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

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## 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<sup>-2</sup>, 1995) to a sink (–21 g C m<sup>-2</sup>, 2004) of CO<sub>2</sub> over the decade, with an average net carbon balance near zero. Annual mean temperatures increased 1–2° 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

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## 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 CO<sub>2</sub>; 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

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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 (Hobbie *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<sup>-2</sup> yr<sup>-1</sup> 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 spring-time onset of photosynthesis in deciduous and coniferous boreal forests is controlled by air and soil temperature (Bergh & 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).

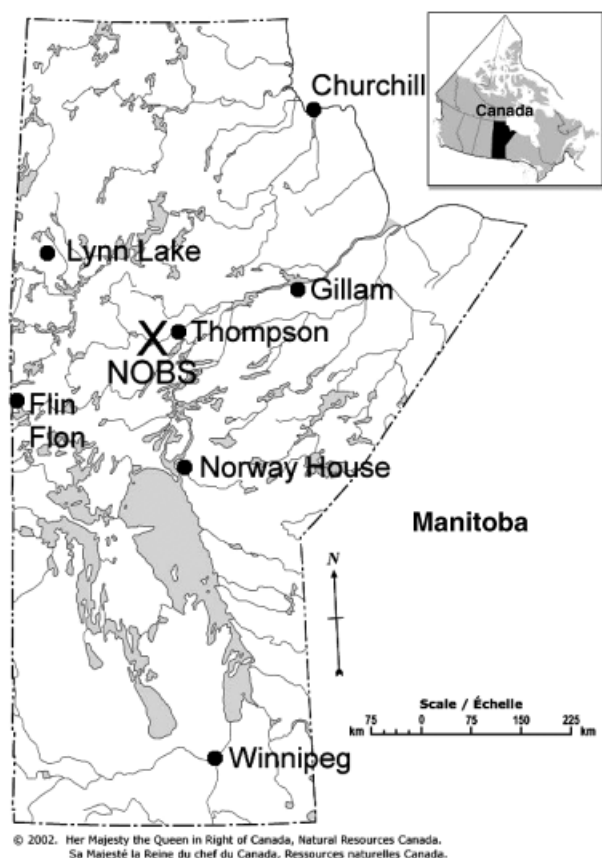
In this paper, we investigate the response of an old (~160 year) boreal black spruce forest (the most widely occurring forest type in the boreal region of North America, O'Connell *et al.*, 2003a) to environmental forcing on instantaneous, seasonal, annual, and inter-annual timescales. We present the long-term record (1994–2004) of eddy-covariance measurements of CO<sub>2</sub> 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<sub>2</sub>, 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.

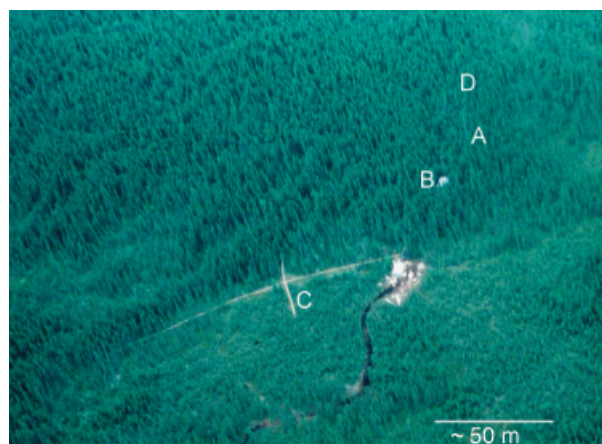
The vegetation at the site consists of regrowth since the last fire, dominated by 160-year-old black spruce trees (*Picea Mariana* (Mill.), Gower *et al.*, 1997); the stand age reported here represents a correction from that of Goulden *et al.* (1997), based on tree-ring data. The average stem density is 5450 trees ha<sup>-1</sup>, with a basal area of 35.6 m<sup>2</sup> ha<sup>-1</sup>, sapwood volume of 82.5 m<sup>3</sup> ha<sup>-1</sup>, 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



**Map 1** Manitoba, Canada, showing the location of the Boreal Ecosystem-Atmosphere Study-Northern Old Black Spruce site (X, 55.88°N, 98.48°W).

