A COMPARISON OF CARBON DIOXIDE, WATER, AND ENERGY FLUXES AT A DRYING SHRUB WETLAND IN NORTHERN WISCONSIN, USA WITH NEARBY WETLAND AND FOREST SITES

by

Benjamin N. Sulman

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

Master of Science
(Atmospheric and Oceanic Sciences)

at the
UNIVERSITY OF WISCONSIN-MADISON
2009

Acknowledgements:

I would first of all like to express my gratitude to my academic and research advisor, Ankur Desai, who has been incredibly responsive, understanding, and helpful. I would not have made much progress without his assistance in data processing and his insightful comments on the interpretation of my results and the directions of my research. The faculty of the University of Wisconsin-Madison Atmospheric and Oceanic Sciences department have been a great resource, both inside and outside of class. I would especially like to thank Dan Vimont and Galen McKinley as well as Ankur Desai, who took the extra time to read and comment on this thesis. The AOS graduate student body, especially my officemates, were an indispensable source of camaraderie, support, and useful discussion. Also, thanks to Scott Ransom of the National Radio Astronomy Observatory, who introduced me to Numerical Python, the software I used for most of my analysis.

I would also like to thank Ron Teclaw and Dan Baumann of the U.S. Forest Service, and Jonathan Thom and Shelley Knuth of the AOS department for field technical support; Jon Martin of Oregon State for assistance with data and measurements; and Paul V. Bolstad of University of Minnesota and Kenneth J. Davis of Penn. State University for continued leadership of the ChEAS cooperative. Bruce Cook (University of Minnesota) and Nicanor Saliendra (U.S. Forest Service Northern Research Station, Rhinelander, WI) were very helpful in providing data as well as information about field sites and data collection.

This research was sponsored by the Department of Energy (DOE) Office of Biological and Environmental Research (BER) National Institute for Climatic Change Research (NICCR) Midwestern Region Subagreement 050516Z19.

Contents

List of Figures

List of Tables

Abstract

Wetland biogeochemistry is strongly influenced by water and temperature dynamics, and these interactions are currently poorly represented in ecosystem and climate models. A decline in water table of approximately 30 cm was observed at a wetland in northern Wisconsin, USA over a period from 2001-2007, which was highly correlated with an increase in daily soil temperature variability. Eddy covariance measurements of carbon dioxide exchange were compared with measured CO_2 fluxes at two nearby forests and two nearby wetlands in order to distinguish wetland effects from regional trends. As wetland water table declined, both ecosystem respiration and ecosystem production increased by over 20% at the main wetland site, while forest CO_2 fluxes had no significant trends. Net ecosystem exchange of carbon dioxide at the wetland sites was not correlated with water table, but wetland evapotranspiration was positively correlated with water table across the three wetland sites. These results suggest that changes in hydrology may not have a large impact on shrub wetland carbon balance over inter-annual time scales due to opposing responses in both ecosystem respiration and productivity, but that there may be important interactions between wetland water table and evapotranspiration rates and associated energy fluxes.

Note: Several sections of this document were published as a paper in the journal Biogeosciences: Sulman, B. N., Desai, A. R., Cook, B. D., Saliendra, N., and Mackay, D. S.: Contrasting carbon dioxide fluxes between a drying shrub wetland in Northern Wisconsin, USA, and nearby forests, Biogeosciences, 6, 1115-1126, 2009. URL: www.biogeosciences.net/6/1115/2009/

1 Introduction and Background

1.1 Ecosystem types and interactions with the atmosphere

Terrestrial ecosystems exist in the atmospheric boundary layer (ABL) and influence the atmosphere through transfers of energy, moisture, momentum, and trace gases. The processes of plant growth and the plasticity of ecosystem responses to climate forcing make biological feedbacks an important part of understanding long-term changes in climate. Major atmosphere-biosphere interactions include energy exchanges, evapotranspiration, and trace gas fluxes, and can change in response to ecosystem processes.

The amount of energy available for interactions between the atmosphere and biosphere is primarily controlled by insolation and albedo. Albedo refers to the reflectivity of the land surface to incoming solar radiation. A surface with high albedo reflects more solar radiation, and therefore absorbs less energy from the sun. Plant-covered areas generally have lower albedo than bare ground, snow, or desert, and different plant types often have different albedos. Expansion of forests, clearing of wild areas for agriculture, and desertification can all have large impacts on the energy budget of the land through changes in the amount of absorbed incoming solar radiation.

Most of the solar energy absorbed by the land is dissipated to the atmosphere through longwave radiation emission, sensible heat flux, and latent heat flux. The emission of longwave radiation is mostly dependent on temperature, and does not vary strongly with landcover type (Campbell and Norman, 1998). The partitioning of the remaining energy between sensible and latent heat fluxes can be strongly dependent on dominant ecosystems and vegetation. Plants absorb water from the soil through their roots and transfer it up stems to their leaves, where it is released to the atmosphere through transpiration. Vegetation can significantly increase the rate at which water is exchanged between the land and atmosphere by efficiently transferring water from the soil to the atmosphere. Plants can also control the rate of water exchange through physiological processes in order to conserve water during dry periods or to moderate leaf temperatures, leading to more powerful feedbacks and interactions in moisture exchange than would exist in a simpler system without biological control of exchange rates. The Bowen ratio, defined as the ratio between sensible and latent heat flux, is an important parameter of land-atmosphere interaction:

$$B = \frac{H}{\lambda E} \tag{1}$$

where B is the Bowen ratio, H is the sensible heat flux, and λE is the latent heat flux. A closely related value is the evaporative fraction (EF):

$$EF = \frac{\lambda E}{H + \lambda E} \tag{2}$$

the ratio of latent heat flux to total turbulent heat flux to the atmosphere. Variations in these parameters can have important impacts on regional climate. Areas with a low EF transfer most heat to the atmosphere through direct temperature exchange, and are likely to have a warmer atmosphere and lower humidity. This is typical of deserts and built-up areas such as cities. Areas with a high EF transfer most energy to the atmosphere as latent heat in evaporated water. Ecosystems with high rates of evapotranspiration and water cycling, such as tropical rainforests, have high EFs, and are associated with lower temperatures and high precipitation and humidity. Shifts between these landscape types and their associated EFs can have important implications for regional climate (Foley et al., 2003; Sampaio et al., 2007).

Transfers of momentum between the land and atmosphere have important impacts on atmospheric circulation, especially in the boundary layer. The surface of the earth is the major frictional forcing on the atmosphere. The amount of friction is related to the roughness, a parameter that depends on the shape of the land surface. Different landcover types lead to different roughness values, which affect turbulence in the boundary layer, friction on atmospheric circulation, and the rates of transfers of energy and trace gases through the boundary layer. Forests with tall trees and cities with tall buildings have high roughness values, promoting more turbulence and higher transfer rates, while deserts, prairies, and other landcover types have low roughness values. Expansion or destruction of forests and increased growth of woody plants can change landscape roughness and momentum transfer over time scales of years to decades.

Transfers of trace gases between the land and atmosphere affect the composition of the atmosphere. The major impact of these composition changes is on the opacity of the atmosphere to longwave radiation (the greenhouse effect). Plants absorb carbon dioxide, the most important greenhouse gas, through photosynthesis as they grow. Terrestrial plant growth is an important sink of CO_2 on a global scale, absorbing approximately 25% of anthropogenic emissions on a yearly basis (Denman et al., 2007). Plants and soils also represent a major pool of carbon that can be converted to CO_2 and released to the atmosphere through decomposition and burning. Peatlands are characterized by thick, rich, organic soils and contain a large portion of global carbon reserves (Limpens et al., 2008; Gorham, 1991). Tropical rainforests contain large carbon reserves as well, but store most of the carbon in above-ground biomass.

Other important greenhouse gases are also produced in terrestrial ecosystems. Methane, an important greenhouse gas, is produced by a number of biogenic processes. While current methane emissions are dominated by anthropogenic sources such as rice agriculture and livestock, natural wetlands are the largest single source (Forster et al., 2007), and are also an important source of N_2O (Junkunst and Fiedler, 2007). Other important trace gas emissions from terrestrial ecosystems include volatile organic compounds (VOCs), which are an important source of atmospheric aerosols in certain regions (the Blue Ridge and Smoky Mountains gained their names due to biogenic aerosol effects) and may play important roles in cloud formation (Guenther et al., 1995; Griffin et al., 1999).

The fluxes of trace gases between the atmosphere and land are almost completely dependent on biological processes, and can be very sensitive to changes in climate, ecology, and land use. CO_2 fluxes from ecosystems depend on the balance between ecosystem respiration (ER) and gross ecosystem production (GEP). The net ecosystem exchange (NEE) of carbon dioxide is equal to the difference between CO_2 removed from the atmosphere by photosynthesis (GEP) and the CO_2 added to the atmosphere when organic compounds are metabolized by organisms to produce energy (ER). If NEE is positive, the ecosystem is emitting CO_2 to the atmosphere, and if NEE is negative then the ecosystem is removing CO_2 from the atmosphere. Typically, ER and GEP are very similar in magnitude and small changes in either can result in large fractional changes in NEE. Other important greenhouse gases such as CH_4 and N_2O are produced by anaerobic decomposition in oxygen-depleted soils, and the production rates are highly dependent on the interactions of ecology, hydrology, and geology that produce anoxic zones.

1.2 Wetlands and peatlands

The terms “wetland” and “peatland,” which appear many times in this document, are often used interchangeably, but have different definitions. Wetlands are defined based on hydrology and typical ecological communities, whereas peatlands are defined by the presence of peat, a thick, purely organic layer of soil. Since the hydrological properties of wetlands often lead to the development of peat, there is much overlap between wetlands and peatlands.

Wetlands have historically been defined in many different ways. Because wetland preservation is an important legal issue, specific legal definitions of wetlands exist, but these may not reflect the ecological and physical processes behind wetland formation. The Ramsar Convention, an international treaty on wetlands preservation, defines wetlands as “areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres” (Ramsar Convention, 1994). This broad definition includes flooded river banks and coastal areas that are inundated by tides, in addition to the groundwater- and rainwater-fed northern wetlands that are the focus of this paper.

Peatlands are defined as ecosystems that have accumulated thick layers of rich, organic soil. Common definitions focus on the thickness of the pure organic layer of soil. Different studies have used minimum peat thicknesses from 20 cm to 40 cm to define peatlands (Mitra et al., 2005). Peat accumulation depends on a positive soil carbon balance, where inputs of detritus from vegetation are larger than the rate of decomposition.

This can occur in tropical areas with high productivity and wet climate, or in high latitudes where climatic and local conditions lead to slow decomposition. The major high latitude peatland types are tundra and wetlands. In tundra ecosystems, sub-freezing temperatures in the soil prevent decomposition, allowing peat to accumulate. High-latitude wetlands occur in areas where warm, wet growing seasons and cold winters lead to high productivity, low evapotranspiration, and a positive water balance, including large portions of the northern United States, Canada, northern Europe, and Siberia (Mitra et al., 2005). Because of wet conditions, the soil is saturated with water for a large proportion of the year. Oxygen has very low diffusivity through saturated soil, so soil layers below the water table quickly become anoxic, leading to very slow rates of decomposition that allow reserves of peat to accumulate (Clymo, 1984). These high-latitude wetlands (which may or may not also be peatlands) are the focus of this paper.

1.3 The northern wetland carbon pool

Peatlands represent an important part of the terrestrial carbon cycle due to their large stores of soil carbon. Northern subarctic peatlands, which exist in a broad belt across the northern hemisphere between about 45°N and 65°N, represent up to one half of the total global wetland area (Harriss et al., 1985; Mitra et al., 2005). Globally, boreal and subarctic peatlands represent only about 3% of terrestrial landcover area but store between 270 and 370 Pg (a Pg is 10^{15} g) carbon as peat, up to one third of the total global soil carbon reserves (Limpens et al., 2008; Gorham, 1991). By comparison, the total mass of carbon dioxide in the atmosphere represents 796 Pg carbon (Forster et al., 2007). Since the process of peat storage is sensitive to climate and hydrology, future changes in climate and hydrology as a result of global climate change could potentially change the carbon balance of northern wetlands. If large portions of the peatland carbon pool were mobilized into the atmosphere, it would represent a large positive feedback to climate change.

1.4 Wetland greenhouse gas production and radiative forcing

The major greenhouse gases associated with wetlands are CO_2 (carbon dioxide) and CH_4 (methane). N_2O is also a potent greenhouse gas produced under anaerobic conditions, but it was not included in this study due to sparse data and small estimated significance. CO_2 is produced as an end product of aerobic decomposition, and is absorbed from the atmosphere by plants during photosynthesis. Peat reserves represent carbon that has been removed from the atmospheric CO_2 pool and stored as organic compounds. Currently, peatlands represent a global carbon sink of approximately 0.076 Pg C/yr (Gorham, 1991).

Since different atmospheric components interact with radiation in different ways, different gases are compared to CO_2 using global warming potentials (GWP). GWP is the ratio of the radiative forcing due to the emission of 1 kg of the gas, compared to that of 1 kg of CO_2, integrated over a specified time period. GWP accounts for differences in the instantaneous heat-trapping efficiency of each gas, as well as lifetime in the atmosphere and the indirect effects of decay products. The GWP of CO_2 is 1 by definition. Methane has a radiative efficiency approximately 26 times higher than CO_2, and a lifetime in the atmosphere of about 12 years. In the actual calculation of GWP, the effects of other decay products on atmospheric chemistry are also taken into account. These indirect effects include increased radiative forcing due to the production of tropospheric ozone and stratospheric water vapor as methane degrades in the atmosphere. Due to the substantial radiative forcing effects of these decay products, methane has a GWP of 25 over a 100 year time horizon even though it has a shorter lifetime than CO_2, meaning that over the next hundred years a kilogram of methane in the atmosphere will cause the same estimated warming effect as 25 kg of CO_2 emitted at the same time.

Methane is produced as a result of anaerobic decomposition in anoxic areas of the soil (Clymo, 1984). Methane exists in the atmosphere in much smaller concentrations than CO_2 (1.7 ppm compared to about 380 ppm). Global total methane emissions are difficult to determine due to high spatial variability, but have been estimated at between 0.05 and 0.1 Pg/yr (Matthews and Fung, 1987; Gorham, 1991). Methane ranks second among long-lived greenhouse gases in terms of atmospheric radiative forcing effects, and wetlands are thought to represent the single largest source of methane to the atmosphere (Denman et al., 2007).

N_2O (nitrous oxide) is another gas produced by anaerobic decomposition in wetland soils. It has a lifetime in the atmosphere of 114 years and a GWP of 298 over a 100-year time horizon. Its concentration in the atmosphere is increasing, and its decay products are important components of ozone depletion in the stratosphere (Forster et al., 2007). However, few wetland gas exchange studies have measured fluxes of N_2O, and most available data show that even after scaling by GWP N_2O fluxes represent less than 1% of total CO_2-equivalent greenhouse gas emissions from typical wetlands, except in cases associated with agricultural fertilizer inputs (Junkunst and Fiedler, 2007). N_2O emissions can thus be neglected for first approximation global estimates, and are not addressed in this paper.

1.5 Predicted climate changes affecting boreal wetlands

Anthropogenic climate change has been observed as a result of carbon dioxide emissions for several decades (Pachauri and Reisinger, 2007). The direct effects of rising concentrations of heat-trapping gases in earths atmosphere have been reasonably well constrained using models of radiative transfer and global climate simulations, but future interactions between climate change and biogeochemistry are not as well understood. On average, terrestrial ecosystems absorb approximately 25% of anthropogenic CO_2 emissions (Denman et al., 2007), providing a significant buffer to climate change. The future of this terrestrial carbon sink is poorly constrained in global ecosystem models due to uncertainties in interactive effects, potential ecosystem change, and the different sensitivities of ecosystem production and respiration to changes in climate (Friedlingstein et al., 2006).

The major impacts of climatic changes on wetlands can be divided into the direct effects of higher temperatures and the indirect effects attributable to lowering water tables. Higher temperatures are primarily expected to impact wetland biogeochemistry by changing the metabolic rates of the microorganisms responsible for decomposition processes in the peat, as well as by changing the length of the growing season for vegetation on the wetland. Changes in water table affect the size and location of anaerobic and aerobic zones in the soil (Clymo, 1984), and may also affect the dominant plants on the wetland.

Studies using general climate models (GCMs) indicate a predicted 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. High latitudes are expected to experience more dramatic changes than the global average, and the northern areas where boreal wetlands 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. Northern areas with large concentrations of wetlands are also expected to experience increases in precipitation, but much of this increase is likely to be in intense precipitation events (Meehl et al., 2007). The increased temperature will lead to greater evapotranspiration, causing soil drying and drops in water table (Meehl et al., 2007). If the overall water balance shifts from positive (more precipitation than evaporation) to negative (more evaporation than precipitation), the impacts on wetland biogeochemistry could be profound.

Large-scale changes in climate must be interpreted in order to understand specific impacts on wetlands. Wetland-specific simulations have predicted a summertime drop in water table of approximately 0.14 m for northern peatlands (Waddington et al., 1998). The effect on individual wetlands will depend on many local factors, including peat depth, local hydrology, dominant plant communities, and the primary water source. Wetlands that are fed by surface or groundwater flows may be resilient to changes in climate until the water source is affected, while rain-fed ecosystems will be more vulnerable to short-term changes in atmospheric inputs. Large-scale changes in climate can still be expected to cause net changes in wetland biogeochemistry when averaged over large areas, since small-scale heterogeneity will average out.

