

Chapter 14

Interacting Controls on Ecosystem Photosynthesis and Respiration in Contrasting Peatland Ecosystems

Lawrence B. Flanagan*

*Department of Biological Sciences, Water and Environmental Science Building,
University of Lethbridge, 4401 University Drive, Lethbridge, AB T1K 3M4, Canada*

Summary	253
I. Introduction.....	254
II. Characteristics of Study Sites and Ecosystem CO ₂ Flux Measurements	254
III. Comparison of a <i>Sphagnum</i> -Dominated Poor Fen and a <i>Carex</i> -Dominated Rich Fen	256
IV. Sensitivity of CO ₂ Exchange in a Moderately-Rich Fen to Warmer and Drier Conditions	259
V. Peatland Succession and Implications for Historical and Future Carbon Sequestration	262
VI. Conclusions.....	264
Acknowledgements.....	265
References	265

Summary

Photosynthesis in moss contributes significantly to carbon gain in northern peatland ecosystems. In turn, these northern peatland ecosystems contain a large fraction of the global soil carbon stock, which has been suggested to be vulnerable to warming and drying associated with climate change. The fate of this vast peatland carbon stock depends on the relative responses of ecosystem photosynthesis and respiration to climate change-induced shifts in environmental conditions. This chapter reviews some recent studies of the controls on ecosystem photosynthesis and respiration in contrasting peatland ecosystems in northern Alberta, Canada, a region where peatlands occupy a significant fraction of the landscape. In particular, it is highlighted how (i) differences in dominant plant functional type, (ii) interactions between variation in water table depth and temperature, and (iii) ecosystem succession, can all strongly control the rate of net carbon sequestration in peatland ecosystems and influence the response of these ecosystems to variation in environmental conditions associated with anticipated climate change. Prediction of future climate change effects on peatland ecosystems would be improved if global-scale models could include more details of the biological variability among peatlands (both spatial and temporal), with realistic parameterizations of the responses of photosynthesis and respiration to variation in temperature, water table depth and soil moisture.

*Author for correspondence, e-mail: larry.flanagan@uleth.ca

I. Introduction

Photosynthesis in *Sphagnum* (peat moss) and several other moss species contribute significantly to carbon gain in northern peatland ecosystems (Glenn et al. 2006; Flanagan and Syed 2011). In turn, these northern peatland ecosystems contain between one-quarter to one-third of the global soil carbon pool (Gorham 1991; Turunen et al. 2002). The carbon stock in peatlands has accumulated over thousands of years because of moderate rates of ecosystem photosynthesis that exceed decomposition and autotrophic respiration, the latter two processes being limited by the cool temperatures and waterlogged conditions that typically occur in peatlands (Gorham 1991; Davidson and Janssens 2006). The fate of this vast peatland carbon stock, under anticipated warmer and drier conditions associated with climate change, depends on the relative responses of ecosystem photosynthesis and respiration to shifts in environmental conditions. Concern has been expressed that exposure of peatlands to warmer and drier conditions could alter the balance between ecosystem photosynthesis and respiration/decomposition thus increasing atmospheric carbon dioxide concentration and providing a positive feedback to further climate change (Moore et al. 1998; Davidson and Janssens 2006; Tarnocai 2006). Simple ecosystem models usually predict that respiration and decomposition are more sensitive than photosynthesis to increases in temperature and reduction in water availability. However, these simple model predictions ignore other important ecological controls that can influence ecosystem CO₂ exchange processes and affect the rate of net carbon sequestration in peatland ecosystems. This chapter reviews some recent studies of the controls on ecosystem photosynthesis and respiration in contrasting peatland ecosystems in northern Alberta, Canada, a region where peatlands

occupy a significant fraction of the landscape. In particular, I highlight how (i) plant functional type, (ii) interactions between variation in water table depth and temperature, and (iii) ecosystem succession, can all strongly control net carbon sequestration in peatland ecosystems and influence the response of these ecosystems to variation in environmental conditions associated with anticipated climate change.

II. Characteristics of Study Sites and Ecosystem CO₂ Flux Measurements

Peatlands are defined in Canada as wetland ecosystems that have a minimum depth of 40 cm of peat soil (National Wetlands Working Group 1988; Johnson et al. 1995; Vitt et al. 1998). Peat refers to the partially decomposed remains of plants, containing over 65 % organic matter by dry weight with less than 20–35 % inorganic material. The criterion of 40 cm depth was chosen because, at this peat thickness, most wetland vascular plants present at a site would be completely rooted within the peat soil (Johnson et al. 1995). Peatlands can be further classified into fens and bogs, with fens having water input from precipitation and groundwater that has come into contact with mineral soils, while bogs only access precipitation. In continental western Canada, peatlands are distributed along a bog-rich fen gradient based on water characteristics and plant species composition (Vitt 1994; Vitt et al. 1998). The water of bogs has low pH, low conductivity, and low base cation concentrations and these three components increase along the gradient axis between bogs and rich fens. Water that is more alkaline, high in conductivity and base cation concentration is characteristic of rich fen ecosystems. The dominant vegetation in rich fens are sedges (*Carex spp.*) and “brown moss” species including *Drepanocladus aduncus* and *Aulacomnium palustre*, while *Sphagnum* moss typically dominates in bogs and poor fens. (Vitt 1994; Johnson et al. 1995; Vitt et al. 1998).

This chapter reviews case studies conducted at three sites, all located in northern Alberta,

Abbreviations: A_{\max} – maximum photosynthetic capacity; GEP – gross ecosystem photosynthesis; NEP – net ecosystem productivity; R_{10} – respiratory capacity at 10 °C; TER – total ecosystem respiration

Canada. The first site, Tony's Fen, is a rich fen dominated by the sedge, *Carex lasiocarpa* with a discontinuous mat of *Drepanocladus aduncus* and *Aulacomnium palastre* (Glenn et al. 2006). Comparative studies were conducted between Tony's fen and May Tower, a poor fen site with open, wet pools or "flarks" alternating with slightly elevated and drier "strings" that were orientated perpendicular to the direction of water flow through the site (Glenn et al. 2006). The poor fen is dominated by *Sphagnum* moss that forms a continuous ground cover with the following species: *S. angustifolium*, *S. magellanicum*, *S. fuscum*. Other species present at the poor fen included *Andromedia polifolia*, *Smilacina trifolia*, *Carex limosa*, along with dwarf trees (*Picea mariana* and *Larix laricina*, less than 0.75 m tall) that were present along the strings of the fen (Glenn et al. 2006). The third site, La Biche River, is a moderately-rich treed fen and is an example of the most common type of peatland found in western Canada (Vitt et al. 1998). The dominant plant species of the La Biche River site are stunted trees (2–3 m tall) of *Picea mariana* and *Larix laricina* which contribute approximately two-thirds of the aboveground biomass (Syed et al. 2006). The site also has a relatively high abundance of a broad-leaf deciduous shrub, *Betula pumila*, and a range of moss species including *Sphagnum angustifolium*, *S. fuscum* and other *Sphagnum* species, *Drepanocladus aduncus*, *Aulacomnium palastre*, and the feather moss, *Pleurozium schreberi*. Several other herb and dwarf shrub species are also present (Syed et al. 2006).

