

# Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest

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## Abstract

To evaluate the carbon budget of a boreal deciduous forest, we measured CO<sub>2</sub> fluxes using the eddy covariance technique above an old aspen (OA) forest in Prince Albert National Park, Saskatchewan, Canada, in 1994 and 1996 as part of the Boreal Ecosystem-Atmosphere Study (BOREAS). We found that the OA forest is a strong carbon sink sequestering  $200 \pm 30$  and  $130 \pm 30$  g C m<sup>-2</sup> y<sup>-1</sup> in 1994 and 1996, respectively. These measurements were 16–45% lower than an inventory result that the mean carbon increment was about 240 g C m<sup>-2</sup> y<sup>-1</sup> between 1919 and 1994, mainly due to the advanced age of the stand at the time of eddy covariance measurements. Assuming these rates to be representative of Canadian boreal deciduous forests (area  $\approx 3 \times 10^5$  km<sup>2</sup>), it is likely they can sequester 40–60 Tg C y<sup>-1</sup>, which is 2–3% of the missing global carbon sink.

The difference in carbon sequestration by the OA forest between 1994 and 1996 was mainly caused by the difference in leaf emergence date. The monthly mean air temperature during March–May 1994, was 4.8 °C higher than in 1996, resulting in leaf emergence being 18–24 days earlier in 1994 than 1996. The warm spring and early leaf emergence in 1994 enabled the aspen forest to exploit the long days and high solar irradiance of mid-to-late spring. In contrast, the 1996 OA growing season included only 32 days before the summer solstice. The earlier leaf emergence in 1994 resulted 16% more absorbed photosynthetically active radiation and a 90 g C m<sup>-2</sup> y<sup>-1</sup> increase in photosynthesis than 1996. The concomitant increase in respiration in the warmer year (1994) was only 20 g C m<sup>-2</sup> y<sup>-1</sup>. These results show that an important control on carbon sequestration by boreal deciduous forests is spring temperature, via the influence of air temperature on the timing of leaf emergence.

**Keywords:** boreal aspen forest, BOREAS, carbon sequestration, climatic variability, eddy covariance, photosynthesis, respiration

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## Introduction

Atmospheric CO<sub>2</sub> concentration increased from 290 to 358 ppmv from the 1880s to 1994 (Keeling *et al.* 1989; Schimel *et al.* 1996) accompanied by a mean global increase in near-surface air temperature of 0.7–0.8 °C (Hansen & Lebedeff 1987; Nicholls *et al.* 1996). The increase in atmospheric CO<sub>2</sub> concentration has been

mainly caused by fossil fuel emissions and land use changes in the tropics. In the 1980s, these sources amounted to  $\approx 7.1$  Pg C y<sup>-1</sup> (1 Pg = 10<sup>15</sup>g), of which  $\approx 3.2$  and  $\approx 2.0$  Pg C y<sup>-1</sup> accumulated in the atmosphere and ocean, respectively (Schimel *et al.* 1996). The fate of the remaining 1.9 Pg C y<sup>-1</sup>, often called the missing carbon sink, is not well known.

Many researchers have suggested that this sink might be found in undisturbed terrestrial ecosystems in which carbon sequestration has increased as a result of increasing atmospheric CO<sub>2</sub> concentration (i.e. CO<sub>2</sub> fertilization) and nutrients in soils (e.g. Houghton 1995).

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The CO<sub>2</sub> fertilization effect has been estimated to be 0.5–2.0 Pg C y<sup>-1</sup> for the 1980s, and the nitrogen fertilization effect to be 0.5–1 Pg C y<sup>-1</sup> (Melillo *et al.* 1996). While terrestrial ecosystems in lower latitude areas are releasing carbon because of deforestation (Lal *et al.* 1995), northern ecosystems (arctic tundra, boreal forest and northern bogs) have been net sinks for carbon (Post 1990) in the historic and recent geological past. Tans *et al.* (1990) hypothesized that the present-day strength of these carbon sinks is about 1–2 Pg C y<sup>-1</sup>. Using  $\delta^{13}\text{C}$  measurements in atmospheric CO<sub>2</sub> from a global air sampling network, Ciais *et al.* (1995) found that northern temperate and boreal ecosystems between 35° and 65°N were a major carbon sink of  $3.5 \pm 1.0$  Pg C y<sup>-1</sup> in 1992. Recent measurements of CO<sub>2</sub> flux in Alaska, however, indicate that tussock and wet sedge tundra are now sources of CO<sub>2</sub> to the atmosphere (Oechel *et al.* 1993). Boreal evergreen conifer forests in central Sweden and in Manitoba, Canada have also been found to be weak sources of CO<sub>2</sub> to the atmosphere based on multiyear continuous CO<sub>2</sub> eddy flux measurements (Lindroth *et al.* 1997; Goulden *et al.* 1998).

To find out the current state of CO<sub>2</sub> exchange between boreal deciduous forests and the atmosphere, we measured the CO<sub>2</sub> eddy flux above mature aspen forest in Prince Albert National Park, Saskatchewan, in 1994 and 1996. This experiment was a part of the large scale, international Boreal Ecosystem–Atmosphere Study (BOREAS), aimed at characterizing the processes that control the exchanges of CO<sub>2</sub> and H<sub>2</sub>O between boreal forests and the atmosphere. BOREAS was conducted over a 1000 × 1000 km boreal forest region in Saskatchewan and Manitoba, Canada, from 1993 to 1996 (1994 and 1996 were intensive-field-campaign years) (Sellers *et al.* 1995, 1996). Data were collected at local scales (a few cm to a few km) using leaf and soil chambers and tower-mounted eddy covariance flux instruments, and at larger scales (10–10<sup>3</sup> km) with meteorological observations and modelling, airborne flux measurements, and satellite remote sensing. In this paper, we report values of annual carbon sequestration by the OA forest in 1994 and 1996. The effects of climatic and biological variations on the respiration and photosynthesis of the OA forest are then analysed.

## Materials and methods

### Description of the OA forest site

The OA forest site (53.7 °N, 106.2 °W), near the southern edge of the boreal forest, is located in Prince Albert National Park, about 50 km NNW of Prince Albert, Saskatchewan, Canada. Its mean annual air temperature and cumulative precipitation are, respectively, about 1 °C and 400 mm. The soil, an Orthic Luvisol, has an 8–10 cm

deep surface organic layer with a bulk density of about 160 kg m<sup>-3</sup>. The mineral soil has a silty-clay texture and a bulk density of about 1300 kg m<sup>-3</sup>. Tree roots penetrate to a depth of about 60 cm.

A natural fire occurred in 1919 (Weir 1996), resulting in an even-aged stand of aspen with presently a mean height of 21 m, a diameter at 1.3 m height of 20 cm (s.d.  $\pm$  4.5 cm) and a stand density of 830 stems ha<sup>-1</sup>. The overstory aspen (*Populus tremuloides* with scattered *Populus balsamifera*) canopy was concentrated within the upper 5–6 m, while the understory, which is mainly composed of hazelnut (*Corylus cornuta* Marsh.) with sparse shrubs (e.g. prickly rose, *Rosa acicularis* Lindl.), was about 2 m high. The topography is relatively level and the fetch is at least 3 km in all directions.