1.6 Methods for measuring land-atmosphere exchange of trace gases in wetlands

Exchanges of trace gases between wetlands and the atmosphere can be studied using models, chamber measurements, laboratory measurements of soil cores, or eddy covariance atmospheric measurements. Models typically represent respiration as a function of temperature, available labile carbon, and soil chemistry and hydrology. They are compared to other measurements to ensure that the results are realistic, and can be used to simulate processes over large temporal and spatial scales that are impractical to study using measurements or manipulations. Models generally include soil processes (e.g. Potter, 1997; Ise et al., 2008), and some include vegetation dynamics (e.g. Frolking et al., 2002; Zhang et al., 2002). They are therefore useful for studying the evolution of wetland CO_2 and methane balance under future climate scenarios, but may be susceptible to hidden assumptions and uncertainties about ecosystem processes.

Chamber measurements are conducted by sealing a container to a small (typically 1 m^2) area of soil and recording the change in trace gas concentration inside the container. The major methods are closed and flow-through chambers (Hutchinson and Livingston, 2002). Closed chambers are sealed away from the atmosphere, and the rise in trace gas concentration with time is measured and converted to an emission measurement. Flow-through chambers use measurements of air at an inlet and outlet, and deduce emissions from the change in trace gas concentration between air entering and leaving the chamber. Chambers can be used to measure CO_2, methane, and many other trace gases. Chambers are relatively simple to use, but are limited to small spatial areas and short time periods because they must typically be hand-deployed in the field. Therefore multiple measurements, upscaling and gap filling are necessary in order to generate estimates of ecosystem-scale fluxes over seasonal time scales (Davidson et al., 2002). Due to their small size, chambers generally cannot include the effect of vegetation except for very small plants such as mosses, and therefore usually only provide estimates of soil respiration, not total ecosystem respiration or GEP.

Laboratory measurements involve removing soil profiles from the wetland and studying them in a controlled setting. They can be very useful for controlled manipulations, and the ability to conduct controlled experiments can provide insights about the effects of changes in environmental parameters such as temperature and moisture on soil processes (e.g. Moore and Knowles, 1989). The controlled setting also makes it easy to measure trace gases and ecological properties that are difficult to measure in the field. Since they involve removing soil from the ecosystem, laboratory measurements are limited to ER, and cannot include many potentially important ecosystem processes, such as vegetation growth and reproduction. Laboratory measurements therefore may produce results that do not occur in natural settings. Mesocosm studies are similar to laboratory measurements, but involve larger volumes of soil, usually with associated plants still intact. They can be used to manipulate temperature and moisture levels in controlled studies while incorporating more ecosystem processes than laboratory-based soil measurements (e.g. Updegraff et al., 2001), but may still introduce artifacts due to the removal and isolation of limited portions of the ecosystem.

Eddy covariance uses measurements of turbulence in the boundary layer to determine exchanges of energy, moisture, and trace gases between the land and atmosphere (see Sect. 2.1). Unlike laboratory and chamber techniques, eddy covariance can be used to measure fluxes of sensible and latent heat fluxes in addition to trace gas fluxes. The technique also provides long, continuous data time series, allowing more reliable estimates of seasonally integrated fluxes. Due to the limitations of available technology, it is currently difficult to measure trace gases other than CO_2 using eddy covariance. Because the technique depends on the statistical nature of atmospheric turbulence, there is significant random error in flux estimates, and there may be bias or missing periods of data due to suboptimal atmospheric conditions.

Long-term carbon accumulation rates in wetlands can also be estimated using peat soil cores. Age of peat at different depths can be estimated using markers such as radioactive isotopes (Kuhry, 1994; Turunen et al., 2001) or preserved pollen (Pitkänen et al., 1999). The mass of peat divided by its average age gives an estimate of long-term apparent rate of carbon accumulation (LORCA), which is useful for comparing with contemporary measurements and for investigating the history of peatlands. Historical fire frequency and climate perturbations can be identified and dated using these peat core investigations, and the effects of disturbances that occurred before continuous flux measurements were possible can be estimated.

1.7 Previous studies on the effects of temperature and hydrology on wetland CO_2 fluxes

CO_2 fluxes from ecosystems depend on the balance between ecosystem respiration (ER) and gross ecosystem production (GEP). The net ecosystem exchange (NEE) of carbon dioxide is equal to the difference between CO_2 removed from the atmosphere by photosynthesis (GEP) and the CO_2 added to the atmosphere by aerobic decomposition of organic matter (ER). If NEE is positive, the ecosystem is emitting CO_2 to the atmosphere, and if NEE is negative then the ecosystem is removing CO_2 from the atmosphere. The large reserves of soil carbon contained in wetland peat are the legacy of long periods of negative NEE, which can persist because excess organic matter is preserved in anoxic soil below the water table.

The impact of climatic changes on wetland NEE depends on both respiration and productivity effects. Changes in hydrology and temperature are expected to impact both ER and GEP. In the dry upper layer of peat where oxygen can penetrate, aerobic decomposition can degrade detritus fairly quickly, releasing CO_2 to the atmosphere. Below the water table, decomposition rates are limited by lack of oxygen, and anaerobic decomposition dominates (Clymo, 1984). Therefore, if the water table declines, the expected effect would be an increase in ER and CO_2 emission as more peat becomes available for aerobic decomposition. Decomposition rates also have a well-known dependence on temperature, since metabolic rates of microorganisms increase at higher temperatures. Thus, higher soil temperatures should be correlated with higher decomposition rates and higher CO_2 emissions.

Changes in water table and temperature can also have significant impacts on GEP. Many wetland plants are limited by their ability to maintain roots in waterlogged soils. If the water table drops, it becomes easier for plants to supply their roots with oxygen, and soil becomes more solid and able to support larger trees. Thus, drier conditions are expected to be correlated with increased plant growth and higher GEP. If there are dramatic changes in hydrology, different plant communities could take over, resulting in large changes to GEP and biomass of the ecosystem. Higher temperatures could also lead to increases in GEP through lengthening of the growing season. However, if changes in hydrology and temperature are out of an optimal range for plant growth, there could be deleterious effects on plants due to water and temperature stress.

Laboratory measurements of the effects of changes in hydrology on wetland soil respiration show that drier conditions promote enhanced CO_2 emission (Moore and Knowles, 1989; Freeman et al., 1992). Many studies conducted in the field using chambers or eddy covariance measurements also agree with the hypothesis that soil respiration increases with declining water table. Bubier et al. (1998) observed that surface soil temperatures and water table were the most important controls on ER in a peatland system in Canada using chambers, and Lloyd (2006) observed a similar effect in a European wetland meadow using eddy covariance. Silvola et al. (1996) observed that draining increased soil CO_2 fluxes by approximately 100%, based on chamber measurements.

Whole-ecosystem studies that include GEP as well as ER can give a more complete sense of the effects of changes in temperature and hydrology on peatland CO_2 fluxes. Several studies have shown that peatlands can change from a sink to a source of carbon dioxide during short dry periods. Alm et al. (1999) observed a rise in respiration at a bog during a dry summer where the water table dropped substantially. Respiration exceeded GEP during the dry period, leading to a net loss of carbon from the wetland. Schreader et al. (1998) observed a similar net release of CO_2 during a hot, dry summer at a sedge fen in Manitoba, and Shurpali et al. (1995) found that a peatland in Minnesota was a source of CO_2 during a dry summer and then a sink during the following wetter summer. A similar contrast in NEE between wet and dry seasons was observed in two European bogs by Arneth et al. (2002).

These results suggest that warming and drying can change peatlands from net sources to net sinks of CO_2, a potential positive feedback to climate change. However, this effect has mostly been observed during short, intense dry periods. While climate change is expected to increase the incidence of droughts and heat waves, these studies do not address possible long-term changes in ecology or soil properties that could compensate for the effects of drying. Several studies of peatlands that experienced longer dry periods have shown that the net emission of CO_2 is not necessarily persistent. As water table drops below a certain level, the thickness of the existing peat layer may prevent soil decomposition at deeper levels even if they are no longer saturated. This hypothesis was supported by the results of Lafleur et al. (2005b), who observed that respiration depended on soil temperature but not water table depth in a bog with a water table persistently more than 30 cm below the soil surface. Nieveen et al. (2005) similarly observed that ER in a peatland that had been drained and converted to pasture did not depend on water table.

Other studies of CO_2 balance at peatlands subjected to long-term draining have shown that drier conditions promoted increased GEP that compensated for increases in ER. Strack and Waddington (2007) conducted a study in which a bog was experimentally drained, with the results that both ER and GEP increased. After three years, there was no significant difference in CO_2 fluxes between experimental and control sites. Studies of even longer periods using peat cores have confirmed that the peatland carbon sink can be resilient to drying. Minkkinen and Laine (1998a) found that 60 years after being drained and converted to forest, a peatland had actually increased the amount of carbon stored in peat, probably because of soil compaction and increased fine root production. In an analogous situation in an Alaskan tundra ecosystem, Oechel et al. (2000) found that the ecosystem initially changed from a sink to a source, but that CO_2 emissions decreased and eventually became negative during summers over a 40-year period. These results suggest that short-term emissions of CO_2 from peatlands during dry periods may not reflect the actual evolution of wetland CO_2 balance under long-term drying and warming conditions. Models that do not include plant succession and changes in soil properties may miss important ecosystem changes that make peatland carbon sinks more resilient to climatic change than would otherwise be expected.

One important effect not considered in the aforementioned studies is fire. Unlike the gradual, largely deterministic changes in biogeochemistry and ecosystem structure investigated above, fire is a fast, stochastic process, which occurs rarely but can have extremely intense impacts. Warming and drying of peatlands is expected to increase the incidence of fire, as both peat and vegetation are more susceptible to burning when dry. In mixed landscapes, the increased risk of forest fires due to favorable climatic conditions could combine with drier peatlands that are less resistant to burning to greatly increase fire frequency. Peat core studies can identify burning events from charcoal layers in the peat. Turunen et al. (2001) found that past fire events in Siberian mires were rare, occurring only 2-3 times over the past 7000 years, and that historical fires had not caused significant carbon losses over the history of their study site. Another study of peatlands in Finland found that an average of 25 fires per sampling plot had occurred, in peatlands with ages between 5000 and 10,000 years, but that burning had essentially ceased about 2000 years ago (Pitkänen et al., 1999). Their results also indicated that frequently burned peatlands had much lower long term carbon accumulation rates, and that there could be large losses of carbon of up to 2.5 kg/m2 during burning events. Kuhry (1994) similarly found that fire frequency decreased substantially about 2500 years ago, and that higher fire frequency was correlated with lower rates of peat accumulation. These results suggest that if fires on peatlands become more common under future climate change, there could be significant reductions in peat accumulation rates and wetland carbon sinks, potentially resulting in net emissions of CO_2 to the atmosphere and operating as a positive feedback to climate change.

1.8 Previous studies on the effects of temperature and hydrology on wetland methane fluxes

Wetland methane is produced primarily as a product of anaerobic decomposition in waterlogged peat. While anthropogenic sources currently dominate the global methane budget, wetlands are thought to represent the largest single source of methane to the atmosphere, making wetland methane emissions an important component of the global greenhouse gas budget (Forster et al., 2007). The metabolic pathway that ends with methane is one of the least efficient sources of energy for microorganisms, so methanogens dominate only in waterlogged soils where oxygen and other chemicals that allow more desirable forms of metabolism are depleted (Clymo, 1984). Methane moving upwards through the soil profile can be absorbed and metabolized in dry soils where oxygen is available (Roulet et al., 1993), so net emission of methane from wetlands to the atmosphere depends on both the existence of anoxic, waterlogged soils and on a water table close enough to the surface that methane can escape. Lowering of water table is expected to decrease emissions of methane by decreasing the waterlogged portion of the soil and increasing the dry layer where methane can be degraded. Higher temperatures are expected to increase rates of methane emission by increasing the metabolic rates of methanogens.

Measurements of methane emissions in peatlands and peat soils have generally confirmed the above hypotheses. Moore and Knowles (1989) found in a study of peat soils under laboratory conditions that changes in water table were positively correlated with methane emission, a result confirmed by several studies using chambers in peatlands (Dise et al., 1993; Smemo and Yavitt, 2006; Turetsky et al., 2008; Strack et al., 2004). Thus, the hypothesis that raising water table increases wetland methane emissions and lowering water table decreases them is widely confirmed. If future changes in climate result in large losses of peatland area due to drying, then there would be a reduction in emissions of methane from peatlands, a negative feedback to climate change.

The interactions of wetland methane emissions with temperature changes complicate this proposed feedback. Field studies of wetland methane emissions have consistently observed a positive correlation between temperature and methane production (Dise et al., 1993; Kettunen et al., 1996; Turetsky et al., 2008; Bubier et al., 1995). If large changes in water table occur, they are likely to dominate control of the methane budget, but if there are not large hydrological changes, warming of peatland soils could cause increased methane emissions. In a modeling study that incorporated a methane emission scheme into a global climate model, Gedney et al. (2004) concluded that rising temperatures would dominate the impacts on future wetland methane emissions, resulting in a future increase in methane emissions from wetlands.

In a modeling study, Frolking et al. (2006) examined the relative effects of methane and carbon dioxide emissions from wetlands over long time scales. They concluded that the increased methane emissions caused by wetland formation should dominate atmospheric effects for an initial time period between several hundred to a few thousand years. The radiative forcing will eventually become negative as CO_2 sequestration effects begin to dominate the balance.

1.9 Experiment description

A trend of declining water table height has been observed over several years at a shrub wetland site in northern Wisconsin, providing an opportunity to directly study the effects of a continuous change in hydrology on land-atmosphere interactions at a wetland ecosystem over a multiple-year time scale. Eddy covariance measurements (see Section 2.1) taken at the drying wetland as well as other wetland and upland sites in the same region over the same time period present a unique opportunity for comparison between ecosystem types subject to the same regional climate forcing, which allows us to separate regional responses from those specific to individual sites and ecosystems, and explore the interactions between climatic effects and biological feedbacks in the wetland ecosystem. This study tested the following hypotheses regarding carbon dioxide exchange between the shrub wetland ecosystem and atmosphere:

1. Lower water table is correlated with increased ER. In theory, a lower water table

exposes more soil to oxygen, increasing the rate of decomposition and the amount of carbon dioxide released to the atmosphere (Clymo, 1984).

2. Lower water table is correlated with increased GEP. In theory, a lower water table makes more nutrients and oxygen available to roots, allowing plants to grow and photosynthesise more efficiently.

3. Since a lower water table increases both ER and GEP, the net effect of water table on NEE is small compared to other sources of variability.

Eddy covariance measurements were also used to investigate changes in energy balance coincident with the change in hydrology. Measurements at the shrub wetland were compared with measurements at a mature forest and an old-growth forest in the same region, as well as with a sedge-dominated wetland and a bog.

2 Sites and Methods

2.1 The eddy covariance technique

Fluxes of heat, moisture, and carbon dioxide between ecosystems and the atmosphere were measured for this study using the eddy covariance technique. Eddy covariance is a micrometeorological method that uses high-frequency measurements in the turbulent boundary layer to determine vertical fluxes of heat, moisture, and trace gases such as carbon dioxide (Baldocchi et al., 1988; Baldocchi, 2003).

2.1.1 Theoretical basis and important assumptions

The theory of eddy covariance is based on Reynolds decomposition of the conservation of mass equation for a tracer in the atmosphere. In this discussion, which follows Baldocchi (2003), overbars indicate the time average of a quantity and primes indicate fluctuations from the mean. The time series of values for a tracer c is $c(t) = \bar{c} + c'(t)$.

This decomposition of measurements between averages and fluctuations can be used to separate fluxes from advection. The conservation of mass equation for a tracer mixing ratio c (ignoring molecular diffusion) is

$$\frac{dc}{dt} = \frac{\partial c}{\partial t} + u\frac{\partial c}{\partial x} + v\frac{\partial c}{\partial y} + w\frac{\partial c}{\partial z} = S(x, y, z) \tag{3}$$

where u, v, and w are wind velocities and S is the source of the tracer due to external processes such as air chemistry or biological activity. Dividing each variable into average and fluctuations and then averaging gives the following equation:

$$\frac{d\bar{c}}{dt} = \frac{\partial \bar{c}}{\partial t} + \left(\bar{u}\frac{\partial \bar{c}}{\partial x} + \frac{\partial \overline{u'c'}}{\partial x}\right) + \left(\bar{v}\frac{\partial \bar{c}}{\partial y} + \frac{\partial \overline{v'c'}}{\partial y}\right) + \left(\bar{w}\frac{\partial \bar{c}}{\partial z} + \frac{\partial \overline{w'c'}}{\partial y}\right) = \bar{S} \tag{4}$$

In this equation, the terms for each wind vector are divided into products of means, which represent advection, and covariances between fluctuations in the wind and the tracer, which represent turbulent fluxes. Thus, conservation of mass requires that the sum of the local time rate of change of a tracer concentration and advection be balanced by the sum of flux divergence of the tracer and the source/sink strength. In the case of CO_2, which has no atmospheric source/sink, this relation can be rearranged into the following:

$$\underbrace{\frac{\partial \bar{c}}{\partial t}}_{\text{I}} + \underbrace{\bar{u}\frac{\partial \bar{c}}{\partial x} + \bar{v}\frac{\partial \bar{c}}{\partial y} + \bar{w}\frac{\partial \bar{c}}{\partial z}}_{\text{II}} = -\underbrace{\left(\frac{\partial \overline{w'c'}}{\partial z} + \frac{\partial \overline{u'c'}}{\partial x} + \frac{\partial \overline{v'c'}}{\partial y}\right)}_{\text{III}} \tag{5}$$

where term I represents the local rate of change, II advection, and III flux divergence. For eddy covariance measurements, this equation is simplified using the following assumptions:

1. Average atmospheric conditions are constant in time
2. The surface is horizontally homogeneous and flat

These assumptions mean that advection (II) and horizontal flux divergences are zero. Thus simplified, the conservation equation becomes:

$$\frac{\partial \bar{c}}{\partial t} + \frac{\partial \overline{w'c'}}{\partial z} = 0 \tag{6}$$

By vertically integrating this equation from the designated surface level ($z = 0$) to a measurement height h, we develop a relationship between the measured vertical tracer flux, the storage of the tracer in air below the measurement point, and the net flux density of the tracer from biological processes below the measurement point:

$$F_z(0) = \overline{w'c'}(h) + \int_0^h \frac{\partial \bar{c}}{\partial t}(z)dz \tag{7}$$

where $F_z(0)$ is the net ecosystem exchange (NEE) of the tracer at the lower bound of the integration. In a complex canopy such as a forest, this level may be at or above the trees, but theoretically represents the interface between the ecosystem and the atmosphere.