In order to study CO₂ exchange processes at the ecosystem-scale, we used the eddy covariance technique to make measurements of net ecosystem CO₂ flux. Eddy covariance is a micro-meteorological technique involving fast-response (10–20 Hz) measurements of vertical wind speed and associated changes in atmospheric CO₂ concentration (Moncrieff et al. 2000; Baldocchi 2003). The fast-response measurements are used to calculate the net flux of CO₂ across a plane between the ecosystem and the atmosphere at the height that the wind speed and CO₂

concentration measurements are made. The net CO₂ flux is sampled over an area upwind of the sensors and its size depends on the height of the instruments and turbulence characteristics of the local atmosphere. During unstable atmospheric conditions, rough guidelines suggest a ratio of 100:1 between the distance sampled upwind from the instruments and their height (Moncrieff et al. 2000). So instruments mounted on a tower 3 m above the surface would sample CO₂ flux across a distance of 300 m upwind of the sensors, although the peak contribution to the measured flux would come from an area much closer (25–50 m) to the tower. The flux footprint rotates on a radius around the instrument tower as the direction of the predominant wind changes. The CO₂ flux measured directly by eddy covariance represents the net difference between the uptake of CO₂ in photosynthesis and the release of CO₂ in respiration by all organisms located above- and below-ground within the flux footprint (Moncrieff et al. 2000; Baldocchi 2003). A number of approaches are available to partition the net CO₂ flux into its major components, ecosystem photosynthesis and total ecosystem respiration (Barr et al. 2004; Moffat et al. 2007; Desai et al. 2008). In general, these approaches make use of a series of nighttime measurements of net ecosystem CO₂ flux (which represent ecosystem respiration only) over a range of different temperatures, in order to develop a temperature-response function for ecosystem respiration. The temperature-response function for respiration is used during the daytime along with temperature measurements to calculate respiration rates while simultaneous net CO₂ flux measurements are made. Ecosystem photosynthesis rates during the day can then be determined from the measured net CO₂ flux rate and the calculated daytime ecosystem respiration measurements. In this paper I use a positive sign convention for both photosynthesis and respiration CO₂ fluxes, and so net ecosystem productivity (NEP) is positive when the photosynthesis rate exceeds the respiration rate and the ecosystem is a net sink for carbon dioxide.

III. Comparison of a *Sphagnum*-Dominated Poor Fen and a *Carex*-Dominated Rich Fen

Recent comparative studies conducted by my lab group have shown distinct differences between a poor fen (May Tower) and an extreme-rich fen (Tony's Fen) for their responses of NEP measured by eddy covariance to inter-annual variation in temperature and water table conditions during three study years (Fig. 14.1; Adkinson et al. 2011). The rates of growing season (May-October) cumulative NEP at the poor fen were very similar among years with an average (\pm SD) of 110.1 ± 0.5 g C m⁻² period⁻¹. By contrast, the growing season cumulative NEP at the extreme-rich fen varied substantially among years and the extreme-rich fen was, on average (76.6 g C m⁻² period⁻¹), a lower net sink for CO₂ than the poor fen. Consistent with the eddy covariance net CO₂ uptake measurements, analysis of ²¹⁰Pb-dated peat cores also showed higher recent net rates of carbon accumulation in the poor fen than in the extreme-rich fen (36.3 versus 20.6 g C m⁻² year⁻¹; Adkinson et al. 2011). The differences between sites resulted from several factors including: (i) contrasting plant functional types; (ii) environmental differences, particularly the importance of water table fluctuations at the extreme-rich fen; and (iii) interactions between temperature and water table depth for effects on ecosystem CO₂ exchange. Each of these three factors will be discussed further in the paragraphs below.

Because of differences in the functional type of the dominant plant species, the poor fen had a longer period of net CO₂ uptake, with net uptake in at least 5 months (May through September), while the rich fen was normally only a net sink during 3 months of the year (June through August). While significant seasonal variation in biochemical capacity for photosynthesis and respiration does occur in *Sphagnum* (Williams and Flanagan 1998), these mosses do not need to build entirely new photosynthetic tissue at the start of the growing season and complete

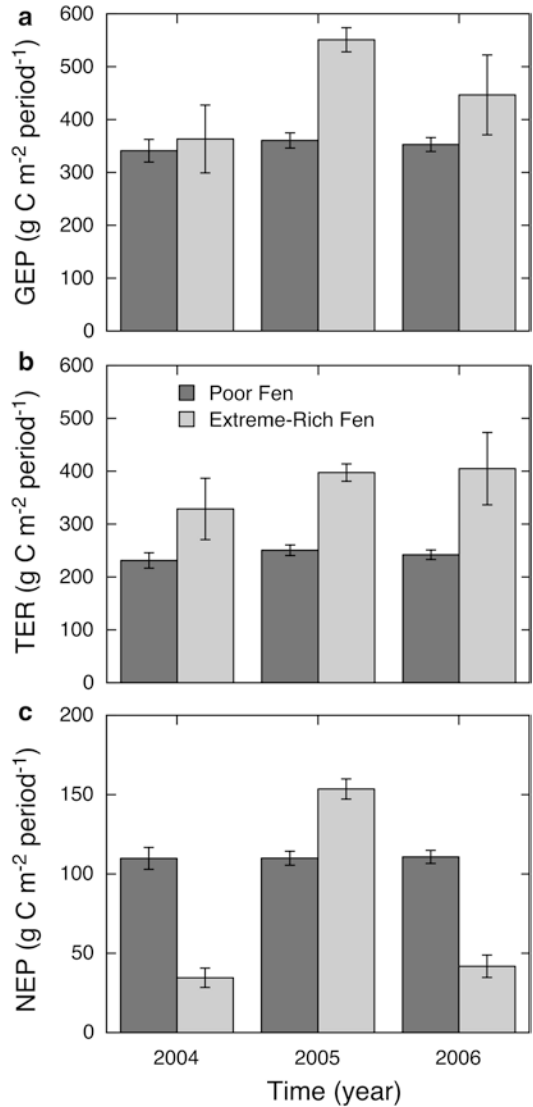


Fig. 14.1. Comparisons of the integrated growing season (1 May to 31 October) values of: (a) gross ecosystem photosynthesis (GEP); (b) total ecosystem respiration (TER); and (c) net ecosystem productivity (NEP; NEP=GEP – TER) in 2004, 2005 and 2006 at the poor fen and extreme-rich fen study sites. Cumulative growing season values were determined using a combination of measured and modeled half-hourly flux data as described by Adkinson et al. (2011). Error bars represent total uncertainty estimates (This figure is based on data in Adkinson et al. (2011)).

senescence of tissue does not occur at the end of the growing season. In addition, *Sphagnum* can also begin to photosynthesize almost immediately following snowmelt when