(*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



**Plate 1** Northern Old Black Spruce site, including: (A) 30 m instrument tower, (B) instrument hut, (C) *Sphagnum* bog study area, (D) upland feathermoss study area. Note the heterogeneity in the tower's footprint; scale is approximate due to oblique angle of photo.

of soil carbon ( $13 \text{ kg C m}^{-2}$ , 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 ( $25 \text{ kg C m}^{-2}$ , 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  $0.51 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  and topographically lower areas producing between  $0.14$  and  $2.83 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  (Moosavi & Crill, 1997), but  $\text{CH}_4$  is a relatively small component of the carbon budget ( $< 10 \text{ g C m}^{-2} \text{ yr}^{-1}$ ).

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 CO<sub>2</sub> and H<sub>2</sub>O were measured by sampling 20 standard L min<sup>-1</sup> at 29 m through a 50-m-long, 0.64-cm inner diameter Teflon PFA tube. A subsample of 4 standard L min<sup>-1</sup> was drawn through a short piece of tubing into a CO<sub>2</sub>/H<sub>2</sub>O 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% CO<sub>2</sub> at 40 and 80 standard mL min<sup>-1</sup>. The IRGA zero was measured every 3 hours by drawing sample air through a CO<sub>2</sub> scrubber (soda lime) and desiccant (Mg(ClO<sub>4</sub>)<sub>2</sub>).

Measurements of the mixing ratio of CO<sub>2</sub> and H<sub>2</sub>O 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 CO<sub>2</sub> 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 CO<sub>2</sub> concentration below 28.8 m (canopy storage of CO<sub>2</sub>). 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 CO<sub>2</sub> fluxes via the modified Bowen ratio method (Meyers *et al.*, 1996; Liu & Foken, 2001).

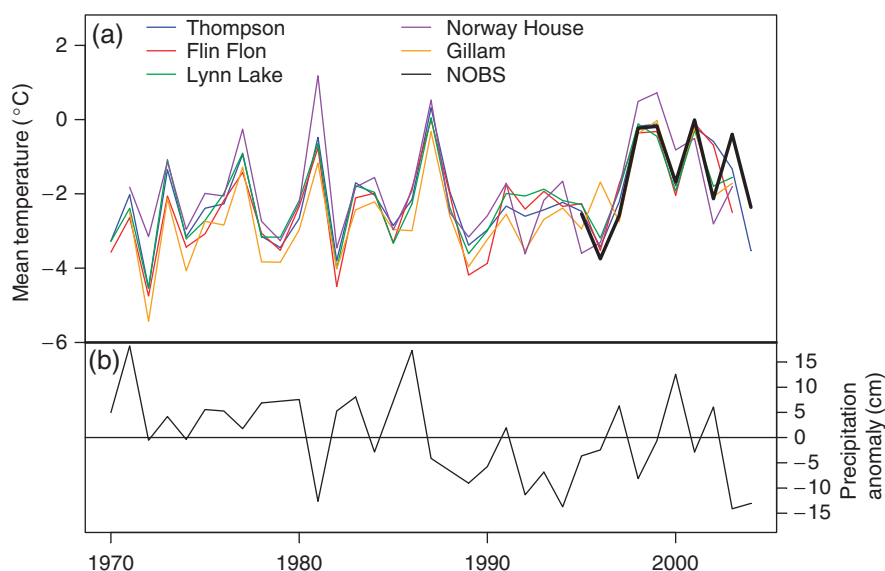
### Analysis

The eddy-covariance technique was used to calculate the turbulent fluxes of sensible heat, latent heat, CO<sub>2</sub>,

and momentum at 29 m. CO<sub>2</sub> flux was calculated as the 30 min covariance of the vertical wind velocity ( $w'$ ) and CO<sub>2</sub> mixing ratio ( $c'$ ). The time lag was determined by maximizing the correlation between  $w'$  and  $c'$ . Fluxes were rotated to the plane in which mean vertical wind speed was zero (McMillen, 1988). The CO<sub>2</sub> 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 CO<sub>2</sub> to the time derivative of the column storage of CO<sub>2</sub> 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 CO<sub>2</sub> flux and canopy storage of CO<sub>2</sub> 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 ( $\sigma_{T_{\text{sonic}}} > 1^\circ$ ). The concentration from the flux IRGA was compared with that of the profile IRGA at 29 m and CO<sub>2</sub> 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 ( $u^* > 0.2 \text{ m s}^{-1}$ ; 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



**Fig. 1** (a) Regional temperature trend, adjusted to Northern Old Black Spruce mean. (b) Precipitation anomaly at Thompson airport relative to 1970–2004 mean.

