Title
A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability, and decadal trends

Permalink
https://escholarship.org/uc/item/8zs839q9

Journal
Global Change Biology, 13(3)

ISSN
1354-1013

Authors
DUNN, ALLISON L
BARFORD, CAROL C
WOFSY, STEVEN C
et al.

Publication Date
2007-03-01

DOI
10.1111/j.1365-2486.2006.01221.x

Copyright Information
This work is made available under the terms of a Creative Commons Attribution License, available at https://creativecommons.org/licenses/by/4.0/

Peer reviewed
A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability, and decadal trends

ALLISON L. DUNN *, CAROL C. BARFORD †, STEVEN C. WOFSY *, MICHAEL L. GOULDEN ‡ and BRUCE C. DAUBE *

*Department of Earth & Planetary Sciences, Harvard University, 20 Oxford St., Cambridge, MA 02138, USA,
†Center for Sustainability and the Global Environment, University of Wisconsin, Madison, 1710 University Ave., Madison, WI 53726, USA, ‡Department of Earth System Science, University of California, Irvine, Croul Hall, Irvine, CA 92697, USA

Abstract

We present a decadal (1994–2004) record of carbon dioxide flux in a 160-year-old black spruce forest/veneer bog complex in central Manitoba, Canada. The ecosystem shifted from a source (+ 41 g C m⁻², 1995) to a sink (−21 g C m⁻², 2004) of CO₂ over the decade, with an average net carbon balance near zero. Annual mean temperatures increased 1–2°C during the period, consistent with the decadal trend across the North American boreal biome. We found that ecosystem carbon exchange responded strongly to air temperature, moisture status, potential evapotranspiration, and summertime solar radiation. The seasonal cycle of ecosystem respiration significantly lagged that of photosynthesis, limited by the rate of soil thaw and the slow drainage of the soil column. Factors acting over long time scales, especially water table depth, strongly influenced the carbon budget on annual time scales. Net uptake was enhanced and respiration inhibited by multiple years of rainfall in excess of evaporative demand. Contrary to expectations, we observed no correlation between longer growing seasons and net uptake, possibly because of offsetting increases in ecosystem respiration. The results indicate that the interactions between soil thaw and water table depth provide critical controls on carbon exchange in boreal forests underlain by peat, on seasonal to decadal time scales, and these factors must be simulated in terrestrial biosphere models to predict response of these regions to future climate.

Keywords: boreal, black spruce, decomposition, global change, interannual variability, net ecosystem exchange, peatland, photosynthesis, Picea mariana, soil carbon

Received 5 May 2005; revised version received 28 September 2005 and accepted 11 October 2005

Introduction

Boreal forests represent 22% of global forest area, and more than half of North American forests (Iremonger et al., 1997; Schlesinger, 1997). These small stature forests contain only 13% of global biomass carbon, but their peat-rich soils hold nearly half (43%) of global soil carbon stores, ~450 Pg (equivalent to 200 ppm atmospheric CO₂; Gorham, 1991; Schlesinger, 1997). Climate has warmed in the boreal forest in the past century, and precipitation has increased (Myneni et al., 1997; Keyser et al., 2000; Zhang et al., 2000; Stone et al., 2002). The IPCC Third Assessment Report (2001) predicted that the high northern latitudes will continue to warm more rapidly than the global average in the 21st century, and will experience the largest changes in precipitation. Primary production may increase in response to a warmer climate (Myneni et al., 1997), but warmer climates may also lead to growth declines in boreal species adapted to cooler climates (Barber et al., 2000; D’Arrigo et al., 2004; Wilmking et al., 2004) and to more frequent and extensive wildfires and insect outbreaks (Flannigan & Van Wagner, 1991; Clark, 1988), as occurred during the warm 1980s (Stocks, 1993).

The sensitivity of boreal soil carbon to climate change is a major uncertainty in predicting responses to climate forcing by the coupled atmosphere–biosphere system. Peatlands accumulate organic matter in part due to cool
temperatures and high water tables, and unless climate warming is accompanied by a substantial increase in precipitation, accumulation of organic carbon in peatlands may cease or reverse (Schreader et al., 1998). The IPCC (2001) predicted that peatland ecosystems may continue to accumulate carbon in the face of water table drawdown, but this ability would be compromised in the case of extended or more frequent droughts, which may leave deep organic soils susceptible to fire.

The net exchange of carbon dioxide is the residual of the coupled processes of respiration and photosynthesis, and small changes in either process can significantly impact the net exchange. During the growing season, boreal forests can act as a sink for atmospheric carbon dioxide (Baldocchi et al., 1997; Black et al., 2000; Griffis et al., 2003; Suni et al., 2003a) or a source (Goulden et al., 1998; Lindroth et al., 1998; Milyukova et al., 2002). The dormant wintertime period is characterized by a slow, steady efflux of carbon (Winston et al., 1997; Goulden et al., 1998; Suni et al., 2003a) which, when taken over the course of a long boreal winter, can contribute significantly to the annual carbon balance (Hobie et al., 2000). As photosynthesis provides the organic substrate for respiration, the processes are strongly coupled when long time scales are considered. But imbalances can persist seasonally, annually, and even for very long periods. In peatlands, carbon has been accumulating at a rate of 3–50 g m\(^{-2}\) yr\(^{-1}\) following deglaciation 12,000–8000 years ago (Clymo, 1984; Gorham, 1991; Harden et al., 1992; Trumbore & Harden, 1997). Hence, to understand the role of boreal systems in the global carbon cycle, we must understand the processes that regulate photosynthesis, respiration, and burning of peat in forest fires on all time scales.