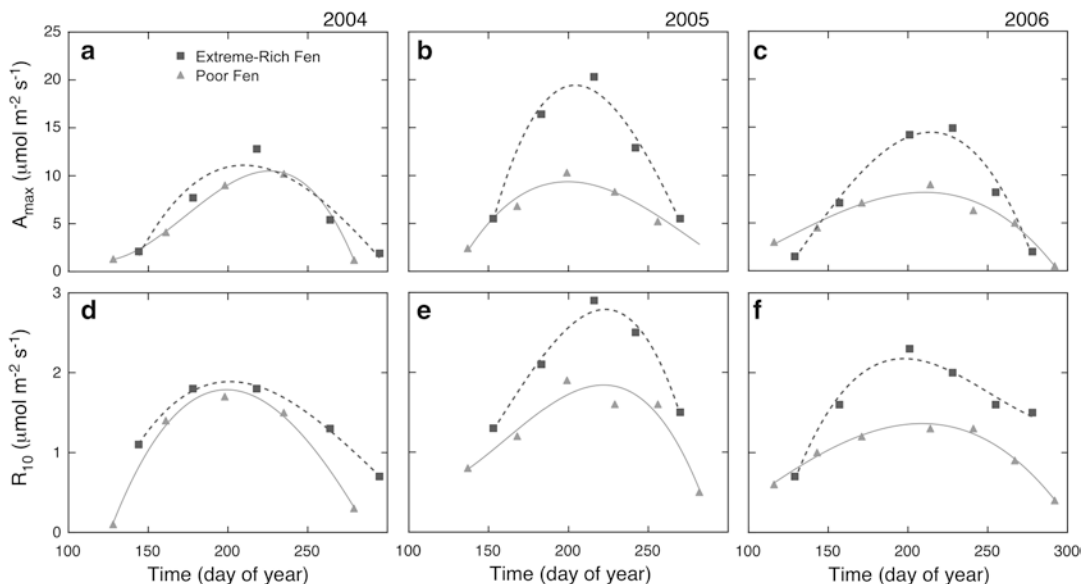


Fig. 14.2. Seasonal trends in fitted parameters describing ecosystem CO₂ exchange in three different study years (2004–2006) at the poor fen and extreme-rich fen sites: (a–c) the maximum photosynthetic capacity (A_{\max}); and (d–f) the respiratory capacity at 10 °C (R_{10}). Points represent parameter estimates derived by fitting the following equation to measured net ecosystem productivity (NEP) data as described by Adkinson et al. (2011):

$$NEP = \frac{A_{\max} \alpha PPF D}{A_{\max} + \alpha PPF D} - R_{10} Q_{10}^{\left(\frac{T-10}{10}\right)}$$

Lines represent third order polynomial regressions fitted to the parameter estimates as a function of time (day of year) (This figure is based on data in Adkinson et al. (2011)).

only the surface of the moss has thawed (Bubier et al. 1998; Lafleur et al. 2003; Moore et al. 2006). Therefore, *Sphagnum* mosses and other evergreen vascular plants at the poor fen can remain photosynthetically active for a longer period of time within the growing season than the deciduous vegetation can at the extreme-rich fen. Also, photosynthetic and respiratory capacities at the poor fen varied less among years, even though both sites were exposed to similar inter-annual variation in environmental conditions (Fig. 14.2, Adkinson et al. 2011). We believe this to result from the fact that *Sphagnum* does not need to develop completely new photosynthetic tissue at the beginning of each growing season. By contrast, the growth of new leaf tissue at the extreme-rich fen, and the capacity for photosynthesis and respiration, may be influenced more strongly by environmental variation among years (Fig. 14.2). The development of new leaf tissue, particularly in *Carex lasiocarpa*, at the extreme-rich fen appeared to respond very quickly to variation in spring

and early summer temperatures (Adkinson et al. 2011; and see additional text below). The differences in dominant plant functional types between the sites, therefore, appeared to control the magnitude of possible response to environmental change.

The two study sites also differed significantly in water table fluctuations and peat density. The extreme-rich fen had relatively large fluctuation in water table depth (Fig. 14.3; Adkinson et al. 2011) and high peat density ($83.1 \pm 18.3 \text{ kg m}^{-3}$, mean \pm SD, $n = 14$). In contrast, the poor fen had low peat density ($46.5 \pm 7.5 \text{ kg m}^{-3}$, mean \pm SD, $n = 16$) and an unstable surface that was likely not anchored to the bottom mineral soil sediments. Variation in the water table at the poor fen, therefore, may have been associated with similar changes in peat surface height, so that there was little or no movement of the water table relative to the peat surface (Adkinson et al. 2011). In this case, moisture availability in the peat at the poor fen would not vary significantly within the growing season or on an inter-annual

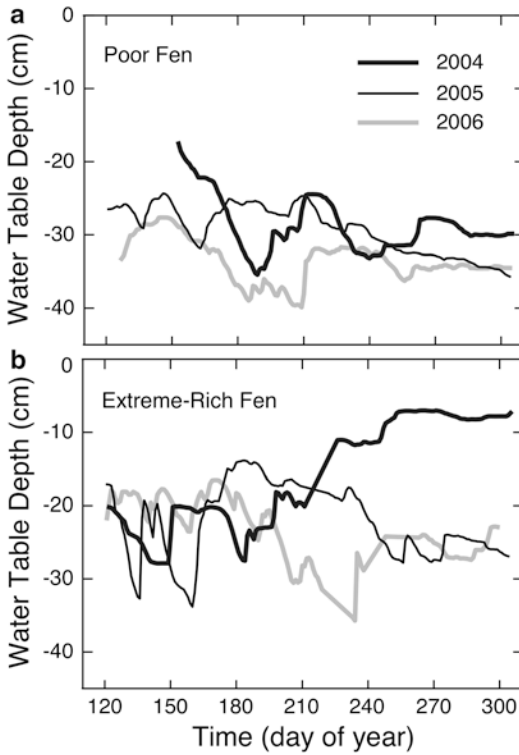


Fig. 14.3. Comparison of growing season daily average water table depths among study years at: (a) the poor fen site; and (b) the extreme-rich fen site. Water table depth was measured relative to a fixed height on the water well and expressed relative to the average hummock height measured in 2004 (This figure is reproduced from Adkinson et al. (2011)).

basis. However, variation in water table depth likely caused significant changes in “soil” moisture availability at the extreme-rich fen. Previous studies have shown that change in water table depth has little influence on peatland ecosystem CO_2 exchange if the water table variation is not accompanied by significant change in soil moisture content (Parmentier et al. 2009).