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  $-10^{\circ}\text{C}$  were assumed to correspond with zero photosynthesis, and all NEE measurements, therefore, represented respiratory fluxes.

GEE was determined as the difference between measured NEE and derived respiration during daytime periods when  $T > -10^{\circ}$  and  $u^* > 0.2 \text{ m s}^{-1}$ :

$$\text{GEE} = \text{NEE} - R. \quad (1a)$$

Note that uptake of  $\text{CO}_2$  from the atmosphere corresponds to  $\text{NEE} < 0$ . To obtain a continuous record of daytime GEE, the data were divided into periods of 150 good GEE observations and tested for linear or quadratic 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

$$\text{GEE} = A + B \times \text{PAR}/(C + \text{PAR}). \quad (1b)$$

Otherwise, a linear least squares fit was used to determine 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 temperature from the Thompson airport weather station, 40 km to the east, for which there is excellent correspondence 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 temperature 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

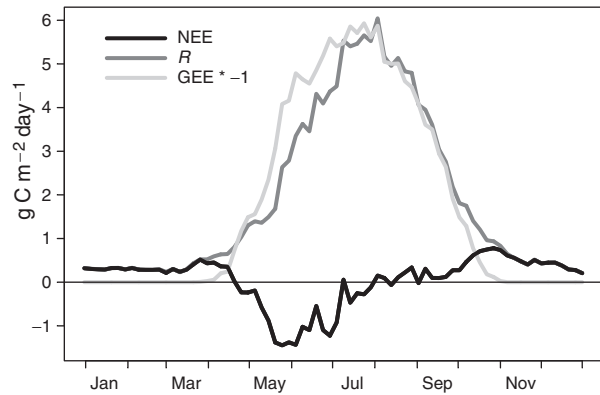
### *Climate at NOBS and the surrounding region*

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

anomalously cold (compared with the 1971–2000 mean of  $-3.2^{\circ}\text{C}$ ) 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  $-3.2^{\circ}\text{C}$ , while 5 of the 7 years from 1998 to 2004 were warmer than the long-term average, with four warmer than  $-1^{\circ}\text{C}$ . 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  $60^{\circ}\text{N}$ . During the 20th century, mean annual temperatures and precipitation increased, by  $0.5$ – $1.5^{\circ}\text{C}$  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  $27.9\text{ kg C m}^{-2}$ ; Trumbore & Harden, 1997). The area within a 500 m radius of the tower is approximately 25% well drained, 50% imperfect 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  $u^* > 0.2\text{ m s}^{-1}$  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



**Fig. 2** Mean annual cycle of net ecosystem exchange,  $R$ , and gross ecosystem exchange (GEE), averaged on 5-day intervals. Note the lag of the  $R$ -curve, peaking a month later than GEE.

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  $12^{\circ}$  to the south (Goulden *et al.*, 1996a). On average the forest has the greatest net uptake of atmospheric  $\text{CO}_2$  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  $\text{CO}_2$  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  $\text{CO}_2$  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,