Previous studies have identified key factors regulating the carbon exchange of boreal forests. The springtime onset of photosynthesis in deciduous and coniferous boreal forests is controlled by air and soil temperatures (Berg & Linder, 1999; Suni et al., 2003b), and varies considerably from year to year (Black et al., 2000; Barr et al., 2002; Suni et al., 2003a). Annual gross ecosystem exchange (GEE) was found to be less variable than ecosystem respiration (R) by Bubier et al. (2003a) and Valentini et al. (2000), but Barr et al. (2002) found more variability in GEE than R at a deciduous boreal site. The shutdown of photosynthesis at the end of the summer appears to depend on photoperiod, as well as climatic factors (Suni et al., 2003a). Valentini et al. (2000) and Bubier et al. (2003a) found that ecosystem respiration was the main determinant of variations in annual net carbon exchange in European forests and an Ontario peatland, respectively. While boreal soil respiration is sensitive to soil temperature (Rayment & Jarvis, 2000; O’Connell et al., 2003b; Wang et al., 2003), the position of the water table also exerts important control on decomposition of soil organic carbon (Funk et al., 1994; Bubier et al., 1998; Schreader et al., 1998).

In this paper, we investigate the response of an old (~160 year) boreal black spruce forest (the most widely occurring forest type in the boreal region of North America, O’Connell et al., 2003a) to environmental forcing on instantaneous, seasonal, annual, and interannual timescales. We present the long-term record (1994–2004) of eddy-covariance measurements of CO\(_2\) and energy exchange, made every 30 min. We supplemented these measurements in 2001 with continuous data for water table depth and soil water content, and in 2003 with smaller-footprint measurements of CO\(_2\) heat and water vapor fluxes in upland and wetland patches of the forest. We use our long data record to quantify the influence of meteorological, hydrological, and related factors on ecosystem carbon balance. These data provide internally consistent information on ecosystem response to environmental forcing for times from hourly to decadal, and at scales from meters to kilometer, allowing us to infer the critical processes underlying ecosystem–atmosphere exchange.

Methods

Site location and description

The study area is located at 55.88°N, 98.48°W, in central Manitoba, Canada (Map 1). It was established in 1993 as the Northern Old Black Spruce (NOBS) site for NASA’s Boreal Ecosystem–Atmosphere Study (BOREAS), an international field experiment examining atmosphere–biosphere interactions in the Canadian boreal forest (Sellers et al., 1995). It is situated on the low-relief terrain of the Canadian Shield, near the northern limit of the continuous boreal forest (Trumbore & Harden, 1997). The site is 40 km from the nearest town (Thompson), and 4 km south of the closest road (Provincial Highway 391). It is accessible only by foot, all-terrain vehicle, or snowmobile.

The vegetation at the site consists of regrowth since the last fire, dominated by 160-year-old black spruce trees (Picea Mariana (Mill.), Gower et al., 1997); the stand age reported here represents a correction from that of Gouldef et al. (1997), based on tree-ring data. The average stem density is 5450 trees ha\(^{-1}\), with a basal area of 35.6 m\(^2\) ha\(^{-1}\), sapwood volume of 82.5 m\(^3\) ha\(^{-1}\), and leaf area index of 4.2 (Gower et al., 1997). Small topographic variations cause large changes in vegetation, with 10-m-tall spruce in the uplands and chlorotic, 1- to 6-m- tall spruce and tamarack (Larix laricina (Du Roi) K. Koch) at slightly lower elevations (Plate 1). Mosses dominate the ground cover: feathermosses
(Pleurozium and Hylocomium) in the dense upland stands and Sphagnum spp. in the low-lying veneer bogs (Trumbore & Harden, 1997). The understory is quite diverse, including bog birch (Betula glandulosa var. hallii), blueberry (Vaccinium spp.), and willow (Salix spp.) in the veneer bogs, wild rose (Rosa spp.) in the uplands, and Labrador tea (Ledum groenlandicum Oeder) throughout. The mosaic of vegetation within a radius of 500 m consists of approximately 25% moderately well drained upland forest, 50% imperfectly to poorly drained feathermoss/Sphagnum veneer bogs, and 25% very poorly drained Sphagnum/brown moss areas, including fens (Harden et al., 1997).

The peat-rich soils at this site developed atop the clay/silt sediments of glacial Lake Agassiz over the past 8000 years (Veldhuis et al., 2002). The soil carbon profile is very heterogeneous, reflecting differences in drainage associated with the same low-relief topography that controls the vegetation cover (Trumbore & Harden, 1997). The moderately well drained feathermoss/spruce uplands can burn deeply during forest fires, and consequently contain relatively modest amounts of soil carbon (13 kg C m\(^{-2}\), Trumbore & Harden, 1997). The poorly drained soils in Sphagnum veneer bogs and other wetlands are protected by high water tables and retain much of their soil organic matter during fires, resulting in higher soil carbon content (25 kg C m\(^{-2}\), Trumbore & Harden, 1997). The site is in the zone of discontinuous permafrost, with thin layers of permafrost occasionally present in veneer bogs and uplands (Veldhuis et al., 2002). Methane production and oxidation are both significant processes during the growing season at this site, with upland areas consuming between 0.14 and 0.51 mg CH\(_4\) m\(^{-2}\) day\(^{-1}\) and topographically lower areas producing between 0.14 and 2.83 mg CH\(_4\) m\(^{-2}\) day\(^{-1}\) (Moosavi & Crill, 1997), but CH\(_4\) is a relatively small component of the carbon budget (< 10 g C m\(^{-2}\) yr\(^{-1}\)).

Flux measurements were made from a 31-m-tall, triangular cross-section (30 cm on a side) tower (Rohn 25G, Peoria, IL, USA; see Plate 1). Other instrumentation and data acquisition equipment were located in a climate-controlled hut 20 m northeast of the tower. Power was provided by two diesel generators, a primary and backup, located 300 m to the east of the tower. The generators were equipped with an automatic switch that activated the backup generator in case of primary generator failure. In conjunction with an uninterruptible power source (APC Smart-UPS 2200, Smart-UPS, APC, W. Kingston, RI, USA), this allowed the site to continue operation without human intervention in the case of generator failure. The data acquisition and control system was automated, with a local technician downloading the raw data weekly and shipping it to the laboratory.
Measurements

All signals associated with determination of turbulent fluxes were measured at 4 Hz from a sampling height of 29 m. The three-dimensional wind vector and virtual temperature were measured with a sonic anemometer (SATI/3K, Applied Technologies Inc., Boulder, CO, USA). The mixing ratios of CO2 and H2O were measured by sampling 20 standard L·min⁻¹ at 29 m through a 50-m-long, 0.64-cm inner diameter Teflon PFA tube. A subsample of 4 standard L·min⁻¹ was drawn through a short piece of tubing into a CO2/H2O infrared gas analyzer (IRGA; Model 6262, LI-COR Inc., Lincoln, NE, USA). The raw voltages from the IRGA were recorded and the gain was calculated every 3 h by a standard addition of 4% CO2 at 40 and 80 standard mL·min⁻¹. The IRGA zero was measured every 3 hours by drawing sample air through a CO2 scrubber (soda lime) and desiccant (Mg(ClO4)2).