### CO<sub>2</sub> flux and supplementary measurements

Continuous half-hourly CO<sub>2</sub> fluxes were measured at 39 m above the ground using the eddy covariance technique from 10 October to 15 November 1993, from 2 February to 20 September 1994, and from 20 April to 31 December 1996. (Measurements have continued uninterrupted until the writing of this paper, but 1997 measurements will not be addressed here.) The instrumentation during the 1993–94 field year consisted of a 3-D sonic anemometer-thermometer (model DAT-310 with model TR-61B probe, Kaijo-Denki, Tokyo, Japan) with a 20-cm path length at the 39-m height and an infrared gas (CO<sub>2</sub>/H<sub>2</sub>O) analyser (IRGA) (model 6262, LI-COR Inc. Lincoln, NE) housed in a temperature-controlled box at the 33-m height on a 36-m high scaffold tower (Black *et al.* 1996). Air was drawn at 6.5 L min<sup>-1</sup> through a 6-m long, 3.2-mm inner diameter heated (to prevent condensation) Bev-a-line tube by two diaphragm pumps connected in parallel (model TD-4 × 2N, Brailsford Co., Rye, NY), which pumped the air through the sample cell of the IRGA. This resulted in a sample cell pressure near atmospheric and a delay time of 1.2 s. The IRGA was operated in differential mode (LI-COR Inc. 1996a) with dry air containing 350  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> flowing through the reference cell at 30 cm<sup>3</sup> min<sup>-1</sup>. From March 20 1996, we used a Solent R2S 3-D sonic anemometer-thermometer (Gill Instruments, Lymington, UK) and an IRGA (LI-COR model 6262) operated in absolute mode. Air was drawn through heated Dekoron tubing (4 mm ID and 4.7 m long) and the sample cell by a diaphragm pump (model DOA-V191-AA, Gast Inc., Dayton, OH) at 10 L min<sup>-1</sup> resulting in sample cell pressure being about 16 kPa less than atmospheric pressure and a delay time 0.8 s. CO<sub>2</sub>- and H<sub>2</sub>O-free nitrogen was passed through the reference cell at 70 cm<sup>3</sup> min<sup>-1</sup>. During the winter, supplemental heating and insulation were added to the IRGA box and the

funnel at the entrance to the sampling tube. The sonic array was not heated. In 1993 and 1994, anemometer and IRGA analogue signals were measured at 100 Hz using a 16-bit analogue-to-digital (A/D) converter (National Instruments model AT-M10-16X) after being low-pass filtered at 50 Hz. Five-point block averaging provided 20 Hz samples for the eddy covariance calculations. In 1996, analogue signals from the IRGA were low-pass filtered at 10 Hz and measured at 20 Hz using the A/D converter in the sonic anemometer-thermometer. CO<sub>2</sub> fluxes were calculated on-line in parallel by two PCs (the eddy covariance PCs) with all high-frequency data being saved on tape drives. The mean vertical and lateral wind velocity components were rotated to zero in the calculation (Tanner & Thurtell 1969).

Since the CO<sub>2</sub> concentration was measured simultaneously with the water vapour concentration in the IRGA, corrections for the pressure broadening and dilution effects of water vapour on CO<sub>2</sub> concentration measurement were required (LI-COR Inc. 1996a, b). The CO<sub>2</sub> mole fraction (μmol CO<sub>2</sub> mol<sup>-1</sup> wet air),  $\chi_c$ , was calculated using the nonoverlapping line approximation (McDermitt *et al.* 1994)

$$\chi_c = F(V \frac{P_0}{P}) \frac{T}{T_0}, \quad (1)$$

where  $F(VP_0/P)$  is a fifth-order polynomial that relates  $\chi_c$  to the measured voltage  $V$  with a zero gas concentration in the reference cell,  $P_0$  and  $P$  are, respectively, the standard barometric pressure and pressure in the sample cell (kPa), and  $T$  and  $T_0$  are, respectively, the temperature of the sample cell and its temperature at calibration (K). Because water vapour in the sample cell broadens the CO<sub>2</sub> infrared absorption band, (1) requires modification as follows (McDermitt *et al.* 1994):

$$\chi_{cb} = (1 + (a_{\chi_w} - 1)\chi_w/1000) F(V \frac{P_0}{P(1 + (a_{\chi_w} - 1)\chi_w/1000)}) \frac{T}{T_0}, \quad (2)$$

where  $\chi_{cb}$  is the broadening-corrected CO<sub>2</sub> mole fraction,  $a_{\chi_w}$  is the broadening coefficient of water vapour (= 1.57, McDermitt *et al.* 1994) and  $\chi_w$  is the water vapour mole fraction (mmol H<sub>2</sub>O mol<sup>-1</sup> wet air). The difference between (1) and (2) is generally less than 0.5% of the measured CO<sub>2</sub> mole fraction in the 0–1000 μmol mol<sup>-1</sup> range.

The CO<sub>2</sub> mole mixing ratio (mol CO<sub>2</sub> mol<sup>-1</sup> dry air,  $s_c$ ) was calculated by accounting for the dilution effect of water vapour in the sample cell as follows (LI-COR Inc. 1996a):

$$s_c = \chi_{cb} \frac{1}{(1 - \chi_w/1000)}. \quad (3)$$

At the OA forest site,  $\chi_w < 20$  mmol mol<sup>-1</sup>, resulting in  $s_c$  being about 0–2% higher than  $\chi_{cb}$ .

The vertical eddy flux of CO<sub>2</sub> ( $F_c$ ) is proportional to the covariance of the vertical velocity ( $w$ ) and  $s_c$  as follows (Webb *et al.* 1980):

$$F_c = (\rho_a/M_a) \overline{w's'_c}, \quad (4)$$

where  $\rho_a$  and  $M_a$  are the density and molecular weight (29 g mole<sup>-1</sup>) of dry air, and the overbar denotes a time average (e.g. a half hour) and the primes denote fluctuations from the average for the period. Instead of using (4) in our on-line calculations, we applied the WPL correction (Webb *et al.* 1980), which is equivalent to the dilution correction, to the covariance of  $w$  and  $\chi_c$  (i.e.,  $\overline{w'\chi'_c}$ ). The broadening correction ( $B$ , μmol m<sup>-2</sup> s<sup>-1</sup>) was not applied on line, but was done later. It was approximated as  $B \approx -0.06E$ , where  $E$  is the water vapour flux (mmol m<sup>-2</sup> s<sup>-1</sup>) at the same height as the CO<sub>2</sub> flux. For  $E = 10$  mmol m<sup>-2</sup> s<sup>-1</sup> (i.e. a latent heat flux of 450 W m<sup>-2</sup>),  $B$  (to be added to the uncorrected CO<sub>2</sub> flux) is about  $-0.6$  μmol m<sup>-2</sup> s<sup>-1</sup>, which is about 3% of the maximum daytime CO<sub>2</sub> flux measured above the OA forest during the growing season. The broadening correction adds about 20 g C m<sup>-2</sup> y<sup>-1</sup> to the carbon sequestration by the OA forest. We recommend the application of the broadening and dilution corrections on-line for CO<sub>2</sub> concentration because (i) the CO<sub>2</sub> flux is more accurate since latent heat flux measurement errors will not contaminate the CO<sub>2</sub> flux through the WPL correction, and because the broadening correction can be more accurate, and (ii) the CO<sub>2</sub> concentration and its statistics are more accurate since they will not vary with fluctuations in water vapour concentration.