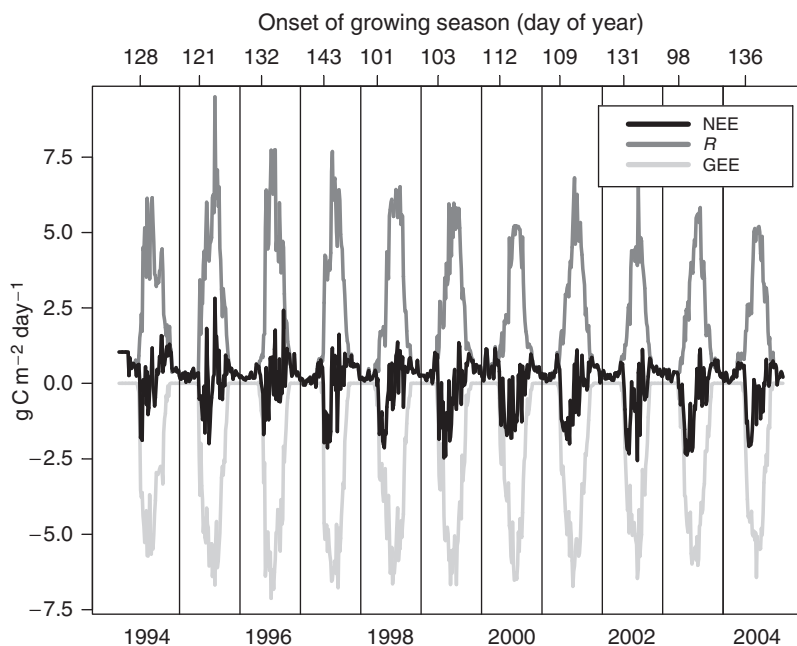


Fig. 3 Carbon exchange averaged on 5-day intervals.

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 CO<sub>2</sub> 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; Schreuder *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 CO<sub>2</sub> 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:

$$R_{\text{predicted}} = 0.0877 \times WT_{\text{depth, bog}} + 0.583 \\ \times T_{\text{soil, 20 cm}} - 0.0106 \times WT_{\text{depth, bog}} \\ \times T_{\text{soil, 20 cm}} - 1.36, \quad (2)$$



where  $R_{\text{predicted}}$  (for the whole ecosystem) is in  $\text{g C m}^{-2} \text{ day}^{-1}$ , and  $WT_{\text{depth, bog}}$  and  $T_{\text{soil, 20 cm}}$  are in cm to water table and  $^{\circ}\text{C}$ , respectively. Based on this relationship, a 2 cm drop in water table depth integrated over the 100 days translates into  $\sim 18 \text{ g C m}^{-2}$  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 ( $30\text{--}130 \text{ g C m}^{-2} \text{ yr}^{-1}$ , 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.

#### *Interannual variability: trends and drivers*

NOBS unexpectedly switched from a modest net annual source to a small annual sink for atmospheric  $\text{CO}_2$  between 1994 and 2004 (Table 1; Fig. 6). There was a significant ( $P = 0.03$ ) trend toward decreased night-time efflux in the summer, likely driving the decreasing  $R$  observed over the study period (Table 1). There was also a significant ( $P = 0.04$ ) trend toward increased

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

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	39	32, 46	–698	743	146	4.2	–3.0	0.18
1998	–7	–14, 2	–773	768	194	4.3	–2.4	0.19
1999	–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.

