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**Impact of declining  
water table on  
wetland carbon  
fluxes**

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# The impact of a declining water table on observed carbon fluxes at a northern temperate wetland

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## 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 6 cm/year was observed at a wetland in northern Wisconsin, USA over a period from 2001–2007. Eddy covariance measurements of carbon dioxide exchange in conjunction with the declining water table revealed an increase in ecosystem respiration of over 20% as water table depth fell through a range between 5 and 35 cm below the surface. Ecosystem respiration was not correlated with water table outside of this range. The limits of the range were dependent on temperature, with the effect of water table penetrating deeper at higher temperatures. Yearly average ecosystem production was approximately 20% higher in years with low water table than in years with high water table. As the water table declined, evapotranspiration decreased and ecosystem water use efficiency increased. Wetland net ecosystem exchange was not correlated with water table, but in 2007, a year with an exceptionally dry growing season, the wetland site was a net carbon source. These results suggest that changes in hydrology may not have a large impact on wetland carbon flux over inter-annual time scales due to opposing responses in both ecosystem respiration and productivity. However, this balance appears to be sensitive to changes in the seasonal distribution of precipitation.

## 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.

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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; Kettunen et al., 1996). 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 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). Most previous studies of wetland carbon fluxes have used chamber measurements, which are limited to small spatial areas and cannot produce long, continuous time series (e.g. Silvola et al., 1996; Alm et al., 1999; Bubier et al., 2003; Corradi et al., 2005; Strack et al., 2006).

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

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ecosystem over a multiple-year time scale. The long continuous record of wetland eddy covariance carbon fluxes and micrometeorological measurements presented in this paper provides a unique opportunity to 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<sub>2</sub> 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<sub>2</sub> due to ER and the absorption of CO<sub>2</sub> 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.
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.

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## 2 Materials and methods

### 2.1 Site descriptions

Eddy covariance fluxes and related bio-and-geophysical data from three wetland sites (Lost Creek, South Fork, and Wilson Flowage) 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 five sites are part of the Chequamegon Ecosystem Atmosphere Study (ChEAS; <http://cheas.psu.edu>). The sites are also affiliated with the AmeriFlux Network (Baldocchi et al., 2001) and measurements and processing are consistent with standard AmeriFlux/FluxNet protocols (Berger et al., 2001; Baldocchi, 2003).

#### 2.1.1 Lost Creek shrub wetland

Lost Creek (LC) is a shrub wetland located in the Northern Highlands State Forest in north central Wisconsin, USA ( $46^{\circ}4.9' N$ ,  $89^{\circ}58.7' W$ ), elevation approximately 480 m above sea level. The vegetation is primarily alder (*Alnus incana* ssp. *rugosa*) and willow (*Salix* sp.), with an understory dominated by sedges (*Carex* sp.). For a more detailed site description, see Cook et al. (2009). The site was established in September, 2000.

#### 2.1.2 South Fork ericaceous 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. It is located in the Chequamegon-Nicolet National Forest, Medford-Park Falls District in North-Central Wisconsin, USA ( $45^{\circ}55.5' N$ ,  $90^{\circ}7.8' W$ ). This site was measured with a portable eddy-covariance system during the growing seasons of 2005–2007.

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### 2.1.3 Wilson Flowage grass-sedge-scrub fen

Wilson Flowage (WF) is a wet meadow/marsh, dominated by sedges and marsh grasses with small patches of labrador tea and leatherleaf. 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). This site was measured with a portable eddy-covariance system during the growing seasons of 2005–2007.

### 2.1.4 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 site was established in May, 1998. For a detailed site description, see Cook et al. (2004).

### 2.1.5 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 site was established in August, 2001. Trees at the Sylvania site range from 0 to 350 years old, and dominant species are sugar maple and eastern hemlock (*Tsuga canadensis*). 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

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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-speed 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).

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 infra-red gas analyser (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.

Water table height (WT) was measured using pressure transducer systems at the three wetland sites, and is defined in this study as height of the water level above the soil surface. Positive WT denotes standing water above the soil, and negative WT represents a water table level below the soil surface.

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.

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## 2.3 Flux calculation

Turbulent fluxes of momentum, heat, water vapour, and CO<sub>2</sub> 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<sub>2</sub> spectra, so the correction factor was computed from theoretical models of air flow through tubing.