$\overline{w'c'}$ can be calculated from high-speed measurements of vertical wind velocity and tracer concentration, and the storage term can be estimated from a vertical profile of tracer concentration and temperature measured at several different heights on the tower.

In practice, c can represent mixing ratios of carbon dioxide for the calculation of CO_2 fluxes, water vapor mixing ratios for latent heat fluxes, air temperature for sensible heat fluxes, or horizontal wind velocities for measuring momentum fluxes.

2.1.2 Equipment and practical measurements

Eddy covariance measurements require time series of wind velocity and the tracer of interest at high temporal resolution. 10 Hz is generally accepted as the minimum sampling frequency necessary to capture the high-frequency portion of the turbulent spectrum (Baldocchi, 2003; Goulden et al., 1996). Typically, sonic anemometers are used in conjunction with high-speed infrared gas analyzers. Sonic anemometers measure the travel time of ultrasonic sound pulses between transducers at three orthogonal angles, which can then be rotated into the desired coordinate system. The average travel time in both directions between transducers gives the speed of sound in the air, which can be converted into a measurement of virtual air temperature. The difference in travel time in opposite directions between transducers gives the wind speed in that direction.

Infrared gas analyzers (IRGAs) use the radiation absorption spectrum of air to determine gas concentrations. Infrared absorption measurements must be corrected for the density of air to be converted into gas concentrations, so fluctuations in air pressure and humidity can have important impacts on measured gas concentrations. Commonly used IRGAs measure concentrations of CO_2 and H_2O in the air, but some IRGAs can be tuned to measure concentrations of other gases, such as methane, and have been used to measure fluxes of different carbon isotopes in CO_2 (Bowling et al., 2001). There are two major kinds of IRGAs, open path and closed path gas analyzers. Closed-path IRGAs draw air down a tube to a closed chamber. They typically require periodical calibration using gas standards due to sensor drift, and must be corrected for time lags and spectral attenuation due to the time taken for air to flow through the tube to the sensor. A major advantage of closed path IRGAs is that the measurement is taken under controlled and measured pressure conditions, so fluctuations in pressure do not influence the gas concentration measurements (Leuning and Judd, 1996).

Open path gas analyzers measure attenuation of infrared light in the open air. Because air is not drawn through a tube, lags and spectral attenuation are less problematic for open path gas analyzers. Open path IRGAs also have much more stable calibrations, so they do not need to be recalibrated with gas standards as often as closed path gas analyzers. However, since the gas measurement is taken in the open air, high-frequency pressure fluctuations affect the measured gas concentrations. Since pressure cannot be precisely measured at high temporal resolution with currently available equipment, open-path IRGA measurements must be corrected using a parameterization called the WPL correction, which accounts for fluctuations in density using measurements of temperature and moisture fluxes (Webb et al., 1980).

Either kind of gas analyzer may be used depending on experiment conditions and the preferences of the investigators. Previous studies have shown that the two methods generate consistent results when the proper design choices are used and necessary corrections are applied (Leuning and Moncrieff, 1990; Lee et al., 1994; Leuning and King, 1992).

Eddy covariance measurements can be taken from land-based or aircraft-based platforms. Only land-based measurements were used for this work. Land-based eddy covariance measuring equipment is typically mounted on a tower, with an optimal height that depends on the roughness and inhomogeneity of the landscape (Schmid and Lloyd, 1999). Eddy covariance measurements have a footprint (the land area that measured fluxes represent) that depends on tower height, surface roughness, and atmospheric conditions (Schmid, 1994). A good rule of thumb is that the average radius of a flux tower footprint is about 10–100 times the height of the tower.

Since the mathematical theory behind eddy covariance assumes horizontal homogeneity, the choice of where to locate a flux tower can be very important. The terrain needs to be flat and essentially homogeneous within an area somewhat larger than the flux footprint or there may be erroneous measured fluxes that depend on wind direction or speed rather than terrestrial processes. In some cases, fluxes measured when the wind is blowing from certain directions may need to be discarded if it is determined that those fluxes are unrepresentative of the landscape of interest (e.g. Cook et al., 2004; Desai et al., 2005).

The other important assumption, that average atmospheric conditions are constant in time, has important implications for the time scale of eddy covariance measurements. The time steps used for calculating covariances must be long enough to capture the large eddies that account for much of the turbulent transfers, but short enough that large-scale advection, diurnal variation, and synoptic-scale changes in temperatures and tracer concentrations do not affect the calculations. The typical time scale for eddy covariance calculations is 30–60 minutes (Baldocchi, 2003).

Because eddy covariance measurements depend on turbulent mixing, they must be screened for low-turbulence conditions. When there is not sufficient vertical mixing, the boundary layer at the measurement height can become decoupled from the surface layer, and fluxes at the measurement height will not be representative of actual tracer exchange between the land and atmosphere. This is most often a problem at night, when the boundary layer becomes stably stratified. Low-level advection and katabatic flow can be important during low-turbulence conditions, meaning that even the profile measurements included in Eq. 7 will not capture the complete tracer exchange. In practice, this results in an underestimation of fluxes during periods of low turbulence (Goulden et al., 1996). Eddy covariance data from these periods must be discarded. Typically a minimum value of the friction velocity, denoted as u_*, is used as a criterion for determining periods when the turbulent mixing condition was not met. u_* is a scaling velocity related to the Reynolds' stress, and can be determined from measurements of vertical and horizontal wind velocities:

$$u_*^2 = \sqrt{\overline{u'w'}^2 + \overline{v'w'}^2} \tag{8}$$

The precision of eddy covariance measurements is limited by the inherent random variability of atmospheric turbulence, which is on the order of 10% (Wesely and Hart, 1985). This is the minimum amount of random variation between individual flux measurements, which are typically at time steps of 30–60 minutes. Averaging many flux measurements together can reduce random uncertainty for longer time periods to within ± 5% (Goulden et al., 1996; Moncrieff et al., 1996).

2.1.3 Missing data and gap filling

Because of the need to discard data from low-turbulence periods and unrepresentative wind directions as well as equipment failures and maintenance, any long time series of eddy covariance measurements will contain some periods of missing data. In a comparative study of many field studies using eddy covariance, Falge et al. (2001) estimated an average of 65% data coverage on a yearly basis. Because eddy covariance measurements are often used to construct long-term averages of carbon sequestration and land-atmosphere interactions, defensible strategies for replacing missing data are of great importance.

Several different methods are used by various research groups to fill gaps in eddy covariance data. These include methods based on mean diurnal variation, look-up tables, and non-linear regressions, as well as other sophisticated techniques such as artificial neural networks and ecosystem models (Falge et al., 2001; Moffat et al., 2007). All these methods attempt to replace missing data with the fluxes that would be expected under similar conditions as measured at other points in the time series. Most methods begin by partitioning NEE into ER and GEP, since these components respond differently to environmental forcing. ER is most dependent on temperature, while GEP depends mostly on photosynthetically active radiation (PAR), the amount of solar radiation in the part of the spectrum that plants can use for photosynthesis.

Methods based on mean diurnal variation (MDV) replace missing data with the mean for the appropriate time period based on adjacent days. The variations in MDV methodologies differ primarily in the choice of the averaging interval, which has varied between 4 and 15 days in previous studies (Falge et al., 2001). This simple method does not attempt to use connections between measured parameters or to model ecosystem processes.

Look-up tables and non-linear regressions are both semi-empirical methods that attempt to preserve the responses to temperature and PAR that are observed in the data. Look-up tables rely on tabulating the measured fluxes under a range of different conditions, and replacing missing flux data with the values observed under similar conditions at different points in time. The tables are usually broken up into appropriate periods in order to represent large changes in ecosystem function over the year. Gaps in parameter space can be interpolated.

Non-linear regression is similarly based on representing fluxes in terms of other measured parameters, but instead of tabulating observed data establishes functional relationships between the components of NEE and their associated controlling factors. Variable parameters are estimated by fitting the function to observed data, usually in a moving window around the period of missing data in order to properly represent changes in model parameters that may occur due to changes in ecosystem function over time. This study used non-linear regression for gap-filling (see Sec. 2.6).

Falge et al. (2001) concluded based on an intercomparison of gap-filling methods at several flux tower sites that each of the three gap-filling methods described here provided similar results, but that the quality of the final results was dependent on the length of gaps and decisions of which data to exclude. In a comparison of 23 different methods for NEE decomposition and gap-filling, Desai et al. (2008b) found good agreement between methods, indicating that partitioning and gap-filling results are not very sensitive to the specific methodology. A similar result was found by Moffat et al. (2007) in a comparison of a wide range of different techniques.

2.2 Site descriptions

Eddy covariance fluxes and related bio-and-geophysical data from three wetland sites (Lost Creek, Wilson Flowage, and South Fork) and two upland forest sites (Willow Creek and Sylvania) in North-Central Wisconsin and the Upper Peninsula of Michigan were analyzed and compared for this study. All the sites are within a 50 km radius, and therefore have roughly similar microclimates. All five sites are part of the Chequamegon Ecosystem Atmosphere Study (ChEAS; http://cheas.psu.edu). Lost Creek, Willow Creek, and Sylvania are also affiliated with the AmeriFlux Network (Baldocchi et al., 2001, http://public.ornl.gov/ameriflux), which synthesizes eddy-covariance based flux networks from sites across North America, South America, and Central America. Measurements and processing are consistent with the standard protocols of AmeriFlux and FluxNet (http://daac.ornl.gov/FLUXNET), the global network of flux measuring organizations with which AmeriFlux is affiliated (Berger et al., 2001; Baldocchi, 2003).

2.2.1 Lost Creek shrub wetland

The primary wetland flux tower (hereafter referred to as LC) is located in a shrub wetland near Lost Creek, in the Northern Highlands State Forest in north central Wisconsin, USA (46° 4.9' N, 89° 58.7' W), elevation approximately 480 m above sea level. Lost Creek and the associated floodplain provide a persistent source of water that provides the conditions necessary for a peat-accumulating wetland ecosystem. The site has been a shrub wetland since at least 1950, based on aerial photographs (R. Hewett, Wisconsin Department of Natural Resources, unpublished). 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. Aboveground biomass measured in 2001 was 613, 215, and 158 g m^{-2} for shrub wood, shrub leaves, and sedge shoots, respectively (J. Martin, personal communications). Basal diameters (mean ± standard error) for alder and willow species were 1.40 ± 0.03 and 0.82 ± 0.05 cm, respectively.

Poorly drained soils surrounding the tower included a Totagatic-Bowstring-Ausable complex and Seelyeville and Markey mucks. These soils form on outwash sand and are composed primarily of sapric material about 0.5 m thick (Natural Resources Conservation Service, 2006). Stream and water table heights at the site responded to precipitation and snowmelt events, as well as dam-building activity by beaver (*Castor canadensis*). The removal of beaver dams from Lost Creek in fall 2000 and summer 2003 may be partially responsible for the observed lowering of the surface water table in subsequent years. Peat subsidence resulting from drainage lowered the soil surface height by approximately 25 cm over the course of the study. Lowering of peatland soils has previously been demonstrated in drawdown experiments (Strack and Waddington, 2007). Water table measurements reported in this paper are referenced to the soil surface in 2001. Changes in plant community and water and soil chemistry that may have accompanied the changes in water table were not measured.

The Lost Creek wetland is typical of minerotrophic wetlands of the Great Lakes region, which commonly occur in long, narrow strips along streams and rivers. Approximately 28% of the wetland plant communities in northern Wisconsin are dominated by broad-leafed shrubs (Wisconsin Department of Natural Resources, 1998).

2.2.2 Wilson Flowage grass-sedge-scrub fen

Wilson Flowage (WF) is a wet meadow/marsh fen, dominated by sedges and marsh grasses with small patches of labrador tea and leatherleaf. Fens are fed by groundwater and surface water, and have significant nutrient inputs. It is located in the Chequamegon-Nicolet National Forest, Medford-Park Falls District in North-Central Wisconsin, USA (45° 49.0' N, 90° 10.3' W). Fluxes at this site were measured with a portable open-path eddy-covariance system during the growing seasons of 2005-2007 (described in Sect. 2.3).

2.2.3 South Fork *Sphagnum* bog

South Fork-Flambeau River (SF) is a *Sphagnum* bog with significant labrador tea (*Ledum groenlandicum*) and leatherleaf (*Chamaedaphne calyculata*), and some black spruce (*Picea mariana*) invading from the edges. As a bog, it is primarily rain-fed, and is very nutrient poor compared to the other two wetland sites. This leads to a characteristic bog plant community, dominated by *Sphagnum* mosses, stunted trees, and shrubs adapted to low-nutrient conditions. Bogs typically have lower primary productivity than fens. SF is located in the Chequamegon-Nicolet National Forest, Medford-Park Falls District in North-Central Wisconsin, USA (45° 55.5' N, 90° 7.8' W). Fluxes at this site were measured with a portable open-path eddy-covariance system during the growing seasons of 2005-2007.

2.2.4 Willow Creek upland hardwood forest

The Willow Creek, Wisconsin, USA AmeriFlux site (WC) is located in the Chequamegon-Nicolet National Forest, WI, USA (45° 48.47' N, 90° 04.72' W), elevation approximately 520 m above sea level. It is a mature hardwood forest, dominated by sugar maple (*Acer saccharum*), basswood (*Tilia americana*), and green ash (*Fraxinus pennsylvanica*). The average age of trees in the stand is 60-80 years, and the height of the canopy is approximately 24 m, with a leaf area index (LAI) of 5.3. The soils around Willow Creek are mostly sandy loam (about 54% sand, 33% silt, and 13% clay) (Cook et al., 2004). Forests in the region were extensively logged in the early 1900s, and trees in the stand were likely harvested at least twice since European settlement. The Ameriflux site was established in May, 1998. For a detailed site description, see Cook et al. (2004).

2.2.5 Sylvania hemlock-hardwood old-growth forest

The old-growth upland forest site (Sylvania) is located about 100 m north of the boundary of the Sylvania Wilderness and Recreation Area, Ottawa National Forest, Michigan, USA (46° 14.52' N, 89° 20.87' W). The Sylvania Wilderness represents one of the few large tracts of old-growth forest remaining in the Midwest (Frelich, 1995). Trees at the Sylvania site range from 0 to 350 years old, and dominant species are sugar maple and eastern hemlock (*Tsuga canadensis*). The average canopy height and LAI measured in 2002 were 23 m and 4.06, respectively (Desai et al., 2005). Dominant soils are moderately well-drained coarse or sandy loam spodosols. The site was established in August, 2001. For a detailed site description, see Desai et al. (2005).

2.3 Measurements

The data time series for each site included eddy covariance measurements of net ecosystem exchange of carbon dioxide (NEE), and momentum, latent heat, and sensible heat fluxes. Eddy covariance wind and gas concentration measurements were taken using fast-response 3D sonic anemometers and open or closed path IRGAs, depending on the site. Data were recorded at 10 Hz, and thirty-minute average fluxes were calculated from the high-speed data. The fluxes were corrected for storage below the eddy covariance measurement height (Eq. 7) and for spectral attenuation using standard established techniques, as described in Desai et al. (2008a). Fluxes were also screened for low-turbulence conditions by discarding measurements from periods when the friction velocity (u_*) was below a minimum value, and the missing values were replaced with the gap-filling methods described in Sect. 2.6. The justification for this is explained in Sect. 2.1.2. The u_* cutoff was determined separately for each site by examining a scatter plot of measured NEE as a function of u_*, and picking a cutoff value at the point where NEE started to depend on u_*. This approach is based on the assumption that biological sources and sinks of carbon dioxide should be independent of turbulence conditions. Anomalous data associated with a specific wind direction were discarded from WC (see Cook et al. (2004) for a full description and justification). At Sylvania, fluxes determined to be nonrepresentative of the forest due to contamination by lakes in the area of the tower were discarded, as described in Desai et al. (2005).

Eddy fluxes at South Fork and Wilson Flowage were measured using a mobile flux tower system during the growing seasons (May-September) of 2005, 2006, and 2007. The system consisted of a portable tower equipped with an open-path IRGA (model LI-7500, Li-Cor, Inc.) and a 3-D sonic anemometer (model CSAT3, Campbell Scientific, Inc.). The tower was mounted on a platform at each wetland site. Flux data were recorded continuously for one-week periods, alternating between the two sites. This approach allowed us to measure fluxes at multiple sites during the growing season using limited equipment, but resulted in time series with large gaps.

Water table height (WT) was measured at 30-minute intervals using differential pressure transducer systems mounted in wells at the wetland sites. Pressure transducer systems use the pressure at a set point below the water level to infer the water depth. Water table depth is defined in this study as height of the water level above the soil surface, referenced to the soil surface height at the beginning of the time series. Positive WT denotes standing water above the soil, and negative WT represents a water table level below the soil surface. The effect of observed soil subsidence at LC on these measurements was removed (see section 2.5).