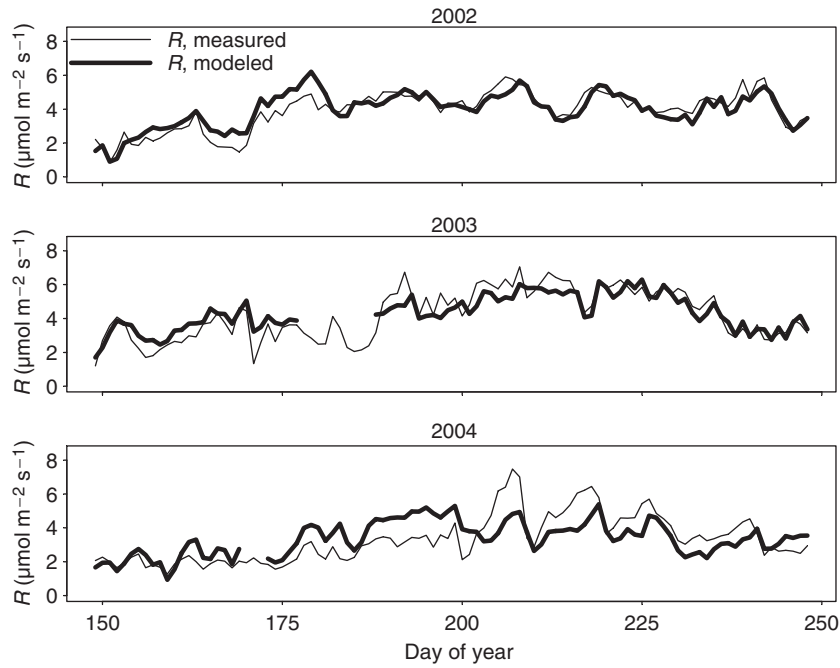


Fig. 4 Measured respiration and respiration modeled as a function of soil temperature and depth to water table during summer 2002, 2003, and 2004.

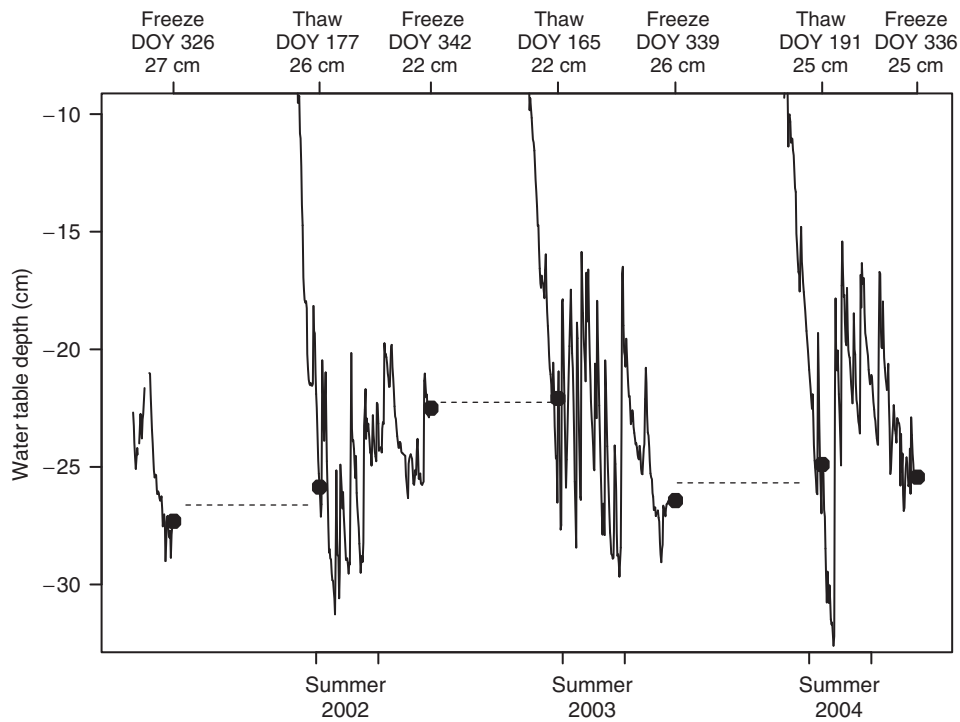


Fig. 5 Interannual variability in water table depth is affected by final position of water table in the preceding year. Thaw times were determined via soil temperature at 20 cm (soil temperature measurement closest to zone of active water table movement); freeze times were defined as last valid measurement 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.

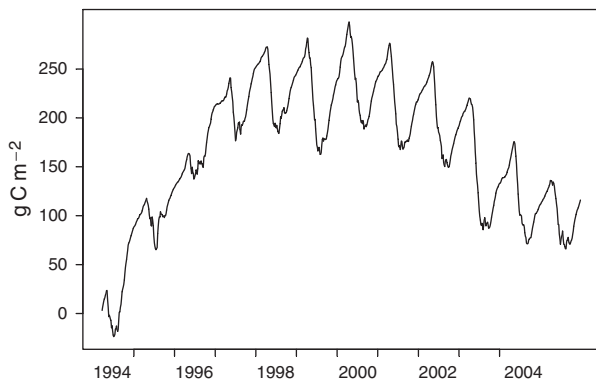


Fig. 6 Cumulative carbon balance at Northern Old Black Spruce.