Measurements of the mixing ratio of CO2 and H2O at 0.3, 1.5, 4.6, 8.4, 12.9, and 28.8 m were made sequentially at 0.5 Hz. These profile measurements were calibrated every 3 hours with two CO2 mixtures traceable to the National Oceanic and Atmospheric Administration (NOAA)/Climate Monitoring and Diagnostics Laboratory (CMDL) standards. These data were used to compute the half-hourly change in CO2 concentration below 28.8 m (canopy storage of CO2). Additional data were collected at 0.5 Hz to characterize the physical environment. Measurements of photosynthetically active radiation (PAR) were made via quantum sensor (PAR, Model LI-190, LI-COR Inc.) at 29 m (upward-facing and downward-facing) and at eight sensors on the moss surface. Net radiation was measured at 29 m with a thermopile net radiometer (Model Q*6, REBS, Seattle, WA, USA). Air temperature at 2, 10, and 30 m was measured using aspirated thermistors. Five arrays of thermistors in the soil measured the soil temperature profile at 5, 10, 20, 50, and 100 cm depths.

Additional instrumentation was added during 2001–2003 to measure soil hydrologic parameters and carbon fluxes at two sites: a Sphagnum veneer bog and a forested upland (Plate 1). Soil moisture and temperature profiles, soil heat flux, and water table depth were measured at these sites with contrasting soil carbon profiles and hydrology (Trumbore & Harden, 1997). These data allowed us to investigate the role of hydrology and substrate quality in the carbon cycle of the boreal forest. In 2003, we added measurements of near-surface CO2 fluxes via the modified Bowen ratio method (Meyers et al., 1996; Liu & Foken, 2001).

Analysis

The eddy-covariance technique was used to calculate the turbulent fluxes of sensible heat, latent heat, CO2, and momentum at 29 m. CO2 flux was calculated as the 30 min covariance of the vertical wind velocity (u') and CO2 mixing ratio (c'). The time lag was determined by maximizing the correlation between u' and c'. Fluxes were rotated to the plane in which mean vertical wind speed was zero (McMillen, 1988). The CO2 and water vapor signals were adjusted to account for dampening in high-frequency fluctuations due to the long sampling tube and closed-path IRGA (Goulden et al., 1997). The net ecosystem exchange (NEE) of carbon dioxide was calculated by adding the turbulent flux of CO2 to the time derivative of the column storage of CO2 between 0 and 28.8 m.

The flux data were carefully examined for errors on a weekly basis and during year-end analysis procedures. NEE was determined by summing the CO2 flux and canopy storage of CO2 except during brief periods for which the storage data were unavailable, when only flux was used. The sonic anemometer experienced occasional failures (spiking) during precipitation (due to water buildup on transducers) and during extreme cold weather (generally < −20 °C). If spikes in the sonic data constituted more than 5% of data in a half-hour, the flux datum from that period was excluded. The sonic temperature signal was monitored and flux data excluded if the data were too noisy (σTsonic > 1 °C). The concentration from the flux IRGA was compared with that of the profile IRGA at 29 m and CO2 data were excluded if there was a mismatch or a divergence between the sensors.

Ecosystem respiration (R) was determined from night-time NEE measurements for well-mixed periods (u' > 0.2 m·s⁻¹; Fig. 3a Goulden et al., 1997), excluding times when wind came from the quadrant containing the generator (45°–135° from north). To obtain a continuous time series of ecosystem respiration (including daytime and poorly mixed nights), the dataset was divided into intervals approximately 10 days in length consisting of 100 valid night-time NEE observations. Data for each interval were tested for a linear relationship with air temperature at 30 m. If a linear fit (R upon T) was significant, the resulting linear function was used to calculate R for the daytime and poorly mixed night-time half-hours in that period. If the linear relationship was not significant, R was interpolated, based on mean valid night-time NEE at 10° intervals. We used a linear rather than exponential fit to temperature based on the following reasoning: while the response of R to temperature may be exponential over the entire temperature range of a site, we calculated R response to temperature in intervals of roughly 10 days. On this timescale, the linear fits to data were more robust than the exponential (median P-values of 0.03 and 0.15, respectively). We investigated whether the use of a
linear rather than exponential fit would affect our
calculation of annual total respiration: the annual sums
calculated both ways were not significantly different.
Treatment of respiration during wintertime was slightly
different than during the growing season. Temperatures
less than \(-10 \, ^\circ C\) were assumed to correspond with zero
photosynthesis, and all NEE measurements, therefore,
represented respiratory fluxes.

GEE was determined as the difference between mea-
sured NEE and derived respiration during daytime
periods when \(T > -10^\circ\) and \(u^* > 0.2 \, \text{m s}^{-1}\):
\[
\text{GEE} = \text{NEE} - R.
\] (1a)

Note that uptake of \(\text{CO}_2\) from the atmosphere corre-
sponds to NEE < 0. To obtain a continuous record of
daytime GEE, the data were divided into periods of 150
good GEE observations and tested for linear or quad-
tratic dependence on PAR. If the quadratic coefficients
were significant, a nonlinear least squares regression
model was used to determine GEE for the poorly mixed
\((u^* < 0.2 \, \text{m s}^{-1})\) daytime periods using the functional
form
\[
\text{GEE} = A + B \times \text{PAR}/(C + \text{PAR}).
\] (1b)

Otherwise, a linear least squares fit was used to deter-
mine GEE for the same periods.