Important interactions can occur between temperature and water availability in peatland ecosystems with significant effects on ecosystem CO_2 exchange processes. For example, some previous studies have shown that warm and dry summer conditions can reduce net CO_2 uptake in peatlands by limiting photosynthesis and/or increasing respiration, and by promoting earlier leaf senescence in

deciduous plants (Bellisario et al. 1998; Alm et al. 1999; Arneth et al. 2002; Bubier et al. 2003; Aurela et al. 2007; Cai et al. 2010). The effects of moisture stress on photosynthesis and respiration have been observed in both sedge-dominated and *Sphagnum*-dominated peatlands (Shurpali et al. 1995; Silvola et al. 1996; Alm et al. 1999; Griffis et al. 2000; Aurela et al. 2007; Sonnentag et al. 2010). In our comparative studies, ecosystem photosynthesis and respiration at the poor fen did not respond to significant inter-annual variation in temperature and water table depth, while the extreme-rich fen showed strong inter-annual variation in ecosystem CO_2 exchange (Figs. 14.1 and 14.2). In addition, the interacting effects of combined variation in temperature and water table depth at the extreme-rich fen contributed to the fluctuations in CO_2 exchange observed at that site (Adkinson et al. 2011). For example, during 2005 warm spring temperatures were accompanied by sufficient water availability throughout the period of leaf growth and this resulted in very high ecosystem photosynthetic capacity (A_{max}) at the extreme-rich fen (Fig. 14.2). This was likely primarily caused by high leaf area index, but possibly also by enhanced photosynthetic rates per unit leaf area. In contrast, the cool spring temperatures in 2004 appeared to inhibit A_{max} and leaf area development at the extreme-rich fen. The reduced water availability at the extreme-rich fen from the beginning of July 2006 onward, however, constrained development of high ecosystem photosynthetic capacity relative to 2005, despite the warm spring and summer temperatures in 2006 (Fig. 14.2). Prior to the decline in water table, conditions for growth were favorable in 2006, with warmer air and soil temperatures and a higher water table than in 2005, suggesting that reduced water availability was the primary factor contributing to the difference in peak photosynthetic capacity between 2005 and 2006 (Adkinson et al. 2011). In addition, warm temperatures in 2006, and the associated increase in evaporative demand, may have exacerbated the effect of declining water table on maximal leaf development in July and August. This

demonstrates the important interactions that occur between temperature and water availability in peatland ecosystems.

Our study of ecosystem response to inter-annual environmental variation has relevance to consideration of the potential responses of these two ecosystems to future climate change. Because of its floating nature, the poor fen will probably be quite resilient to anticipated warmer and drier conditions, as long as the current hydrological features of the site are not disrupted. By contrast, our data indicate that the extreme-rich fen should be much more susceptible to predicted warmer and drier conditions. The response of the extreme-rich fen to the very warm conditions in 2006 was constrained by reduced moisture availability in mid-growing season, and this occurred in a year when the cumulative precipitation during May-October was higher than normal (439 mm in 2006 versus the long-term average (\pm SD) of 381 ± 81 mm; Adkinson et al. 2011). This suggests that in the future, combined warmer- and drier-than-normal conditions could substantially affect ecosystem CO_2 exchange and net carbon sequestration at the extreme-rich fen site.

IV. Sensitivity of CO_2 Exchange in a Moderately-Rich Fen to Warmer and Drier Conditions

In this second case study, the sensitivities of gross ecosystem photosynthesis (GEP), total ecosystem respiration (TER) and NEP to variations in temperature and water table depth were examined in a moderately-rich treed fen (La Biche River), the most abundant peatland type in western Canada, in a region where peatland ecosystems are a significant landscape component (approximately 20 %; National Wetlands Working Group 1988; Vitt et al. 1998; Tarnocai 2006). During the 6-year study period, the average growing season (May-October) water depth declined approximately 38 cm (Fig. 14.4b), with the reduction in water table depth primarily caused by progressively lower precipitation in May-August throughout the study period

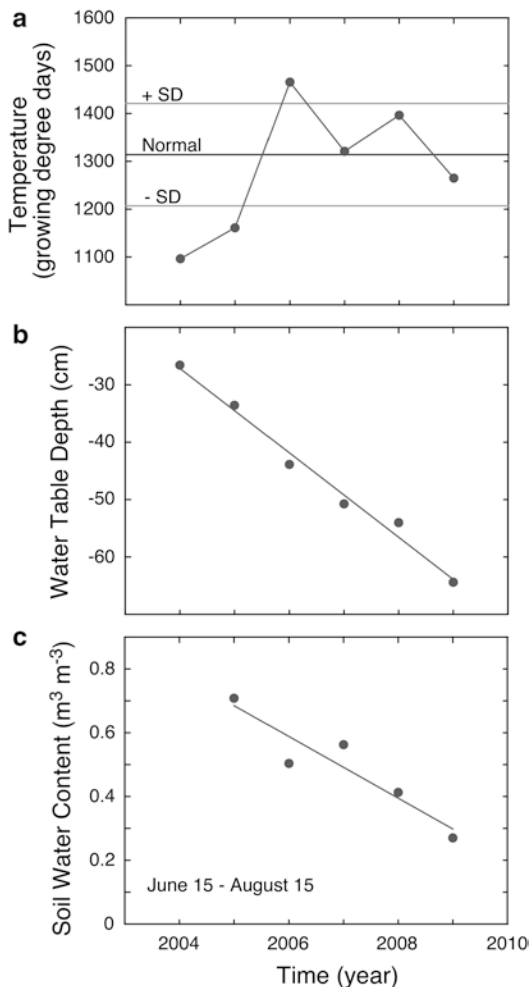


Fig. 14.4. Comparison of inter-annual variation in: (a) temperature (expressed as cumulative growing degree days, March-October); (b) water table depth (average value during May-October); and (c) average soil (peat) water content during mid-summer (June 15–August 15) at the La Biche River flux station. The line fitted to the data in panel (b) was: $y = -7.3531x + 14,709$, $r^2 = 0.98$. The line fitted to the data in panel (c) was: $y = -0.0967x + 194.61$, $r^2 = 0.87$. Soil water content measurements represent the average of three probes located at depths of 7.5, 10 and 12.5 cm below the surface in *Sphagnum* moss (This figure is based on data published in Flanagan and Syed (2011)).

(Fig. 14.5). For example, the cumulative precipitation during May-August in the final year of the study (134 mm in 2009) was less than 50 % of the long-term average \pm SD (306 ± 68 mm) during this summer time period. In addition, during the study there

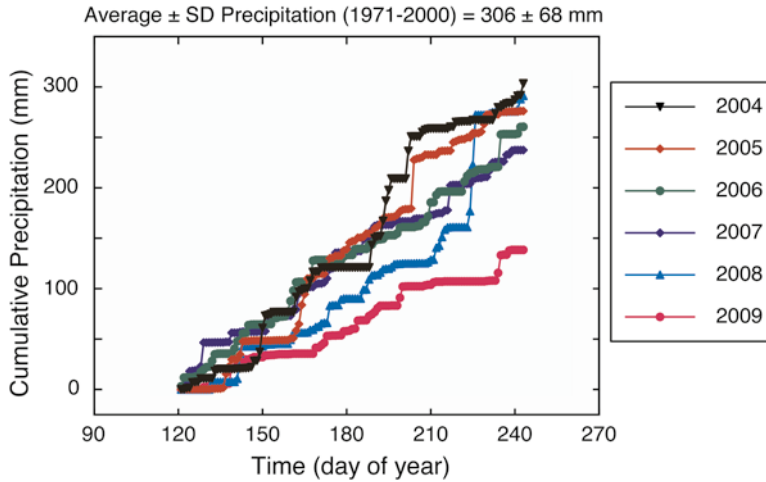


Fig. 14.5. Comparison of inter-annual variation in daily precipitation recorded during May–August at the La Biche River flux station in northern Alberta, Canada. The indicated average (\pm SD) is based on the long-term (1971–2000) Environment Canada weather records measured at nearby Athabasca, Alberta (This figure is reproduced from Flanagan and Syed (2011)).

