Biogeosciences

Contrasting carbon dioxide fluxes between a drying shrub wetland in Northern Wisconsin, USA, and nearby forests

B. N. Sulman[1], A. R. Desai[1], B. D. Cook[2], N. Saliendra[3], and D. S. Mackay[4]

[1]Dept. of Atmospheric and Oceanic Sciences, University of Wisconsin – Madison, Madison, WI, USA
[2]Dept. of Forest Resources, University of Minnesota – Twin Cities, Minneapolis, MN, USA
[3]Institute for Applied Ecosystem Studies, US Forest Service Northern Research Station, Rhinelander, WI, USA
[4]Dept. of Geography, State University of New York – Buffalo, Buffalo, NY, USA

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 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 wetland, while forest CO_2 fluxes had no significant trends. Net ecosystem exchange of carbon dioxide at the wetland was not correlated with water table, but wetland evapotranspiration decreased substantially as the water table declined. 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.

1 Introduction

Terrestrial carbon fluxes represent a major source of uncertainty in estimates of future atmospheric greenhouse gas accumulation and consequently models of climate change (Friedlingstein et al., 2006). Wetlands represent one of the largest sources of this uncertainty. In the Upper Great

Lakes states (Minnesota, Wisconsin, and Michigan), wetlands cover 14% of the land area, and comprise up to one third of the land cover in the forest-wetland landscapes that dominate the northern half of the region. Worldwide, wetlands contain up to one third of the total soil carbon reservoir (Gorham, 1991; Turunen et al., 2002).

One major source of error in wetland modelling is the lack of mechanisms linking wetland biogeochemistry and hydrology. Fluxes of both carbon dioxide and methane are expected to respond to changes in water table height (Moore and Knowles, 1989; Freeman et al., 1992; Kettunen et al., 1996; Vourlitis and Oechel, 1999; Yurova et al., 2007; Jungkunst and Fiedler, 2007). Many climate change models predict increases in summer precipitation in the areas of the world with the highest concentration of wetlands. However, increases in summer temperature and evapotranspiration are expected to result in a net lowering of summer water table in high latitudes where most of the world's wetlands are found (Wetherald and Manabe, 2002; Meehl et. al., 2007). In a modelling study of a warming climate scenario, Ise et al. (2008) predicted high future losses of soil carbon from peatlands as water tables decline. Given the sensitivity of wetlands to water dynamics, the expected climatic changes, and the large carbon reservoir contained in wetlands, interactions between wetland hydrology and carbon fluxes represent a climate feedback mechanism of potentially great importance. A better understanding of the wetland response to changes in hydrology could materially improve the accuracy of land-atmosphere interaction modelling of temperate regions.

Understanding of ecosystem responses over long time scales is crucial to characterising expected responses to climate change, because climate change is fundamentally a long-term process, occurring over a time scale of decades or

Correspondence to: B. N. Sulman
(bnsulman@wisc.edu)

longer (Meehl et. al., 2007). Eddy covariance measurements provide data reflecting a large spatial area and form a long, continuous time series, making the measurements useful for characterising ecosystem-level processes (Baldocchi, 2003). The multi-year time series of data presented here is useful for providing insights on the longer-term processes and ecosystem changes that may occur under future climatic changes.

A trend of declining water table height has been observed over several years at a wetland site in Northern Wisconsin, providing an opportunity to directly study the effects of a continuous change in hydrology on the carbon dynamics of the wetland ecosystem over a multiple-year time scale. Eddy covariance measurements taken at 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.