Micrometeorological data were collected continuously at all sites. Data included photosynthetically active radiation (PAR), air and soil temperature at multiple levels, net radiation, soil heat flux, precipitation, and soil water content. Due to gaps and concerns about the reliability of precipitation data measured at the sites, the precipitation reported here is from the National Climate Data Center Minocqua station (cooperative station number 475516), located approximately 25 km from Lost Creek. These precipitation measurements were well correlated with the on-site measurements.

2.4 Flux calculation

Turbulent fluxes of momentum, heat, water vapour, and CO_2 were calculated at half-hourly intervals for all sites using the methodology described in Berger et al. (2001), basically identical to that applied in Desai et al. (2008a). 10 Hz measurements of scalar quantities were detrended and 10 Hz measurements of wind were rotated into the mean horizontal wind direction using a long-term planar fit correction to account for possible non-level mounting of the sonic anemometer. Lags between measurements of vertical wind velocity and carbon dioxide or water vapour were corrected by maximizing the lagged covariance. High frequency attenuation was corrected by applying a spectral correction, as described in Berger et al. (2001). Spectral corrections for water vapour were computed by spectrally degrading the power spectrum of sonic virtual temperature to match that of water vapour and then calculating the ratio of degraded to non-degraded spectra. No degradation was found for CO_2 spectra, so the correction factor was computed from theoretical models of air flow through tubing.

2.5 Modeling of soil subsidence

Peat subsidence and compaction resulting from the declining water table at LC lowered the soil surface by approximately 25 cm over the course of the study. Because water table measurements were referenced to the height of the soil surface at the beginning of the study, the lowering of the soil surface needed to be removed from the measured water table time series. A time course of soil surface height was not available, so soil subsidence was modeled using a relationship suggested by Wösten (1997). The rate of change of soil height is proportional to the depth of the water table:

$$\frac{dz}{dt} = A \times (\mathrm{WT}_{\mathrm{meas}}(t) - z(t)) \tag{9}$$

where z is the soil surface height, $\mathrm{WT}_{\mathrm{meas}}(t)$ is the uncorrected measured water table depth, and A is a variable parameter adjusted to match observed data. $(\mathrm{WT}_{\mathrm{meas}}(t) - z(t))$ is the corrected water table depth. The modeled subsidence was normalized to match the observed total change in soil surface height, and the final results were not sensitive to the value of A. The time series of calculated soil subsidence is shown in Fig. 1. A repetition of the calculations presented in this paper using the uncorrected measured water table depth did not produce results materially different from those presented here.

2.6 Partitioning of carbon fluxes and gap-filling

Missing and screened data were replaced using the non-linear regression methodology of Falge et al. (2001), with slight modifications (Cook et al., 2004; Desai et al., 2005). The basic strategy was to represent ER as measured NEE during nighttime, when photosynthesis is not occurring. A model that expressed ER as a function of temperature was fit to observed nighttime NEE for each day using a moving window of ± 15-60 days, with the width of the window depending on the amount of missing data and quality of fit. Modeled ER was then calculated based on observed soil temperatures and GEP was determined by subtracting modeled ER from observed NEE and fitting the residual to a model that expressed GEP as a function of PAR. Gaps in observed NEE were filled by summing modeled ER and GEP for the missing periods. The use of a moving window allowed model parameters to change over time, allowing modeled ER and GEP to incorporate seasonal variations and changes caused by the effects of factors not included in the functional models, such as changes in hydrology and plant community.

ER was modeled by fitting nighttime CO_2 flux to the Eyring function, a theoretically derived chemical reaction kinetics model that depends on soil temperature:

$$\text{ER} = 10^{-6}\frac{k}{h}T_s e^{-(\Delta G^{++}/R^{*}T_s)} \tag{10}$$

where ER is the modeled ecosystem respiration rate (μmol m^{-2}s^{-1}), T_s the soil temperature in K, k Boltzmann's constant (1.38×10^{-23} J K^{-1}), h Planck's constant (6.626×10^{-34} J s), and R^* is the universal gas constant (8.3143 J mol^{-1} K^{-1}). ΔG^{++} is the Gibbs activation energy of the reaction (J mol^{-1}):

$$\Delta G^{++} = \Delta H^{++} - T_s \Delta S^{++} \tag{11}$$

where ΔH^{++} is enthalpy (J mol^{-1}) and ΔS^{++} is entropy (J mol^{-1} K^{-1}). These are the variable parameters of the function, and were determined for each point in the time series by empirically fitting the equation to nighttime measured CO_2 flux and soil temperature in a moving window of ± 15-60 days, with the width of the window depending on the amount of missing data and quality of fit.

GEP was computed by subtracting modeled ER from daytime observed NEE and fitting the result to a Michaelis-Menton reaction rate equation (Falge et al., 2001):

$$\text{GEP} = \frac{b_1 \cdot \text{PAR}}{b_2 + \text{PAR}} \tag{12}$$

where PAR is photosynthetically active radiation (μmol m^{-2} s^{-1}), and b_1 and b_2 are the variable parameters of the function. The variable parameters were determined for each point in the time series by fitting the equation to measured values in a moving window, as in the calculation of modeled ER.

Estimates of GEP and ER by this method were not found to differ significantly from other methods across a range of sites (Desai et al., 2008b).

2.7 Calculation of ecosystem water use efficiency

One important measure of ecosystem interactions is water use efficiency (WUE), the amount of water plants transpire when fixing a certain amount of carbon. Plants control gas exchange through their leaves by opening and closing pores in their leaves called stomata. When stomata are open, CO_2 and water are transferred between leaves and the air. Plants can open and close their stomata in response to a number of factors including water stress, temperature, and light conditions. Different plant species are adapted to different environmental conditions and amounts of available water, and have different water use efficiencies. Plants adapted to dry conditions are more likely to have water-conserving adaptations that lead to high WUE, while wetland plants are more likely to have low WUE since water is almost always available for transpiration.

The eddy covariance measurements from this study provided time series of latent heat flux, which is equivalent to evapotranspiration (ET). ET includes transpiration, water evaporated through plant leaves, as well as water evaporated from the soil through processes that are not plant-mediated. It is difficult to reliably separate the two components of ET, so for this study estimated ecosystem water use efficiency was calculated as the ratio between GEP and evapotranspiration as measured by eddy-covariance:

$$\mathrm{WUE} = \frac{\mathrm{GEP}}{\mathrm{ET}} \tag{13}$$

This definition avoids errors introduced by attempting to model soil evaporation, since we had no direct measurements to separate evaporation from transpiration. It is not able to isolate biological effects from physical changes that affect total ET, but still reflects changes in the energy and water balance of the ecosystem. The same definition of WUE was used by Humphreys et al. (2006).

3 Results

3.1 Climate and annual patterns

The region has a northern continental climate, characterized by short, moist growing seasons (June-August) and cold, relatively dry winters. Table 1 shows yearly averages of carbon fluxes and climatological data for Lost Creek. The average annual temperature at LC over the time period of this study was 5.2° C, with January the coldest month (average temperature $-9.9°$ C) and July the warmest (average temperature 18.7° C). The last three years of the record (2005-2007) were warmer than the previous years, with an average air temperature of 5.8° C.

The average yearly total precipitation over the seven-year record (2001-2007) was 900 mm. The wet season was April-October, with October the wettest month (average precipitation 110 mm over the record). November-March were comparatively dry, and January was the driest month with an average of 23 mm precipitation over the record.

3.2 Declining water table trend at LC

The record of water table at Lost Creek shows a clear decline, with yearly average water table lowering by approximately 30 cm between 2001 and 2006 (Fig. 2). Beaver dams were removed from Lost Creek during fall 2000 and summer 2003, which may be the cause of the large decline visible in mid-2003. Peat subsidence relating to the declining water table lowered the soil surface by approximately 25 cm over the observed time period (B. Cook, personal communication). Water table measurements were corrected for peat subsidence using the methodology discussed in Sect. 2.5. The calculated soil subsidence correction is shown in Fig. 1.

Trends in precipitation appear connected with the water table decline at Lost Creek. Growing season average water table and yearly total precipitation have a correlation coefficient of 0.88 ($p = 0.01$) over the seven-year record (Fig. 3). A decline in precipitation in the region was also observed in a gridded meteorological dataset (Kucharik and Serbin, 2008). These observations are consistent with a regional trend of declining lake levels observed by Stow et al. (2008). A decline in both lake and water table levels in conjunction with decreasing rainfall suggest a drying climatic trend across the region over the period of study.

There was no significant correlation between yearly average water table depth and yearly average soil temperature ($r = 0.27, p = 0.6$) or air temperature ($r = -0.004, p = 0.99$). However, water table depth was correlated with yearly averages of daily maximum soil temperature ($r = -0.76, p = 0.08$), daily minimum soil temperature ($r = 0.98, p = 0.0006$), and daily variance in soil temperature ($r = -0.88, p = 0.02$). The high correlations are probably due to increased variability in soil temperature as upper levels of soil dried and thermal mass was reduced. Decreasing soil water content decreases the soil heat capacity and conductivity. The effects of changes in soil water content on soil temperature fluctuations have been previously observed (e.g. Hinkel et al., 2001; Behaegel et al., 2007).

3.3 NEE, ER, and GEP at LC

The monthly-averaged time series of NEE, ER, and GEP at LC are shown in Fig. 4. The seasonal cycle is clear, with both ER and GEP highest during the summer. NEE is negative during the growing season when the ecosystem is absorbing carbon from the atmosphere due to high rates of photosynthesis, is most positive in spring and fall, and is near zero in the winter when low temperatures limit respiration. The yearly averages of these values are shown in Table 1. Lost Creek was a net absorber of CO_2 in all years of the record. ER, GEP, and NEE averaged over the entire 6-year time series were 1.94, 2.15, and –0.22 μmol $m^{-2}s^{-1}$, respectively. Yearly average GEP and ER were highly correlated with each other (correlation coefficient 0.98).

Residuals between modeled ER and nighttime NEE were not correlated with either water table or soil temperature, nor were residuals between modeled and measured NEE. This indicates that the gap filling and partitioning did not miss important water table or temperature interactions.

3.4 Comparison of LC with nearby upland sites

3.4.1 ER correlation with water table

Hypothesis 1 states that lower water table should be correlated with a higher ecosystem respiration rate, since more peat is exposed to oxygen and can be decomposed by aerobic processes. Yearly-average ER was most highly correlated with WT when soil temperature was greater than 0°C (hereafter referred to as warm-period WT), as was yearly-average GEP. Including water table values from colder periods reduced the correlation substantially. Both ER and GEP were greatest during these periods, and only including warm-period WT in annual averages better captures the interactions between water table and ecosystem processes. Warm-period WT was therefore used for all the annual average analysis in this study.

The time series in Fig. 2 shows that warm-period WT had a clear declining pattern, despite variability in spring WT. The yearly-averaged ER and warm-period WT data from Lost Creek (Fig. 5, filled circles) have a correlation coefficient of -0.90 ($p = 0.015$). LC ER increased from an average of 1.65 μmol $\mathrm{m}^{-2}\mathrm{s}^{-1}$ in the first two years of the record to an average of 2.06 μmol $\mathrm{m}^{-2}\mathrm{s}^{-1}$ in the last four years of the record. This represents an increase of approximately 25% over the record. Yearly average ER at the upland sites (open symbols) was not significantly correlated to Lost Creek water table (correlation coefficient of –0.56 ($p = 0.33$) for Sylvania and –0.1 ($p = 0.85$) for WC). This indicates that the change in wetland ER with changing water table was a real wetland effect, not a statistical artifact or regional trend.

Since ER is strongly dependent on soil temperature, it is illuminating to investigate the variability in ER as an interaction between both WT and soil temperature. Soil temperatures below the water table or very near the soil surface do not accurately reflect the conditions under which most soil respiration is taking place. Multiple levels of soil temperature were available for Lost Creek, so for these calculations a time series of soil temperature at the lowest level above the water table for each time point was used. A repetition of the calculations using only one level of soil temperature showed that this did not significantly skew the results. Figure 6 shows binned averages of Lost Creek ER, formed from half-hourly data divided into different temperature ranges and averaged over water table bins. In each temperature range, ER decreases with increasing water table height above a critical level below the surface. Below this level, there is little dependence on water table depth. The depth of the critical level increases with increasing temperature, from about 20 cm below the surface at temperatures below 7° C to a depth of 35 cm at temperatures above 20° C. This cutoff is consistent with the observations of Lafleur et al. (2005b), a study of ER in a wetland with a water table level consistently below –30 cm. The study found no correlation between water table and ER, and the authors hypothesised that wetter peatlands would have a stronger relationship between ER and water table.

Figure 7 shows binned average ER calculated from half-hourly data at the Lost Creek wetland site as well as Willow Creek and Sylvania, the upland forest sites, during the growing season, combined over all temperatures. The 20-30 cm cutoff for Lost Creek ER identified in Fig. 6 is visible in this plot as well. ER is flat at water table heights below 20 cm, with an average of approximately 5.1 μmol m^{-2}s^{-1}. When water table is above a level 20 cm below the surface, ER is flat with an average of approximately 4.2 μmol m^{-2}s^{-1}. This represents an increase in ER of over 20% between the high and low water table regimes. WC (open circles) and Sylvania (open diamonds) are plotted against LC water table height, and show no similar dependence, indicating that the observed effect is a real wetland effect and not a statistical artifact.

3.4.2 GEP correlation with water table

Hypothesis 2 states that lower water table should be connected with higher ecosystem productivity, which would counteract the increase in respiration observed with lower water table. A plot of yearly average GEP as a function of warm-period WT (Fig. 8) shows that wetland GEP (filled circles) was highly correlated with water table levels (correlation coefficient $-0.94, p = 0.005$), while Willow Creek (open circles) and Sylvania (open diamonds) had no apparent dependence on wetland water table. The average GEP at LC in the two years with the highest water table was 1.87 μmol m^{-2}s^{-1}, while the average GEP in years with lower water table was 2.23 μmol m^{-2}s^{-1}, representing an increase in GEP of approximately 22% between years with high and low water tables. The observed increase in GEP was accompanied by an increase the in aboveground biomass of the plant community at LC. Aboveground woody biomass increased by 64% between 2001 and 2005, from 613 to 1008 g m^{-2}, and woody leaf biomass increased 53% over the same time period, from 215 to 328 g m^{-2} (J. Martin, unpublished data).

3.4.3 NEE correlation with water table

Yearly average GEP and ER at LC were highly correlated with each other ($r = -0.98$). Since years with lower water table had increases of similar magnitude in both GEP and ER, the two effects offset, resulting in little change in NEE, as predicted by Hypothesis 3 (Fig. 9). There was no significant correlation between yearly NEE and warm-period water table at LC ($r = 0.1$). There was also no significant trend in NEE at the upland sites. Therefore, the lowering water table at the wetland did not result in a net increase of carbon dioxide emissions, confirming the results of ecosystem studies that found that peatland carbon pools could be resilient to draining (Strack and Waddington, 2007; Minkkinen and Laine, 1998a; Oechel et al., 2000).

3.4.4 Changes in water and energy fluxes

An investigation of evapotranspiration (ET) at Lost Creek showed a clear decrease over the record that coincided with the declining water table (Fig. 10). While we were not able to reliably separate evaporation from transpiration, this trend in total ET still indicates important changes in water availability as water table declined. The decrease in ET was accompanied by a slight increase in sensible heat flux, with the result that the energy balance of Lost Creek changed from a scenario where the majority of energy dissipated to the atmosphere was in the form of latent heat to one where sensible heat flux dominated (Fig. 11). Calculated on a yearly basis, the evaporative fraction (EF, Eq. 2) changed from 0.61 in 2001 to 0.43 in 2006 (Fig. 12). LC EF and WT were highly correlated

($r = 0.975$, $p = 0.0009$), while EF was not significantly correlated with LC WT at WC ($r = 0.17$, $p = 0.75$) or Sylvania ($r = 0.69$, $p = 0.13$).

Since ET decreased and GEP increased as water table declined at LC, the yearly average ecosystem water use efficiency (WUE) increased ($r = -0.91$, $p = 0.01$). This is shown in Fig. 13. The increase in WUE indicates that plants were not water stressed as a result of the declining water table. The ecosystem was able to reduce the amount of water lost to the atmosphere through ET without reducing the amount of CO_2 assimilation. This could be a result of changes in the plant community that favored species with higher water use efficiencies, or simply a reflection of the resilience of shrub wetland plants to changes in hydrology.

Theoretically, the components of energy balance shown in Fig. 11 should add up so that the sum of latent heat flux, sensible heat flux, and heat flux into the ground equal the net radiation. This energy balance was not closed at Lost Creek, as is visible in the figure. Energy balance closure, the ratio of the heat fluxes to net radiation, ranged from 83% to 100% over the record shown. Lack of energy balance closure is a well-documented issue with eddy covariance measurements (Wilson et al., 2002).

3.5 Comparison of nearby wetland sites

In addition to LC, two other wetland sites were investigated for this study. Wilson Flowage (WF, Sect. 2.2.2) and South Fork (SF, Sect. 2.2.3) were instrumented during three growing seasons with a portable eddy covariance system that was moved between the two sites every two weeks. There is therefore a more limited body of data for these two sites, but they are still useful for comparison with the results from LC. The three wetland sites represent different ecosystem types with different dominant plant communities, and thus may have different responses to changes in hydrology. LC is a shrub fen, WF is a sedge and grass dominated fen, and SF is a nutrient-poor, *Sphagnum*-moss-dominated bog.

