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

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[1] This study compares eddy-covariance measurements of carbon dioxide fluxes at six northern temperate and boreal peatland sites in Canada and the northern United States of America, representing both bogs and fens. The two peatland types had opposite responses of gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER) to inter-annual fluctuations in water table level. At fens, wetter conditions were correlated with lower GEP and ER, while at bogs wetter conditions were correlated with higher GEP and ER. We hypothesize that these contrasting responses are due to differences in the relative contributions of vascular plants and mosses. The coherence of our results between sites representing a range of average environmental conditions indicates ecosystem-scale differences in resilience to hydrological changes that should be taken into account when considering the future of peatland ecosystem services such as carbon sequestration under changing environmental conditions. **Citation:** Sulman, B. N., A. R. Desai, N. Z. Saliendra, P. M. Lafleur, L. B. Flanagan, O. Sonnentag, D. S. Mackay, A. G. Barr, and G. van der Kamp (2010), CO_2 fluxes at northern fens and bogs have opposite responses to inter-annual fluctuations in water table, *Geophys. Res. Lett.*, *37*, L19702, doi:10.1029/2010GL044018.

1. Introduction

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

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

2. Methods and Sites

2.1. Site Notes

[4] We calculated fluxes of carbon dioxide based on eddy-covariance measurements from six sites in northern North America, representing four fens and two bogs. Important data about the sites are compiled in Table 1. For site descriptions, see the citations for each site. US-Los-fen, US-WFL-fen, and US-SFK-bog are located close to each other in northern Wisconsin, USA. Ca-Mer-bog is located in southeastern Ontario, Canada; Ca-WP1-fen is located in eastern central Alberta, Canada; and Ca-SDH-fen is located in central Saskatchewan, Canada.

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

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Table 1. Site Descriptions[a]

Site name	Identifier	Latitude	Longitude	T (°C)	Precip	WT	NEE	ER	GEP	Citation
Lost Creek	US-Los-fen	46.082	89.978	15.7	900	−24	−2.2	4.8	6.9	[*Sulman et al.*, 2009]
Western Peatland	Ca-WP1-fen	54.954	112.467	13.6	504	−32	−2.3	4.5	6.8	[*Syed et al.*, 2006]
Wilson Flowage	US-WFL-fen	45.817	90.172	15.2	900	−4	−1.0	4.2	5.1	NA
Sandhill Fen	Ca-SDH-fen	53.80	104.62	15.6	467	−3.5	−2.1	1.8	3.9	[*Sonnentag et al.*, 2010]
South Fork	US-SFK-bog	45.925	90.13	14.0	900	−19	−0.18	3.7	3.8	NA
Mer Bleue	Ca-Mer-bog	45.40	75.50	19.2	910	−39	−0.96	3.3	4.3	[*Roulet et al.*, 2007]

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

For the purposes of the present study, we only present the results from the wetland sites.

2.1.1. Wilson Flowage

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

2.1.2. South Fork

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

2.2. Measurements and Flux Processing

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

[9] We estimated the effect of the large gaps at US-WFL-fen and US-SFK-bog by artificially introducing repeated one-week gaps into the US-Los-fen dataset, gap-filling, and comparing the result with the complete gap-filled record for US-Los-fen. To estimate the uncertainty due to random variability at those sites, we repeated the gap-filling procedure 1000 times with artificially added random noise. Random uncertainty estimates at Ca-Mer-bog, US-Los-fen, and Ca-WP1-fen were calculated using the method of *Richardson and Hollinger* [2007], and uncertainty resulting from the friction velocity (u*) threshold for these sites was estimated using a bootstrapping procedure. Uncertainty estimates for Ca-SDH-fen were generated using the method described by *Sonnentag et al.* [2010].