Carbon exchange between an ecological system and the atmosphere can be represented as the sum of two separate processes. One, aerobic ecosystem respiration (ER), produces carbon dioxide through the decomposition of organic matter, and represents the emission of carbon dioxide to the atmosphere. Anaerobic respiration emits other chemical products such as methane, and was not investigated for this study. The other process, gross ecosystem production (GEP), is the conversion of atmospheric CO_2 to organic matter through photosynthesis, and represents the removal of carbon from the atmosphere. These processes, while not completely independent, can be modelled separately (Falge et. al., 2001). The sum of the emission of CO_2 due to ER and the absorption of CO_2 due to GEP is net ecosystem exchange (NEE), and is a balance between the two. ER and GEP are similar in magnitude when averaged over the seasonal cycle, so small changes in either component can result in large fractional changes in NEE. This study tested the following hypotheses regarding the response of ER, GEP, and NEE to changes in water table depth:

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 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.

2 Materials and methods

2.1 Site descriptions

Eddy covariance fluxes and related bio-and-geophysical data from one wetland site (Lost Creek) and two upland sites (Willow Creek and Sylvania) in North-Central Wisconsin and the Upper Peninsula of Michigan were analysed and compared for this study. All the sites are within a 50 km radius, and therefore have roughly similar microclimates. All three sites are part of the Chequamegon Ecosystem Atmosphere Study (ChEAS; http://cheas.psu.edu). The sites are also affiliated with the Ameri-Flux Network (Baldocchi et al., 2001) and measurements and processing are consistent with standard Ameri-Flux/Flux-Net protocols (Berger et al., 2001; Baldocchi, 2003).

2.1.1 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).

2.1.2 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).

2.1.3 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, 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).

2.2 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 3-D sonic anemometers and open or closed path infrared gas analysers. Data were recorded at 10 Hz, and thirty-minute average fluxes were calculated from the high-frequency data. The fluxes were corrected for storage below the eddy covariance measurement height and for spectral attenuation using standard established techniques (Desai et. al., 2008a). Fluxes were also screened

for low-turbulence conditions using a friction velocity criterion for each site. 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).

Water table height (WT) was measured using pressure transducer systems at LC, and is defined in this study as height of the water level above the soil surface, referenced to the soil surface height in 2001. 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 on these measurements was removed (see Sect. 2.4).

Micrometeorological data were collected continuously at all sites, including 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.

2.3 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 maximising 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.

2.4 Modelling of soil subsidence

Peat subsidence and compaction resulting from the declining water table 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 modelled using a relationship suggested by Wösten et. al. (1997). The rate of change of soil height is proportional to the depth of the water table:

$$\frac{dz}{dt} = A \times (\mathrm{WT_{meas}}(t) - z(t)) \qquad (1)$$

where z is the soil surface height, $\mathrm{WT_{meas}}(t)$ is the uncorrected measured water table depth, and A is a variable parameter adjusted to match observed data. $(\mathrm{WT_{meas}}(t) - z(t))$ is the corrected water table depth. The modelled subsidence was normalised to match the observed total change in soil surface height, and the final results were not sensitive to the value of A. 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.

2.5 Partitioning of carbon fluxes and gap-filling

Missing and screened data were replaced using the methodology of Falge et. al. (2001), with slight modifications (Cook et. al., 2004; Desai et. al., 2005). ER was modelled by fitting nighttime CO_2 flux to the Eyring function, a theoretically derived chemical reaction kinetics model that depends on soil temperature:

$$\mathrm{ER} = 10^{-6}\frac{k}{h}T_s e^{-(\Delta G^{++}/R^*T_s)} \qquad (2)$$

where ER is the modelled 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}):

$$\Delta G^{++} = \Delta H^{++} - T_s \Delta S^{++} \qquad (3)$$

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 modelled ER from daytime observed NEE and fitting the result to a Michaelis-Menton reaction rate equation (Falge et. al., 2001):

$$\mathrm{GEP} = \frac{b_1 \times \mathrm{PAR}}{b_2 + \mathrm{PAR}} \qquad (4)$$

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 modelled 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).