## 2.4 Transpiration calculation

Transpiration was calculated by subtracting modelled soil evaporation from eddy covariance measurements of water flux. The evaporation model used was the Penman-Monteith model under the assumption of saturated soil conditions (Allen et al., 1998):

$$E = \frac{\rho C_p}{\gamma} \frac{1}{\lambda} \frac{e_s(T_s) - e_a}{r_d + r_s} \quad (1)$$

where  $E$  is evaporation in units of  $\text{kg m}^{-2} \text{s}^{-1}$ ,  $\rho$  the density of air ( $1.3 \text{ kg m}^{-3}$ ),  $C_p$  the specific heat of air at constant pressure ( $1005 \text{ J kg}^{-1} \text{ K}^{-1}$ ),  $\gamma$  the psychrometric constant ( $66 \text{ Pa K}^{-1}$ ),  $\lambda$  the latent heat of vaporisation for water ( $2.5 \times 10^6 \text{ J kg}^{-1}$ ),  $e_s$  and  $e_a$  the vapour pressures for air and soil, respectively, and  $r_s$  and  $r_d$  the (bulk) surface and aerodynamic resistances, respectively.  $r_d$  was calculated using the formula

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$r_d = 36.5/U$ , where  $U$  is the wind speed,  $r_s$  was calculated using the formula

$$r_s = \exp(8.2 - 4.3 \cdot \% \text{soilsaturation}) \quad (2)$$

using 100% soil saturation, and  $e_s$  used the formula

$$e_s = 100 \cdot 6.112 \cdot \exp\left(\frac{17.67T_s}{243.5 + T_s}\right) \quad (3)$$

5 where  $T_s$  is the soil temperature.

## 2.5 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:

$$\frac{dz}{dt} = A \times (WT_{\text{meas}}(t) - z(t)) \quad (4)$$

15 where  $z$  is the soil surface height,  $WT_{\text{meas}}(t)$  is the uncorrected measured water table depth, and  $A$  is a variable parameter adjusted to match observed data.  $(WT_{\text{meas}}(t) - z(t))$  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.

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## 2.6 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<sub>2</sub> flux to the Eyring function, a theoretically derived chemical reaction kinetics model that depends on soil temperature:

$$ER = 10^{-6} \frac{k}{h} T_s e^{-(\Delta G^{++}/R^*T_s)} \quad (5)$$

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

$$\Delta G^{++} = \Delta H^{++} - T_s \Delta S^{++} \quad (6)$$

where  $\Delta H^{++}$  is enthalpy ( $\text{J mol}^{-1}$ ) and  $\Delta S^{++}$  is entropy ( $\text{J mol}^{-1} \text{ K}^{-1}$ ). 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<sub>2</sub> flux and soil temperature in a moving window.

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):

$$GEP = \frac{b_1 \cdot PAR}{b_2 + PAR} \quad (7)$$

where PAR is photosynthetically active radiation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), 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).

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### 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 declining trend, with the water table lowering by approximately 6 cm per year over the seven-year record (Fig. 1). 2006 had the lowest average water table in the record, but the average water table level in 2007 was only 3 cm higher than in 2006. 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, and also may be partially responsible for the long-term trend. Peat subsidence relating to the declining water table lowered the soil surface by approximately 25 cm over the observed time period (Cook et al., 2009). Water table measurements were corrected for peat subsidence using the methodology discussed in Sect. 2.5.

Trends in precipitation also appear connected with the water table trend at Lost Creek. Yearly-averaged water table and precipitation have a correlation coefficient

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of 0.90 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.

### 5 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 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<sub>2</sub> in all years except 2007, the last year of the record, when it was a net emitter due to below-average GEP.

### 3.4 ER interaction with water table

Hypothesis 1 states that lower water table should correspond to a higher ecosystem respiration rate, since more peat is exposed to oxygen and can be decomposed by aerobic processes. The yearly-averaged ER and WT data from Lost Creek (Fig. 4, filled circles) have a correlation coefficient of  $-0.84$ , supporting this conclusion. The ER data for the upland sites (open symbols) are less correlated to Lost Creek water table (correlation coefficient of  $-0.71$  for Sylvania and  $0.05$  for WC). The smaller but still significant correlation in the Sylvania data suggests that a common factor may affect both Sylvania carbon fluxes and Lost Creek water table (see Sect. 4.2). ER at LC in the two years with the highest water table was significantly less than in the five years with lower water table ( $p < 0.01$ ). ER at Sylvania and WC did not change significantly between high and low LC water table levels (at the 95% level, using a two-tailed t-test). This indicates that the change in wetland ER with changing water table was a real wetland effect, not a statistical artefact.

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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 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  $5.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ . When water table is above a level 20 cm below the surface, ER is flat with an average of approximately  $4.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ . 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 artefact.