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

[11] Water table height (WT) was measured using pressure transducer systems at US-Los-fen, US-WFL-fen, and US-SFK-bog [*Sulman et al.*, 2009]; with a float and weight system at Ca-WP1-fen [*Syed et al.*, 2006]; with a float and weight system [*Roulet et al.*, 2007] at Ca-Mer-bog; and calculated as the difference between continuous measurements of ground surface elevation and hydraulic head at Ca-SDH-fen [*Sonnentag et al.*, 2010]. WT at US-Los-fen and Ca-WP1-fen was corrected for peat subsidence using the method described by *Sulman et al.* [2009]. No significant changes in peat surface level were observed at US-WFL-fen, US-SFK-bog, or Ca-Mer-bog. In the present paper, WT is referenced to the mean hummock surface. Negative values indicate a water table below hummock surfaces. WT levels and anomalies have an uncertainty on the order of a few cm due to spatial variations in site topography. We were not able to determine this uncertainty with greater precision because we did not have access to appropriate micro-topographical survey information.

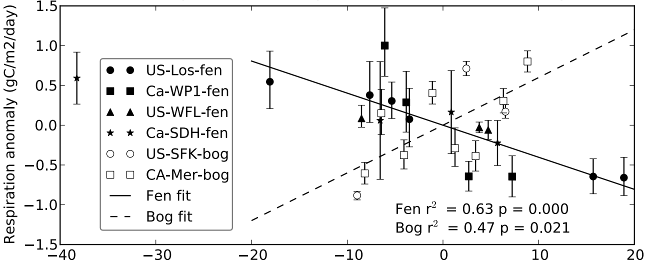
[12] The relationships presented in this study were calculated using June–July–August flux anomaly and growing season WT anomaly for each site, because it was a portion of the growing season when flux magnitudes were greatest and flux and WT measurements were available for all sites [*Lafleur et al.*, 2001; *Sonnentag et al.*, 2010; *Sulman et al.*, 2009]. For WT calculations, growing season is defined as the portion of the year when daily average soil temperature is above 0°C. We focused on anomalies rather than flux magnitude and absolute WT because differences in topography and ecosystem characteristics between sites made direct comparisons of measured WT and flux magnitudes problematic. Anomalies were calculated for each site by subtracting the mean growing season value of the measurement over the study period (time series of measurements for each site) from the growing season average value for each year, where growing season is June–July–August for carbon fluxes and the soil temperature criterion described above for WT. Longer periods were used for WT averages to capture the potential effects of spring hydrology on

summer growth. Data from the 2003 season at Ca-SDH-fen were excluded from the anomaly calculation because of atypical hydrological conditions (described below).

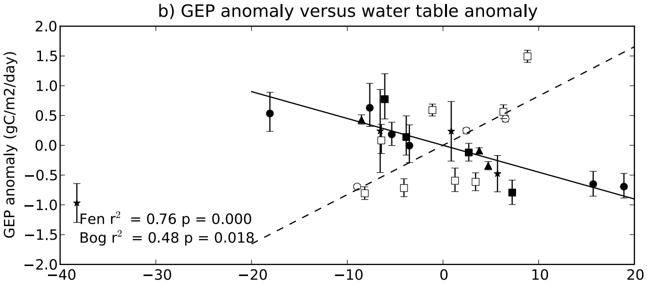
3. Results

[13] The first year of the flux record at Ca-SDH-fen (2003) was unusually warm and dry for the site, resulting in an anomalously low WT. Plant growth in that year was suppressed due to the drought stress [*Sonnentag et al.*, 2010]. Because the conditions were atypical compared to the rest of the study period, data from 2003 at Ca-SDH-fen were excluded from the statistical analyses in this study, although the data point for that year is retained in the plots in Figure 1.