2.6 Calculation of ecosystem water use efficiency

Estimated ecosystem water use efficiency was calculated as the ratio between GEP and evapotranspiration as measured by eddy-covariance:

$$\mathrm{WUE} = \frac{\mathrm{GEP}}{\mathrm{ET}} \qquad (5)$$

This definition avoids errors introduced by attempting to model soil evaporation, since we had no direct measurements to separate evaporation from transpiration. The same definition was used by Humphreys et al. (2006).

3 Results

3.1 Climate and annual patterns

The region has a northern continental climate, characterised 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

The record of water table at Lost Creek shows a clear decline, with yearly average water table lowering by approximately 30 cm between 2002 and 2006 (Fig. 1). 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, 2009). Water table measurements were corrected for peat subsidence using the methodology discussed in Sect. 2.4.

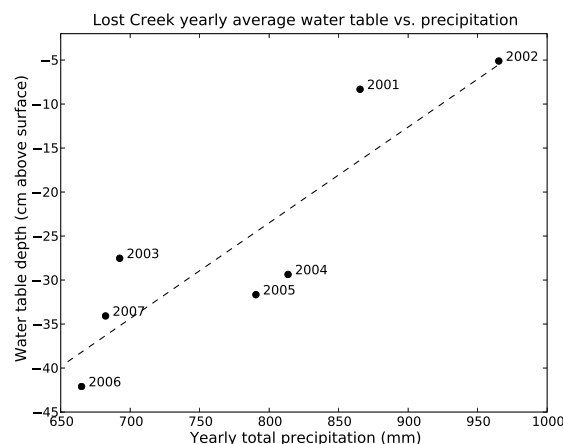Trends in precipitation also appear connected with the water table decline at Lost Creek. Growing season

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 is in cm above soil surface.

Year	NEE	ER	GEP	WT	Total precip (mm/yr)	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
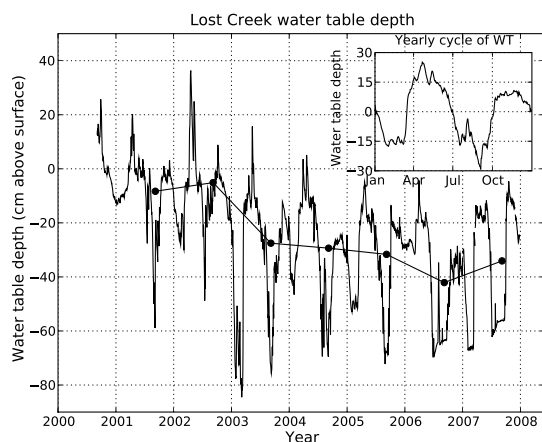
Fig. 1. Time series of Lost Creek water table measurements. Positive numbers denote standing water, and negative numbers denote depth of water table below the soil surface. Water table height declined substantially over the record, primarily between 2002 and 2003. The black dots connected by solid lines 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.

Fig. 2. 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.

average water table and yearly total precipitation have a correlation coefficient of 0.88 ($p=0.01$) over the seven-year record (Fig. 2). 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.

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; Béhaegel et al., 2007).

