hydrological change.

This study did not distinguish between types of wetland soil carbon loss. In fact, how soil carbon loss is partitioned between CO_2, CH_4, and dissolved organic carbon (DOC) can have important implications for both carbon balance and climate impacts. Anaerobic respiration will primarily produce CH_4 rather than CO_2 [*Clymo*, 1984], and as a result decomposition in inundated peat soils is a major source of methane [*Harriss et al.*, 1985; *Matthews and Fung*, 1987; *Frolking et al.*, 2006]. In addition to methane, DOC fluxes of carbon can be important components in wetland carbon budgets [*Roulet et al.*, 2007; *Billett et al.*, 2004; *Buffam et al.*, 2011]. The climate effects of increasing CO_2 emissions following wetland drainage could therefore be counteracted by decreases in methane emissions [*Moore and Knowles*, 1989; *Strack et al.*, 2004]. Despite these omissions, it is clear that wetland drying would have substantial impacts on the future of peatland carbon pools and the carbon cycle in boreal and subarctic regions.

4.5 Conclusions

This study introduced a novel method for modeling peatland succession and peat decomposition within a landscape succession model originally intended for forests. Peatlands have not been previously simulated using the LANDIS-II model, and plant community succession has not historically been a focus in peatland modeling studies. The strategies introduced here simplified or omitted some potentially important processes, but the results were plausible and consistent with previous field and modeling studies. We hope our strategy will inform future implementations of peatland biogeochemistry within landscape succession models in order to improve understanding of these important processes.

Our results suggest that drainage of wetlands can lead to increases in carbon over time scales of a few hundred years, but that the longer-term effect is potential loss of carbon as biomass accumulation reaches a maximum while soil carbon loss continues. These long time scales proved more important than the time scale of the initial water table decline. The depth of drainage was the most important factor, with 40 cm water table declines leading to net carbon loss and 100 cm declines leading to net carbon gain. The responses were significant at the regional scale, confirming one of our original hypotheses. These results highlight the importance of hydrology in maintaining long-term carbon storage in peatlands. Plant community responses were integral to the net carbon cycle response, suggesting that both peat and plant community responses must be considered in any complete assessment of peatland carbon storage and its response to climate change.

Our results should encourage caution when interpreting the results of short-term studies, because they could suggest very different conclusions depending on the time scale being considered. Over $5 - 10$ year time scales, simulations indicated net loss or only a small increase in ecosystem carbon. Time scales of $50 - 100$ years indicated large increases in carbon following 100 cm water table decline and neutral carbon balance following 40 cm decline, while the results over longer time scales suggested eventual net losses of carbon. Discussions of wetland land use and climate responses need to consider the long-term impacts of wetland hydrological change in addition to the immediate responses. While there may be a short-term benefit to peatland drainage in increased NPP, this comes at the expense of the long-term ecosystem service of carbon storage.

Chapter 5

Conclusions

5.1 Key findings and implications for peatland modeling

Our key results generally concerned areas where ecosystem models may need improvement to accurately capture peatland responses to hydrological change. The comparison of measured CO_2 fluxes from multiple peatland sites in Chapter 2 demonstrated important differences in sensitivity to interannual fluctuations in water table between northern peatland types. This finding was corroborated by the results of the model intercomparison presented in Chapter 3, which found that simulated CO_2 fluxes were significantly less accurate at the bog site than at the fen sites. The intercomparison found substantial bias in simulated mean fluxes, and identified additional bias during wet periods. Together, these chapters suggest some key processes that could improve ecosystem model simulations of peatland CO_2 fluxes at diurnal, annual, and interannual time scales:

1. Improved simulations of hydrology: Ecosystem models could be coupled to spatial hydrological models, or the necessary processes and boundary conditions to simulate

water table fluctuations could be added.

2. Inundation effects on soil decomposition: Include suppressed soil respiration under saturated conditions.
3. Inundation effects on plant growth and photosynthesis: Plant growth should be suppressed under very wet conditions.
4. Differences in soil properties and plant communities between bogs and fens: Distinct plant functional types and soil parameterizations should be developed and calibrated for the two peatland types.