During the whole field experiment period in 1993–94 and part of 1996, changes in CO<sub>2</sub> storage in the air column below the flux measurement height were calculated from a profile of CO<sub>2</sub> concentrations measured at 0.8, 2.3, 9.5, 15.7, 18.8, 21.9, 25 and 34.2 m above the ground. Using an 8-input manifold, a 200 L min<sup>-1</sup> rotary pump drew air down 20-mm inner diameter Dekoron tubing from each height (25 L min<sup>-1</sup> per height) to one of the data logging huts. Using 8 solenoid valves in the hut, air from each level was sequentially pumped (using a diaphragm pump) through a LI-COR 6262 gas analyser. All 8 levels were sampled twice every half hour and the system was calibrated automatically every 6 hs. During periods when the profile was not available, changes in CO<sub>2</sub> storage in the air column below the flux measurement height were estimated from the CO<sub>2</sub> concentration data at 39 m.

The CO<sub>2</sub> concentration measurement at 39 m was automatically calibrated once daily to correct for zero and span drift. A solenoid valve was opened permitting nitrogen gas to flow into the sampling tube entrance for 12 s establishing the voltage corresponding to zero CO<sub>2</sub> concentration. A second solenoid was then opened for 12 s permitting dry air with 350 μmol mol<sup>-1</sup> CO<sub>2</sub>

(calibration gas traceable to a Scripps analysis in 1993) to enter the sampling tube establishing the span voltage. The IRGA calibration was found to be extremely stable. The calibration procedure ensured that CO<sub>2</sub> concentration was accurate to within  $\pm 1 \mu\text{mol mol}^{-1}$ .

Downwelling and upwelling photosynthetic photon flux densities (PPFD) were measured using a model 190-SB quantum sensor (LI-COR Inc.). The measurement of upwelling PPFD was made 9 m above the aspen canopy from a 5 m horizontal boom mounted on the flux tower. Air temperature and humidity at 39 m were measured with a ventilated platinum resistance thermometer and a dewpoint hygrometer (model M1 with sensor model D2, General Eastern Instruments Corp., Watertown, MA), respectively, in 1993–94. In 1996, humidity was measured with a humidity sensor (model HMP-35C, Vaisala Inc., Woburn, MA) and the IRGA. Soil temperatures at depths of 2, 5, 10, 20, 50 and 100 cm were measured using direct-burial copper-constantan thermocouples (CSI). In 1993–94, volumetric soil water content ( $\theta_v$ ) of the 0–10 cm deep forest floor was measured every 2–3 days gravimetrically. In addition, time-domain reflectometry (TDR) segmented rods were used to measure  $\theta_v$  from the surface to a depth of 120 cm (Hook & Livingston 1996). In 1996, soil water content was measured using an automated TDR system (Gabel Corp., Victoria, Canada).

All data loggers (models 21X and CR7, CSI) were networked (using CSI multi-drop interfaces) and connected to a PC (the data logger PC). Every three hours, this PC automatically transferred all data from the loggers to its hard disc. The data logger PC was accessed daily using pcANYWHERE, Symantec Corp. from our laboratory at UBC through a communication system, which comprised a modem, cellular phone and Yagi antenna at the site, and a phone and modem in the laboratory. The Yagi antenna was mounted above the trees on the flux tower and the cellular phone was housed in a thermostatically controlled box near the antenna. Every day at mid-night (just before the calibration) the eddy covariance PCs compressed the previous 24 h of half-hour turbulence statistics and flux data, and one of them called the laboratory using the cellular phone and in three minutes transferred, using Kermit, the compressed data to the laboratory computer. The following morning the data were checked to determine that the sensors were functioning properly, transferred to the data archive, and used to update carbon flux and evaporation analyses. This communication system enabled us to monitor system performance daily and to make changes to the operating system if necessary. The data measurement/communication system is still operating as part of our long-term flux monitoring program at the OA forest site (see below).

### Determination of biotic flux from CO<sub>2</sub> eddy flux

Within a control volume with an upper boundary at 39 m and a lower boundary at a depth well into the ground so that there is no CO<sub>2</sub> flux, the net biotic flux (i.e. respiration rate,  $R$ , minus photosynthetic rate,  $P$ ) is balanced by the time rate of change of CO<sub>2</sub> storage in the air volume above the ground,  $\Delta S_a/\Delta t$ , and in the air-filled soil pore volume,  $\Delta S_s/\Delta t$ , (term I), by the mean horizontal and vertical advection (term II), and by the mean horizontal turbulent flux divergence (term III) and the vertical turbulent flux at 39 m (term IV), so that:

$$R - P = \frac{\Delta S_a}{\Delta t} + \frac{\Delta S_s}{\Delta t} + (\rho_a/M_a) \quad (5)$$

(.....I.....)

$$[\overline{u\Delta s_{cx}} + \overline{v\Delta s_{cy}} + \overline{w\Delta s_{cz}} + \Delta(\overline{u's'_c})_x + \Delta(\overline{v's'_c})_y] + F_c, \quad (IV)$$

(.....II.....) (.....III.....)

where  $u$ ,  $v$  and  $w$  are wind velocity components, respectively, in the longitudinal ( $x$ ), lateral ( $y$ ) and vertical ( $z$ ) directions. Overbars denote a time average over a measurement period (e.g. a half hour) and primes denote fluctuations from the mean. Terms II and III are not measurable at present and are believed to average to zero over long periods (e.g. a year) above a flat site like the OA forest. The storage terms also average to virtually zero over long periods, and so the annual net biotic flux equals the integrated CO<sub>2</sub> eddy fluxes at 39 m. The carbon sequestration or net ecosystem productivity (NEP) equals  $P - R$ , i.e. minus the net biotic flux. Half-hourly values of  $R$  were obtained using  $F_c + \Delta S_a/\Delta t + \Delta S_s/\Delta t$  during the leafless period and the nighttime during the growing season, and were then related to soil temperatures at the 2-cm depth. Because the soil storage term is difficult to measure, we estimated it by assuming it is proportional to  $R$  and is modulated by a wind speed function  $M$ , which is a function of the friction velocity, i.e.  $\Delta S_s/\Delta t = (1 - M)R$ . Several pieces of evidence indicate that the CO<sub>2</sub> storage in the air-filled soil pores increases during calm nights due to the lack of turbulent mixing so that  $M < 1$ , and decreases during the daytime when it is usually windy so that  $M > 1$  (Yang *et al.* 1997). Mathematically,  $M$  was determined by an iterative procedure using the following equations  $M = (F_c + \Delta S_a/\Delta t)/R$  and  $R = F_c + \Delta S_a/\Delta t + (1 - M)R$  where  $R$  was assumed to be a function of soil temperature at 2-cm depth, with the constraining condition that  $\sum(\Delta S_s/\Delta t) = 0$  (Yang *et al.* 1997). The values of  $P$  were then calculated as  $R - (F_c + \Delta S_a/\Delta t + \Delta S_s/\Delta t)$  during the growing season.