3.3 NEE, ER, and GEP

The monthly-averaged time series of NEE, ER, and GEP are shown in Fig. 3. 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
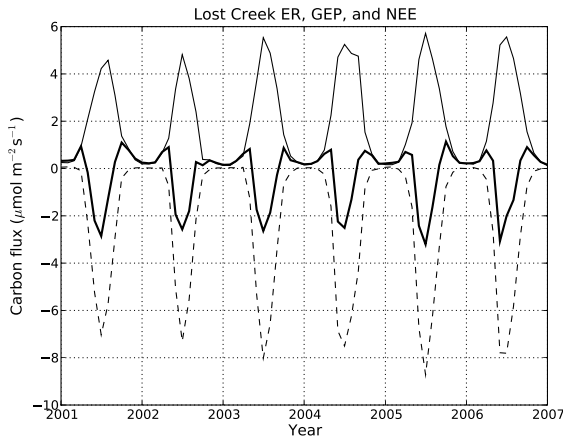
Fig. 3. Monthly-averaged ER (solid line), GEP (dashed line), and NEE (thick solid line) at Lost Creek. Negative numbers represent absorption of carbon from the atmosphere, and positive numbers represent emission of carbon to the atmosphere.
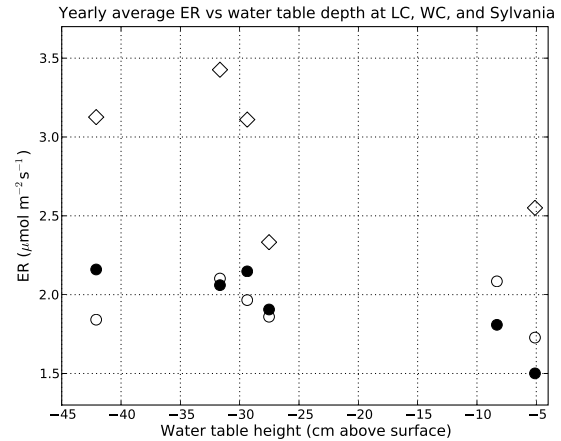

Fig. 4. Yearly-averaged ER as a function of WT averaged over the period of each year when soil temperature was greater than 0°C at LC (●), Sylvania (◇), and WC (○). LC shows a strong negative correlation between WT and ER (correlation coefficient −0.90). Yearly average wetland ER increased by over 20% 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).

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

3.4 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, 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-season WT was therefore used for all the annual average analysis in this study.

The time series in Fig. 1 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. 4, filled circles) have a correlation coefficient of −0.90 (p=0.015). LC ER increased from an average of 1.65 μmol m^{-2} s^{-1} in the first two years of the record to an average of 2.06 μmol m^{-2} s^{-1} in the last four years of the

record. This represents an increase of approximately 25% over the record. The ER data for the upland sites (open symbols) are less 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 artefact.

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 5 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
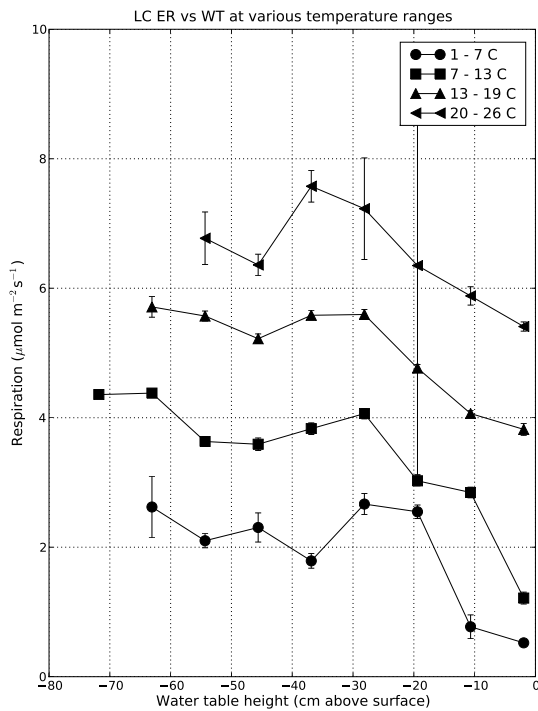
Fig. 5. Binned averages of half-hourly ER during the growing season at LC plotted against water table depth, for different soil temperature ranges. The depth of soil temperature used was determined based on water table. This did not have an appreciable effect on the shape of the curve, and more accurately reflects the physical processes taking place (see Sect. 3.4). 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.