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### 3.5 GEP interaction with water table

Hypothesis 2 states that lower water table should be connected with higher ecosystem productivity, counteracting the increase in respiration also connected with lower water table. GEP is higher at higher levels of PAR, saturating at values of PAR above approximately  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Averaging GEP under conditions above this saturation level produces an estimate of the peak ecosystem productivity. Figure 7 shows half-hourly measurements of this peak productivity during the growing season, averaged in bins according to water table depth. This is a measure of the peak productivity of the ecosystem under different water table regimes. GEP at Lost Creek (●) shows a very similar dependence on water table to that of Willow Creek (○). The binned-average data from the Lost Creek wetland site and the Willow Creek upland forest shown in Fig. 7 have a correlation coefficient of 0.87. The correlation coefficient between LC and Sylvania is only 0.35. Since wetland water table cannot be a true control on upland carbon dynamics, this indicates that GEP in both LC and WC sites is affected by a parameter that is also connected with water table in the wetland site. One possibility is that GEP depends on seasonal rainfall, which also affects water table, but GEP is not independently affected by groundwater levels. The lower correlation with Sylvania is probably because LC and WC are much closer to each other than to Sylvania. Interpretation of this plot is also complicated by the seasonal patterns of both water table and GEP.

A plot of yearly average GEP (Fig. 8) shows that wetland GEP is lower at higher water table levels. Averaging over the entire year eliminates interactions between the seasonal patterns of water table and GEP. Lost Creek (●) has lower average GEP at water table levels above  $-20 \text{ cm}$ , while Willow Creek (○) and Sylvania (◇) have no apparent dependence on wetland water table. The average GEP at LC in the two years with the highest water table is  $1.87 \mu\text{mol m}^{-2} \text{s}^{-1}$ , while the average GEP in years with lower water table is  $2.23 \mu\text{mol m}^{-2} \text{s}^{-1}$ , representing an increase in GEP of approximately 20% between years with high and low water tables.

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In 2007, the year with the lowest average water table, the average growing season GEP at LC was significantly lower than in the four previous years ( $p < 0.02$ ), which had similar average water table compared to the first two years of the record. LC had nearly equal average water table and respiration in 2006 and 2007, but very different average GEP. The anomalously low GEP was the main contributor to the net emission of carbon at LC in 2007. For a discussion, see Sect. 4.4.

### 3.6 NEE interaction with water table

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. Yearly averages of NEE and water table depth at LC confirm this hypothesis (Fig. 9). Neglecting the anomalously high NEE in 2007, when LC was a net carbon emitter, there was no significant correlation between yearly NEE and water table at LC (evaluated using a t-test at the 95% level). GEP in 2007 at LC was the lowest of the record, probably representing the effect of an unusually dry growing season. For further discussion, see Sect. 4.4.

### 3.7 Transpiration and water use efficiency interactions with water table

An investigation of transpiration at Lost Creek showed a clear decrease over the record that coincided with the declining water table (Fig. 10). GEP increased over the same time period. The ecosystem water use efficiency (WUE), defined as

$$WUE = \frac{GEP}{Transpiration} \tag{8}$$

increased as the water table declined. This is shown in Fig. 11.

## 4 Discussion

### 4.1 Threshold effect of water table on ER

The data in Sect. 3.4 indicate that water table levels in a wetland have a significant effect on ecosystem respiration. Soil that is saturated with water is low in oxygen, and decomposition is dominated by anaerobic bacteria. When the water table lowers, this soil is exposed to oxygen and much more efficient aerobic bacteria dominate respiration (Clymo, 1984). Total measured ecosystem respiration would be expected to increase as poorly-decomposed organic matter in peat is respired more efficiently in the presence of oxygen. The results of this study suggest that the ecosystem responds to water table as predicted by this hypothesis in a range of water table depth between 5 and 35 cm below the surface, with the range of depths depending on temperature. The change in respiration occurs over a much smaller range of water table depths when combined over all measured temperature ranges, with respiration flat above and below a critical range of water table depth between 18 and 30 cm below the surface. When the water table is below the lower threshold, additional oxygen cannot penetrate the depth of soil, and respiration at lower depths does not increase. This hypothesis was discussed by Lafleur et al. (2005), whose study of wetland ER found no significant correlation between ER and water table at a site where water table was consistently below –30 cm, and by Strack et al. (2006). An earlier study using chamber measurements at several sites (Silvola et al., 1996) found a similar increase in CO<sub>2</sub> emission with lowering water table, with the dependence reaching a saturation point at 30–40 cm below the surface.

These results suggest that rapid drying of peatlands would not cause a rapid release of carbon from the soil to the atmosphere. The acceleration of soil respiration and loss of carbon to the atmosphere would be modulated by the limited thickness of the layer where respiration rates respond to changes in hydrology. In deep peatlands with large soil carbon reserves, a large proportion of soil carbon would be preserved from decomposition even after drying. This result is valid for inter-annual time scales, but

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may break down over longer time scales when ecological succession, changes in soil chemistry, and bulk decomposition of soil become important.