### Measuring and calculating leaf area index and absorbed PPFD

One-sided (projected) leaf area index (LAI) was measured using a LI-COR Plant Canopy Analyser (model LAI-2000,

LI-COR Inc., Lincoln, NB), which uses the transmission of the diffuse visible radiation less than 490 nm in wavelength through the canopy. For the aspen canopy, measurements were made at heights of 25 m and 3 m at six predetermined locations on overcast days or near sunset. Hazelnut LAI measurements consisted of pairs of below and above hazelnut readings at six predetermined locations along a 60-m east-west transect. LAI values were corrected for clumping and preleaf wood (boles and branches) area index (Chen *et al.* 1997) as follows:

$$A_L = A_m / \Omega_L - A_w, \quad (6)$$

where  $A_L$  and  $A_m$  are, respectively, the corrected and measured LAI,  $\Omega_L$  is the clumping index of the leaves ( $\Omega_{La} = 0.7$  for the aspen and  $\Omega_{Lh} = 0.98$  for the hazelnut), and  $A_w$  is preleaf wood area index (measured to be 0.62 for aspen and 0.34 for hazelnut) (Black *et al.* 1996). Because only one measurement was made using the LAI-2000 technique in 1996, we calculated aspen LAI,  $A_{La}$ , using daily average ratio of PPFD below to that above the aspen canopy between 10:00 and 16:00 CST,  $\tau$ , which was measured continuously, that is:

$$A_{La} = c \left( \frac{\ln \tau}{k_a \Omega_{La}} - \frac{A_w}{\Omega_{La}} \right), \quad (7)$$

where  $c$  is the coefficient determined by calibrating against the LAI-2000 measurement and  $k_a$  is the extinction coefficient (0.54, see below). Because the values of  $\tau$  fluctuated significantly from day-to-day as weather conditions changed, while LAI varied slowly, we smoothed  $\tau$  using a 5th-order polynomial function before it was used in the calculation.

The absorbed PPFD,  $Q_a$ , was calculated from measured incident PPFD,  $Q_0$ , as follows:

$$Q_a = Q_0 [1 - e^{-k_a A_{La}} + e^{-k_a (A_{La} + A_{wa})} \times (1 - e^{-k_h A_{Lh}})] \times [1 - \alpha] \quad (8)$$

(...I...)                      (...II...)                      (...III...)

where  $k_a$  and  $k_h$  are extinction coefficients of the aspen and hazelnut (0.540 and 0.756, respectively, Blanken 1997),  $A_{Lh}$  is the LAI of the hazelnut, and  $\alpha$  ( $\approx 0.03$ ) is the reflectivity of the forest to the incident PPFD. Term I is the proportion of  $Q_0$  intercepted by the aspen leaves, term II is the proportion of  $Q_0$  transmitted through the aspen canopy, and term III is the proportion of the transmitted radiation flux intercepted by the hazelnut leaves.

## Results and discussion

### Annual courses of CO<sub>2</sub> eddy flux in 1994 and 1996

Figure 1 shows the annual courses of daily mean CO<sub>2</sub> eddy flux,  $F_c$ , at 39 m above the ground at the OA forest site in 1994 and 1996. Data on daily and longer time scales were used throughout this analysis, following the recommendation by Ruimy *et al.* (1995) that more data sets be presented on a daily basis, in particular for long-term flux measurements in forests, because statistics at this time scale are important for large-scale modelling. Analyses on a half-hourly basis will be reported in later papers. During winter and early spring, values of  $F_c$  were positive (i.e. release of CO<sub>2</sub> to the atmosphere) and increased with increasing temperature before leafing. The most negative  $F_c$ , i.e. maximum CO<sub>2</sub> uptake by the forest, occurred soon after leaf emergence. Carbon uptake decreased gradually during the middle of the growing season and then rapidly late in the growing season as the leaves senesced. Carbon release into the atmosphere reached a maximum just after the leaves had fallen, when soil temperatures were highest for the part of the year

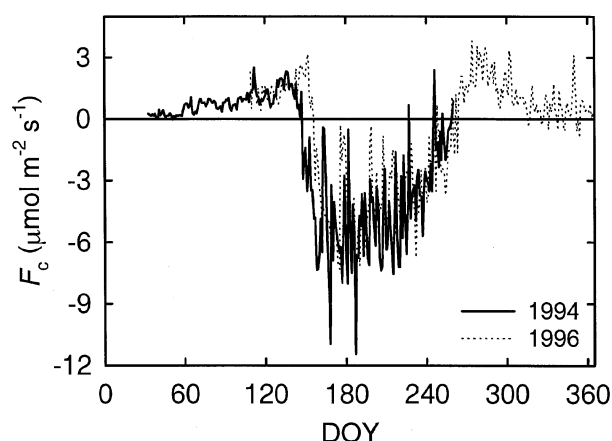


Fig. 1 Annual courses of daily mean CO<sub>2</sub> eddy flux at the 39-m height above the ground in a 21-m tall boreal old aspen (OA) forest in Prince Albert National Park, Saskatchewan, Canada, in 1994 and 1996.

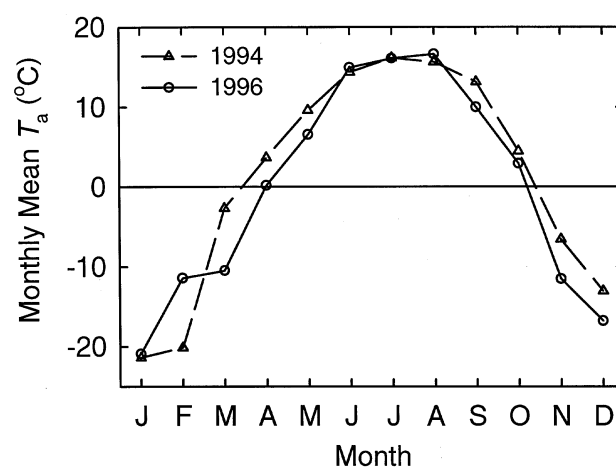


Fig. 2 Annual courses of monthly mean air temperatures at the 39-m height above the ground at the OA forest site in 1994 and 1996.

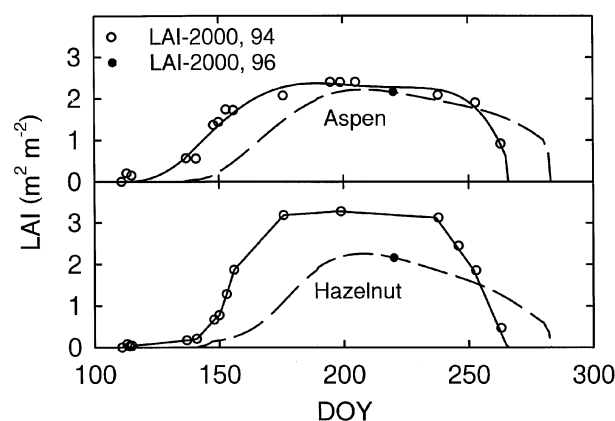
that the forest was leafless. Such an annual course of  $F_c$  is typical for deciduous forests, including those at mid-latitudes (Wofsy *et al.* 1993; Goulden *et al.* 1996).

$F_c$  in 1994 became negative 9 days earlier, and was more negative during most of the growing season than in 1996. This difference was mainly due to the late spring in 1996, with its mean air temperature being more than 3 °C lower in both April and May than in 1994 (Fig. 2). Consequently, the trees started leafing 18–24 days later in 1996 than in 1994 (Fig. 3). In both years, the trees started to leaf when the accumulated heat units ( $T_a > 5$  °C) exceeded 40 °C day. The growing season (defined as the period when the forest was in leaf) was only 7 days shorter in 1996 than in 1994. Maximum forest LAI (LAI of the aspen and hazelnut) in 1996 was 4.3, less than the LAI of 5.6 in 1994.