was an associated significant linear decline in the average soil water content in the middle of the growing season (June 15–August 15; Fig. 14.4c). Temperature, expressed as cumulative growing degree days (GDD) during March–October, varied from a minimum of approximately 1,096 in 2004 to a high of 1,466 in 2006 (Fig. 14.4a). Based on the long-term (1971–2000) Environment Canada weather records at nearby Athabasca, Alberta, the average (\pm SD) GDD for the region was $1,310 \pm 105$ (Flanagan and Syed 2011). The difference of 370 GDD apparent among years of our study is equivalent to a change in elevation of approximately 600 m. We suggest, therefore, that observation of ecosystem response to the relatively large inter-annual environmental variation in temperature and moisture conditions apparent during our study period has relevance to understanding the potential response of this important ecosystem type to future climate change (Flanagan and Syed 2011).

Both GEP and TER showed similar increases in response to the warmer and drier conditions experienced during the 6-year study period (Fig. 14.6a–d). Photosynthesis and respiration were positively correlated with cumulative GDD (Pearson product–moment

correlation coefficient (r); GEP, $r=0.762$; TER, $r=0.743$), and they were both negatively correlated with average water table depth (GEP, $r=-0.781$; TER, $r=-0.839$). In an observational study such as this, it is difficult to separate the effects temperature and water table changes because the two environmental changes were coincident and negatively correlated ($r=-0.569$). We conducted a variety of statistical analyses, however, to evaluate the relative importance of temperature and moisture effects on ecosystem photosynthesis and respiration, as described below.

The two-dimensional graphs shown in Fig. 14.6a–d assume independent responses to variation in temperature and changes in water table depth, when the environmental conditions were actually negatively correlated. Partial correlation analysis suggested that the response to changes in water table depth were more important than changes in temperature (Flanagan and Syed 2011). In addition, as shown in Fig. 14.6a–d we fitted the observed ecosystem photosynthesis and respiration data to optimum (bell-shaped) response functions for simultaneous change in both GDD and water table depth (dotted lines) and compared this with the optimum response function considering only one

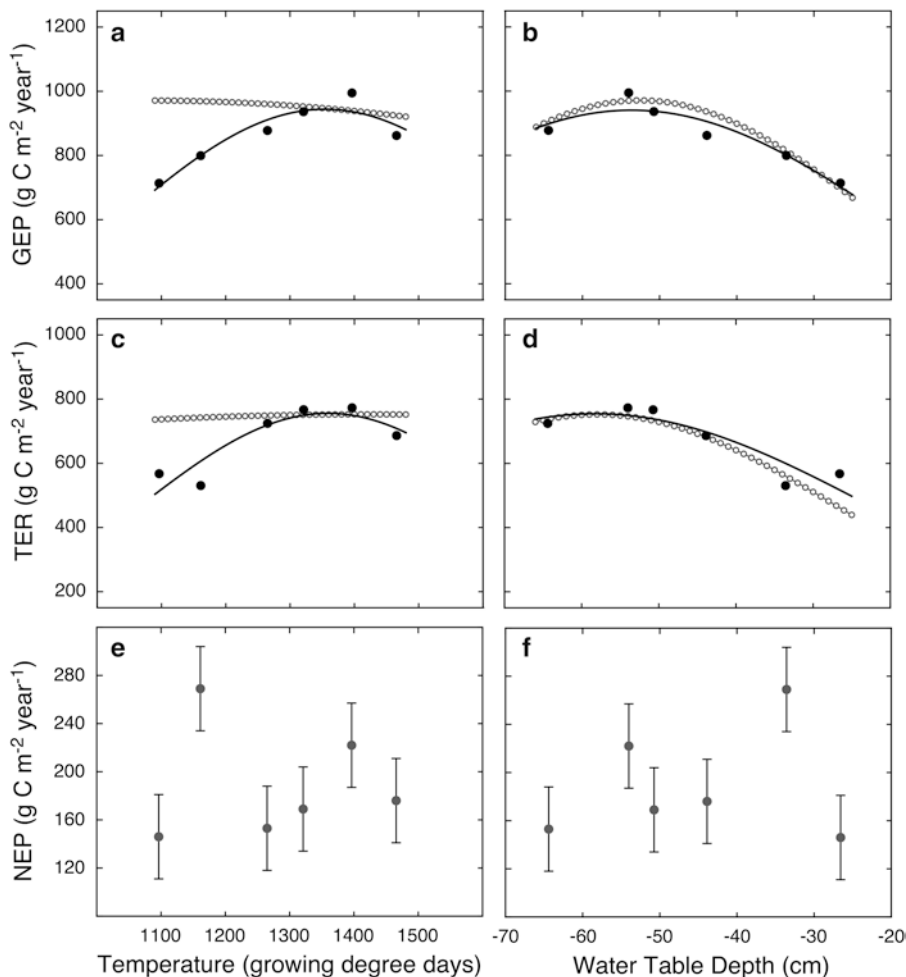


Fig. 14.6. Response of annual-integrated values of: (a, b) gross ecosystem photosynthesis (*GEP*); (c, d) total ecosystem respiration (*TER*); and (e, f) net ecosystem productivity (*NEP*), to variation in temperature (expressed as cumulative growing degree days, March–October) and water table depth (average value during May–October) at the La Biche River flux station in northern Alberta, Canada. The *solid lines* represent calculations done by assuming that variations in *GEP* and *TER* were only a result of changes caused by variation in temperature (a, c) or water table depth (b, d). The *dotted lines* represent calculations done by including the simultaneous effects of changes in both temperature and water table depth on *GEP* and *TER*, but the graphs (a–d) show the predicted response to due to changes in temperature (a, c) and water table depth (b, d) separately. The similarity of the *dotted* and *solid lines* responses to variation in water table depth indicated that inter-annual variation in water table depth controlled changes in *GEP* and *TER*, while inter-annual variation in temperature had virtually no effect. Error bars for the *NEP* measurements represent an estimate of total uncertainty in the eddy covariance measurements and associated data processing of $\pm 35 \text{ g C m}^{-2} \text{ year}^{-1}$ (This figure is based on data published in Flanagan and Syed (2011)).

environmental factor at a time (solid lines) (Zhuang et al. 2004; Flanagan and Syed 2011). In the case of changes in water table depth, the fitted response considering both temperature and water table was almost identical to the fitted response considering only

changes in water table depth. By contrast, for changes in temperature, the fitted response considering both temperature and water table depth was very different from the response that only included variation in temperature. The function that included consideration of

both environmental variables indicated that change in temperature had no significant effect (i.e. a flat-line response) on ecosystem photosynthesis and respiration. In other words, the reductions in photosynthesis and respiration observed in years with low temperature were not actually caused by low temperature, but were rather caused by the associated high water table that was present in those years. Our statistical analysis, therefore, strongly suggested that inter-annual variation in water table depth was the major cause of the variation we observed in GEP and TER (Flanagan and Syed 2011).