In order to determine seasonal and annual NEE,
GEE, and \(R\), gaps in the data record must be filled,
and gap-filling methodologies have generated much
discussion (Goulden et al., 1996b; Falge et al., 2001).
Several types of events lead to gaps in the record, and
the treatment of these gaps differs. Gaps due to a
malfunctioning sonic anemometer, IRGA, or pump
are filled by using the estimated \(R\) (from temperature,
using the fit from proximate days) and GEE (from
PAR) to fill for NEE. More serious gaps occur when
the entire system goes down due to generator failure,
lightning strikes, or computer problems, leaving no
temperature or PAR data to calculate NEE from \(R\) and
GEE. In this case, PAR was estimated using a lookup
table consisting of the average PAR for each half-hour
of an average year as determined from the entire
dataset. Temperature was filled with mean daily tem-
perature from the Thompson airport weather station,
40 km to the east, for which there is excellent corre-
spondence with NOBS temperatures (Fig. 1). These
temperatures were corrected to account for the mean
systematic difference between NOBS and Thompson
airport temperatures. These estimated PAR and tem-
perature values were used to calculate \(R\) and GEE,
respectively, which were then summed to arrive at an
estimate of NEE during system downtime. After gap
filling, annual NEE was derived from the cumulative
NEE over the calendar year. GEE and respiration sums
were calculated in the same way.

**Results**

**Climate at NOBS and the surrounding region**

Air temperatures at NOBS correspond well with other
climate stations in a 300 km radius (Fig. 1), suggesting
that the climate variations at NOBS are typical of a
much larger region. Temperatures in the region were

![Fig. 1](image-url)
anomalously cold (compared with the 1971–2000 mean of −3.2 °C) from the late-1980s to 1997, recovering during our study period. From 1994 to 1997, mean annual temperatures (at the Thompson airport climate station) were less than or equal to −3.2 °C, while 5 of the 7 years from 1998 to 2004 were warmer than the long-term average, with four warmer than −1 °C. Although this difference in mean annual temperature between 1994–1997 and 1998–2004 was significant ($P = 0.01$), it has not yet led to a significant increase in length of the growing season (LGS). In addition, the beginning of the study period coincided with the end of a prolonged period of below-average precipitation (for 8 of the 10 years from 1987 to 1996; Fig. 1, bottom panel), suggesting that the early years of our study may show the response to a decadal water deficit. These decadal variations are larger than the long-term climatic trends in this region of Canada, south of 60°N. During the 20th century, mean annual temperatures and precipitation increased, by 0.5–1.5 °C and 12%, respectively, although springtime snowfall decreased (Zhang et al., 2000).

**Tower footprint and source areas**

The area surrounding the tower is quite heterogeneous (Plate 1), comprising a continuum of drainage classes (from moderately well drained to very poorly drained; Harden et al., 1997) and soil carbon profiles (from 4.3 to 27.9 kg C m$^{-2}$; Trumbore & Harden, 1997). The area within a 500 m radius of the tower is approximately 25% well drained, 50% imperfectly to poorly drained, and 25% very poorly drained (Harden et al., 1997). We analyzed the data to test for influence of source area on the carbon exchange measured at the tower. We divided the data into four quadrants representing the four cardinal wind directions; we excluded the eastern quadrant from subsequent analyses as its source area includes the diesel generator (this quadrant was also excluded from our determination of $R$). The number of measurements with $u^* > 0.2$ m s$^{-1}$ from the three remaining quadrants did not differ significantly, suggesting that there is no sampling bias in the tower data in terms of the source area. We examined data from each quadrant separately to test for differing photosynthesis response to PAR and respiration response to temperature. Drainage class and vegetation cover differed markedly between the quadrants: the southern and western quadrants were 40% well drained and 60% imperfectly to very poorly drained; the northern quadrant only had 8% well drained, with 92% of the cover imperfectly to very poorly drained. There was no appreciable difference in light curve response between the data from each quadrant. Respiration response to temperature was similar in the western and southern quadrants, and was slightly smaller (approximately 25%) in the northern quadrant.

**Seasonal cycle of carbon exchange**

The average seasonal cycles of NEE, GEE, and $R$, as calculated from the nearly 10 years of eddy-covariance data, are shown in Fig. 2. The mean date for onset of photosynthesis in mid-April is similar to observations at a southern black spruce forest 475 km to the WSW (Griffis et al., 2003), but is several weeks before measurable photosynthesis is seen at deciduous forests in the region (Black et al., 2000), and even at Harvard Forest 12° to the south (Goulden et al., 1996a). On average the forest has the greatest net uptake of atmospheric CO$_2$ during the months of May and June, also similar to observations in southern black spruce and jack pine forests (Griffis et al., 2003). The system is roughly carbon neutral from July until the end of September, when a peak in CO$_2$ emission occurs that slowly declines through the winter (Goulden et al., 1998).

Initiation of photosynthesis in boreal conifer forests is largely regulated by air temperature, requiring daytime temperatures above freezing (Goulden et al., 1997; Bergh & Linder, 1999; Suni et al., 2003b). NEE turns positive in July and August because of high respiration rates, and hence we could not define the growing season simply by the sign of net daily CO$_2$ exchange. We instead designated the onset and end of the growing season (OGS and EGS, respectively) as the first and last day of the year where forest GEE achieves 10% of the summertime maximum GEE. There was significant variation in the onset of photosynthesis (Fig. 3), with OGS as early as day of year (DOY) 99 (2003) or as late as DOY 143 (1997), a difference of more than 6 weeks. There was considerably less variability at the end of the growing season, which ranged from DOY 284 to 302,
suggesting that decreasing day length and/or low light intensity limited late-season photosynthesis (Suni et al., 2003a), even in the warm autumns of 1998 and 2000.