#### Relationship between respiration and climatic factors

Temperature and soil moisture are the dominant climatic factors controlling the respiration rate  $R$  of the OA forest ecosystem. Figure 4 compares the 1994 and 1996 relationships between  $R$  and soil temperature  $T_s$  at 2-cm depth. The relationships were quite similar in both years except when  $T_s > 10$  °C for which  $R$  was slightly higher in 1996. Using an ensemble averaging with a bin size of 0.5 °C, the best fit among a number of functions tested, including an exponential function, was found with a logistic function as follows:

$$R = \frac{6.88}{1 + \exp(0.2474(8.4 - T_s))}, \quad n = 42, r^2 = 0.96, 1994 \quad (9)$$



**Fig. 3** Measurements of leaf area index (LAI) of the aspen and hazelnut canopies in 1994 and 1996 using a LI-COR LAI-2000, Plant Canopy Analyser. The lines for the aspen were calculated with (7) using PPFD measurements above and below the canopy by obtaining  $c$  for each year from the LAI-2000 measurements. The dashed line for the hazelnut in 1996 was fit to the measured value and its pattern calculated using the relationship between the hazelnut and aspen LAI for 1994.

$$R = \frac{7.31}{1 + \exp(0.2606(8.6 - T_s))}, \quad n = 40, r^2 = 0.96, 1996$$

These relationships indicate that the maximum respiration rate of the forest ecosystem was 6.88 and 7.31  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , and  $R$  reached half the maximum at  $T_s = 8.4$  and 8.6 °C in 1994 and 1996, respectively. Since the logistic function described the data best,  $Q_{10}$  (the ratio of the rate of a process at one temperature to that at a temperature 10 °C lower) values were not constant over the entire temperature range. As an example, we estimate  $Q_{10}$  to be 5.4 and 2.8 for  $T_s$  in the 0–10 and 5–15 °C ranges, respectively, in 1994. These values are higher than expected and may be the effect of seasonal changes in live root biomass and in soil temperature and moisture profiles with depth (Black *et al.* 1996).

Effects of soil moisture were derived after the influence of  $T_s$  on  $R$  had been accounted for, i.e. using  $R$  measured divided by that calculated using (9). Respiration rate increased about 35% as  $\theta_v$  at the 15-cm depth increased from 0.1 to 0.4  $\text{m}^3 \text{m}^{-3}$ , using data from 21 April to 19 September 1994 (Fig. 5). Low values of  $\theta_v$  (i.e. < 0.15) only occurred in August 1994, which may help to explain why  $R$  was slightly lower and  $T_s$  slightly higher in this period in 1994 than in 1996. Since the liquid water content usually approaches zero in winter as  $T_s$  drops below 0 °C, it is likely that the low liquid water content in winter may further hinder soil respiration in addition to the effect of low temperature, resulting in the higher  $Q_{10}$  for  $T_s$  in the 0–10 °C range.

In spite of the effects of soil moisture, temperature was still the most important factor controlling respiration. Soil temperature alone explained 84% (1994) and 67% (1996) of the variance in daily (leafless period) and night-time mean (growing season)  $R$ , respectively, and 94% of the variance of monthly mean  $R$  (Fig. 6). The proportion of variance explained in 1994 increased by 6% for daily and night-time mean  $R$ , when the effect of  $\theta_v$  was included. Because of the relatively small influence of  $\theta_v$  on  $R$ , and more importantly the lack of soil moisture data during periods when  $F_c$  was not measured, we used only the relationships between  $R$  and  $T_s$  in filling data gaps and calculating photosynthetic rates.

#### Relationship between photosynthesis and climatic factors

Figure 7 compares the courses of daily mean photosynthetic rate during 1994 and 1996. Photosynthesis started earlier in 1994 and its rate was higher during most of the growing season than in 1996. Factors affecting photosynthesis include  $Q_a$ , air temperature ( $T_a$ ), saturation deficit  $D$  and  $\theta_v$  (Baldocchi *et al.* 1997).

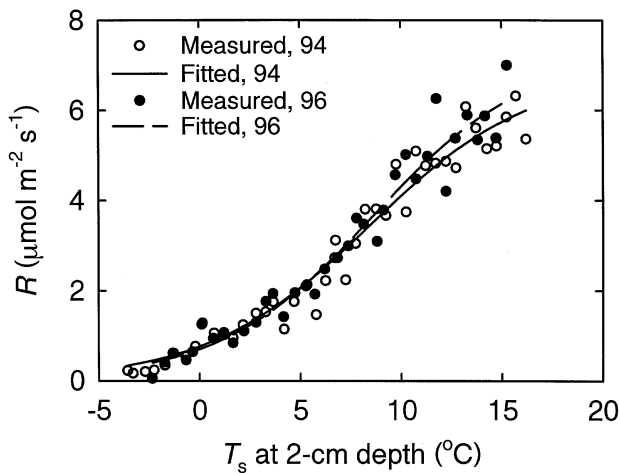
The response of photosynthetic rate to  $Q_a$  was almost identical in 1994 and 1996 (Fig. 8). A rectangular hyperbolic function best described the influence of  $Q_a$  on the photosynthetic rate of the OA forest, as follows:

$$P_1(Q_a) = \frac{0.0453 \times 20.70 Q_a}{0.0453 Q_a + 20.70}, 1994, \quad (10)$$

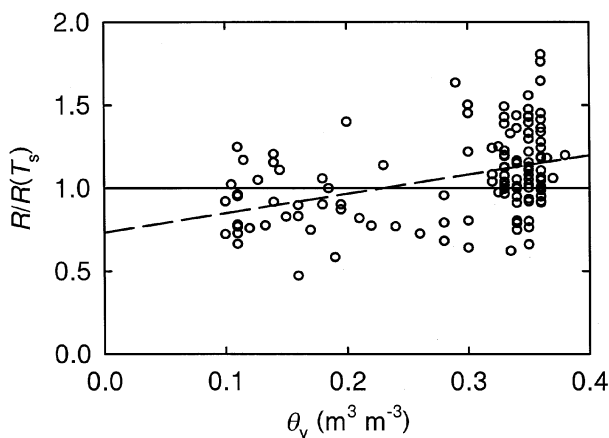
$$P_1(Q_a) = \frac{0.0515 \times 16.53 Q_a}{0.0515 Q_a + 16.53}, 1996.$$

The apparent quantum yields were 0.0453 and 0.0515, and the photosynthetic capacities were 20.70 and  $16.53 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, in 1994 and 1996. These results are consistent with Ruimy *et al.*'s (1995) findings (using  $Q_0$ ) for broadleaf forests that the apparent quantum yield and photosynthetic capacity are about 0.035 and  $20.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, using half-hourly or hourly data sets. They are about half of the highest quantum yield of a single leaf of 0.09 ever measured (Bugbee & Monje 1992).

The curvilinear response of  $P$  to  $Q_a$  implies a decrease in photosynthetic energy-use efficiency with increasing  $Q_a$

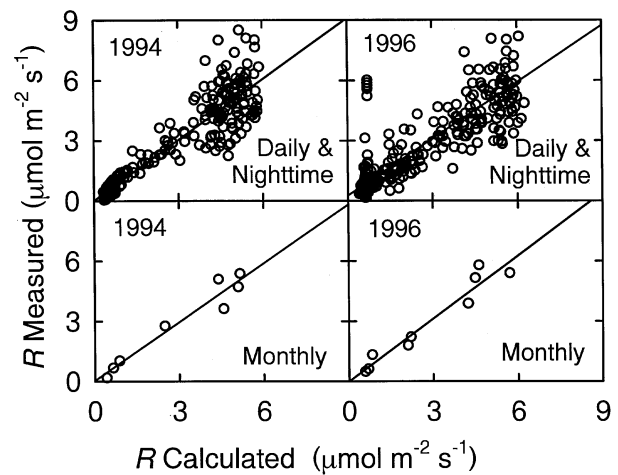


**Fig. 4** Relationships between the respiration rate  $R$  of the OA forest and soil temperature at the 2-cm depth (with a  $T_s$  bin size of  $0.5^\circ\text{C}$ ) in 1994 and 1996. Data were daily (24-h) mean values during the leafless period and night-time mean values during the growing season.