a) Respiration anomaly versus water table anomaly



b) GEP anomaly versus water table anomaly



c) NEE anomaly versus water table anomaly

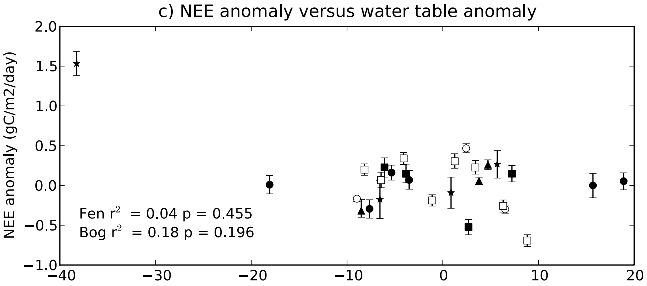


Figure 1. June–July–August average CO_2 flux anomaly at fen and bog sites as a function of growing season average water table (WT) anomaly. Fen sites are marked with black symbols, and bog sites with white symbols. Vertical error bars represent 95% confidence intervals. WT measurements have an uncertainty on the order of a few cm, but horizontal error bars are omitted in order to preserve clarity of the plots. The 2003 site-year at Ca-SDH-fen (stars) is shown, but was excluded from calculations. (a) Ecosystem respiration anomaly was negatively correlated with WT anomaly at fen sites and positively correlated with WT anomaly at bog sites. (b) Gross ecosystem photosynthesis anomaly was also negatively correlated with WT anomaly at fens and positively correlated with WT anomaly at bogs. (c) Net ecosystem exchange anomaly was not significantly correlated with WT anomaly at fens or bogs.

Table 2. Relationships Between June–July–August CO_2 Flux Anomaly and Growing-Season Water Table Anomaly at Each Site[a]

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

[a] Slopes were calculated using linear regression, and are expressed in gC m^{-2} day^{-1} per cm of water table change. Standard error of the estimate is indicated in parentheses.

[14] ER anomaly at fen sites (Figure 1a) was negatively correlated with WT anomaly ($r^2 = 0.63$; $p < 0.001$) while ER anomaly at bog sites was positively correlated with WT anomaly ($r^2 = 0.47$; $p = 0.02$). GEP anomaly (Figure 1b) at fen sites was also negatively correlated with WT anomaly ($r^2 = 0.76$; $p < 0.001$), while GEP anomaly at bog sites had a significant positive correlation with WT anomaly ($r^2 = 0.48$; $p = 0.018$). Each individual site had the same direction of correlation, although not all were significant (Table 2). NEE anomaly had no significant correlation with WT anomaly at either fen or bog sites (Figure 1c). CO_2 flux anomalies were not significantly correlated with summer soil temperature anomaly (not shown), with the exception of ER at fen sites, which had a significant correlation with temperature that was substantially smaller than the correlation with WT ($r^2 = 0.30$; $p = 0.027$).

4. Discussion and Conclusions

[15] The contrasting correlations of GEP with WT at fens and bogs may result from differences in the contribution of vascular plants to total GEP between sites. The species listings in Table S1 of the auxiliary material[1] show that the fen sites included in this study had substantially more shrub and sedge biomass than the bog sites, which had larger populations of mosses. These species differences can lead to contrasting responses to environmental perturbations as well as differences in peat properties [*Limpens et al.*, 2008]. Many vascular species can tolerate wet conditions, but grow faster during dry periods, causing an increase in GEP since generalist herbs and woody plants typically have higher maximum productivity than mosses. Such increased growth was evident at US-Los-fen, where shrub biomass increased during a multi-year decline in WT [*Sulman et al.*, 2009]. *Weltzin et al.* [2003] observed similar shifts in species composition in response to WT and temperature manipulations in mesocosms, and *Ewers et al.* [2007] observed distinct adaptations to flooding between different tree species in a study in northern Wisconsin using sap flux data. In contrast, the mosses that make up a large proportion of live biomass at the bog sites are more sensitive to fluctuations in hydrology [*Laitinen et al.*, 2008; *Talbot et al.*, 2010]. The presence of significant live *Sphagnum* biomass at Ca-WP1-fen and shrub biomass at Ca-Mer-bog expose potential weaknesses in this hypothesis, although *Sphagnum* capitu-

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[1] Auxiliary materials are available in the HTML. doi:10.1029/2010GL044018.

lum makes up a smaller percentage of total aboveground biomass at the fen compared to the bog (17% and 29%, respectively). The presence of shrubs at Ca-Mer-bog may contribute to the high variability and lower sensitivity of the bog to WT fluctuations.

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

[17] The observed fluxes from 2003 at Ca-SDH-fen are an exception to the relationships described above. During this exceptionally dry year, early senescence and dieback of drought-intolerant sedges occurred, and GEP was lower than in other years [*Sonnentag et al.*, 2010]. This suggests that the advantage of certain wetland species in drier conditions breaks down when the fluctuations exceed a threshold. Similar effects have been observed during anomalously dry years in both fens and bogs [*Alm et al.*, 1999; *Schreader et al.*, 1998; *Shurpali et al.*, 1995; *Arneth et al.*, 2002]. Such results, however, do not apply to long-term changes, which could drive succession [*Laine et al.*, 1995; *Talbot et al.*, 2010] or cause changes in peat surface height that counteract the effects of declining WT [*Dise*, 2009].