The seasonal increase in respiration begins at approximately the same time as photosynthesis, but is initially weaker than photosynthesis for two reasons. First, conifers may initially allocate more photosynthate to replenishing carbohydrate reserves than to growth, limiting growth respiration in spring and early summer (Goulden et al., 1997). Second, heterotrophic respiration is limited in early summer by soil climate in thawing, meltwater-saturated soils. Respiration rates continue to rise until August, as the slow thawing of the carbon-rich, deeper soil layers progressively provide additional substrate for heterotrophic respiration (Goulden et al., 1998); this phenomenon gives the seasonal course of ecosystem respiration a significant lag relative to photosynthesis (Fig. 2). The reverse process, gradual freezing of soils during the cold season, leads to even longer lags in the fall. Respiration rates decline slowly and CO₂ efflux continues throughout the winter.

Effect of water tables on carbon exchange

Soils below the water table are typically low in oxygen or anoxic (Clymo, 1984; Clymo & Pearce, 1995), which inhibits decomposition (Funk et al., 1994; Bubier et al., 1998; Schreder et al., 1998). We investigated the role of summertime (DOY 150–250) water table position on ecosystem respiration using measurements at a Sphagnum veneer bog in the northern portion of the eddy-covariance tower footprint, the locus of the largest reservoir of soil carbon at the site (Plate 1). We found that increased depth to water table was significantly correlated with increased CO₂ flux during well-mixed night-time periods (daily: \( p = < 1 \times 10^{-10}, r = 0.36 \)) during summer 2002–2004. Depth to water table in the veneer bog was a predictor for ecosystem respiration observed at the main tower, accounting for 11% of the half-hourly variance in \( R \) during the summers of 2002–2004 (\( P < 1 \times 10^{-10} \)). This result is not surprising given the dominance of wetlands in the tower footprint.

We constructed two multiple linear regression models, using half-hourly and daily time steps, to investigate the relative contribution of water table depth and soil temperature to total ecosystem respiration. We found that depth to water table and soil temperatures at the carbon-rich 20 cm depth predicted 57% of the half-hourly variance in \( R \) (\( P < 1 \times 10^{-10} \)), with 10% of the variance attributable to depth to water table, 46% to soil temperature, and 1% to the interaction between the two variables. On a daily time step, these two factors accounted for 64% of the daily variance in \( R \); 15% attributable to water table depth, 48% to soil temperature, and 1% to the interaction between the two variables. The daily model fit took the form of:

\[
R_{\text{predicted}} = 0.0877 \times WT_{\text{depth.bog}} + 0.583 \\
\times T_{\text{soil,20 cm}} - 0.0106 \times WT_{\text{depth.bog}} \\
\times T_{\text{soil,20 cm}} - 1.36,
\]

© 2007 The Authors
Journal compilation © 2007 Blackwell Publishing Ltd, Global Change Biology, 13, 577–590
where $R_{\text{predicted}}$ (for the whole ecosystem) is in g C m$^{-2}$ day$^{-1}$, and $WT_{\text{depth, bog}}$ and $T_{\text{soil, 20 cm}}$ are in cm to water table and °C, respectively. Based on this relationship, a 2 cm drop in water table depth integrated over the 100 days translates into ~18 g C m$^{-2}$ additional $R$ – enough to tip the overall carbon balance from a sink to a source in some years (Table 1). Note that this investigation only considered a 100-day thawed period (DOY 150–250) for 3 years, and would not be applicable during other seasons. Our data showing $R$ positively correlated to temperature and negatively correlated with higher water tables corroborate the findings of Bubier et al. (1998) and Funk et al. (1994).

It is important to note that the position of the water table is an important contributor to the observed variability in $R$, even though most of the ecosystem respiration is autotrophic or derived from the aerobic upper soil layers, and controlled by soil temperature: the variations in water table depth between 20 and 30 cm represent a critical factor regulating variability in $R$ on seasonal and annual time scales. Water table movement at these depths brings into play a relatively old, abundant reservoir of organic matter and makes a significant contribution to total deep decomposition (30–130 g C m$^{-2}$ yr$^{-1}$, Goulden et al., 1998).

The water table in the Sphagnum veneer bog responded both to precipitation and to seasonal progression associated with low permeability at the frost line, which inhibits the drainage of snowmelt and precipitation. Frozen soil layers and perched springtime water tables prevent oxygen from reaching deeper soil layers, and our data show that respiration rates respond directly to these conditions (Fig. 4). The interaction between soil thaw and water table depth in poorly drained areas is a key factor in controlling whole-forest respiration rates observed at the eddy-covariance tower at seasonal time scales.

Our results from the Sphagnum veneer bog also suggest that these interactions are important on longer timescales, and that water table depths in the bog appear to be influenced by the preceding year. In all years for which we have data, the position of the water table once thaw was complete appeared to be correlated with the previous year’s position at freeze-up (Fig. 5). The water tables at the veneer bog reflect the ecosystem’s overall water balance, with a net rise in water table over the course of a wet summer (2002, Fig. 5) and a net fall in water table in a dry summer (2003, Fig. 5). As the veneer bog lies in a topographical low underlain by clay, it likely experiences very little runoff (H. Veldhuis, personal communication), allowing water table depth to reflect the time-integrated water balance.

**Table 1** Annual net ecosystem exchange (NEE), gross ecosystem exchange (GEE), and ecosystem respiration ($R$) at BOREAS–NOBS (g C m$^{-2}$ yr$^{-1}$), length of growing season (LGS), mean summer (DOY 150–250) night-time and daytime, and mean January fluxes (μmol m$^{-2}$ s$^{-1}$)

| Year | NEE  | 95% CI | GEE  | $R$  | LGS | $F_{\text{CO}_2}$ summer night | $F_{\text{CO}_2}$ summer day | $F_{\text{CO}_2}$ January |
|------|------|--------|------|------|-----|-------------------------------|-----------------------------|---------------------------|
| 1995 | 41   | 31, 45 | −782 | 826  | 173 | 4.6                           | −2.7                        | 0.22                      |
| 1996 | 84   | 76, 89 | −706 | 795  | 159 | 4.0                           | −2.9                        | 0.19                      |
| 1997 | −7   | −14, 2 | −773 | 768  | 194 | 4.3                           | −2.4                        | 0.19                      |
| 1998 | −7   | −13, 1 | −746 | 746  | 183 | 3.7                           | −2.8                        | 0.19                      |
| 2000 | −3   | −5, 8  | −693 | 705  | 186 | 3.1                           | −2.6                        | 0.20                      |
| 2001 | −23  | −31, −16 | −728 | 707  | 184 | 3.4                           | −2.8                        | 0.24                      |
| 2002 | −27  | −35, −19 | −610 | 586  | 153 | 3.0                           | −3.1                        | 0.31                      |
| 2003 | −58  | −68, −53 | −698 | 640  | 191 | 3.5                           | −2.7                        | 0.36                      |
| 2004 | −21  | −28, −19 | −622 | 611  | 151 | 2.4                           | −3.2                        | 0.23                      |