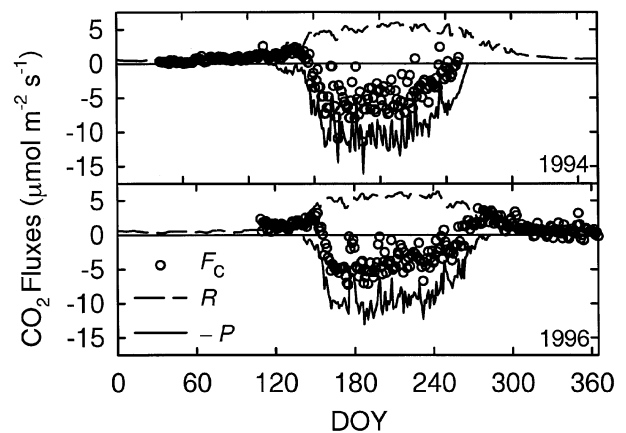


**Fig. 5** Effects of soil moisture  $\theta_v$  on respiration at the OA forest site. Data were from 21 April to 19 September 1994.

(Fig. 8). The photosynthetic energy-use efficiency was calculated as the proportion of  $Q_a$  (217 kJ per mole of photons) that becomes chemical energy in the carbohydrate produced (479 kJ per mole) (Bugbee & Monje 1992). On clear days (i.e. daily (24-h) mean  $Q_a > 250 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), the mean photosynthetic energy-use efficiency was about 5.6% in 1994 and 6% in 1996 (Fig. 9). Under cloudy or overcast conditions (i.e. daily mean  $Q_a < 250 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), however, the photosynthetic energy-use efficiency averaged 12.5% during July and August in both years, which approaches the optimal efficiency of 14–17% (Bugbee & Monje 1992). This indicates that the OA forest can use absorbed radiation energy very efficiently during the growing season. The annual photosynthetic energy conversion efficiency, calculated as the ratio of the total energy in the carbohydrate produced to the total absorbable PPFD, was 2.5% in 1994



**Fig. 6** Comparison of measured and calculated (using eqn 9) daily (during the leafless periods) and night-time mean (during the growing seasons) (upper panels) and monthly mean (lower panels) respiration rate  $R$  at the OA forest site in 1994 and 1996.



**Fig. 7** Annual courses of daily (24-h) mean  $\text{CO}_2$  eddy flux  $F_c$ , respiration rate  $R$  and photosynthetic rate  $P$  at the OA forest site in 1994 and 1996.

and 2.3% in 1996. In comparison, the annual photosynthetic energy conversion efficiency is 4.5% for tropical rain forests and 1.1% for boreal coniferous forests (Larcher 1975).

Figure 10 shows the effect of  $T_a$  on photosynthesis, derived after accounting for the influence of  $Q_a$ , i.e.  $P/P_1(Q_a) [= P_2(T_a)]$ :

$$P_2(T_a) = \frac{0.9612 \times 212.19T_a}{0.9612T_a + 212.19} - 0.8229T_a - 0.1277, 1994, \quad (11)$$

$$P_2(T_a) = \frac{0.2622 \times 3.401T_a}{0.2622T_a + 3.401} - 0.0562T_a + 0.1074, 1996.$$

The low energy-use efficiency at the beginning and end of the growing seasons (Fig. 9) was mainly due to low  $T_a$ . Low temperature (i.e.  $T_a < 10^\circ\text{C}$ ) limited photosynthesis in both years.

Similarly, the effect of  $D$  ( $\text{mmol mol}^{-1}$  dry air) was derived by examining the relationship between  $P/[P_1(Q_a)P_2(T_a)] [= P_3(D)]$  and  $D$  (Fig. 11), and resulted in:

$$P_3(D) = \exp(-340.57D + 0.4474) + 0.8951, 1994 \quad (12)$$

$$P_3(D) = \exp(-241.82D - 0.4947) + 0.8947, 1996,$$

which indicates that photosynthetic rate decreased as  $D$  increased. No or little effect of  $\theta_v$  on photosynthesis was found for 21 April to 19 September 1994 (data not shown), probably because the low values of  $\theta_v$  occurred for only about one month and the tree roots may tap into deeper soil layers for water (Baldocchi *et al.* 1997).

The relationships between  $P$  and  $Q_a$ ,  $T_a$  and  $D$  are not necessarily independently valid because of the interactions between these factors. For example, the slight decrease in  $P/P_1(Q_a)$  in the range of  $T_a > 20^\circ\text{C}$  could be due to the higher  $D$ . Their combined effect on  $P$  (i.e.  $P_1(Q_a)P_2(T_a)P_3(D)$ ), however, is valid no matter how they interact.  $P_1(Q_a)P_2(T_a)P_3(D)$  accounted for 68% and 72% of variance in  $P$  in 1994 and 1996, respectively (Fig. 12).

#### Annual carbon sequestration in 1994 and 1996

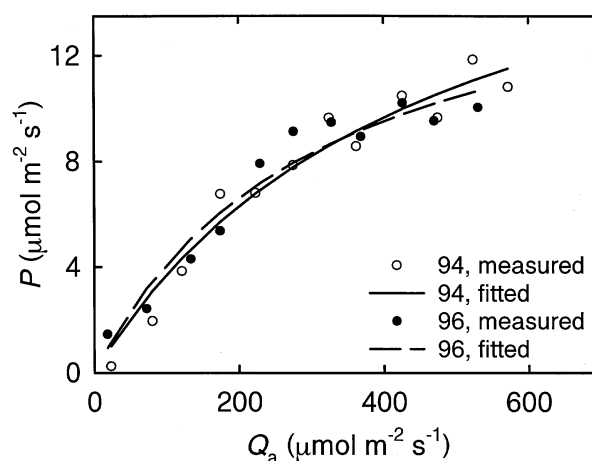
The values of annual carbon sequestration or NEP calculated by integrating  $-F_c$  were  $200 \pm 30$  and  $130 \pm 30$   $\text{g C m}^{-2} \text{y}^{-1}$  in 1994 and 1996, respectively (Table 1). Data gaps when  $F_c$  was not measured were filled using the relationships described above between photosynthesis and respira-

**Table 1** Values and uncertainties of annual photosynthetic rate ( $P$ ), respiration rate ( $R$ ), and net ecosystem productivity (NEP) at the OA forest site in 1994 and 1996 based on eddy covariance measurements ( $\text{g C m}^{-2} \text{y}^{-1}$ )