There was no significant correlation between annual NEP and either cumulative growing degree days ($r = -0.016$, $P > 0.05$) or average water table depth ($r = 0.189$, $P > 0.05$) (Fig. 14.6e, f). Inter-annual variation in NEP appeared to be associated with relatively subtle differences in the response of ecosystem photosynthesis and respiration to environmental conditions during the growing season. The ecosystem was a strong net sink for CO₂ with an average (\pm SD) NEP of 189 ± 47 g C m⁻² year⁻¹ based on integrated eddy covariance measurements during the 6 year study.

The similar responses of ecosystem photosynthesis and respiration to warmer and drier conditions was contrary to previous predictions of peatland response to climate change which have suggested that respiration increases should override changes in photosynthesis and result in net losses of CO₂ as peatland ecosystems respond to warmer temperatures and lower water tables (Moore et al. 1998; Davidson and Janssens 2006; Tarnocai 2006). However, such predictions of a stronger response for respiration than photosynthesis may only occur if changes in temperature are the most important environmental change. If reduction in water table depth was the only significant environmental change, then more equitable responses of photosynthesis and respiration should be expected. In support of this suggestion, recent studies in a shrub-dominated wetland (Sulman et al. 2009) and in several fens (Sulman et al. 2010) have shown that reductions in the

water table stimulated almost equal increases to ecosystem photosynthesis and respiration, so that there was no effect of water table changes on net ecosystem CO₂ exchange. Lower water tables can increase soil temperature, enhance oxygen supply to roots and improve nutrient availability, all factors that should stimulate both higher photosynthesis and respiration (Shaver et al. 1992; Larcher 1995). This has implications for future ecosystem responses to environmental change because draining of forested peatlands in Finland has resulted in continued net carbon sequestration in trees and soils for decades after the lowering of the water table (Minkkinen et al. 2002). In contrast, classic eco-physiological studies have shown that warmer temperatures alone do normally result in asymmetric responses of respiration and photosynthesis (Larcher 1995).

V. Peatland Succession and Implications for Historical and Future Carbon Sequestration

The average NEP value (189 g C m⁻² year⁻¹) we measured via eddy covariance at the moderately-rich fen site was 3.8 times higher than the value (50 g C m⁻² year⁻¹) predicted from peat core carbon accumulation and carbon losses associated with methane emission and organic and inorganic carbon in runoff (Flanagan and Syed 2011). In addition our NEP measurements were higher than values reported by other eddy covariance studies in several peatland types in Canada and Europe (Flanagan and Syed 2011). There are a number of factors that have contributed to the high rates of NEP we have measured over the last 6 years. First, our study site has a relatively high leaf area index (2.6) compared with many other peatland sites (range 0.4–2.3; Humphreys et al. 2006; Lund et al. 2010), and LAI is increasing with recent tree growth and tree density changes. Approximately 50 % of the peak summer leaf area was contributed by a broad-leaf shrub (*Betula pumila*) and the two tree species, and both *Betula* and *Larix laricina* have relatively high leaf-level

photosynthetic rates (Syed et al. 2006). The increasing woody plant biomass, with high C/N ratio, allows significant rates of carbon sequestration to occur even in a relatively nutrient limited peatland environment (Shaver et al. 1992, 2000). In addition, the nutrient availability at our study site was also likely higher than at many of the other peatlands reported in the literature, sites that are generally oligotrophic and mostly bogs (Flanagan and Syed 2011). Beyond these factors, the successional status of our moderately-rich fen site will strongly influence the observed current rates of ecosystem net carbon sequestration, as will be discussed more fully below.

A general pattern of successional development occurs in peatlands in continental, boreal regions of Canada (Kuhry et al. 1993). In this successional pattern a site develops through a series of stages from a pond, to marsh or open fen, to a treed rich fen, to a treed poor fen, to a forested dry bog. The terms “rich” and “poor” relate to species richness, not nutrient availability (Vitt et al. 1998). The transition from a rich fen to a poor fen is strongly correlated with a change in pH of the near-surface water from above pH 6 to below pH 5 (Kuhry et al. 1993). This temporal pattern of vegetation change is largely an internal (autogenic) process that is controlled by peat accumulation and a shift from early dominance of brown moss species (particularly *Drepanocladus*) to later dominance of *Sphagnum* moss, with the *Sphagnum* species responsible for an acidification of the water. Continued *Sphagnum* peat accumulation and acidification creates conditions for establishment and growth of *Picea mariana* trees and results in the surface of the peatland becoming elevated and separated from the mineral-rich ground water. Ultimately this process leads to the development of a forested bog where the surface vegetation relies strongly on precipitation input for water and nutrients (Kuhry et al. 1993).

Our study site is currently classified as a moderately-rich treed fen, but it appears to be near the stage of transition toward a poor fen. This suggestion is supported by the fact that a mixture of brown moss species and *Sphagnum* moss species are currently present

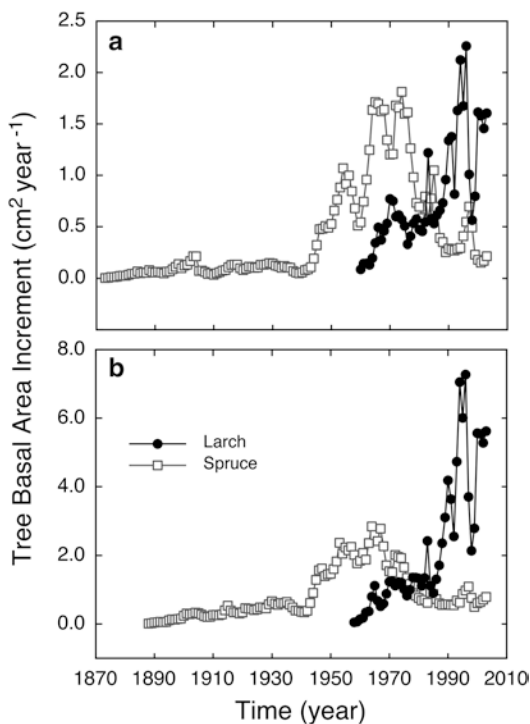


Fig. 14.7. Comparison of average basal area increment (BAI) of *Picea mariana* (Spruce) and *Larix laricina* (Larch) trees at the La Biche River flux station in northern Alberta, Canada. Tree cores were sampled in 2004. The calculated BAI was averaged for each year in the chronology for the five trees of a species. This was done separately for the two locations where the increment cores were collected: (a) approximately 100 m north of the flux tower; and (b) approximately 100 m south of the flux tower (This figure is reproduced from Flanagan and Syed (2011)).

at the site, but the surface water pH is still 6.2 (Syed et al. 2006). Analysis of increment cores of the oldest trees (Fig. 14.7) and examination of time sequences of air photographs of the site (data not shown) indicate that significant tree growth was not apparent until the early 1960s. The oldest *Picea mariana* trees at the site were established in approximately 1870, although peak basal area increment growth in these *Picea* trees did not occur until approximately 1960, the approximate time when the oldest *Larix laricina* trees became established at the site (Fig. 14.7). These data suggest that it was only about 50 years ago that peat accumulation reached the point where the peatland surface was

stable enough to support significant tree growth rates, although the majority of the larger trees present at the site still have stunted growth features consistent with the influence of water logging caused by a high water table (Syed et al. 2006). While the growth rate of oldest *Picea* trees has passed its peak (Fig. 14.7), there has been significant recruitment of a new cohort of *Picea* trees as shown by the proportionally high biomass (approximately 20 % of total above ground biomass) for small trees with a DBH less than 1 cm (Syed et al. 2006).