#### 4.2 Correlation of wetland and upland GEP with wetland water table

Half-hourly measurements of growing-season GEP in both the Willow Creek upland site and the Lost Creek wetland site showed similar dependencies on the wetland water table depth, with lower GEP at the lower and higher extremes of water table and higher GEP in the middle. GEP at Sylvania, the old-growth forest site, did not show a similar dependence. Since wetland water table depth cannot be a true control on upland carbon dynamics, this shared dependence suggests that a precursor to water table depth controls GEP at both LC and WC. One possibility is seasonal rainfall. Yearly precipitation and Lost Creek water table were well correlated, with a correlation coefficient of 0.9 (see Fig. 2). A regional trend of lowering lake levels has also been observed (Stow et al., 2008), which would be consistent with a climatic change across the study area. The observed pattern of GEP could be explained as a plant response to precipitation, where both very dry and very wet periods are detrimental to productivity, and plants can fix carbon most efficiently during moderately wet periods. Sylvania is located about 60 km away from WC and LC, while the distance between WC and LC is about 30 km, and may therefore experience different precipitation and hydrology, both of which are very variable in space. This would explain why Sylvania GEP was not correlated with LC.

Cook et al. (2009) found that including water table measurements improved calculations of Lost Creek GPP from remote sensing data on both daily and annual time scales. This is consistent with our finding that water table is correlated with wetland GEP. However, the fact that wetland water table was also correlated with upland GEP implies that the short-term wetland effect is not solely due to water table. If water table responds to a precursor that also affects upland productivity, including regional wetland water table measurements would also improve calculations of nearby upland productivity. This hypothesis could be tested using an investigation of regional precipitation

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and water table measurement networks to determine the relationship between wetland water table and precipitation within the watershed.

The correlation of ER at Sylvania with LC water table could be due to a similar precursor effect, or could result from the presence of wetland areas within Sylvania's flux footprint, as described in Desai et al. (2005). Also, as an old-growth forest Sylvania contains large pools of carbon in soil and woody debris compared to WC, a younger forest (see Luyssaert et al. (2008) for a discussion of old-growth carbon dynamics). The mean and interannual variability of ER were higher at Sylvania than at WC. If the differences in ER at Sylvania result from major differences in the characteristics of the carbon pool, ER at Sylvania could be expected to respond differently to precipitation and other climate forcings.

#### 4.3 ER and GEP balance and changes in plant community composition

The changes in ER and GEP in conjunction with a declining water table at Lost Creek offset each other, resulting in no significant net change in NEE, with the exception of the last year of the record (see Sect. 4.4). Soil respiration increased as upper layers of peat were exposed to oxygen, but the loss of carbon from soil was counteracted by an increase in above-ground carbon storage in woody biomass due to the shrub growth described by Cook et al. (2009). The net result was a shift in stored carbon from soil to above-ground living biomass rather than a large emission of soil carbon to the atmosphere. In the context of climate feedbacks, this suggests that changes in wetland hydrology will not greatly affect wetland net carbon exchange over inter-annual time scales. However, the change in species dominance will likely cause changes in NEE over longer time periods, as well as changes to other important parameters of ecosystem-atmosphere interaction and radiative forcing, such as albedo, roughness, and water balance. Furthermore, the increase in GEP with lowering water table may saturate over time as plants reach the end of their life cycle and die, producing more detritus and increasing ER as is observed in old-growth forests (Desai et al., 2005).

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#### 4.4 Net emission of carbon from LC in 2007

2007 was the first year of the record in which Lost Creek was a net emitter of CO<sub>2</sub>. July GEP in 2007 was 11% lower than the mean over the record for that month, and August GEP was 29% lower than the mean, while growing season ER was only 4% lower than the mean. JJA precipitation in 2007 was 25% lower than the average over the record, and was 45% lower than in 2006, while the water table level was comparable to that in 2006. Previous studies have shown that peatlands can become carbon sources during dry periods (Alm et al., 1999).

This result suggests that the important climatological forcings on wetland carbon fluxes are more complex than simple yearly means of water table and precipitation. If ecosystem respiration responds primarily to water table and GEP responds to growing season precipitation, then the components of NEE could exhibit very different responses depending on the distribution of precipitation over the year. Simulations of future warming predict changes in seasonal patterns of precipitation (Meehl et al., 2007), which could affect wetland carbon balances even if the response to yearly total precipitation is small.