Confidence intervals were estimated by first determining an error distribution for each half-hour, consisting of: (1) instrumentation error calculated via daily difference method of Hollinger & Richardson (2005) and Richardson et al. (2006), (2) error associated with the model fit for $R$/GEE, and (3) error associated with filling $T$ and PAR during gaps. These error distributions were used to generate different 500 simulations of the NEE time series, from which confidence intervals were bootstrapped. The confidence intervals vary between the years due to distribution of gaps in different years.

BOREAS, Boreal Ecosystem-Atmosphere Study; NOBS, Northern Old Black Spruce.

© 2007 The Authors

Journal compilation © 2007 Blackwell Publishing Ltd, Global Change Biology, 13, 577–590
Fig. 4 Measured respiration and respiration modeled as a function of soil temperature and depth to water table during summer 2002, 2003, and 2004.

Fig. 5 Interannual variability in water table depth is affected by final position of water table in the preceding year. Thaw times were determined via soil temperature at 20 cm (soil temperature measurement closest to zone of active water table movement); freeze times were defined as last valid measurement of water table before transition to ice. Note changes in water table depth due to wet (2002) and dry (2003) summers. Dashed lines (-----) during the frozen and spring thaws periods are included as visual aids.
January efflux (Table 1), possibly due to warmer soil temperatures during the latter part of the study period. We observed no trend in growing season daytime CO₂ flux. Likewise, we observed no trend in annual energy budget closure, suggesting that the trends observed in CO₂ flux do not reflect instrumentation or calculation error. There were significant trends toward decreased respiration (P < 0.001, respectively). There was nearly 50% more RNE, but increased annual NEE, suggesting that more of the variability in NEE is attributable to photosynthesis rather than GEE, as observed by Bubier et al. (2003b) using chambers in a mid-latitude bog. There was no relationship between annual GEE and NEE, but increased annual R was significantly (P = 0.01) correlated with increased NEE (less uptake).

We investigated the influence of mean annual air temperature, precipitation, PAR, and potential evapotranspiration (PET) on annual carbon balance using three different annual bases: calendar year, April 1–March 31, and November 1–October 31. No significant difference in controlling variables was observed between the annual bases, so our analysis is reported according to calendar year carbon exchange. We determined PET via the simplified Penman–Monteith equation of Hogg (1997), calculating each year from the previous September through current August in order to capture the time period most relevant to growing season water balance. Warmer annual temperatures were associated with increased net uptake (53% of the variance, P = 0.02), but had no significant association with annual R nor GEE. PET was associated with enhanced photosynthesis (44% of the variance, P = 0.04). Annual precipitation did not explain any of the variability in NEE, R, or GEE.

We tested for longer-term effects of water balance on carbon exchange as the results given above show that water table depth at the veneer bog in the tower’s footprint provided an important control on whole-forest respiration rates, and depended on climate in previous years. Hogg (1997) defined a climate moisture index (CMI)

\[
\text{CMI} = \text{precipitation} - \text{PET}
\]

to estimate the availability of water in excess of evaporative demand. We calculated CMI on a monthly basis, and determined annual CMI from the previous September through the current August. We then created a variety of lagged indices (CMI1, CMI2, CMI3, CMI4) consisting of the mean CMI for the previous 1, 2, 3, or 4 years to test for longer-term moisture effects on carbon exchange (current year is excluded). We found significant negative correlations between CMI2, CMI3, and CMI4 and annual NEE, supporting the view that abundant moisture enhances net carbon uptake. CMI3 was particularly well correlated with NEE, accounting for 66% of the variance (P = 0.005). Annual values for NEE, T anomalies, and CMI3 anomalies are shown in Fig. 7.

When combined with other climatic variables, the role of these lagged indices in explaining interannual variability was striking. CMI3 (representing past years) and PET (current year) explained 75% of the interannual variability in NEE (P = 0.008; Table 2). A similar relationship was observed in R, with high values of CMI3 decreasing R and high values of PET increasing R. For GEE, high values of CMI3 were associated with increased GEE (less photosynthesis) and increased PET with decreased GEE (more photosynthesis). These results suggest that the effects of precipitation anomalies on carbon exchange may only be evident after several years of drought or wetness, as the water table at NOBS integrates the water balance over several years. The strong autocorrelations of annual NEE and R time series (1-year lagged autoregression coefficients were 0.7 and 0.45, respectively) also indicate that processes with long timescales are important. Our results are consistent with Arneth et al. (2002), Bubier et al. (2003a,b), and Alm et al. (1999), all of who found that dry conditions increased NEE by enhancing R in peat bogs.

Myneni et al. (1997) reported progressively earlier onset, and longer duration, of the growing season in

![Fig. 6 Cumulative carbon balance at Northern Old Black Spruce.](image)

Table 2 Results of regressions between annual carbon exchange, 3-year lagged climate moisture index (CMI3), and current year potential evapotranspiration (PET)
northern high latitudes between 1981 and 1991, based on satellite observations of NDVI and CO₂ concentration data. White et al. (2000) and Berthelot et al. (2002) predicted that increases in growing season length would translate into a marked decrease in NEE (more uptake) in boreal regions. We tested this hypothesis by investigating the influence of OGS, EGS, and LGS on the annual carbon budget at NOBS. In contrast to expectations, years with earlier OGS (1998, 1999) were not associated with decreased NEE (i.e., annual uptake of CO₂ was not enhanced), and neither NEE nor R responded directly to LGS. Longer growing seasons did enhance photosynthesis (38% of the variance, \( P = 0.06 \)), but this did not translate into greater net uptake in years with earlier OGS. R may also have been enhanced by LGS when taken into conjunction with CML3 (\( P = 0.04 \) for LGS). As factors controlling R, such as soil thaw and drainage, may be as sensitive to LGS as is GEE, we are not surprised that LGS has little effect on annual net carbon balance.