The significance of this information on peatland successional development and patterns of tree establishment is that the study site is currently changing from a relatively open fen with small stunted trees toward a poor fen with a greater density of *Picea* trees that, in the absence of external disturbance, will eventually form a closed canopy forested bog. The site is now in a phase of relatively rapid tree establishment and associated increase in LAI. An analogous mid-successional stage in upland forest ecosystems is a period when high rates of ecosystem NEP are usually apparent (Bond-Lamberty et al. 2006; Goulden et al. 2011). This has implications for comparisons between current rates of ecosystem NEP as measured by eddy covariance, with historical rates of net carbon accumulation measured in peat cores. In addition, the transition from rich fen to forested dry bog may require 50–350 years (Kuhry et al. 1993). As the succession occurs and above ground biomass accumulates, there should be an associated increase in ecosystem respiration and a decline in NEP until it reaches a near zero steady state value (Bond-Lamberty et al. 2006; Goulden et al. 2011). Therefore, in the absence of fire or other major disturbance, significant net carbon sequestration could continue for decades at this site and help to reduce the positive feedback of climate change on increasing atmospheric CO₂ concentration. However, climate change-induced warmer and drier conditions could also increase the risk of fire disturbance, which would release significant amounts of stored carbon and reset the succession to an early,

less productive stage (Turetsky et al. 2002; Amiro et al. 2009; Goulden et al. 2011).

VI. Conclusions

Northern peatland ecosystems have been consistent carbon sinks for millennia, but it has been predicted that exposure to warmer temperatures and drier conditions associated with climate change will shift the balance between ecosystem photosynthesis and respiration providing a positive feedback to atmospheric CO₂ concentration. I suggest that this prediction is over simplified and ignores a number of important interacting biological and environmental factors that influence ecosystem photosynthesis, respiration and net carbon sequestration in peatland ecosystems. Peatland ecosystems exist in a wide variety of types with contrasting plant community composition associated with variation in water chemistry and hydrological features and water inputs. Because of contrasting dominant plant functional types in these different peatlands, the response of ecosystem CO₂ exchange to temperature and moisture variation can differ dramatically among peatland types. Biological succession can also result in significant changes in plant species composition over time that can influence patterns of ecosystem carbon sequestration for extended periods of time (e.g. potentially hundreds of years). Coupled to this complex biological variability are the strong interactions that occur between temperature and moisture effects on ecosystem photosynthesis and respiration. As shown here, if water table depth and soil moisture are the dominant environmental change influencing peatlands, initial reductions in water table depth may actually increase both photosynthesis and respiration because water tables currently tend to be higher than is optimal for supplying adequate root zone oxygen, which in turn is necessary for high levels of biological metabolism in peatlands. If trees are able to establish on peatland sites, net carbon sequestration in trees and peat soils may continue for decades after the

lowering of the water table, as long as the local hydrology does not change dramatically and the ecosystems are not exposed to severe soil moisture shortages. Prediction of the implications of future climate change effects on peatlands would be improved if global-scale models could include more details of the biological variability among peatlands (both spatial and temporal), with realistic parameterizations of the interacting responses of these ecosystems to variation in temperature, water table depth and soil moisture.

Acknowledgements

This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada, the Canadian Foundation for Climate and Atmospheric Sciences, and Biosphere Implications of CO₂ Policy in Canada (BIOCAP). I thank Angela Adkinson, Peter Carlson, Aaron Glenn, Kamran Syed, and Eric Van Gaalen for their contributions to the research that is reviewed here.

References

- Adkinson AC, Syed KH, Flanagan LB (2011) Contrasting responses of growing season ecosystem CO₂ exchange to variation in temperature and water table depth in two peatlands in northern Alberta, Canada. *J Geophys Res* 116:G01004. doi:[10.1029/2010JG001512](https://doi.org/10.1029/2010JG001512)
- Alm J, Schulman L, Walden J, Nykanen H, Martikainen PJ, Silvola J (1999) Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology* 80:161–174
- Amiro BD, Cantin A, Flannigan MD, de Groot WJ (2009) Future emissions from Canadian boreal forest fires. *Can J For Res* 39:383–395
- Arneeth A, Kurbatova J, Kolle O, Shibistova OB, Lloyd J, Vygodskaya NN, Schulze E-D (2002) Comparative ecosystem-atmosphere exchange of energy and mass in a European Russian and a central Siberian bog II. Interseasonal and interannual variability in CO₂ fluxes. *Tellus* 54B:514–530
- Aurela M, Riutta T, Laurila T, Tuovinen J-P, Vesala T, Tuittila E-S, Rinne J, Haapanala S (2007) CO₂ exchange of a sedge fen in southern Finland – the impact of a drought period. *Tellus* 59B:826–837
- Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present, and future. *Glob Change Biol* 9:479–492
- Barr AG, Black TA, Hogg EH, Kljun N, Morgenstern K, Nesic Z (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
- Bellisario LM, Moore TR, Bubier JL (1998) Net ecosystem CO₂ exchange in a boreal peatland, northern Manitoba. *Ecoscience* 5:534–541
- Bond-Lamberty B, Gower ST, Goulden ML, McMillan A (2006) Simulation of boreal black spruce chronosequences: comparison to field measurements and model evaluation. *J Geophys Res* 11, G02014. doi:[10.1029/2005JG000123](https://doi.org/10.1029/2005JG000123)
- Bubier JL, Crill PM, Moore TR, Savage K, Varner RK (1998) Seasonal patterns and controls on net ecosystem CO₂ exchange in a boreal peatland complex. *Global Biogeochem Cycles* 12:703–714
- Bubier JL, Bhatia G, Moore TR, Roulet NT, Lafleur PM (2003) Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. *Ecosystems* 6:353–367
- Cai T, Flanagan LB, Syed KH (2010) Warmer and drier conditions stimulate respiration more than photosynthesis in a boreal peatland ecosystem: analysis of automatic chambers and eddy covariance measurements. *Plant Cell Environ* 33:394–407
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440:165–173
- Desai AR, Richardson AD, Moffat AN, Kattge J, Hollinger DY, Barr A, Falge E, Noormets A, Papale D, Reichstein M, Stauch VJ (2008) Cross-site evaluation of eddy covariance GPP and RE decomposition techniques. *Agric For Meteorol* 148:821–838
- Flanagan LB, Syed KH (2011) Stimulation of both photosynthesis and respiration in response to warmer and drier conditions in a boreal peatland ecosystem. *Glob Change Biol* 17:2271–2287
- Glenn AJ, Flanagan LB, Syed KH, Carlson PJ (2006) Comparison of net ecosystem CO₂ exchange in two peatlands in western Canada with contrasting dominant vegetation, *Sphagnum* and *Carex*. *Agric For Meteorol* 140:115–135
- Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol Appl* 1:182–195
- Goulden ML, McMillan AMS, Winston GC, Rocha AV, Manies KL, Harden JW, Bond-Lamberty BP (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Glob Change Biol* 17:855–871