The results presented in Chapter 4 complement the previous chapters by expanding the focus to the longer time scales that are relevant to climate change and land use scenarios. This research also advanced the field by presenting a novel strategy for including peatland vegetation and soil processes in a landscape succession model that lacked explicit internal processes for hydrology and biogeochemistry. The model results suggest that the gradual, offsetting changes in respiration and productivity identified in inter-annual studies will be overwhelmed by changes in plant communities and soil carbon pools over century time scales. Furthermore, these changes could be globally relevant. When scaled by total wetland area, the modeled changes in carbon pools were equivalent to between a $4 - 15\%$ decrease or a $1 - 5\%$ increase in anthropogenic carbon emissions over 100 years, depending on the scenario (see page 98). These results suggest a fifth important process to be included in ecosystem models that will be used over time scales longer than a few years:

5. Changes in plant communities in response to long-term hydrological change: Hydrology-driven succession processes should be added.

Given the uncertainty in global carbon cycle feedbacks to climate, and large carbon pools contained in northern peatlands, and the magnitude of predicted warming in boreal regions, it is extremely important that coupled climate-carbon cycle earth system models include accurate representations of peatlands. Our results identify problems with current implementations, but also provide a roadmap for improving future simulations.

5.2 Time scales and ecosystem services

One of the most surprising results of this research was the large contrast between results at different time scales. Over inter-annual time scales, small fluctuations in water table cause relatively equal and opposite responses in both productivity and respiration (Chapter 2). These short-term changes contributed to biases in productivity and respiration simulated by commonly used ecosystem models (Chapter 3), with important implications for simulating interannual variability in peatlands, but did not lead to large interannual variations in NEE. The longer time scales investigated in Chapter 4 produced markedly different results, with large changes in carbon pools occurring over century and multi-century time periods.

Due to limitations in funding and the characteristic time scale of research projects, field studies of carbon fluxes have generally been limited to time periods of a few years. Only a small number of flux sites exist with time series of greater than a decade (such as Harvard Forest). Techniques such as chronosequences and historical inventories can be used to supplement these short-term results, but constructing reliable time series of ecosystem behavior over time scales relevant to land use planning and climate change remains difficult. As a result, it is tempting to extrapolate short-term studies to longer time scales in order to predict the outcomes of ecological changes. Our results highlight the danger of this approach, showing that short-term wetland responses to hydrological change can be quite different from long term responses. Based on inter-annual studies, decision makers might conclude that wetlands are resilient to lowering of water tables, since these studies showed little change in net ecosystem CO_2 balance. Over century time scales, our model results indicated that wetland drainage could result in a large increase in carbon uptake for large water table declines or no net effect for moderate declines, which could be used to justify converting wetlands to forest as a means of sequestering carbon. However, over time scales of several centuries, our results predicted nearly the opposite outcome, with the trajectory of carbon pools indicating a large continual loss of carbon into the future. Therefore, when interpreting the results of ecosystem studies, it is extremely important to consider whether the time scale of measurements or models matches the time scale of the problem being considered.

Another important consideration is the specific ecosystem service of interest. Peatlands provide multiple distinct ecosystem services, and their responses to ecological change at different time scales could produce tradeoffs (Table 5.1). For example, our results indicate that drainage could enhance peatland carbon uptake rates over century time scales as well as producing timber for potential harvest, but this occurs at the expense of decreased long term carbon storage, and would be accompanied by an immediate reduction in wetland habitat area. Over very long time scales, net carbon uptake would also be reduced due to the continued loss of soil carbon. So when making management choices, decision makers must be careful to consider the full impact on all important ecosystem services and time scales.

Table 5.1: Effects of wetland drainage on ecosystem services. Columns show the time scale being considered, and rows show different example ecosystem services.

Ecosystem service	Interannual	Century	Multi-century
C uptake	Neutral	Gain	Loss
Soil C	Loss	Gain	Loss
Vegetation C	Gain	Gain	Neutral
Total C storage	Neutral	Gain	Loss
Timber production	Gain	Gain	Gain
Wetland habitat	Loss	Loss	Loss

5.3 Limitations and future work

No study is perfect, and the methods used in this dissertation leave room for improvement in future research. Intercomparisons such as those presented in Chapters 2 and 3 are limited by the availability of data. In the North American peatland carbon cycling literature, Mer Bleue is by far the best represented bog site, and available data therefore may not represent the behavior of different sites, such as wetter bogs. Furthermore, only growing season measurements were available for some of the sites included in Chapter 2, which prevented analysis of the total annual carbon budget and its dependence on water table. There is a need for carbon flux measurements from a greater variety of peatland sites representing a range of climates, plant communities, and hydrological regimes, in order to better understand the variability between sites and peatland types.