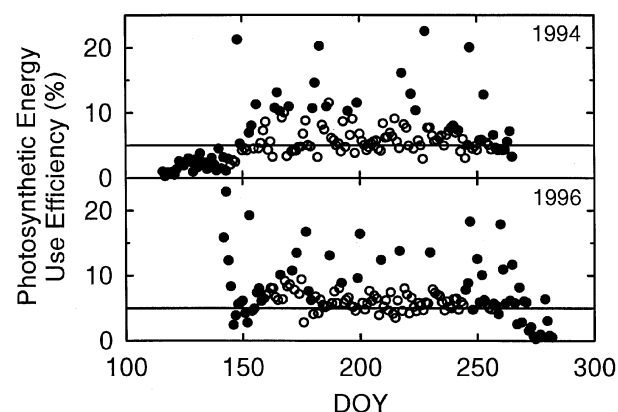
	$P$	$R$	NEP
1994	$1120 \pm 60$	$920 \pm 90$	$200 \pm 30$
1996	$1030 \pm 60$	$900 \pm 90$	$130 \pm 30$

tion and various climatic and biological variables. Errors in the annual carbon sequestration values were largely the result of the uncertainty introduced by the filling process, and were calculated by multiplying the total  $R$  in the periods of missing data by the ratio of one standard deviation to the monthly mean  $R$  ( $= 17\%$  based on Fig. 6). The uncertainty in  $R$  was about  $90 \text{ g C m}^{-2} \text{y}^{-1}$  in both years. Of this about  $60 \text{ g C m}^{-2} \text{y}^{-1}$  came from the estimation of daytime respiration rates using the relationships between  $R$  and  $T_s$  at the 2-cm depth during the growing seasons and  $30 \text{ g C m}^{-2} \text{y}^{-1}$  from gap filling during the rest of both years using these relationships.  $P$ , which is equal to  $R - F_c$ , had an uncertainty of about  $60 \text{ g C m}^{-2} \text{y}^{-1}$  because it had mainly the effect of the uncertainty in daytime respiration rate.

The  $70 \text{ g C m}^{-2} \text{y}^{-1}$  (or 35%) decrease in carbon sequestration in 1996 compared with 1994 was mainly caused by the



**Fig. 8** Relationships between the daily mean photosynthetic rate  $P$  and absorbed photosynthetic photon flux density  $Q_a$  at the OA forest site in 1994 and 1996.



**Fig. 9** Annual courses of daily mean photosynthetic energy use efficiency, calculated as the ratio of energy stored in carbohydrate (479 kJ per a mole) to the absorbed photosynthetic photon flux density  $Q_a$  (217 kJ per a mole of photons). Open circles represent daily mean  $Q_a > 250 \mu\text{mol m}^{-2} \text{s}^{-1}$ , and the filled ones otherwise.

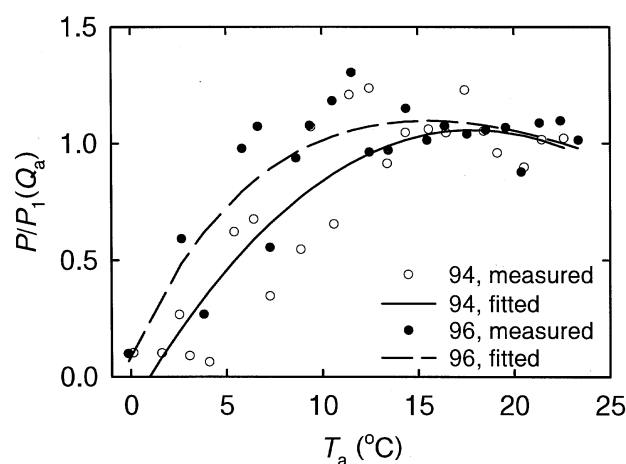


**Table 2** Statistics showing the slopes of linear regressions between the annual and seasonal mean air temperatures  $T_a$  and cumulative precipitation  $p$  for the period 1943–96 and the number of years since 1943 measured at Prince Albert Airport climate station, standard deviations of  $T_a$  and  $p$  over this period, and differences in  $T_a$  and  $p$  between the 54-year averages ( $\bar{T}_a$  and  $\bar{p}$ ) and values in 1994 and 1996

	Annual	Winter (Nov–Feb)	Spring (Mar–May)	Summer (Jun–Aug)	Autumn (Sept–Oct)
Slope, $T_a$ ( $^{\circ}\text{C y}^{-1}$ )	0.0196	0.0174	0.0556	0.0097	–0.0140
STD of $T_a$ ( $^{\circ}\text{C}$ )	1.09	2.30	2.13	0.92	1.36
Slope, $p$ ( $\text{mm y}^{-1}$ )	0.8376	–0.4271	0.3372	0.6477	0.2798
STD of $p$ ( $\text{mm}$ )	74.70	20.70	33.30	60.51	31.21
$T_a(94) - \bar{T}_a$ ( $^{\circ}\text{C}$ )	0.29	–2.07	2.94	–0.28	1.85
$T_a(96) - \bar{T}_a$ ( $^{\circ}\text{C}$ )	–1.17	–2.63	–1.85	1.05	–0.6
$p(94) - \bar{p}$ ( $\text{mm}$ )	89.68	6.78	44.15	40.41	–1.67
$p(96) - \bar{p}$ ( $\text{mm}$ )	20.98	–25.02	37.45	–40.45	49.00

90 g C m $^{-2}$  y $^{-1}$  decrease in  $P$  (Table 1). This was the result of the combined effect of the late spring in 1996 and the asymmetrical distribution of incident PPFD over the growing season (Fig. 13). In 1996 the forest started to leaf about 20 May, only 32 days before the summer solstice, and the leaves remained on for another 110 days, whereas in 1994 the corresponding numbers of days were 56 and 93. Consequently, the forest absorbed about 16% less PPFD in 1996 than in 1994. Of this 16%, 12% was due to the different leaf emergence dates, 1.5% was due to the difference in the length of the growing seasons, and 2.5% was due to the difference in LAI between the two years. Figure 14 shows the monthly differences in  $P$  and  $R$  between the two years. Except at the end of the growing season,  $P$  was much higher in 1994 than in 1996, especially early in the growing season, whereas the average respiration rate in 1994 was only 20 g C m $^{-2}$  y $^{-1}$  higher than in 1996 (see Table 1).

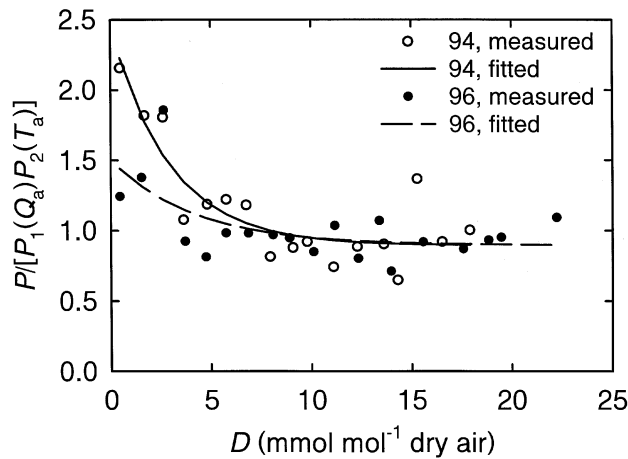
At Prince Albert airport, the annual mean  $T_a$  and cumulative precipitation in 1994 were 0.29  $^{\circ}\text{C}$  and 89.7 mm higher, respectively, than the 54-year (1943–96) average (Table 2). In contrast 1996 was a cold year (1.17  $^{\circ}\text{C}$  less than the 54-year average), with its cumulative precipitation being slightly above the average. The annual mean air temperature increased about 1  $^{\circ}\text{C}$  during the 54-year period, despite significant fluctuations from year to year (Fig. 15 and Table 2). Over this period, the mean air temperature in spring increased by about 3  $^{\circ}\text{C}$ . These annual and seasonal temperature trends were consistent with those at regional scales (Environment Canada 1995). During the same period, annual precipitation increased 45 mm, with the increase occurring mainly in the summer. On the basis of the relationships described above between photosynthesis, respiration and climate 1994 was a good growth year, whereas 1996 was a bad year. We hope that in the near future the occurrence of a 'normal-climate' year and a dry year will enable us to determine the effect of these climatic conditions on photosynthesis and respiration. In view of the importance of long-term monitoring in better understanding the biological and climatic processes controlling carbon exchange pro-