- Griffis TJ, Rouse WR, Waddington JM (2000) Interannual variability of net ecosystem CO₂ exchange at a sub-arctic fen. *Global Biogeochem Cycles* 14:1109–1121
- Humphreys ER, Lafleur PM, Flanagan LB, Hedstrom N, Syed KH, Glenn AJ, Granger R (2006) Summer carbon dioxide and water vapor fluxes across a range of northern peatlands. *J Geophys Res* 111:G04011. doi:10.1029/2005JG000111
- Johnson D, Kershaw L, MacKinnon A, Pojar J (1995) Plants of the western boreal forest and Aspen Parkland. Lone Pine, Edmonton
- Kuhry P, Nicholson BJ, Gignac LD, Vitt DH, Bayley SE (1993) Development of *Sphagnum*-dominated peatlands in boreal continental Canada. *Can J Bot* 71:10–22
- Lafleur PM, Roulet NT, Bubier JL, Frolking S, Moore TR (2003) Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochem Cycles* 17:1036. doi:10.1029/2002GB001983
- Larcher W (1995) Physiological plant ecology: ecophysiology and stress physiology of functional groups, 3rd edn. Springer, Berlin
- Lund M, Lafleur PM, Roulet NT, Lindroth A, Christensen TR, Aurela M, Chojnick BH, Flanagan LB, Humphreys ER, Laurila T, Oechel WC, Olejnik J, Rinne J, Schubert P, Nilsson MB (2010) Variability in exchange of CO₂ across 12 northern peatland and tundra sites. *Glob Change Biol* 16:2436–2448
- Minkinen K, Korhonen R, Savolainen I, Laine J (2002) Carbon balance and radiative forcing of Finnish peatlands 1900–2100 – the impact of forestry drainage. *Glob Change Biol* 8:785–799
- Moffat AM, Papale D, Reichstein M, Hollinger DY, Richardson AD, Barr AG, Beckstein C, Braswell BH, Churkina G, Desai AR, Falge E, Gove JH, Heimann M, Hui D, Jarvis AJ, Kattge J, Noormets A, Stauch VJ (2007) Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. *Agric For Meteorol* 147:209–232
- Moncrieff JB, Jarvis PG, Valentini R (2000) Canopy fluxes. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) *Methods in ecosystem science*. Springer, New York, pp 161–180
- Moore TR, Roulet NT, Waddington JM (1998) Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Clim Chang* 40:229–245
- Moore TR, Lafleur PM, Poon DMI, Heumann BW, Seaquist JW, Roulet NT (2006) Spring photosynthesis in a cool temperate bog. *Glob Change Biol* 12:2323–2335
- National Wetlands Working Group (1988) *Wetlands of Canada*. Ecological land classification series no. 24. Sustainable Development Branch, Environment Canada/Polyscience Publications, Inc., Ottawa/Montreal
- Parmentier FJW, van der Molen MK, de Jeu RAM, Hendriks DMD, Dolman AJ (2009) CO₂ fluxes and evaporation on a peatland in the Netherlands appear not affected by water table fluctuations. *Agric For Meteorol* 149:1201–1208
- Shaver GR, Billings WD, Chapin FS, Giblin LF, Nadelhoffer KJ, Oechel WC, Rastetter EB (1992) Global change and the carbon balance of arctic ecosystems. *Bioscience* 42:433–441
- Shaver GR, Billings WD, Chapin FS, Gurevitch J, Harte J, Henry G, Ineson P, Jonasson S, Melillo J, Pitelka L, Rustad L (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *Bioscience* 50:871–882
- Shurpali NJ, Verma SB, Kim J (1995) Carbon dioxide exchange in a peatland ecosystem. *J Geophys Res* 100:14319–14326
- Silvola J, Alm J, Ahlholm U, Nykanen H, Marikainen PJ (1996) CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions. *J Ecol* 84:219–228
- Sonnentag O, van der Kamp G, Barr AG, Chen JM (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
- Sulman BN, Desai AR, Cook BD, Saliendra N, Mackay DS (2009) Contrasting carbon dioxide fluxes between a drying shrub wetland in Northern Wisconsin, USA, and nearby forests. *Biogeosciences* 6:1115–1126
- Sulman BN, Desai AR, Saliendra N, Lafleur PM, Flanagan LB, Sonnentag O, Mackay DS, Barr AG, van der Kamp G (2010) CO₂ fluxes at northern fens and bogs have opposite responses to interannual fluctuations in water table. *Geophys Res Lett* 37:L19702. doi:10.1029/2010GL044018
- Syed KH, Flanagan LB, Carlson PJ, Glenn AJ, Van Gaalen KE (2006) Environmental control of net ecosystem CO₂ exchange and carbon balance in a treed, moderately rich fen in northern Alberta. *Agric For Meteorol* 140:97–114
- Tarnocai C (2006) The effect of climate change on carbon in Canadian peatlands. *Glob Planet Change* 53:222–232
- Turetsky MR, Weider RK, Halsey LA, Vitt DH (2002) Current disturbance and the diminishing peatland carbon sink. *Geophys Res Lett* 29:L526. doi:10.1029/2001GL014000
- Turunen J, Tomppo E, Tolonen K, Reinikainen A (2002) Estimating carbon accumulation rates of undrained

- mires in Finland – application to boreal and subarctic regions. *Holocene* 12:69–80
- Vitt DH (1994) An overview of the factors that influence the development of Canadian peatlands. *Mem Entomol Soc Can* 169:7–20
- Vitt DH, Halsey LA, Thormann MN, Martin T (1998) Peatland Inventory of Alberta. Phase 1: Overview of peatland resources in the natural regions and subregions of the province. Sustainable Forest Management Network, University of Alberta, Edmonton
- Williams TG, Flanagan LB (1998) Measuring and modelling environmental influences on photosynthetic gas exchange in *Sphagnum* and *Pleurozium*. *Plant Cell Environ* 21:555–564
- Zhuang Q, Melillo JM, Kicklighter DW, Prinn RG, McGuire AD, Steudler PA, Felzer BS, Hu S (2004) Methane fluxes between terrestrial ecosystems and the atmosphere at northern high latitudes during the past century: a retrospective analysis with a process-based biogeochemistry model. *Global Biogeochem Cycles* 18:GB3010. doi:[10.1029/2004GB002239](https://doi.org/10.1029/2004GB002239)