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

[19] Because the results presented here include only fluxes of CO_2, and omit other carbon fluxes such as methane and dissolved carbon, they do not represent a complete peatland carbon budget. At Ca-Mer-bog, methane and dissolved carbon losses were significant portions of the total carbon balance, but on average were smaller in magnitude than NEE [*Roulet et al.*, 2007]. Measurements of methane emissions at US-Los-fen, US-WFL-fen and US-SFK-bog suggested that carbon losses through methane emissions at these sites were small compared to NEE (B. Cook, unpublished data, 2008). Measurements of carbon fluxes other than CO_2 were not available at the other sites.

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

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References

Alm, J., L. Schulman, J. Walden, H. Nykänen, P. J. Martikainen, and J. Silvola (1999), Carbon balance of a boreal bog during a year with an exceptionally dry summer, *Ecology*, *80*(1), 161–174.

Arneth, A., J. Kurbatova, O. Kolle, O. B. Shivistova, J. Lloyd, N. N. Vygodskaya, and E.-D. Schulze (2002), Comparative ecosystem-atmosphere exchange of energy and mass in a European Russian and a central Siberian bog II. Interseasonal and interannual variability of CO_2 fluxes, *Tellus, Ser. B*, *54*(5), 514–530.

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

Barr, A., T. Black, E. Hogg, N. Kljun, K. Morgenstern, and Z. Nesic (2004), Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production, *Agric. For. Meteorol.*, *126*, 237–255, doi:10.1016/j.agrformet.2004.06.011.

Bubier, J. L., P. M. Crill, T. R. Moore, K. Savage, and R. K. Varner (1998), Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex, *Global Biogeochem. Cycles*, *12*(4), 703–714.

Clymo, R. S. (1984), The limits to peat bog growth, *Philos. Trans. R. Soc. B*, *303*(1117), 605–654, doi:10.1098/rstb.1984.0002.

Desai, A., P. V. Bolstad, B. D. Cook, K. J. Davis, and E. Carey (2005), Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA, *Agric. For. Meteorol.*, *128*, 33–55.

Desai, A., et al. (2008), Cross-site evaluation of eddy covariance GPP and RE decomposition techniques, *Agric. For. Meteorol.*, *148*, 821–838.

Dise, N. B. (2009), Peatland response to global change, *Science*, *326*(5954), 810–811, doi:10.1126/science.1174268.

Ewers, B. E., D. S. Mackay, and S. Samanta (2007), Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species, *Tree Physiol.*, *27*(1), 11–24.

Freeman, C., M. Lock, and B. Reynolds (1992), Fluxes of CO_2, CH_4 and N_2O from a Welsh peatland following simulation of water table draw-down: Potential feedback to climate change, *Biogeochemistry*, *19*(1), 51–60, doi:10.1007/BF00000574.

Gorham, E. (1991), Northern peatlands: Role in the carbon cycle and probable responses to climatic warming, *Ecol. Appl.*, *1*(2), 182–195, doi:10.2307/1941811.

Humphreys, E. R., P. M. Lafleur, L. B. Flanagan, N. Hedstrom, K. H. Syed, A. J. Glenn, and R. Granger (2006), Summer carbon dioxide and water vapor fluxes across a range of northern peatlands, *J. Geophys. Res.*, *111*, G04011, doi:10.1029/2005JG000111.

Lafleur, P. M., N. T. Roulet, and S. W. Admiral (2001), Annual cycle of CO_2 exchange at a bog peatland, *J. Geophys. Res.*, *106*, 3071–3081.

Lafleur, P. M., N. T. Roulet, J. L. Bubier, S. Frolking, and T. R. Moore (2003), Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog, *Global Biogeochem. Cycles*, *17*(2), 1036, doi:10.1029/2002GB001983.

Laine, J., H. Vasander, and R. Laiho (1995), Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland, *J. Appl. Ecol.*, *32*(4), 785–802.