#### 4.5 Effect of water table on water use efficiency

The results in Sect. 3.7 show that growing season transpiration at LC decreased as the water table declined, while GEP increased. Therefore, water use efficiency, the ratio of GEP to transpiration, was not constant. Photosynthesis can be conceptualised as plants “trading” water for carbon dioxide, since leaves must release water through stomata in order to absorb CO<sub>2</sub> from the atmosphere (Jackson et al., 2005). The change in ecosystem WUE with water table height indicates that the amount of water the plants in the wetland released in exchange for a specific amount of CO<sub>2</sub> changed in response to environmental conditions. Either this is a mutable property of individual plants, or the composition of the flora has changed over the record in favour of plants that transpire less water during photosynthesis. The change in WUE could be a result

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of the large observed growth in shrubs at the expense of understory plants such as sedges (Cook et al., 2009).

#### 4.6 Other wetland sites

This paper presents results from the analysis of data primarily from a single wetland site, Lost Creek. Due to the large number of factors affecting the dynamics of any natural ecosystem, results from a single site can be difficult to interpret with confidence. The other two wetland sites described in Sect. 2.1 represent a supplemental data set that can be used to confirm the findings from Lost Creek. We performed a preliminary analysis of data from the two sites measured with the portable eddy covariance system, WF and SF. These sites were instrumented for a much shorter time than Lost Creek, and because a single portable system was used for both, the resulting time series are very fragmented. Yearly totals of ER, GEP, and NEE could not be calculated with confidence since only growing-season data are available, but averages over the growing season periods measured are presented in Table 2.

Over the three growing seasons with available water table data, Wilson Flowage experienced a large rise in water table that was coincident with a substantial drop in both ER and GEP. NEE at WF became less negative. These results are consistent with the results for Lost Creek. South Fork experienced a small drop in water table, which was coincident with slight drops in ER and GEP, and no overall trend in NEE. These responses to water table are the opposite of those observed at LC and WF. One explanation for this discrepancy is that SF is a bog, whereas LC and WF are fens. Bogs have different nutrient regimes and support different plant communities from fens, and could be expected to have different biogeochemistry. Further work with this data set is needed to better identify the similarities and differences in responses between the wetland sites.

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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. The exception was 2007, the last year of the record, when an unusually dry growing season led to a net loss of carbon from the wetland. These results suggest that changes in wetland hydrology should not affect net carbon exchange over inter-annual time scales, although this behaviour appears to be sensitive to the yearly distribution of precipitation. The increase in shrub cover did lead to changes in evapotranspiration, and could be expected to change other important parameters of interaction between the ecosystem and atmosphere, such as albedo and roughness, although these were not investigated for this study.

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.

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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**Table 1.** Yearly average measurements for LC. NEE, ER, and GEP are average fluxes in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , precipitation is total mm for each year, and water table is in cm above soil surface. Note that in 2007 Lost Creek was a net producer of  $\text{CO}_2$ .

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
2007	0.13	2.14	2.02	-36.38	682	5.77

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**Table 2.** Growing season average carbon flux measurements and water table for South Fork and Wilson Flowage. Units are the same as in Table 1. Water table measurements for these sites are not available for 2007.

Site	Year	NEE	ER	GEP	WT
South Fork	2005	-0.30	3.08	3.32	-18.0
	2006	-0.07	2.65	2.56	-21.8
	2007	-0.28	2.17	2.45	-29.3
Wilson Flowage	2005	-0.80	3.58	4.38	-20.3
	2006	-0.27	2.47	2.72	-2.9
	2007	-0.33	2.99	3.29	-3.0

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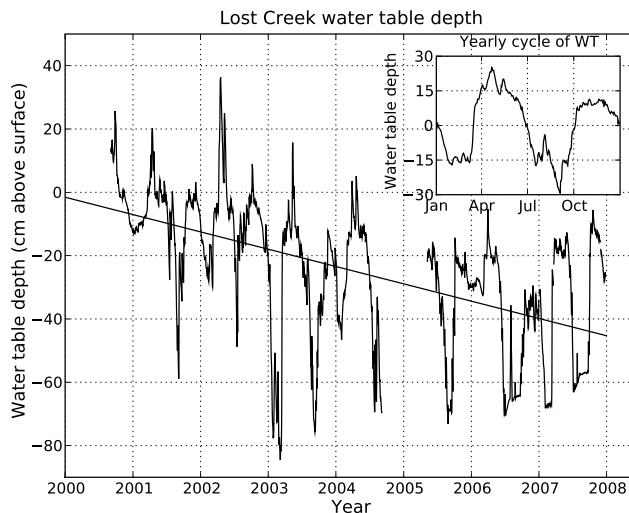
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**Fig. 1.** Time series of Lost Creek water table measurements. Positive numbers denote standing water, and negative numbers denote depth of water table below the soil surface. A linear fit shows the declining trend of approximately 6 cm per year. 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.