3.5.1 Carbon fluxes and water table

A comparison of carbon fluxes as a function of water table at the three wetland sites reveals both coherence and differences. ER at LC, SF, and WF as a function of water table at each site is shown in Fig. 14. At water table heights above –20 cm ER at all three sites has similar magnitude. This level is above the cutoff where changes in water table were important for LC ER (Fig. 7). ER at WF, where WT was above –20 cm for all three years, had no significant correlation with WT. At SF, the bog site, ER was significantly lower during 2007, when water table at the site had an average height of 27 cm below the surface during the period when soil temperature was above 0° C. This was the opposite pattern to that seen at LC, a shrub fen.

GEP at LC, SF, and WF as a function of water table at each site is shown in Fig. 15. The magnitude of GEP at WF was lower than at LC, and GEP at SF was substantially lower than both. It is not surprising that LC is more productive than the other sites. LC is dominated by shrubs, which are larger and have more leaf area than the grasses and sedges that dominate WF, just as a forest is typically more productive than a grassland. Bogs such as SF generally have low productivity because they are very nutrient-poor. The correlations between GEP and WT at the two fen sites were both negative, indicating a decrease in productivity with higher water table as predicted by Hypothesis 2. In contrast to the fen sites, GEP and WT were positively correlated at SF ($r = 0.9997, p = 0.02$), the bog, indicating that productivity decreased as water table declined. Despite the high r^2 value, the significance of this correlation is not extremely high due to the small number of data points. Additional years of data would allow a more confident assessment of this correlation.

NEE as a function of water table at the three wetland sites is shown in Fig. 16. LC had the most negative yearly average NEE (highest net absorption of CO_2 from the atmosphere) of the three wetland sites. WF was a lesser carbon sink than LC for all three growing seasons, and SF was a slight carbon sink for two growing seasons and a source for one. There was no correlation between WT and NEE at LC or SF, but NEE had a slightly significant positive correlation with WT at WF ($r = 0.997, p = 0.05$), indicating that the site was actually less of a carbon sink during high water table seasons. Note that despite the high r^2 value the significance of the correlation is relatively low, due to the limited number of data points.

3.5.2 Latent and sensible heat fluxes

The dependence of latent heat fluxes on water table observed at Lost Creek was supported by a similar dependence observable between the three different wetland sites. Figure 17 shows growing season latent and sensible heat fluxes for all three wetland sites as a function of average warm period ($T_s > 0°\text{C}$) water table depth for each year. Latent heat fluxes were significantly correlated with water table across the three sites ($r = 0.71, p = 0.005$). Warm-period water table depth explained 50% of the variance in growing season latent heat flux across sites. In contrast, sensible heat fluxes were not significantly correlated with water table across wetland sites ($r = 0.04$). Sensible heat flux was higher under wetter conditions at WF, and lower under wetter conditions at SF and LC.

4 Discussion

Our observed average values of wetland ER, GEP, and NEE (1.94, 2.15, and -0.22 μmol m^{-2}s^{-1}, respectively for Lost Creek) were comparable to those reported in previous eddy covariance studies of wetlands. Syed et al. (2006) reported ER, GEP, and NEE of 1.5, 1.89, and –0.38 μmol m^{-2}s^{-1} in a wetland dominated by shrubs and stunted trees, and Humphreys et al. (2006) also reported fluxes of similar magnitudes in a comparison of several northern wetland sites. Both these studies also observed a strong correlation between ER and GEP, which our results confirm at our wetland site. However, because GEP was calculated based on a residual from the calculation of ER, there is likely a high automatic correlation between the two values, as observed by Vickers et al. (2009), and the correlation should not be interpreted as significant without careful analysis.

The range of ecosystem WUE observed at LC ($1.67 - 3.57$ gC/kgH$_2$O) was similar in magnitude to water use efficiencies reported for different wetland types by Humphreys et al. (2006) (1.88 – 4.4 gC/kgH$_2$O). The increase in WUE as the wetland dried and biomass increased was consistent with the observation of Humphreys et al. (2006) that average WUE was higher at sites with higher biomass and LAI. However, the variations in WUE that they observed were mostly due to variations in GEP, and did not correlate with differences in water table as was observed in this study.

As reported in Sec. 3.4.4, the energy fluxes measured at Lost Creek did not add up to the estimated available energy. Lack of energy balance closure is a persistent and well-documented issue in eddy covariance measurements. The observed lack of energy balance closure in the Lost Creek measurements, which had a maximum yearly average deficit (percentage of available energy not accounted for in flux measurements) of 17% in 2006, is within the range observed in previous eddy covariance studies. In a study incorporating data from 22 eddy covariance sites in the FLUXNET network, Wilson et al. (2002) found an average yearly energy balance closure deficit on the order of 20%. Proposed explanations for this consistent bias include: errors due to the unmatched footprints of flux measurements and the equipment for measuring other components of energy balance (such as radiation meters and soil heat flux plates); inherent bias in instrumental measurements; sinks of energy beyond those being measured at sites, such as heating of above-ground biomass; unintentional filtering of the turbulent spectrum due to measurement constraints; and advection of heat (Wilson et al., 2002). The implications of energy balance closure for the reliability of CO_2 fluxes measured using eddy covariance are still a subject of debate in the eddy covariance community. Because lack of energy balance closure can be caused by a number of different mechanisms which may or may not be independent of CO_2 fluxes, Wilson et al. (2002) concluded that lack of closure does not necessarily indicate errors in flux measurements, and that the reliability of measurements should be evaluated on an individual basis for each site. Because energy balance closure at Lost Creek was as good or better than the average reported by other eddy covariance studies and because the measured patterns in fluxes were consistent with biometric measurements such as increased shrub growth, we conclude for this study that the lack of energy balance closure does not indicate a large error in flux measurements.

The high correlation between water table depth and variance in daily soil temperature at LC makes separating the effects of soil temperature and water table difficult. The observed increases in GEP and ER could be due to changes in soil moisture and associated effects on oxygen availability in soil, or due to the greater temperature variability in drier peat, or a combination of the two. The lack of correlation between water table and air temperature indicate that the changes in soil temperature were related to soil properties, and not direct results of climatic forcing. Changes in soil water content are known to affect soil thermal properties (Behaegel et al., 2007).

Previous studies have reported that microtopography is important in determining whether water table or soil temperature is more important to carbon fluxes. Sullivan et al. (2008) found that soil temperatures varied significantly between hummocks and hollows, and that microtopography had significant effects on ER and GEP but not on NEE. Strack and Waddington (2007) reported that hummocks, lawns, and hollows all responded with different sensitivities to water table drawdown, and Sommerkorn (2008) found that dry and wet microsites had different sensitivities to changes in water table and temperature. In a comparison of different wetland sites, Silvola et al. (1996) found that drier sites had lower sensitivity of soil respiration to temperature. Due to the large footprint of eddy covariance measurements, our study was unable to separate different microsite effects within the wetland of interest. However, the LC tower is situated in a fairly flat area of the wetland, so the water table measurements are representative of most of the tower footprint and microtopography is probably not critically important to our results.

A number of previous studies have found that wetland carbon balance is sensitive to changes in hydrology. Silvola et al. (1996) found that soil respiration increased in response to lowering water table, and several other studies have observed changes in wetland carbon balance from a net sink to a source during unusually warm, dry seasons (Shurpali et al., 1995; Schreader et al., 1998; Alm et al., 1999; Joiner et al., 1999; Bubier et al., 2003; Arneth et al., 2002). These studies reported short-term reductions in GEP attributed to water stress and early senescence, as well as temporary rises in ER or soil respiration. However, other studies have observed little correlation between water table and ER, both in manipulated mesocosms (Updegraff et al., 2001) and in field sites (Lafleur et al., 2005b; Nieveen et al., 2005). The results presented here for Lost Creek represent a relatively long time period of GEP measurements coincident with a multi-year change in hydrology, which was not correlated with increasing average temperatures. In fact, the two years following the largest drop in water table at Lost Creek were cooler than the average for the record, which may have contributed to the lack of increase in NEE as WT dropped. Similar balancing increases in both ER and GEP to those reported here have been observed at wetlands subjected to controlled draining (Strack and Waddington, 2007). In a study that addressed the impact of ecosystem changes over a longer time scale, Minkkinen and Laine (1998a,b) found that forested peatlands had continued to accumulate carbon over a 60 year period after being drained. The increase in seasonal average GEP observed in this study was consistent with acclimation of the ecosystem to different climatic conditions. In an analogous study in an Alaskan tundra ecosystem, Oechel et al. (2000) found that the ecosystem initially changed from a CO_2 sink to a source due to warming and drying, but that CO_2 emissions decreased and eventually became negative during summers over a 40-year period.

Several studies of CO_2 fluxes at wetlands have also indicated the importance of vegetation, both stand age for forested wetlands (Ball et al., 2007) and dominant plant community among different wetland types (Humphreys et al., 2006; Glenn et al., 2006; Vourlitis et al., 2000; Waddington et al., 1998). While the small body of data for the two secondary wetland sites makes drawing strong conclusions difficult, our results suggested different magnitudes of NEE as well as different changes in ER, GEP, and NEE with changes in water table between the three wetland sites that were compared. Magnitudes of ER and GEP at both fen sites were similar at similar water table depths, but NEE at the grass-sedge site was highly correlated with WT, while NEE at the shrub fen was not significantly correlated with water table. In contrast to the results observed at the fen sites, ER and GEP at the bog site were both positively correlated with water table. This also contrasts with previous studies of bogs in which dry periods were associated with increases in both ER and GEP. Further investigation of the mechanisms behind these correlations is warranted. Understanding the impact of dominant plant communities on an ecosystem's response to changing climatic and hydrological conditions will be important for complete understanding of this issue.

In the context of feedbacks to climate change, several studies have predicted that future drying of boreal wetlands due to climatic change would result in a large release of carbon dioxide to the atmosphere (Junkunst and Fiedler, 2007; Ise et al., 2008). The results presented in this study of a shrub wetland indicated that increases in primary productivity counteracted increased ER, resulting in little change to NEE as water table declined. This suggests that drying of some peatlands may lead to ecosystem changes that prevent large losses of carbon to the atmosphere. However, the complete greenhouse gas budget of wetlands may still respond to hydrological changes through changes in fluxes of methane, which were not investigated in this study. Previous studies have indicated that wetland methane fluxes decrease with declining water table and increase with increasing temperature (Moore and Knowles, 1989; Dise et al., 1993; Freeman et al., 1992; Turetsky et al., 2008), and these changes could be an important feedback to climate change (Gedney et al., 2004).

While no significant change in net exchange of carbon dioxide was observed at Lost Creek, the shifts in energy balance observed at the wetland site could have important implications for regional climate. The correlation between evapotranspiration (ET) and water table depth observed across all three wetland sites suggests a strong connection between wetland hydrology and latent heat fluxes, independent of the wetland ecosystem type. These results contrast with those of Humphreys et al. (2006), who found that daily evapotranspiration rates were not correlated with wetland water table levels. Lafleur et al. (2005a) found in a shrub covered bog that ET rates were lower during periods with lower water table levels, but only when water table was below a critical depth of approximately 60 cm. They also found that total growing season ET was lower in years with lower average water tables, which agrees with the findings presented here. As discussed in Sect. 1.1, changes in energy balance and especially evaporative fraction at the landscape scale can cause changes in regional average surface temperatures and precipitation. The results of this study suggest that the climatic effects of changes in energy balance could in fact be more important than those of changes in carbon exchange for some drying wetlands. The increase in above-ground biomass observed at Lost Creek could also result in changes to surface roughness. The moderate growth observed there so far is unlikely to have large impacts on boundary layer processes, but if growth continues and the wetland is converted into a much taller forest, there could be important impacts on boundary layer turbulence and the strength of land-atmosphere coupling.

5 Conclusions

This analysis found that a trend of lowering water table coincided with an increase in both ecosystem respiration and productivity at the main wetland site. The effects balanced, resulting in net carbon exchange with the atmosphere being independent of water table. These results suggest that changes in shrub wetland hydrology may not ultimately affect net carbon dioxide exchange over inter-annual time scales. Based on our results, wetland management plans focused on maintaining high water tables in order to preserve carbon sink and storage services may be overly simplistic. Our results show that wetland carbon dioxide sinks can be resilient to hydrological changes through responses in plant community structure, so other impacts of hydrological change, such as those affecting biodiversity, methane fluxes, and other ecosystem services, should perhaps take priority in management decisions.

While there was no significant change in net carbon dioxide exchange at Lost Creek, the decline in water table and increase in shrub cover on the wetland did coincide with changes in evapotranspiration and water use efficiency. The correlation between water table and evapotranspiration was consistent across the three wetland sites included in the study, indicating a strong relationship independent of nutrient status or dominant vegetation. Other important parameters of interaction between the ecosystem and atmosphere, such as albedo and roughness, could also be expected to change in response to changes in hydrology, although these were not investigated for this study. Shifts in these surface properties could have important impacts on local climate if they occurred on a large scale, as discussed in Sec. 1.1. Models of climate-biosphere interactions that do not include these types of ecological responses may miss important changes in the interactions between wetland ecosystems and the atmosphere with important implications for future climate feedbacks.

References

Alm, J., Schulman, L., Walden, J., Nykänen, H., Martikainen, P. J., and Silvola, J.: Carbon Balance of a Boreal Bog during a Year with an Exceptionally Dry Summer, Ecology, 80, 161–174, 1999.

Arneth, A., Kurbatova, J., Kolle, O., Shivistova, O. B., Lloyd, J., Vygodskaya, N. N., and Schulze, E.-D.: Comparative ecosystem-atmosphere exchange of energy and mass in a European Russian and a central Siberian bog II. Interseasonal and interannual variability of CO_2 fluxes, Tellus, 54B, 514–530, 2002.

Baldocchi, D.: Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present, and future, Global Change Biology, 9, 479–492, 2003.

Baldocchi, D., Hincks, B., and Meyers, T.: Measuring Biosphere-Atmosphere Exchanges of Biologically Related Gases with Micrometeorological Methods, Ecology, 69, 1331–1340, 1988.

Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K. T., Pilgaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, T., Wilson, K., and Wofsy, S.: FLUXNET: A new tool to study the temporal and spatial variability of ecosystem–scale carbon dioxide, water vapor, and energy flux densities, Bulletin of the American Meteorological Society, 82, 2415–2434, 2001.

Ball, T., Smith, K., and Moncrieff, J.: Effect of stand age on greenhouse gas fluxes from a Sitka spruce [*Picea sitchensis* (Bong.) Carr.] chronosequence on a peaty gley soil, Global Change Biology, 13, 2128–2142, 2007.

Behaegel, M., Sailhac, P., and Marquis, G.: On the use of surface and ground temperature data to recover soil water content information, Journal of Applied Geophysics, 62, 234–243, doi:10.1016/j.jappgeo.2006.11.005, 2007.

Berger, B., Davis, K., Yi, C., Bakwin, P., and Zhao, C.: Long-Term Carbon Dioxide Fluxes from a Very Tall Tower in a Northern Forest: Flux Measurement Methodology, Journal of Atmospheric and Oceanic Technology, 2001.

Bowling, D., Tans, P., and Monson, R.: Partitioning net ecosystem carbon exchange with isotopic fluxes of CO_2, Global Change Biology, 7, 127–145, 2001.

Bubier, J., Moore, T., Bellisario, L., Comer, N., and Grill, P.: Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada, Global Biogeochemical Cycles, 9, 455–470, 1995.

Bubier, J., Crill, P., Moore, T., Savage, K., and Varner, R.: Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex, Global Biogeochemical Cycles, 12, 703–714, 1998.

Bubier, J., Bhatia, G., Moore, T., Roulet, N., and Lafleur, P. M.: Spatial and Temporal Variability in Growing-Season Net Ecosystem Carbon Dioxide Exchange at a Large Peatland in Ontario, Canada, Ecosystems, 6, 353–367, 2003.

Campbell, G. S. and Norman, J. M.: An Introduction to Environmental Biophysics, Springer Science+Business Media, Inc., New York, NY, second edn., 1998.

Clymo, R. S.: The Limits to Peat Bog Growth, Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences (1934-1990), 303, 605–654, doi:10.1098/rstb.1984.0002, 1984.

Cook, B., Davis, K., Wang, W., Desai, A., Berger, B., Teclaw, R., Martin, J., Bolstad, P., Bakwin, P., Yi, C., and Heilman, W.: Carbon exchange and venting anomalies in an upland deciduous forest in northern Wisconsin, USA, Agricultural and Forest Meteorology, 126, 271–295, doi:10.1016/j.agrformet.2004.06.008, 2004.

Davidson, E., Savage, K., Verchot, L., and Navarro, R.: Minimizing artifacts and biases in chamber-based measurements of soil respiration, Agricultural and Forest Meteorology, 113, 21–37, doi:10.1016/S0168-1923(02)00100-4, 2002.

Denman, K., Brasseur, G., Chidthaisong, A., Ciais, P., Cox, P., Dickinson, R., Hauglustaine, D., Heinze, C., Holland, E., Jacob, D., Lohmann, U., Ramachandran, S., da Silva Dias, P., Wofsy, S., and Zhang, X.: Couplings Between Changes in the Climate System and Biogeochemistry., in: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., M.Tignor, and Miller, H., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2007.

Desai, A., Bolstad, P., Cook, B., Davis, K., and Carey, E.: Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA, Agricultural and Forest Meteorology, 128, 33–55, 2005.

Desai, A., Noormets, A., Bolstad, P., Chen, J., and Cook, B.: Influence of vegetation and seasonal forcing on carbon dioxide fluxes across the Upper Midwest, USA: Implications for regional scaling, Agricultural and Forest Meteorology, 148, 288–308, 2008a.

Desai, A., Richardson, A., Moffat, A., Kattge, J., Hollinger, D. Y., Barr, A., Falge, E., Noormets, A., Papale, D., Reichstein, M., and Stauch, V. J.: Cross-site evaluation of eddy covariance GPP and RE decomposition techniques, Agricultural and Forest Meteorology, 148, 821–838, 2008b.