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 CO<sub>2</sub> flux. Likewise, we observed no trend in annual energy budget closure, suggesting that the trends observed in CO<sub>2</sub> flux do not reflect instrumentation or calculation error. There were significant trends toward decreased annual NEE (more uptake) and respiration ( $P = 0.002$  and  $0.0001$ , respectively). There was nearly 50% more interannual variability in respiration than photosynthesis, suggesting that more of the variability in NEE is attributable to  $R$  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)

$$\text{CMI} = \text{precipitation} - \text{PET} \quad (3)$$

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 (CMI.1, CMI.2, CMI.3, CMI.4) 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 CMI.2, CMI.3, and CMI.4 and annual NEE, supporting the view that abundant moisture enhances net carbon uptake. CMI.3 was particularly well correlated with NEE, accounting for 66% of the variance ( $P = 0.005$ ). Annual values for NEE, T anomalies, and CMI.3 anomalies are shown in Fig. 7.

When combined with other climatic variables, the role of these lagged indices in explaining interannual variability was striking. CMI.3 (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 CMI.3 decreasing  $R$  and high values of PET increasing  $R$ . For GEE, high values of CMI.3 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 Arneeth *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

**Table 2** Results of regressions between annual carbon exchange, 3-year lagged climate moisture index (CMI.3), and current year potential evapotranspiration (PET)

	CMI.3 coefficient	PET coefficient	$R^2$	$P$
NEE	-9.5	0.4	0.75	0.008
$R$	-18.4	2.0	0.87	0.0008
GEE	8.7	-1.6	0.77	0.006

northern high latitudes between 1981 and 1991, based on satellite observations of NDVI and CO<sub>2</sub> 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 CO<sub>2</sub> 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 CMI.3 ( $P = 0.04$  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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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 CO<sub>2</sub> 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: CMI.3 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), CMI.3 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, CMI.3 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

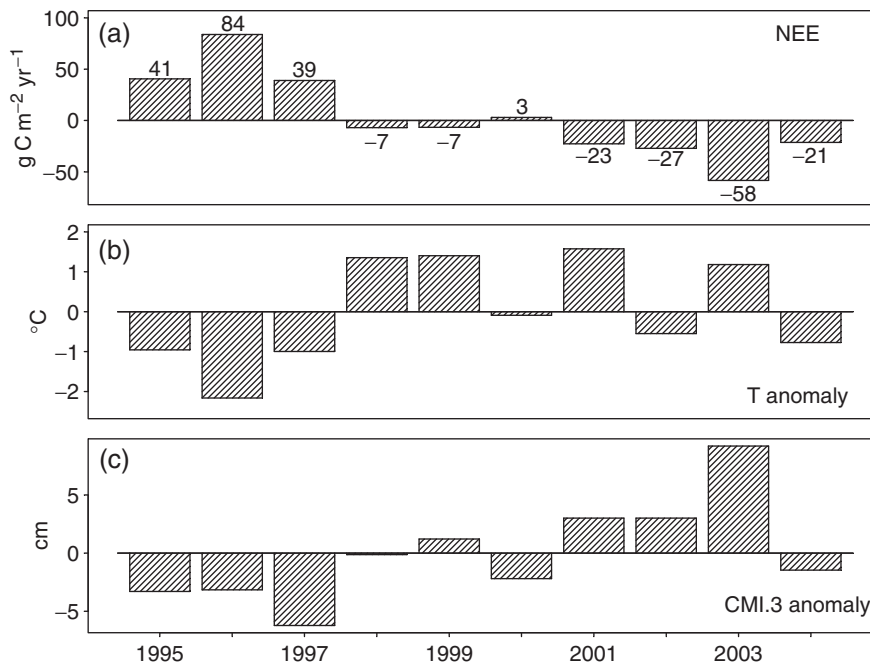


Fig. 7 Comparison with (a) net ecosystem exchange, (b) temperature anomaly, (c) 3-year lagged climate moisture index anomaly.

it from a modest source into a weak sink for atmospheric CO<sub>2</sub>. 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 CO<sub>2</sub> 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.

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