consistent with the observations of Lafleur et. al. (2005), 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 6 shows binned average ER calculated from half-hourly data at the Lost Creek wetland site as well as Willow Creek and Sylvania, the upland sites, during the growing season, combined over all temperatures. The 20–30 cm cutoff for Lost Creek ER identified in Fig. 5 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
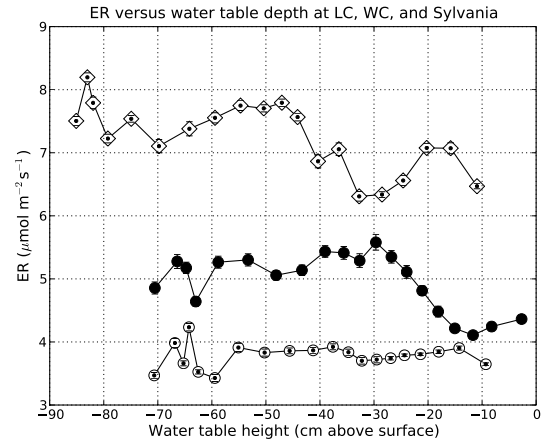

Fig. 6. ER plotted against water table height for LC (●), WC (○), and Sylvania (◇). The plot is a binned average of growing-season ER, calculated from half-hourly data. Each point is the mean of a water table range containing an equal number of points. WC and Sylvania, the upland forest sites, are plotted 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 artefact. Error bars represent 95% confidence limits on the mean of each bin.

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 artefact.

3.5 GEP correlation with water table

Hypothesis 2 states that lower water table should be connected with higher ecosystem productivity, countering the increase in respiration also connected with lower water table. A plot of yearly average GEP as a function of warm-season WT (Fig. 7) 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) have 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 in aboveground biomass. 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).
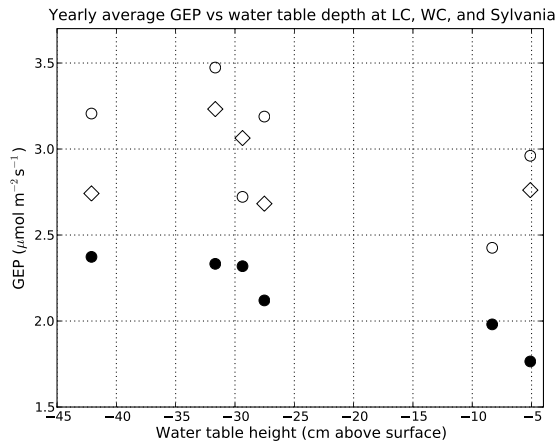
Fig. 7. Yearly average GEP plotted against WT averaged over the period of each year when soil temperature was greater than 0°C at LC (•), WC (○), and Sylvania (◇). The upland sites WC and Sylvania are plotted against LC water table for comparison. Wetland GEP is highly correlated with water table (correlation 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.
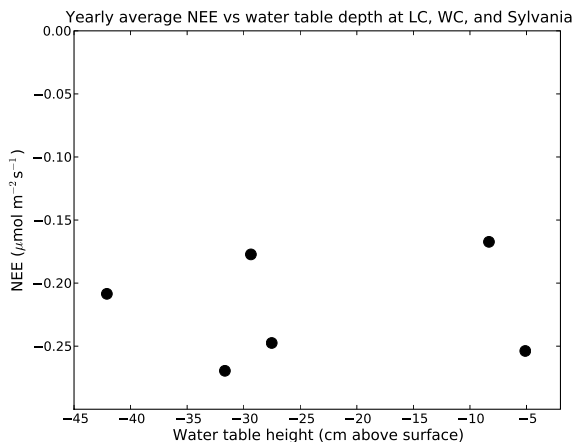

Fig. 8. Yearly-averaged NEE as a function WT averaged over the period of each year when soil temperature was greater than 0°C at Lost Creek. There was no apparent correlation over the record. The relationship between NEE and whole-year average WT was not materially different.