Dise, N., Gorham, E., and Verry, E.: Environmental factors controlling methane emissions from peatlands in northern Minnesota, Journal of Geophysical Research-Atmospheres, 98, 10 583–10 594, 1993.

Falge, E., Baldocchi, D., Olson, R., and Anthoni, P.: Gap filling strategies for defensible annual sums of net ecosystem exchange, Agricultural and Forest Meteorology, 107, 43–69, 2001.

Foley, J., Costa, M., Delire, C., Ramankutty, N., and Snyder, P.: Green surprise? How terrestrial ecosystems could affect earth's climate, Frontiers in Ecology and the Environment, 1, 38–44, 2003.

Forster, P., Ramaswamy, V., Artaxo, P., Berntsen, T., Betts, R., Fahey, D., Haywood, J., Lean, J., Lowe, D., Myhre, G., Nganga, J., Prinn, R., Raga, G., Schulz, M., and Dorland, R. V.: Changes in Atmospheric Constituents and in Radiative Forcing, in: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., M.Tignor, and Miller, H., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2007.

Freeman, C., Lock, M., and Reynolds, B.: Fluxes of CO_2, CH_4 and N_2O from a Welsh peatland following simulation of water table draw-down: Potential feedback to climate change, Biogeochemistry, 19, 51–60, doi:10.1007/BF00000574, 1992.

Frelich, L. E.: Old forest in the Lake States today and before European settlement, Natural Areas Journal, 15, 157–167, 1995.

Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K.-G., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N.: Climate–Carbon Cycle Feedback Analysis: Results from the C4MIP Model Intercomparison, Journal of Climate, 19, 3337–3353, 2006.

Frolking, S., Roulet, N., Moore, T., Lafleur, P., Bubier, J., and Crill, P.: Modeling seasonal to annual carbon balance of Mer Bleue Bog, Ontario, Canada, Global Biogeochemical Cycles, 16, 1030, 2002.

Frolking, S., Roulet, N., and Fuglestvedt, J.: How northern peatlands influence the

Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration, Journal of Geophysical Research, 111, G01 008, 2006.

Gedney, N., Cox, P., and Huntingford, C.: Climate feedback from wetland methane emissions, Geophysical Research Letters, 31, L20 503, doi:10.1029/2004GL020919, 2004.

Glenn, A., Flanagan, L., Syed, K., and Carlson, P.: Comparison of net ecosystem CO_2 exchange in two peatlands in western Canada with contrasting dominant vegetation, Sphagnum and Carex, Agricultural and Forest Meteorology, 140, 115–135, doi:10.1016/j.agrformet.2006.03.020, 2006.

Gorham, E.: Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming, Ecological Applications, 1, 182–195, doi:10.2307/1941811, 1991.

Goulden, M., Munger, J., Fan, S., Daube, B., and Wofsy, S.: Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy, Global Change Biology, 2, 169–182, 1996.

Griffin, R. J., Cocker, III, D. R., Seinfeld, J. H., and Dabdub, D.: Estimate of global atmospheric organic aerosol from oxidation of biogenic hydrocarbons, Geophysical Research Letters, 26, 2721–2724, doi:10.1029/1999GL900476, 1999.

Guenther, A., Hewitt, C. N., Erickson, D., Fall, R., Geron, C., Graedel, T., Harley, P., Klinger, L., Lerdau, M., McKay, W. A., Pierce, T., Scholes, B., Steinbrecher, R., Tallamraju, R., Taylor, J., and Zimmerman, P.: A global model of natural volatile organic compound emission, Journal of Geophysical Research-Atmospheres, 100, 8873–8892, 1995.

Harriss, R. C., Gorham, E., Sebacher, D., Bartlett, K. B., and Flebbe, P. A.: Methane flux from northern peatlands, Nature, 315, 652–654, doi:10.1038/315652a0, 1985.

Hinkel, K., Paetzold, F., Nelson, F., and Bockheim, J.: Patterns of soil temperature and moisture in the active layer and upper permafrost at Barrow, Alaska: 1993–1999, Global and Planetary Change, 29, 293–309, 2001.

Humphreys, E. R., Lafleur, P. M., Flanagan, L. B., Hedstrom, N., Syed, K. H., Glenn, A. J., and Granger, R.: Summer carbon dioxide and water vapor fluxes across a range of northern peatlands, Journal of Geophysical Research, 111, G04 011, doi: 10.1029/2005JG000111, 2006.

Hutchinson, G. L. and Livingston, G. P.: Gas flux, in: Methods of Soil Analysis: Part 1, Physical Methods, edited by Dane, J. H. and Topp, G. C., Soil Society of America, Madison, WI, third edn., 2002.

Ise, T., Dunn, A. L., Wofsy, S. C., and Moorcroft, P. R.: High sensitivity of peat decomposition to climate change through water-table feedback, Nature Geoscience, 1, 763–766, 2008.

Joiner, D., Lafleur, P., McCaughey, J., and Bartlett, P.: Interannual variability in carbon dioxide exchanges at a boreal wetland in the BOREAS northern study area, Journal of Geophysical Research, 104, 27 663–27 672, 1999.

Junkunst, H. F. and Fiedler, S.: Latitudinal differentiated water table control of carbon dioxide, methane and nitrous oxide fluxes from hydromorphic soils: feedbacks to climate change, Global Change Biology, 13, 2668–2683, 2007.

Kettunen, A., Kaitala, V., Alm, J., Silvola, J., Nykänen, H., and Martikainen, P. J.: Cross-correlation analysis of the dynamics of methane emissions from a boreal peatland, Global Biogeochemical Cycles, 10, 457–471, 1996.

Kucharik, C. J. and Serbin, S. P.: Impacts of recent climate change on Wisconsin corn and soybean yield trends, Environmental Research Letters, 3, 034 003, 2008.

Kuhry, P.: The role of fire in the development of *Sphagnum*-dominated peatlands in western boreal Canada, Journal of Ecology, 82, 899–910, 1994.

Lafleur, P. M., Hember, R. A., Admiral, S. W., and Roulet, N. T.: Annual and seasonal variability in evapotranspiration and water table at a shrub-covered bog in southern Ontario, Canada, Hydrological Processes, 19, 3533–3550, 2005a.

Lafleur, P. M., Moore, T. R., Roulet, N. T., and Frolking, S.: Ecosystem respiration in a cool temperate bog depends on peat temperature but not water table, Ecosystems, 8, 619–629, 2005b.

Lee, X., Black, T., and Novak, M.: Comparison of flux measurements with open-and closed-path gas analyzers above an agricultural field and a forest floor, Boundary-Layer Meteorology, 67, 195–202, 1994.

Leuning, R. and Judd, M. J.: The relative merits of open-and closed-path analysers for measurement of eddy fluxes, Global Change Biology, 2, 241–253, 1996.

Leuning, R. and King, K.: Comparison of eddy-covariance measurements of CO_2 fluxes by open-and closed-path CO_2 analysers, Boundary-Layer Meteorology, 59, 297–311, 1992.

Leuning, R. and Moncrieff, J.: Eddy-covariance CO_2 flux measurements using open- and closed-path CO_2 analysers: corrections for analyser water vapour sensitivity and damping of fluctuations in air sampling tubes, Boundary-Layer Meteorology, 53, 63–76, 1990.

Limpens, J., Berendse, F., Blodau, C., Canadell, J., Freeman, C., Holden, J., Roulet, N., Rydin, H., and Schaepman-Strub, G.: Peatlands and the carbon cycle: from local processes to global implications–a synthesis, Biogeosciences, 5, 1475–1491, 2008.

Lloyd, C.: Annual carbon balance of a managed wetland meadow in the Somerset Levels, UK, Agricultural and Forest Meteorology, 138, 168–179, 2006.

Matthews, E. and Fung, I.: Methane emission from natural wetlands: Global distribution, area, and environmental characteristics of sources, Global Biogeochemical Cycles, 1, 61–86, 1987.

Meehl, G., Stocker, T., Collins, W., Friedlingstein, P., Gaye, A., Gregory, J., Kitoh, A., Knutti, R., Murphy, J., Noda, A., Raper, S., Watterson, I., Weaver, A., and Zhao, Z.-C.: Global Climate Projections, in: Climate Change 2007: The Physical Science

Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, edited by Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K., Tignor, M., and Miller, H., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2007.

Minkkinen, K. and Laine, J.: Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland, Can. J. For. Res, 28, 1267–1275, 1998a.

Minkkinen, K. and Laine, J.: Effect of forest drainage on the peat bulk density of pine mires in Finland, Can. J. For. Res, 28, 178–186, 1998b.

Mitra, S., Wassmann, R., and Vlek, P.: An appraisal of global wetland area and its organic carbon stock, Current Science, 88, 25–35, 2005.

Moffat, A., Papale, D., Reichstein, M., Hollinger, D., Richardson, A., Barr, A., Beckstein, C., Braswell, B., Churkina, G., and Desai, A.: Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes, Agricultural and Forest Meteorology, 147, 209–232, 2007.

Moncrieff, J., Malhi, Y., and Leuning, R.: The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water, Global Change Biology, 2, 231–240, 1996.

Moore, T. and Knowles, R.: The influence of water table levels on methane and carbon dioxide emissions from peatland soils., Canadian Journal of Soil Science, 69, 33–38, 1989.

Natural Resources Conservation Service: Soil Survey Geographic (SSURGO) database for Iron County, Wisconsin, USA, United States Department of Agriculture, Fort Worth, TX, 2006.

Nieveen, J. P., Campbell, D. I., Schipper, L. A., and Blair, I. J.: Carbon exchange of grazed pasture on a drained peat soil, Global Change Biology, 11, 607–618, doi: 10.1111/j.1365-2486.2005.00929.x, 2005.

Oechel, W. C., Vourlitis, G. L., Hastings, S. J., Zulueta, R. C., Hinzman, L., and Kane, D.: Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming, Nature, 406, 978–981, doi:10.1038/35023137, 2000.

Pachauri, R. and Reisinger, A., eds.: Climate Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, IPCC, Geneva, Switzerland, 2007.

Pitkänen, A., Turunen, J., and Tolonen, K.: The role of fire in the carbon dynamics of a mire, eastern Finland, The Holocene, 9, 453–462, doi:10.1191/095968399674919303, 1999.

Potter, C. S.: An ecosystem simulation model for methane production and emission from wetlands, Global Biogeochemical Cycles, 11, 495–506, 1997.

Ramsar Convention: Convention on Wetlands of International Importance especially as Waterfowl Habitat, United Nations Educational, Scientific and Cultural Organization (UNESCO), Paris, France, URL `http://www.ramsar.org/key_conv_e.htm`, 1994.

Roulet, N., Ash, R., Quinton, W., and Moore, T.: Methane flux from drained northern peatlands: effect of a persistent water table lowering on flux, Global Biogeochemical Cycles, 7, 749–769, 1993.

Sampaio, G., Nobre, C., Costa, M., Satymurty, P., Soares-Filho, B. S., and Cardoso, M.: Regional climate change over eastern Amazonia caused by pasture and soybean cropland expansion, Geophysical Research Letters, 34, L17 709, doi:10.1029/2007GL030612, 2007.

Schmid, H.: Source areas for scalars and scalar fluxes, Boundary-Layer Meteorology, 67, 293–318, 1994.

Schmid, H. and Lloyd, C.: Spatial representativeness and the location bias of flux footprints over inhomogeneous areas, Agricultural and Forest Meteorology, 93, 195–209, 1999.

Schreader, C., Rouse, W., Griffis, T., Boudreau, L. D., and Blanken, P.: Carbon dioxide fluxes in a northern fen during a hot, dry summer, Global Biogeochemical Cycles, 12, 729–740, 1998.

Shurpali, N., Verma, S., Kim, J., and Arkebauer, T.: Carbon dioxide exchange in a peatland ecosystem, Journal of Geophysical Research, 100, 14 319–14 326, 1995.

Silvola, J., Alm, J., Alholm, U., Nykänen, H., and Martikainen, P. J.: CO_2 fluxes from peat in boreal mires under varying temperature and moisture conditions, Ecology, 84, 219–228, 1996.

Smemo, K. and Yavitt, J.: A multi-year perspective on methane cycling in a shallow peat fen in central New York State, USA, Wetlands, 26, 20–29, 2006.

Sommerkorn, M.: Micro-topographic patterns unravel controls of soil water and temperature on soil respiration in three Siberian tundra systems, Soil Biology and Biochemistry, 40, 1792–1802, 2008.

Stow, C., Lamon, E., Kratz, T., and Sellinger, C.: Lake Level Coherence Supports Common Driver, Eos Trans. AGU, 89, 389–390, 2008.

Strack, M. and Waddington, J.: Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment, Global Biogeochemical Cycles, 21, GB1007, 2007.

Strack, M., Waddington, J. M., and Tuittila, E.-S.: Effect of water table drawdown on northern peatland methane dynamics: Implications for climate change, Global Biogeochemical Cycles, 18, GB4003, doi:10.1029/2003GB002209, 2004.

Sullivan, P., Arens, S., Chimner, R., and Welker, J.: Temperature and microtopography interact to control carbon cycling in a high arctic fen, Ecosystems, 11, 61–76, doi: 10.1007/s10021-007-9107-y, 2008.

Syed, K., Flanagan, L., Carlson, P., Glenn, A., and Gaalen, K. E. V.: Environmental control of net ecosystem CO_2 exchange in a treed, moderately rich fen in northern Alberta, Agricultural and Forest Meteorology, 140, 97–114, doi: 10.1016/j.agrformet.2006.03.022, 2006.

Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., and Mcguire, A. D.: Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland, Journal of Geophysical Research, 113, G00A10, doi:10.1029/2007JG000496, 2008.

Turunen, J., Tahvanainen, T., Tolonen, K., and Pitkänen, A.: Carbon accumulation in west Siberian mires, Russia, Global Biogeochemical Cycles, 15, 285–296, 2001.

Updegraff, K., Bridgham, S., Pastor, J., Weishampel, P., and Harth, C.: Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation, Ecological Applications, 11, 311–326, 2001.

Vickers, D., Thomas, C. K., Martin, J. G., and Law, B.: Self-correlation between assimilation and respiration resulting from flux partitioning of eddy-covariance CO_2 fluxes, Agricultural and Forest Meteorology, 149, 1552–1555, 2009.

Vourlitis, G., Harazono, Y., Oechel, W., Yoshimoto, M., and Mano, M.: Spatial and temporal variations in hectare-scale net CO_2 flux, respiration and gross primary production of Arctic tundra ecosystems, Functional Ecology, 14, 203–214, 2000.

Waddington, J., Griffis, T., and Rouse, W.: Northern Canadian Wetlands: Net Ecosystem CO_2 Exchange and Climatic Change, Climatic Change, 40, 267–275, 1998.

Webb, E., Pearman, G., and Leuning, R.: Correction of flux measurements for density effects due to heat and water vapour transfer, Quarterly Journal of the Royal Meteorological Society, 106, 85–100, 1980.

Wesely, M. L. and Hart, R. L.: Variability of short term eddy correlation estimates of mass exchange, in: Forest-Atmosphere Interaction, edited by Hutchinson, B. A. and Hicks, B. B., pp. 591–612, Reidel Publications, Dordrecht, Netherlands, 1985.

Wilson, K., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Berbigier, P., Bernhofer, C., Ceulemans, R., Dolman, H., Field, C., Grelle, A., Ibrom, A., Law, B., Kowalski, A., Meyers, T., Moncrieff, J., Monson, R., Oechel, W., Tenhunen, J., Valentini, R., and Verma, S.: Energy balance closure at FLUXNET sites, Agricultural and Forest Meteorology, 113, 223–243, 2002.

Wisconsin Department of Natural Resources: WISCLAND Land Cover, Wisconsin Department of Natural Resources, Madison, WI, 1998.

Wösten, J.: Peat subsidence and its practical implications: a case study in Malaysia, Geoderma, 78, 25–36, doi:10.1016/S0016-7061(97)00013-X, 1997.

Zhang, Y., Li, C., Trettin, C., Li, H., and Sun, G.: An integrated model of soil, hydrology, and vegetation for carbon dynamics in wetland ecosystems, Global Biogeochemical Cycles, 16, 1061, 2002.

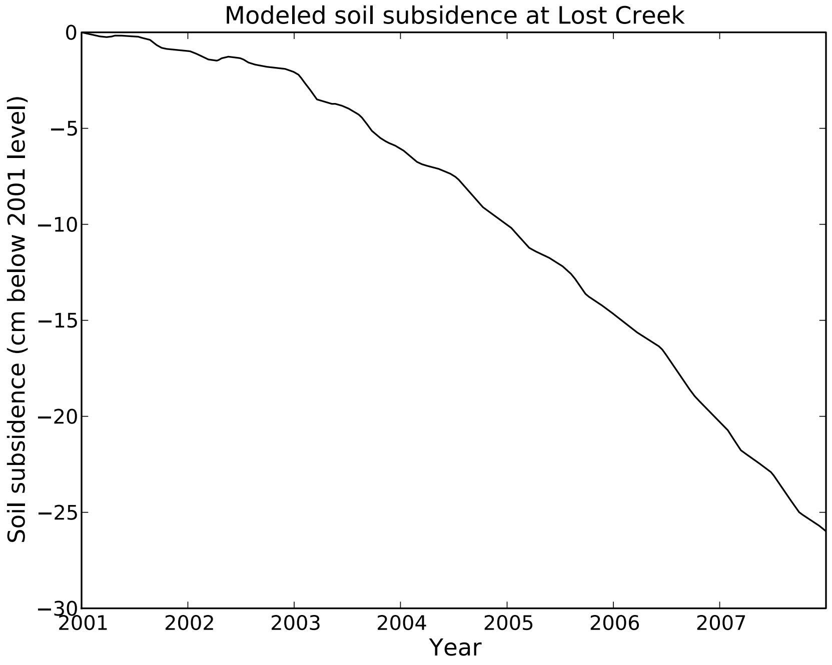

Figure 1: Time series of soil subsidence at Lost Creek, calculated using Eq. 9. This level was subtracted from water table measurements in order to properly reference water table to the soil surface over the time series.