The NOBS results must also be considered in light of their regional context, especially because Picea forests are the most widely occurring forest type in the North American boreal forest biome (39%, Black et al., 2004). Temperatures in Canada south of 60°N have warmed 0.5–1.5 °C during the 20th century, and precipitation has increased by 5–35% in the same time period (Zhang et al., 2000; Gillett et al., 2004). The close correspondence between climate at NOBS and local climate stations (Fig. 1) suggests that our results are representative of processes occurring at other mature black spruce forests in the region. The portion of the growing season favorable to heterotrophic respiration is currently limited at NOBS due to slow thaw and drainage of the soil column, causing the seasonal cycle of R to lag that of GEE. Atmospheric CO₂ concentrations across boreal regions are closely linked to the timing of these two offsetting processes, so proper representation of this cycle is clearly essential for inverse models using observed CO₂ concentrations, and for assessment of long-term carbon balances.

**Discussion**

The annual carbon budget of the site has changed over the last 10 years in a manner that cannot be fully explained by the prompt responses of plant and ecosystem physiology to weather. The longer-term ecosystem water balance, and particularly the depth of the water table, are clearly important, and may explain much of the observed interannual variability and trend. Factors such as ecosystem water balance operate on timescales longer than most physiological and ecological studies, and, as a result, are poorly described and understood. Nonetheless, these factors may have key implications for ecosystem resistance and resilience in the face of changes in climate or climate variability.

There is a long-term trend of increasing annual temperature in the region (Fig. 1), which was particularly pronounced during the middle part of the study period (Fig. 7, second panel), and was unexpectedly correlated with increased net carbon uptake. Warming during the decade of observations provided an excellent opportunity to test ideas about ecosystem response to projected future climatic warming. Most interactive vegetation–climate models represent respiration as a strongly increasing function of temperature, with photosynthesis assumed a function of light, subject to limitations due to temperature, LGS, and availability of water and nutrients. The results from NOBS show that these simplified functional representations are incomplete in the case of boreal peatlands, particularly with respect to ecosystem respiration.

Our results show that while temperature and LGS exerted important controls on photosynthesis, respiration rates were influenced by both temperature and seasonal and interannual patterns of ecosystem water availability. No increase in ecosystem respiration was observed during the mid–late years of the study, which experienced warmer temperatures than the 30-year mean (Fig. 7, middle panel). Instead, a trend toward decreased respiration was observed in the night-time CO₂ fluxes from the summer (Table 1), which have showed a significant (\( P = 0.03 \)) decline since the start of the study, and in the annual R sums (Table 1). While wintertime CO₂ fluxes have increased during the study period (Table 1), perhaps as a result of warmer temperatures, wintertime effluxes are low when compared with summertime respiration.

The observed decrease in overall respiration is a direct consequence of the increase in water availability in the growing season during this time period: CML3 values, on average, increased over the study period (Fig. 7, panel 3), indicating a shift in the overall water balance from a deficit to a surplus. Before 1997, the region experienced nearly 10 years of below-average rainfall (Fig. 1), CML3 values were low, and 1995 and 1996 were the years of largest R at our site. In comparison, the two dry years of 2003–2004 followed several years of above average or average rainfall, CML3 values were average to high, and R rates remained low. Our results thus suggest that several consecutive years of drought or water surplus have a greater impact on respiration rates than one or two anomalous years in isolation, reflecting long-term shifts in regional water tables.

The net result is that the NEE of the forest has decreased under this warmer, wetter regime, turning
it from a modest source into a weak sink for atmospheric CO₂. As depth of the water table appears to be an important factor, the warmer–wetter regime may also lead to reduced losses of peat in a fire.

There are several factors that contribute to the retention of water in these soils, with important implications for decomposition of organic matter. Low-permeability glaciolacustrine clays, exposed only 8000 years ago at the retreat of Lake Agassiz, underlie much of Manitoba, western Ontario, and central Saskatchewan, and drainage in the region is poorly developed (Veldhuis et al., 2002). As a result of this poor drainage, water tables in our veneer bog exhibit a notable carryover effect, whereby water table depth at the end of one growing season strongly influence water table depth early in the next summer, after soil thaw is complete. The poor drainage and cold temperatures in the soils inhibit breakdown of organic matter, favoring the development of deep organic soils. The presence of a distinct frost line in the soil for much of the early growing season limits infiltration of snowmelt and precipitation in the wettest parts of the tower’s footprint, which also contain the largest soil organic carbon stores. As a result, early- and mid-summer water tables in the wetland areas are kept higher than they would be in the absence of a frost line, especially when enhanced by early-season precipitation.

The role of soil moisture in depressing respiration rates is seen at all time scales, from instantaneous (depth to water table explains 15% of the daily variance in R in for DOY 150–250 of 2002–2004) to interannual, providing a rationale for why the multiyear climate moisture index, in combination with the year’s evaporative demand, explains 87% of the interannual variability in R. The significance of precipitation, evaporative demand, and depth to water table reflects the central importance of the seasonal soil freeze–thaw cycle and associated hydrologic variations in controlling annual carbon exchange. Our findings illustrate that soil water balance may be as critical as temperature in controlling the long-term carbon balance in boreal forests underlain by peat, and must be factored into predictions of ecosystem response to future climate. Carbon balance in these areas is very sensitive to water table depth, and small fluctuations in its position may be enough to shift the net carbon balance to a source or sink.