3.6 NEE correlation with water table

Yearly average GEP and ER at LC were highly correlated (correlation coefficient −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,
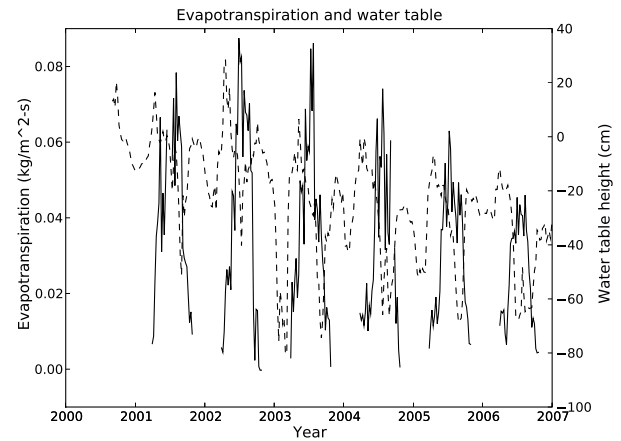

Fig. 9. Weekly-average growing season evapotranspiration (solid line), and water table (dashed line) at Lost Creek. Evapotranspiration decreased as water table declined.

as predicted by hypothesis 3 (Fig. 8). There was no significant correlation between yearly NEE and warm-season water table at LC (correlation coefficient 0.1).

3.7 Evapotranspiration and water use efficiency interactions with water table

An investigation of evapotranspiration (ET) at Lost Creek showed a clear decrease over the record that coincided with the declining water table (Fig. 9). GEP increased over the same time period. The yearly average ecosystem water use efficiency (WUE) increased as the water table declined (correlation coefficient −0.91, p=0.01). This is shown in Fig. 10.

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) 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. 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
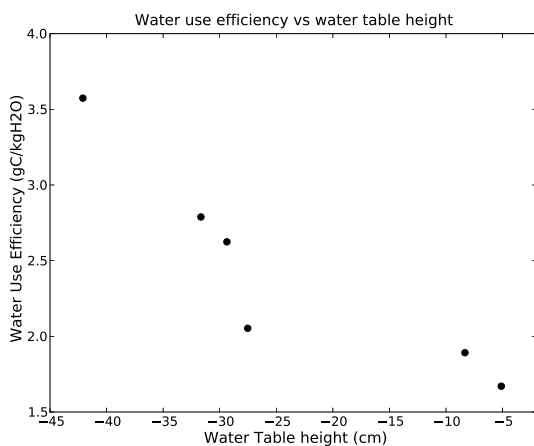
Fig. 10. Yearly Lost Creek water use efficiency (defined here as the ratio between evapotranspiration and GEP) as a function of WT averaged over the period of each year when soil temperature was greater than 0°C. Evapotranspiration decreased as the water table declined while GEP increased, resulting in a net increase in WUE. The correlation coefficient is −0.91.

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.

The high correlation between water table depth and variance in daily soil temperature at LC makes separating the effects of soil moisture 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 (Béhaegel 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., 2005; Nieveen et al., 2005). The results presented here represent a longer 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 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). 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 (Jungkunst 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).

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 NEE being independent of water table. Taking the increased shrub growth over the record into account, the decline in water table led to a net shift in stored carbon from soil to living woody biomass. 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, the increase in shrub cover on the wetland did coincide with changes in evapotranspiration and water use efficiency, and could be expected to change other important parameters of interaction between the ecosystem and atmosphere, such as albedo, roughness, and energy balance, 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 (Foley et al., 2003). Models of climate-biosphere interactions that do not include these types of ecological responses may miss important ecosystem changes with important implications for future climate interactions and feedbacks.

The findings from this study provide some basis for incorporating the effects of water table dynamics into models of wetland biogeochemistry. We plan to pursue this in future work. A properly parameterised model would allow us to investigate the relative responses of autrophic and heterotrophic respiration, which we were unable to separate in our measured data.

Only a single wetland was intensively analysed for this study. Further analysis of eddy covariance data from other wetland sites is necessary to determine whether the findings of this study are consistent across different sites, wetland types, and latitudes. Boreal wetlands and tundra areas are especially important to study, since these form the largest continuous wetland areas in the world and could potentially be a large climate feedback if water dynamics change in the future.

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