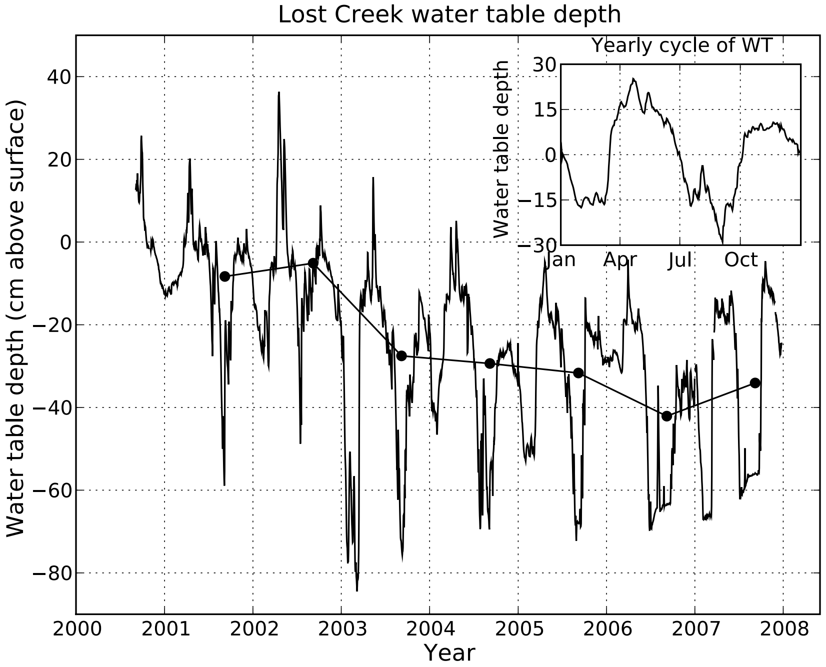

Figure 2: Time series of Lost Creek water table measurements. Positive numbers denote standing water, and negative numbers denote depth of water table below the soil surface. Water table height declined substantially over the record, primarily between 2002 and 2003. The black dots connected by solid lines show WT averaged over the period of each year when the soil temperature was greater than 0°C. The inset shows the detrended mean yearly cycle of water table at LC. Water table is high in spring and fall and lowest in late summer and in winter before snowmelt.

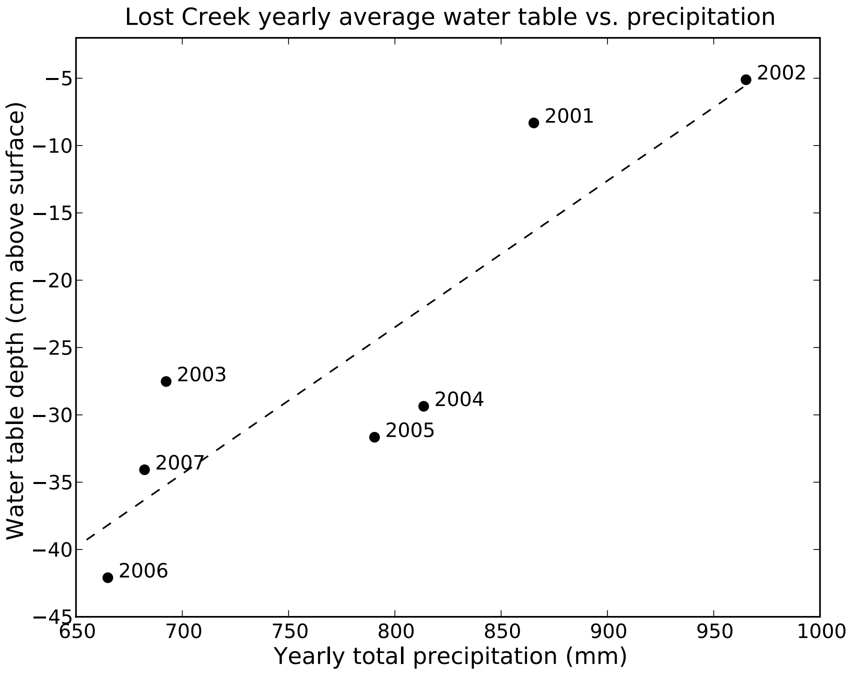

Figure 3: Water table averaged over the period of each year when soil temperature was greater than 0°C vs yearly total precipitation at Lost Creek. Each point is labelled with the year. The dashed line is a linear regression, with a slope of 0.11 cm water table/mm precipitation. The correlation coefficient is 0.88.

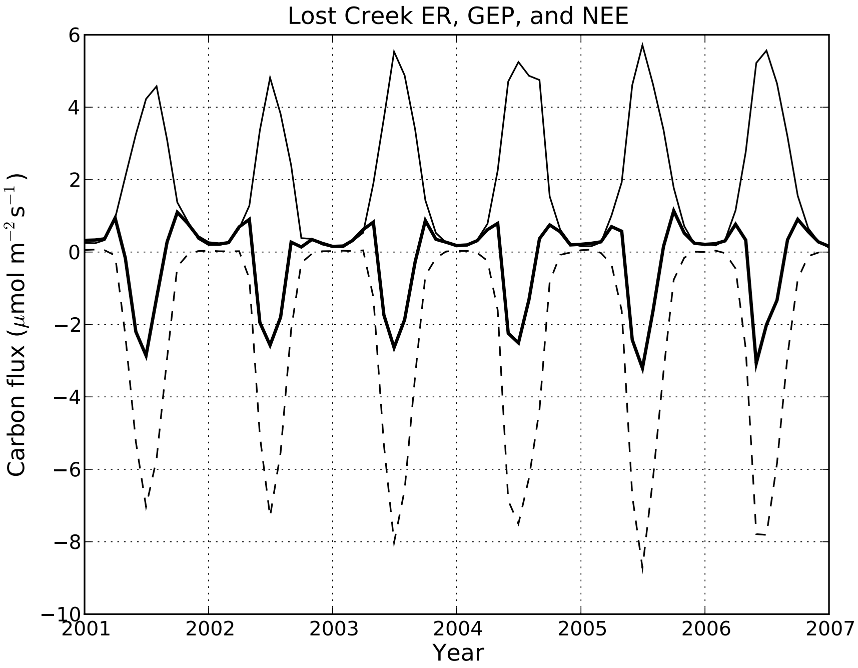

Figure 4: Monthly-averaged ER (solid line), GEP (dashed line), and NEE (thick solid line) at Lost Creek. Negative numbers represent absorption of carbon from the atmosphere, and positive numbers represent emission of carbon to the atmosphere.

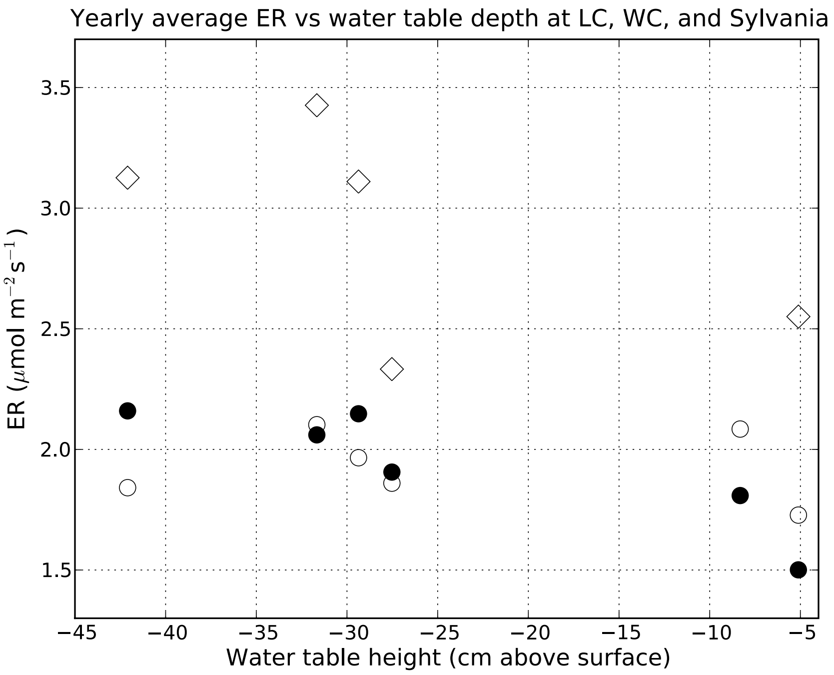

Figure 5: Yearly-averaged ER as a function of WT averaged over the period of each year when soil temperature was greater than 0°C at LC (•), Sylvania (♢), and WC (◯). LC shows a strong negative correlation between WT and ER (correlation coefficient -0.90). Yearly average wetland ER increased by over 20% over the record. ER at Sylvania is also negatively correlated with LC water table to a lesser extent (correlation coefficient -0.56), while ER at WC is not significantly correlated with LC water table (correlation coefficient –0.1).

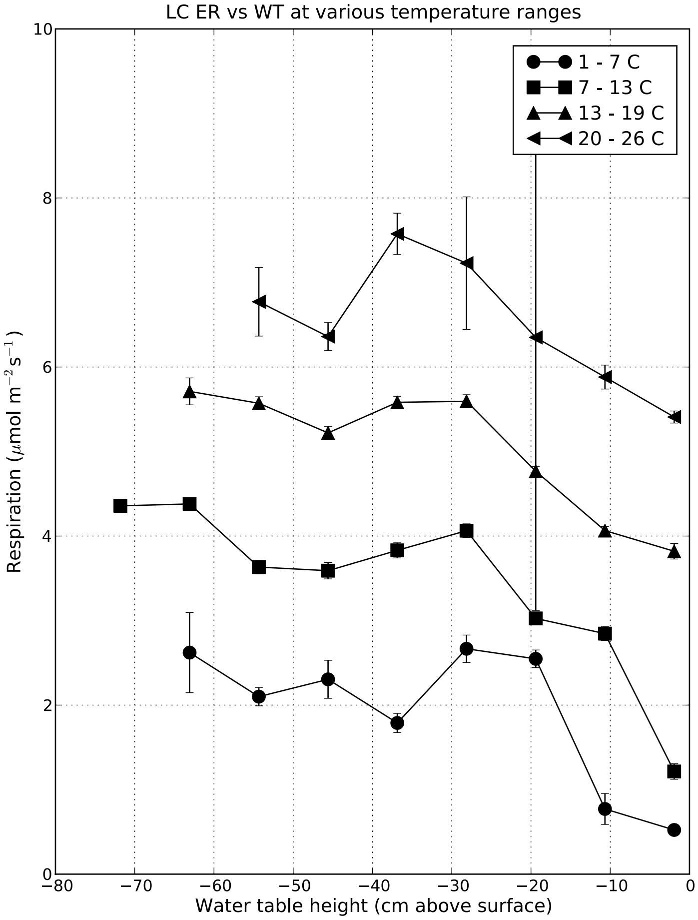

Figure 6: Binned averages of half-hourly ER during the growing season at LC plotted against water table depth, for different soil temperature ranges. The depth of soil temperature used was determined based on water table. This did not have an appreciable effect on the shape of the curve, and more accurately reflects the physical processes taking place (see section 3.4.1). Higher temperature bins have higher ER rates. ER decreases with increasing water table height up to a critical depth, below which ER does not depend on temperature. The dependence on water table penetrates deeper at higher temperatures. Error bars represent 95% confidence limits on the mean of each bin.

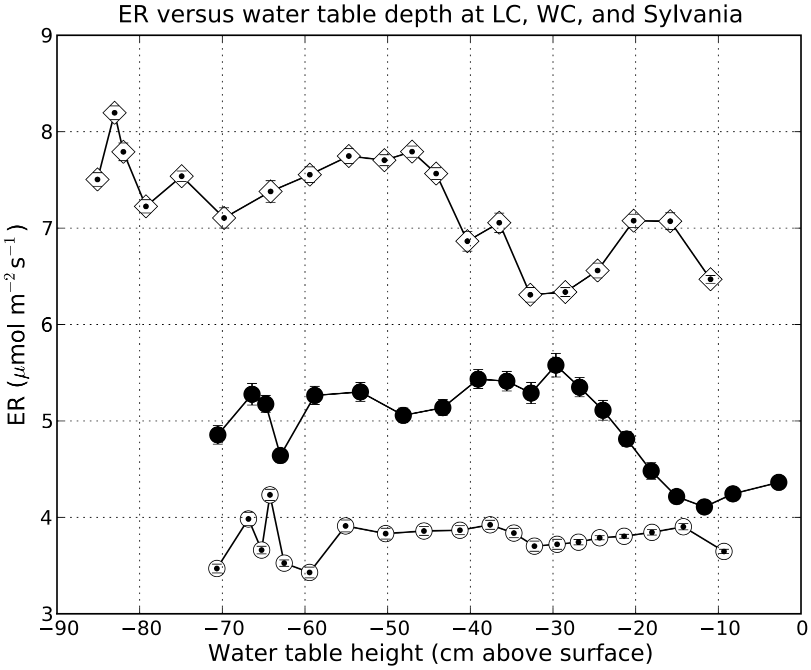

Figure 7: ER plotted against water table height for LC (●), WC (◯), and Sylvania (◊). The plot is a binned average of growing-season ER, calculated from half-hourly data. Each point is the mean of a water table range containing an equal number of points. WC and Sylvania, the upland forest sites, are plotted against LC WT for comparison. The wetland site exhibits a large decrease in ER with higher WT at a level about 30 cm below the surface. WC and Sylvania, the upland sites, do not show the same relationship between ER and water table, indicating that the dependence in the wetland site is not a statistical artifact. Error bars represent 95% confidence limits on the mean of each bin.

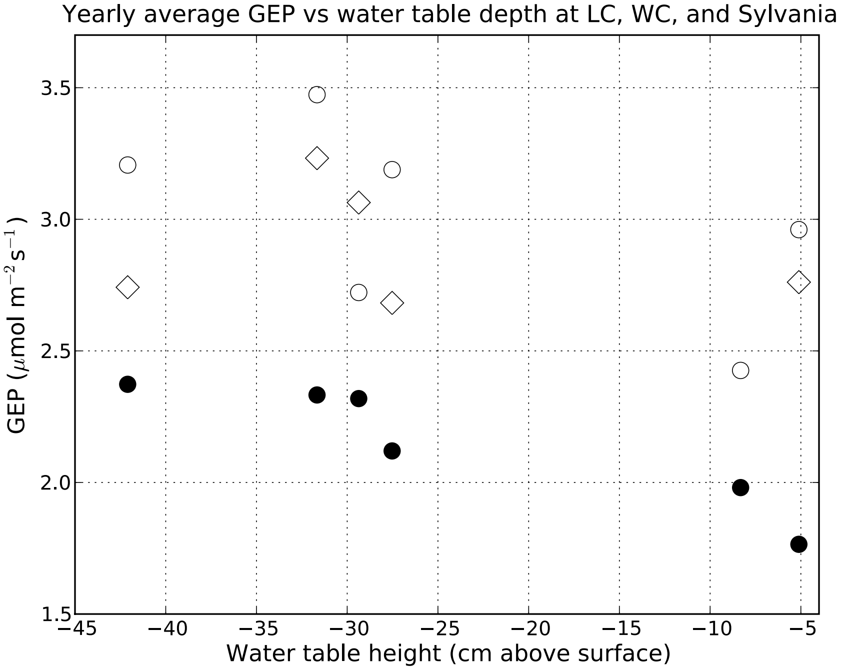

Figure 8: Yearly average GEP plotted against WT averaged over the period of each year when soil temperature was greater than 0°C at LC (●), WC (○), and Sylvania (◊). The upland sites WC and Sylvania are plotted against LC water table for comparison. Wetland GEP is highly correlated with water table (correlation coefficient –0.94), while upland GEP has no significant correlation with wetland water table. Yearly average wetland GEP increased by over 20% over the record.

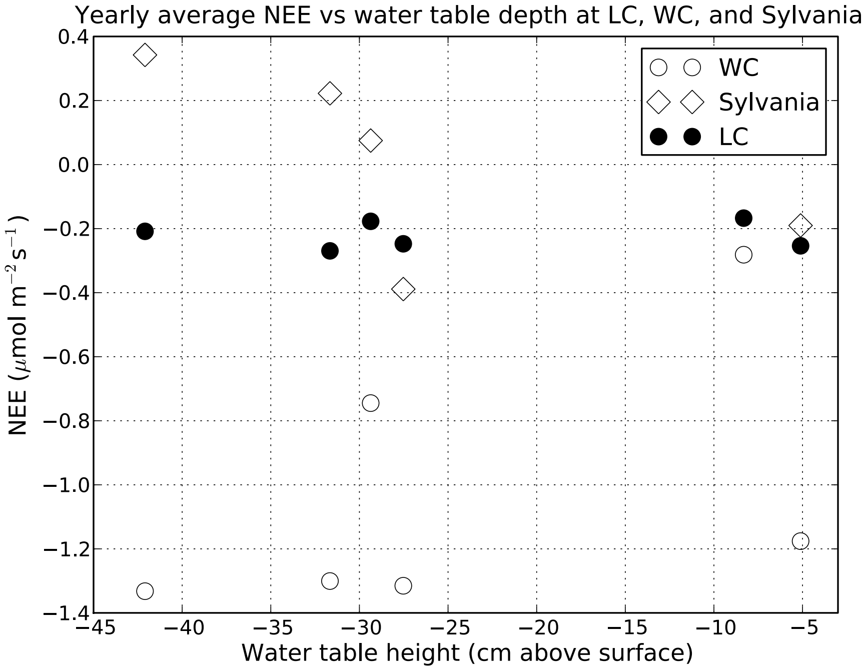

Figure 9: Yearly-averaged NEE at Lost Creek, Willow Creek, and Sylvania as a function of Lost Creek warm period WT. NEE was not correlated with LC water table at any of the sites. The relationships between NEE and whole-year average WT were not materially different.