The strong influence of slowly changing parameters, such as water balance, reminds us that boreal systems tend to change slowly, and that observations to assess long-term factors are critical for understanding climate–carbon cycle interactions in this biome. A warmer climate may lead to release of CO₂ from deep organic soils in the boreal region if they became drier, but if the climate were also wetter than the long-term mean, these soils could continue to accumulate organic matter. It is, therefore, critical to properly represent soil hydrologic processes, rainfall, and soil thaw in order to predict the response to changing climate of the extensive black spruce-Sphagnum wetland biome of North America.
Acknowledgements

This work was supported by the US National Aeronautics and Space Administration (NAG5-11154, NAG5-7534, NAG5-2253) and by a NASA Earth System Science Fellowship (A. Dunn, R-ESSF/03-0000-0092). We especially thank Alfram Bright, John Budney, Lucy Hutyr, Christine Jones, Bill Munger, Leo Grenier, Bert Lesley, and Ted Hogg.

References

Alm J, Schulman L, Walden J et al. (1999) Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology, 80, 161–174.

Arness A, Kurbatova J, Kolle O et al. (2002) Comparative ecosystem-atmosphere exchange of energy and mass in a European Russian and a central Siberian bog II: seasonal and interannual variability of CO2 fluxes. Tellus, 54B, 514–530.

Baldocchi DD, Vogel CA, Hall B (1997) Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agricultural and Forest Meteorology, 83, 147–170.

Barber VA, Juday GP, Finney BP (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature, 405, 668–673.

Barr AG, Griffis TJ, Black TA et al. (2002) Comparing the carbon budgets of boreal and temperate deciduous forest stands. Canadian Journal of Forest Research, 32, 813–822.

Bergh J, Linder S (1999) Effects of soil warming during spring on photosynthetic recovery in boreal Norway spruce stands. Global Change Biology, 5, 245–253.

Berthelot M, Friedlingstein P, Ciais P et al. (2002) Global response of the terrestrial biosphere to CO2 and climate change using a coupled climate-carbon cycle model. Global Biogeochemical Cycles, 16, 1084.

Black TA, Chen WJ, Barr AG et al. (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. Geophysical Research Letters, 27, 1271–1274.

Black TA, Gaumont-Guay D, Jassal RS et al. (2004) Carbon balance research in boreal biomes. In: Carbon Balance of Forest Ecosystems (eds Griffiths H, Jarvis Pj), Garland Science/Taylor & Francis, Abingdon, UK.

Bubier JL, Bhatia G, Moore TR et al. (2003a) Spatial and temporal variability in growing-season net ecosystem carbon dioxide exchange at a large peatland in Ontario, Canada. Ecosystems, 6, 353–367.

Bubier JL, Crill PM, Moore TR et al. (1998) Seasonal patterns and controls on net ecosystem CO2 exchange in a boreal peatland complex. Global Biogeochemical Cycles, 12, 703–714.

Bubier J, Crill P, Mosedale A et al. (2003b) Peatland responses to varying interannual moisture conditions as measured by automatic CO2 chambers. Global Biogeochemical Cycles, 17, 1066, doi: 10.1029/2002GB001946.

Clark JS (1988) Effect of climate change on fire regimes in northwestern Minnesota. Nature, 334, 233–235.

Clymo RS (1984) The limits to peat bog growth. Philosophical Transactions of the Royal Society of London B, 303, 605–654.

Clymo RS, Pearce DME (1995) Methane and carbon dioxide production in, transport through, and efflux from a peatland. Philosophical Transactions of the Royal Society of London A, 350, 249–259.

D’Arrigo RD, Kaufmann RK, Davi N et al. (2004) Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. Global Biogeochemical Cycles, 18, 3021, doi: 10.1029/2004GB002249.

Falge E, Baldocchi D, Olson R et al. (2001) Gap filling strategies for defensible annual sums of NEE. Agricultural and Forest Meteorology, 107, 43–69.

Flannigan MD, Van Wagner CE (1991) Climate change and wildfire in Canada. Canadian Journal of Forest Research, 21, 66–72.

Funk DW, Pullman ER, Peterson KM et al. (1994) Influence of water table on carbon dioxide, carbon monoxide, and methane fluxes from taiga bog microcosms. Global Biogeochemical Cycles, 8, 271–278.

Gillett NP, Weaver AJ, Zwiers FW et al. (2004) Detecting the effect of climate change on Canadian forest fires. Geophysical Research Letters, 31, 18211, doi: 10.1029/2004GL020876.

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecological Applications, 1, 182–195.

Goulden ML, Daube BC, Fan S-M et al. (1997) Physiological responses of a black spruce forest to weather. Journal of Geophysical Research, 102, 28987–28996.

Goulden ML, Munger JW, Fan S-M et al. (1996a) Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science, 271, 1576–1578.

Goulden ML, Munger JW, Fan S-M et al. (1996b) Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. Global Change Biology, 2, 169–182.

Goulden ML, Wofsy SC, Harden JW et al. (1998) Sensitivity of boreal forest carbon balance to soil thaw. Science, 279, 214–217.

Gower ST, Vogel JG, Norman JM et al. (1997) Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. Journal of Geophysical Research, 102, 29029–29041.

Griffis TJ, Black TA, Morgenstern K et al. (2003) Ecophysiological controls on the carbon balance of three southern boreal forests. Agricultural and Forest Meteorology, 117, 53–71.

Harden JW, O’Neill KP, Trumbore SE et al. (1997) Moss and soil contributions to the annual net carbon flux of a maturing boreal forest. Journal of Geophysical Research, 102, 28805–28816.

Harden JW, Sundquist ET, Stallard RF et al. (1992) Dynamics of soil carbon during deglaciation of the Laurentide ice sheet. Science, 258, 1921–1924.

Hobbs SE, Schimel JP, Trumbore SE et al. (2000) Controls over carbon storage and turnover in high-latitude soils. Global Change Biology, 6 (Suppl. 1), 196–210.

Hogg EH (1997) Temporal scaling of moisture and the forest-grassland boundary in western Canada. Agricultural and Forest Meteorology, 84, 115–122.

Hollinger DY, Richardson AD (2005) Uncertainty in eddy covariance measurements and its application to physiological models. Tree Physiology, 25, 873–885.

IPCC (2001) Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Inter-