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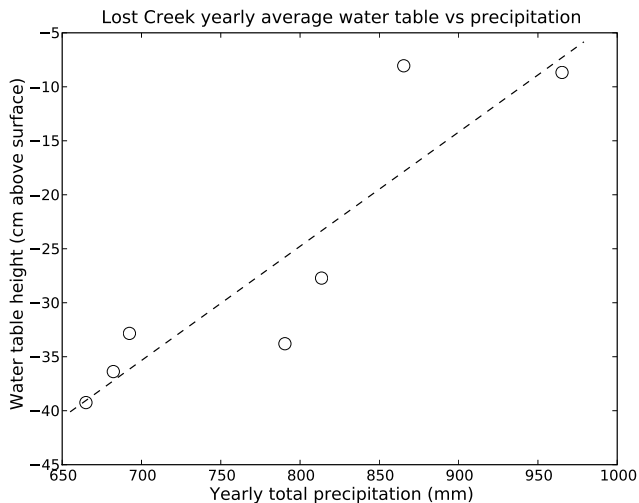
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**Fig. 2.** Yearly averaged water table vs. yearly total precipitation at Lost Creek. The dashed line is a linear regression, with a slope of 0.11 cm water table/mm precipitation. The correlation coefficient is 0.90.

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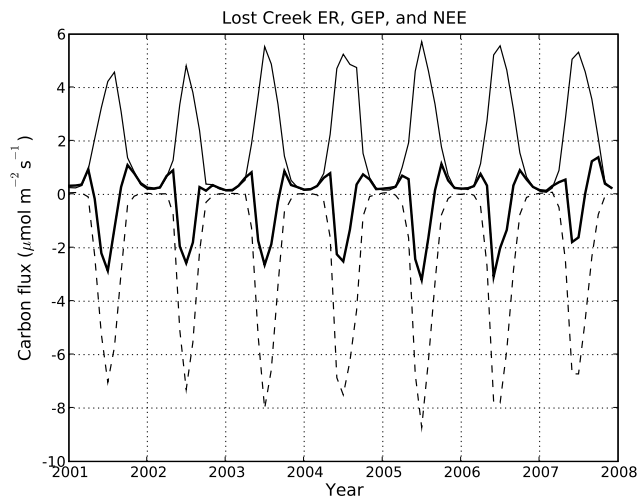
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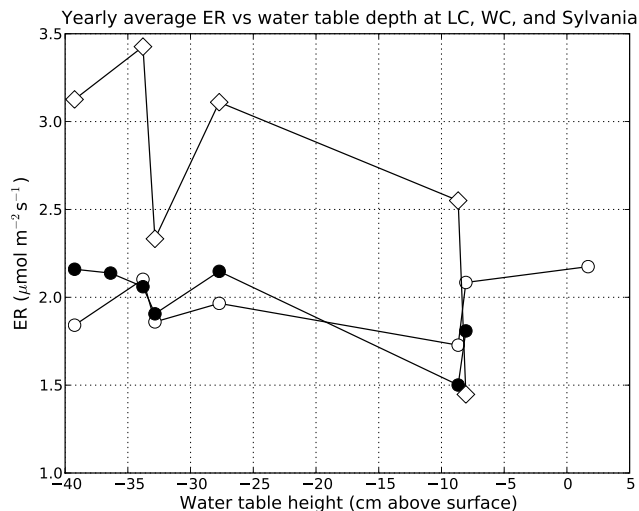
**Fig. 3.** Monthly-averaged ER (solid line), GEP (dashed line), and NEE (thick solid line) at Lost Creek. Negative numbers represent absorption of carbon from the atmosphere, and positive numbers represent emission of carbon to the atmosphere. In 2007, Lost Creek was a net CO<sub>2</sub> emitter due to the above-normal fall NEE.

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**Fig. 4.** Yearly-averaged ER as a function of LC water table depth at LC (●), Sylvania (◇), and WC (○). LC shows a negative correlation between WT and ER (correlation coefficient  $-0.84$ ). ER at Sylvania is also negatively correlated with LC water table to a lesser extent (correlation coefficient  $-0.71$ ), while ER at WC is not significantly correlated with LC water table (correlation coefficient  $0.05$ ).