Laitinen, J., S. Rehell, and J. Oksanen (2008), Community and species responses to water level fluctuations with reference to soil layers in different habitats of mid-boreal mire complexes, *Plant Ecol.*, *194*(1), 17–36, doi:10.1007/s11258-007-9271-3.

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

Lund, M., et al. (2009), Variability in exchange of CO_2 across 12 northern peatland and tundra sites, *Glob. Change Biol.*, doi:10.1111/j.1365-2486.2009.02104.x, in press.

Minkkinen, K., and J. Laine (1998), Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland, *Can. J. For. Res.*, *28*(9), 1267–1275.

Moffat, A., et al. (2007), Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes, *Agric. For. Meteorol.*, *147*, 209–232, doi:10.1016/j.agrformet.2007.08.011.

Moore, T., and R. Knowles (1989), The influence of water table levels on methane and carbon dioxide emissions from peatland soils, *Can. J. Soil Sci.*, *69*, 33–38.

Peichl, M., J. J. Brodeur, M. Khomik, and M. A. Arain (2010), Biometric and eddy-covariance based estimates of ecosystem carbon exchange in an age-sequence of temperate pine forests, *Agric. For. Meteorol.*, in press.

Richardson, A. D., and D. Y. Hollinger (2007), A method to estimate the additional uncertainty in gap-filled nee resulting from long gaps in the CO_2 flux record, *Agric. For. Meteorol.*, *147*, 199–208, doi:10.1016/j.agrformet.2007.06.004.

Roulet, N., P. M. Lafleur, P. Richard, and T. Moore (2007), Contemporary carbon balance and late Holocene carbon accumulation in a northern peatland, *Glob. Change Biol.*, *13*, 397–411.

Schreader, C., W. Rouse, T. Griffis, L. D. Boudreau, and P. Blanken (1998), Carbon dioxide fluxes in a northern fen during a hot, dry summer, *Global Biogeochem. Cycles*, *12*(4), 729–740.

Shurpali, N., S. B. Verma, J. Kim, and T. Arkebauer (1995), Carbon dioxide exchange in a peatland ecosystem, *J. Geophys. Res.*, *100*(D7), 14,319–14,326.

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

Sonnentag, O., G. van der Kamp, A. G. Barr, and J. M. Chen (2010), On the relationship between water table depth and water vapor and carbon dioxide fluxes in a minerotrophic fen, *Glob. Change Biol.*, *16*, 1762–1776, doi:10.1111/j.1365-2486.2009.02032.x.

Strack, M., and J. M. Waddington (2007), Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment, *Global Biogeochem. Cycles*, *21*, GB1007, doi:10.1029/2006GB002715.

Sulman, B., A. Desai, B. D. Cook, N. Saliendra, and D. S. Mackay (2009), Contrasting carbon dioxide fluxes between a drying shrub wetland in northern Wisconsin, USA, and nearby forests, *Biogeosciences*, *6*, 1115–1126.

Syed, K. H., L. B. Flanagan, P. Carlson, A. Glenn, and K. E. V. Gaalen (2006), Environmental control of net ecosystem CO_2 exchange in a treed, moderately rich fen in northern Alberta, *Agric. For. Meteorol.*, *140*, 97–114, doi:10.1016/j.agrformet.2006.03.022.

Talbot, J., P. J. H. Richard, N. T. Roulet, and R. K. Booth (2010), Assessing long-term hydrological and ecological responses to drainage in a raised bog using paleoecology and a hydrosequence, *J. Veg. Sci.*, *21*(1), 143–156, doi:10.1111/j.1654-1103.2009.01128.x.

Turunen, J., E. Tomppo, K. Tolonen, and A. Reinikainen (2002), Estimating carbon accumulation rates of undrained mires in Finland—Application to boreal and subarctic regions, *Holocene*, *12*(1), 69–80.

Weltzin, J., S. Bridgham, J. Pastor, J. M. Chen, and C. Harth (2003), Potential effects of warming and drying on peatland plant community composition, *Global Change Biol.*, *9*(2), 141–151.

Wheeler, B., and M. Proctor (2000), Ecological gradients, subdivisions and terminology of north–west European mires, *J. Ecol.*, *88*(2), 187–203.

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