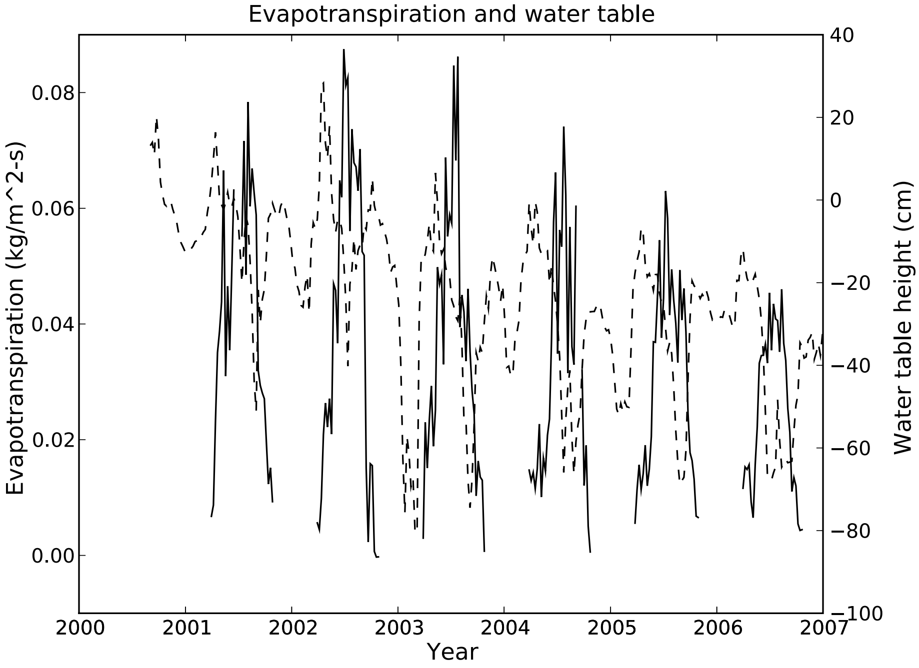

Figure 10: Weekly-average growing season evapotranspiration (solid line), and water table (dashed line) at Lost Creek. Evapotranspiration decreased as water table declined.

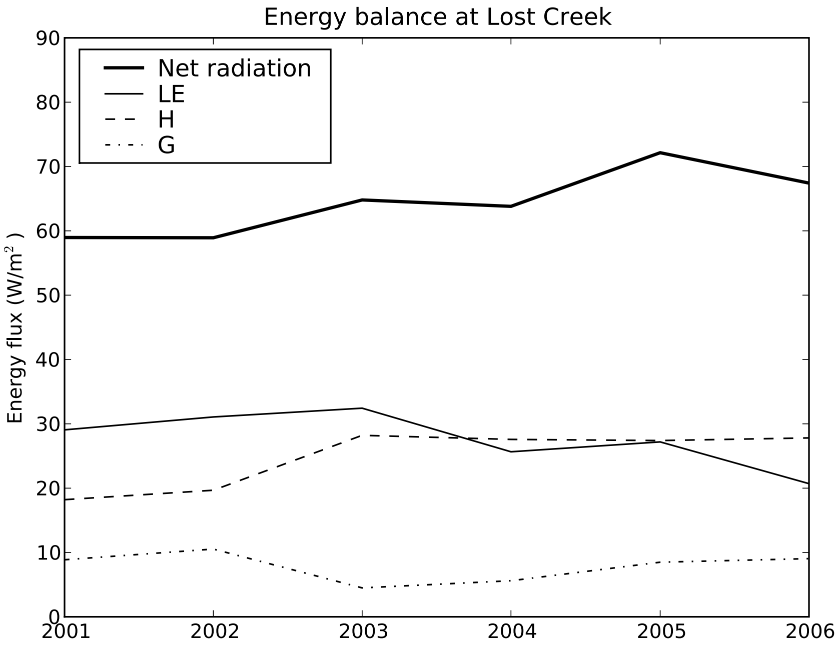

Figure 11: Yearly average energy fluxes at Lost Creek. LE is latent heat, H sensible heat, and G heat flux into the ground. The largest heat sink changed from latent heat to sensible heat flux as water table declined over the time series.

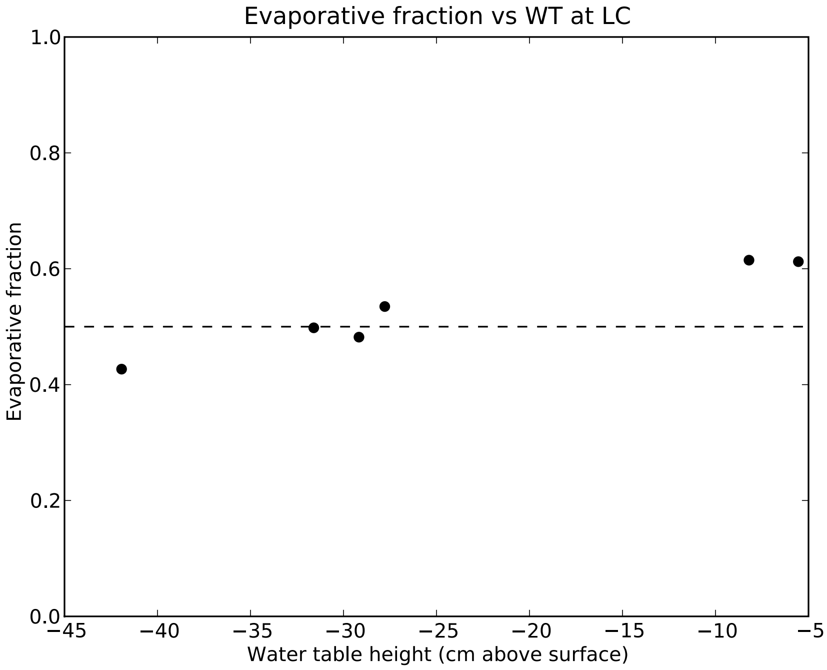

Figure 12: Yearly average evaporative fraction (Eq. 2) as a function of warm-period water table at LC. The dashed line indicates the level where latent heat flux and sensible heat flux are equal. EF declined as water table declined ($r = 0.975$) and EF crossed below the 0.5 level, indicating that sensible heat flux became a larger part of the energy budget than latent heat flux.

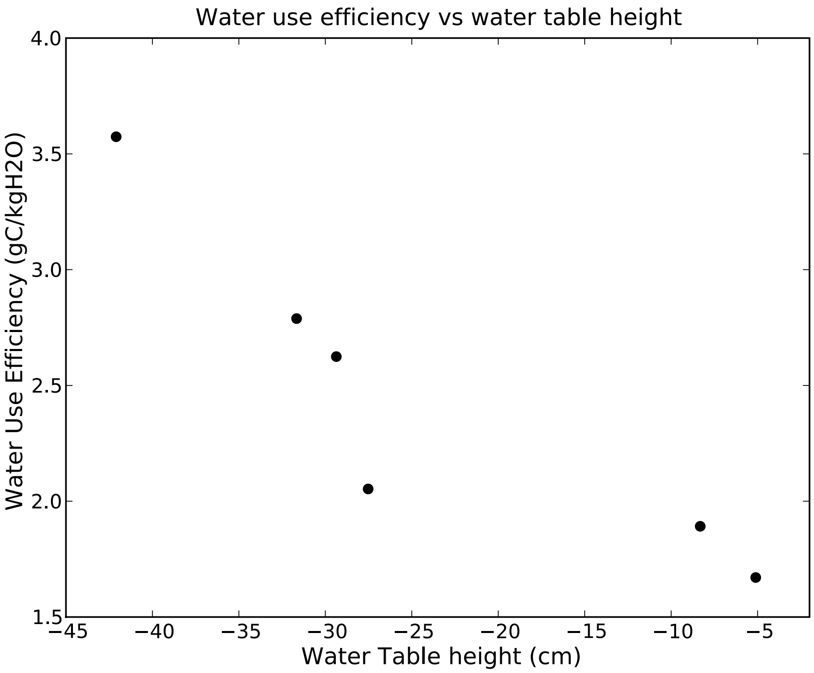

Figure 13: Yearly Lost Creek water use efficiency (defined here as the ratio between evapotranspiration and GEP) as a function of WT averaged over the period of each year when soil temperature was greater than 0°C. Evapotranspiration decreased as the water table declined while GEP increased, resulting in a net increase in WUE. The correlation coefficient is –0.91.

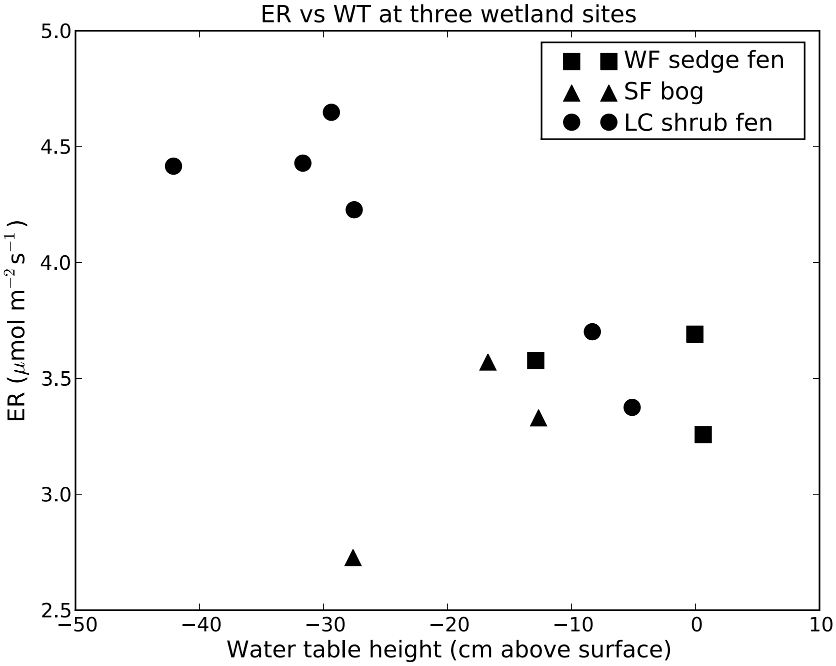

Figure 14: ER at the three wetland sites. LC (shrub fen) is circles, WF (sedge and grass fen) is squares, and SF (bog) is triangles.

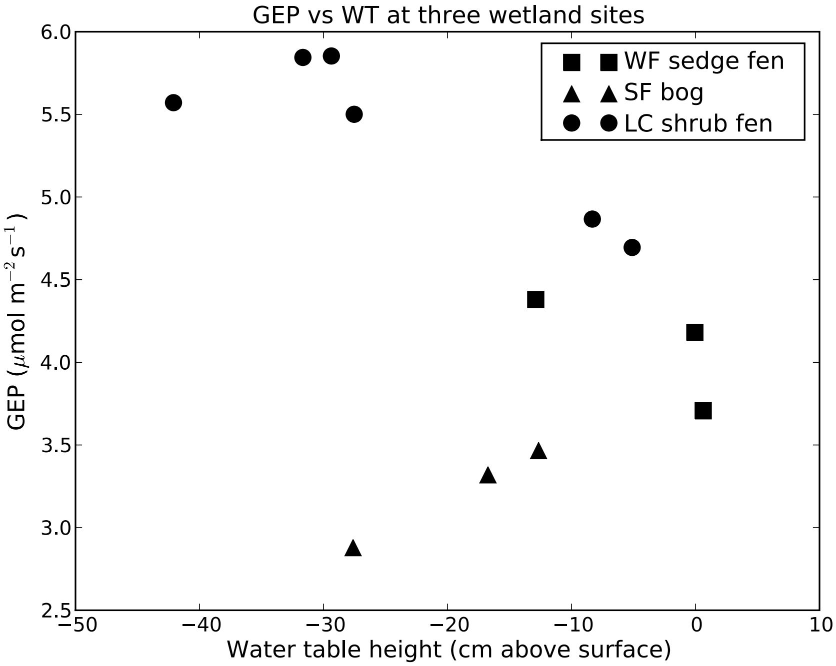

Figure 15: GEP at the three wetland sites. LC (shrub fen) is circles, WF (sedge and grass fen) is squares, and SF (bog) is triangles.

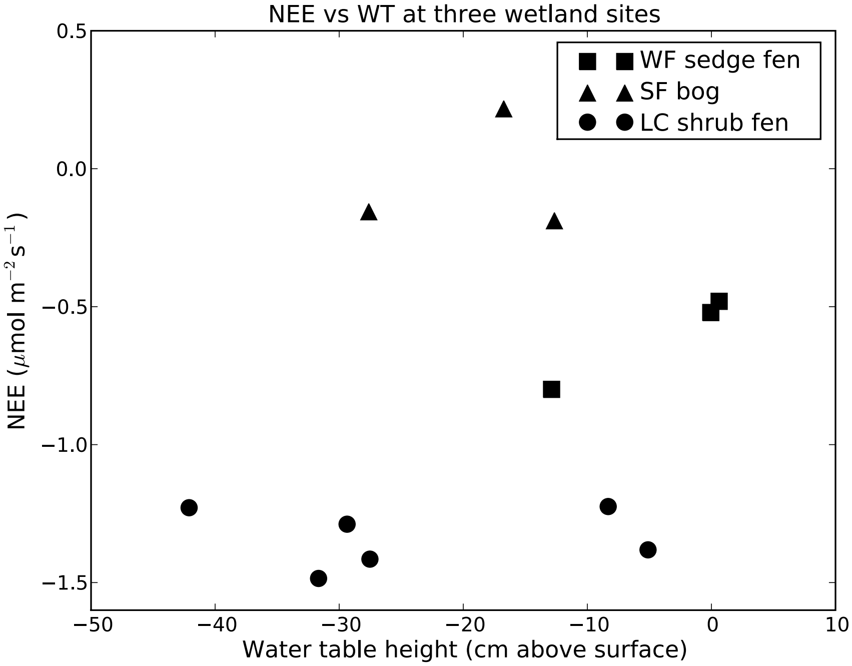

Figure 16: Net ecosystem CO_2 exchange at the three wetland sites. LC (shrub fen) is circles, WF (sedge and grass fen) is squares, and SF (bog) is triangles.

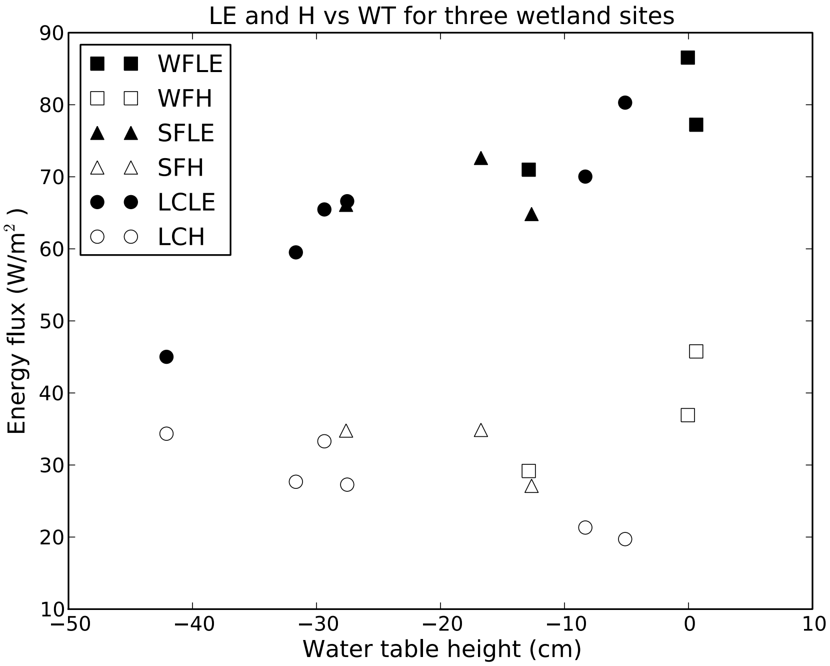

Figure 17: Latent and sensible heat fluxes as a function of warm-period water table at the three wetland sites. Black symbols are latent heat fluxes and open symbols are sensible heat fluxes. Circles are LC (shrub fen), squares are WF (sedge and grass fen), and triangles are SF (bog). Latent heat flux was correlated with water table across the sites ($r = 0.71, p = 0.005$), while sensible heat flux was not significantly correlated with water table ($r = 0.04$)

Table 1: Yearly average measurements for LC. NEE, ER, and GEP are average fluxes in μmol m^{-2}s^{-1}, precipitation is total mm for each year, and water table (WT) is in cm above soil surface.

Year	NEE	ER	GEP	WT	Total precip	Average T (C)
2001	-0.17	1.81	1.98	-8.05	865	5.61
2002	-0.25	1.56	1.76	-8.67	965	4.86
2003	-0.25	1.91	2.12	-32.84	692	4.11
2004	-0.18	2.15	2.32	-27.72	814	4.04
2005	-0.27	2.06	2.33	-33.79	790	5.74
2006	-0.21	2.16	2.37	-39.25	665	6.09