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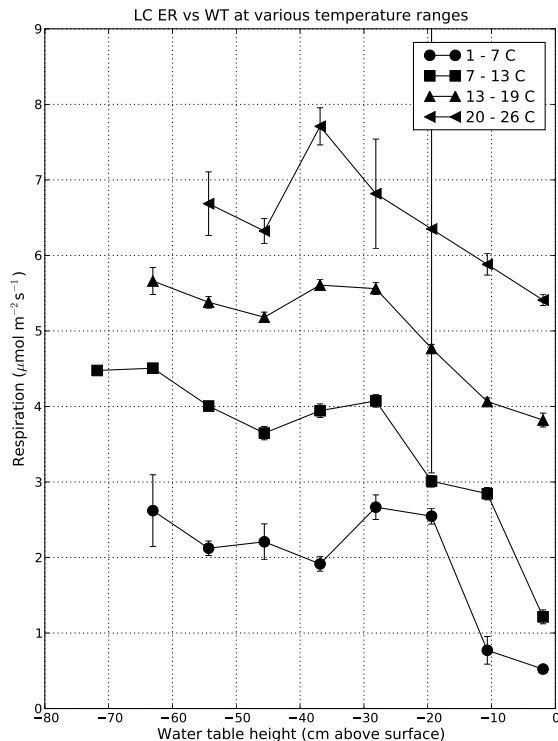
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**Fig. 5.** Binned averages of half-hourly ER during the growing season at LC plotted against water table depth, for different soil temperature ranges. The depth of soil temperature used was determined based on water table. This did not have an appreciable 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.

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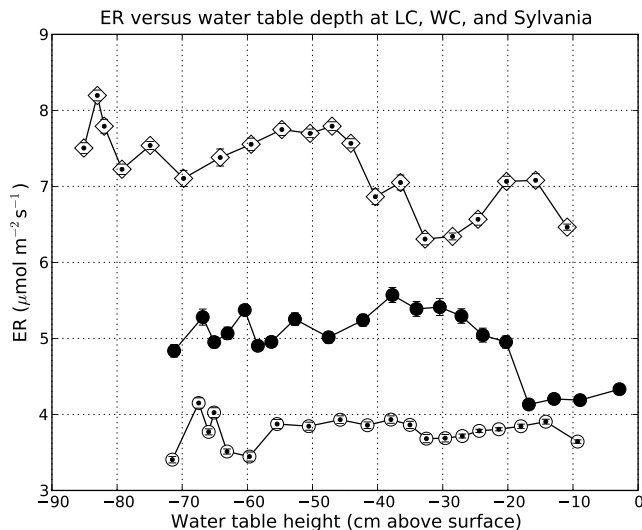
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**Fig. 6.** ER plotted against water table height for LC (●), WC (○), and Sylvania (◇). The plot is a binned average of growing-season ER, calculated from half-hourly data. Each point is the mean of a water table range containing an equal number of 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 20 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.

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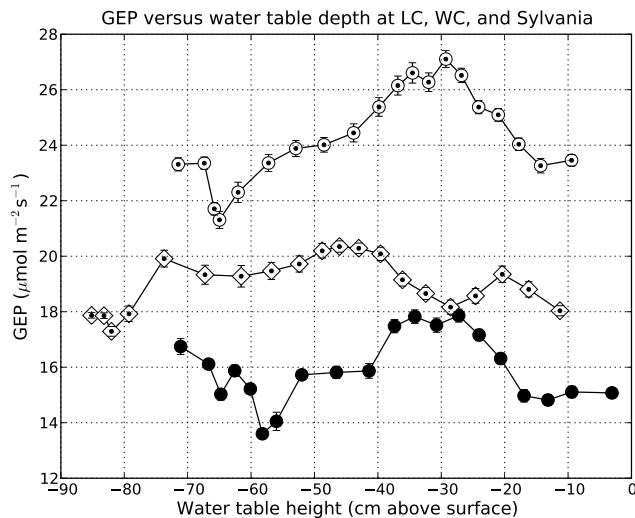
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**Fig. 7.** GEP during the growing season at PAR levels higher than  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  plotted against water table depth at LC (●), WC (○), and Sylvania (◇). This is a measure of the peak productivity of the ecosystem at different water table levels. The upland sites WC and Sylvania are plotted against LC water table for comparison. The Lost Creek and Willow Creek exhibit similar responses to wetland water table, indicating a common precursor that influences both wetland and upland GEP as well as water table.