Intercomparison studies are inherently limited to diagnostic statistical interpretations. Direct causality cannot be established without controlled studies, and therefore the direct relationship between drivers (e.g. water table) and responses (e.g. carbon fluxes) cannot be established with certainty. Controlled manipulation studies could solve this issue, but these can be difficult in peatlands due to operational difficulties and regulatory requirements for wetland preservation. Historical manipulations exist [e.g. *Minkkinen and Laine*, 1998b; *Laiho et al.*, 2003], but these can only be studied after the fact by comparing carbon pools, rather than directly measuring changes in carbon fluxes.

Model intercomparisons also face issues with determining causality. Different models contain different strategies for a wide range of ecosystem processes, so it is difficult to isolate the reasons for differences in model accuracy. A more ideal comparison would involve using different versions of a single model, so that specific processes could be modified. This would allow direct attribution of model error to specific model processes, as well as quantitative evaluation of the most effective areas for model improvement.

Another way to produce a more robust model comparison would be to include a “gold standard” model that was well-parameterized and designed to include peatland processes as realistically as possible. This model could serve as a basis of comparison for the other models, and would help identify how much room there is for improvement. A study designed around a hierarchical set of models chosen to represent a range of strategies, complexities, and spatial and temporal resolutions could produce more systematic and broadly applicable results.

The modeling study presented in Chapter 4 had a number of limitations related to the simple modeling strategy. The greatest weakness of the model was probably the assumption that soil properties did not change over time. This assumption was clearly violated by the increased inputs of carbon from vegetation growth in water table decline simulations, which changed the age profile of the soil. Additional decomposition was applied to soil pools to correct for this effect, but this correction was obviously less robust than including these changes directly in the simulation. In future versions of this model, one of the top priorities should be integrating changes in soil age over time into the model framework. The model also did not include soil subsidence, which could act as a negative feedback to water table fluctuations [*Dise*, 2009].

The area-based framework used to simulate the effects of water table on vegetation processes was also a simplification that ignored potentially interesting and important processes, and could be improved by using species-specific biological interactions related to soil saturation and related adaptations, and by directly including processes relating plant reproduction and establishment to soil wetness. These specific parameterizations could drive predictions of changes in specific species distributions, which would be useful for predicting changes in wetland wildlife habitat. A further improvement would be the explicit inclusion of nitrogen cycling and limitations on plant growth. More sophisticated carbon cycle models certainly exist, and a promising avenue for future research would be to apply the peatland processes identified above to a biogeochemistry and landscape succession model such as the ED2 model [*Medvigy et al.*, 2009].

Our model tests used simple water table scenarios (declines of 40 or 100 cm) that were applied equally to the entire landscape. These results could be better integrated into the context of climate change feedbacks by using a regional elevation map and a spatial hydrological model to directly compute changes in hydrology resulting from changes in temperature and precipitation. The ultimate goal would be to include this type of simulation in a fully coupled climate-carbon cycle earth system model, in order to directly evaluate peatland feedbacks to climate change.

A general weakness of this work was the focus on CO_2 fluxes. Fluxes of methane and dissolved carbon can be significant components of peatland carbon budgets [*Roulet et al.*, 2007; *Buffam et al.*, 2011]. Because methane emissions can be very sensitive to water table, and because methane is a more potent greenhouse gas than CO_2, it is important to place peatland CO_2 fluxes in the context of the complete greenhouse gas budget. Fluxes of dissolved carbon connect wetlands with the broader hydrological cycle, as significant amounts of carbon can be carried laterally and then either buried or outgassed downstream [*Hope et al.*, 2001; *Billett et al.*, 2004]. Clearly, constraining CO_2 flux responses to hydrological change is important due to the primary role of CO_2 in forcing climate change, but future work should expand the scope of this research to include the other important components of the peatland carbon balance.

Despite some weaknesses in scope and methods, this work advances the understanding of wetland carbon cycle responses to hydrological change and associated climate feedbacks. It highlights the roles of peatland **community types** and **community succession** in determining short- and long-term responses to hydrological change; identifies **overestimates of productivity and respiration**, responses to short-term **hydrological variations**, and differences between **bog and fen plant communities** as key sources of bias in model simulations of peatland carbon fluxes; and shows that consideration of peatland carbon cycles at **different time scales** can lead to dramatically different conceptions of how peatlands respond to hydrological change. It is my hope that these results will help ecosystem modelers to improve their simulations, and that they will inform discussions of the role of peatland management and climate responses in the earth system responses to climate change.

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