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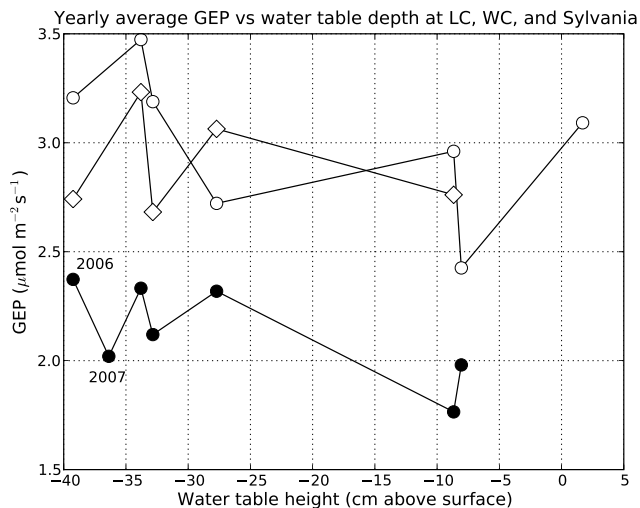
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**Fig. 8.** Yearly average GEP plotted against water table depth at LC (●), WC (○), and Sylvania (◇). The upland sites WC and Sylvania are plotted against LC water table for comparison. Wetland GEP is suppressed at high water table, while upland GEP has no correlation with wetland water table.

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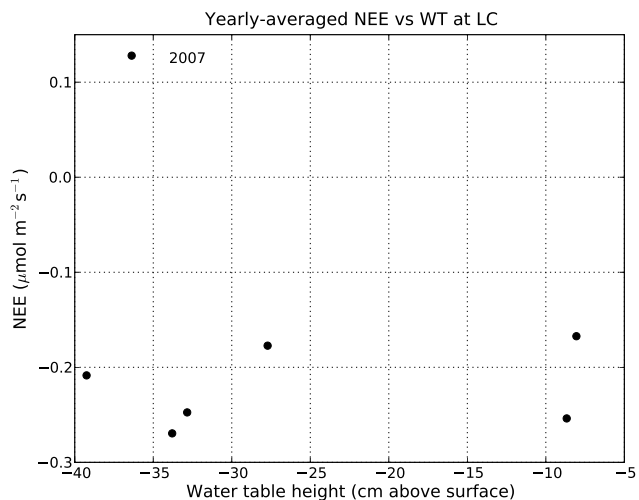
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**Fig. 9.** Yearly-averaged NEE as a function of water table height at Lost Creek. There was no apparent correlation over the record. In 2007, Lost Creek was a net emitter of CO<sub>2</sub>.

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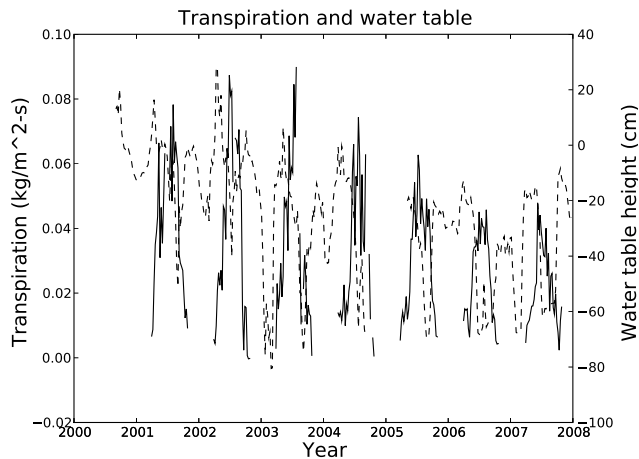
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**Fig. 10.** Weekly-average growing season transpiration (solid line), and water table (dashed line) at Lost Creek. Transpiration decreased as water table declined.

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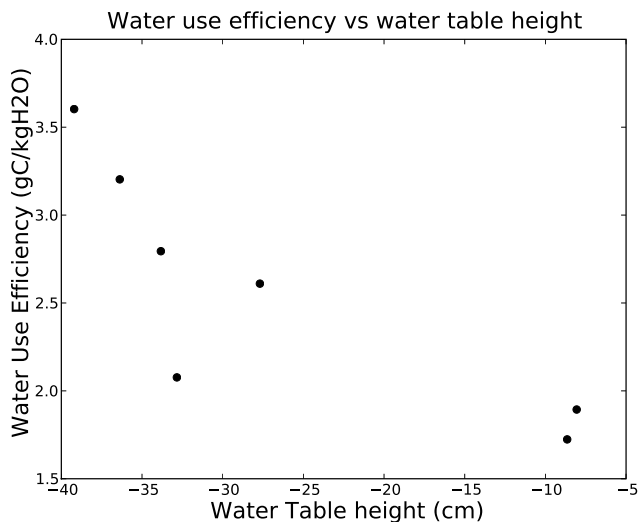
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**Fig. 11.** Yearly Lost Creek water use efficiency as a function of water table height. Since transpiration decreased along with the declining water table and GEP did not, the water use efficiency increased as the water table declined.

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