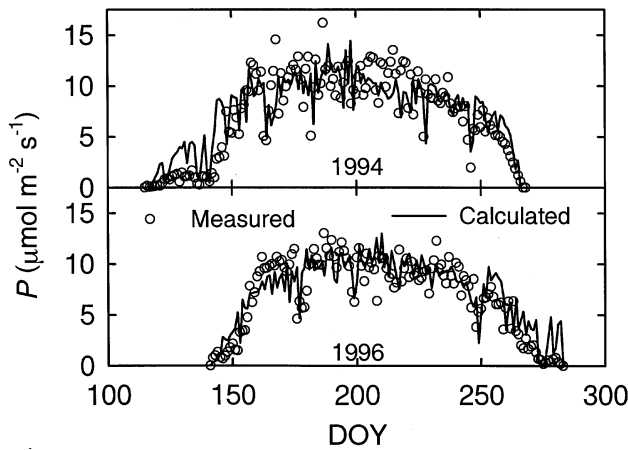
**Fig. 10** Effects of daily mean air temperature  $T_a$  on the photosynthetic rate  $P$  at the OA forest site in 1994 and 1996.  $P_1(Q_a)$  accounts for the effect of the absorbed photosynthetic photon flux density  $Q_a$  on  $P$ .

cesses (Baldocchi *et al.* 1996), a long-term flux monitoring program has been initiated at the OA forest site as part of the Boreal Ecosystem Research and Monitoring Sites (BERMS) project, which will continue flux measurements at some former BOREAS sites. The OA forest site is also part of the recently initiated AmeriFlux regional CO $_2$ /H $_2$ O flux network (D.Y. Hollinger, pers. comm.).

The 1994 carbon stock in the OA forest ecosystem, which includes the boles, twigs, branches and roots of aspen trees, stems of hazelnut, and the organic matter on the forest floor, but excludes the carbon stock in the soil mineral layers (not known at present and 75 years ago), was calculated to be 17.8 kg C m $^{-2}$ . In the calculation, we used 0.45 for the ratio of the actual bole volume determined from measurements of a 16-cm diameter felled aspen to that assuming the bole is a cylinder with a diameter equal to that at the 1.3-m height, measured dry wood density of 422.5 kg m $^{-3}$  (Blanken 1997). The carbon-dry matter conversion factors were 0.58 and 0.55 kg C per kg dry matter for wood and forest-floor

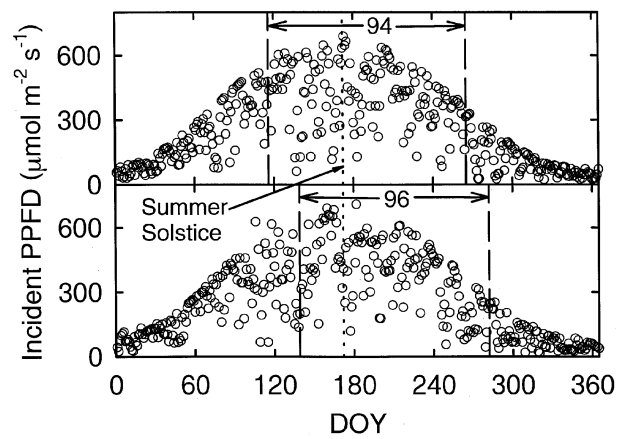


**Fig. 11** Effects of daily mean saturation pressure deficit  $D$  on the photosynthetic rate  $P$  at the OA forest site in 1994 and 1996.  $P_1(Q_a)P_2(T_a)$  accounts for the effects of the absorbed photosynthetic photon flux density  $Q_a$  and air temperature  $T_a$  on  $P$ . At the site,  $10 \text{ mmol mol}^{-1}$  corresponds to  $\approx 0.94 \text{ kPa}$  vapour pressure.

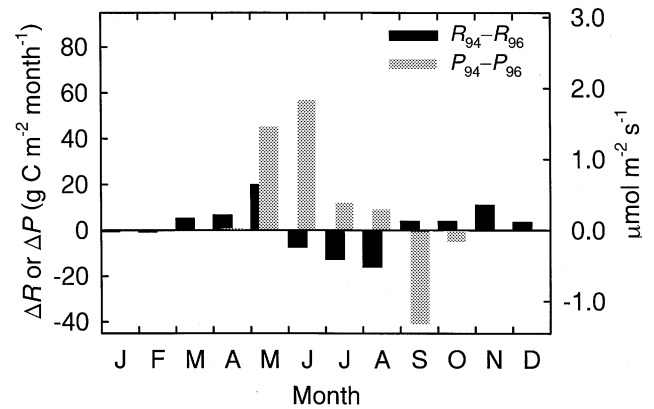


**Fig. 12** Comparison of measured and calculated daily mean photosynthetic rate  $P$  at the OA forest site in 1994 and 1996. Calculated values equal  $P_1(Q_a)P_2(T_a)P_3(D)$ .

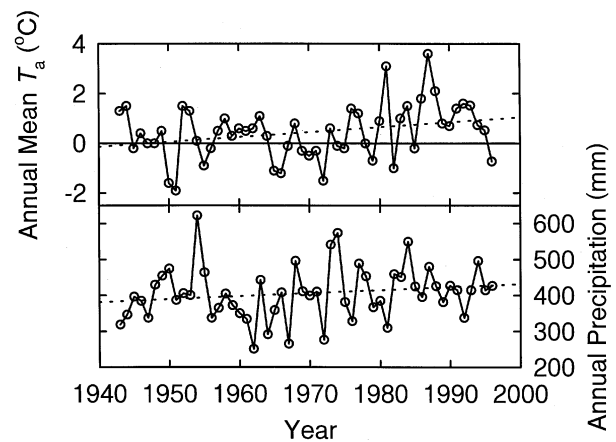
material (Page *et al.* 1982; T.M. Ballard, pers. comm.). The carbon stock of the aspen boles and forest-floor material were calculated to be, respectively,  $6.04$  and  $7.92 \text{ kg C m}^{-2}$ . The carbon stored in the roots was measured to be  $3.13 \text{ kg C m}^{-2}$  (Steele *et al.* 1997), and carbon in the twigs and branches was assumed to be 5% of that in the boles (i.e.  $0.30 \text{ kg C m}^{-2}$ ). The hazelnut understorey (above ground) was harvested from three  $3 \text{ m} \times 3 \text{ m}$  plots during early August of 1994 (Blanken 1997), which gave the above-ground carbon stock of the understorey to be  $0.51 \text{ kg C m}^{-2}$ . Assuming the fire in 1919 burned all the organic matter above the mineral horizons and the carbon stock in the mineral layer has remained the same since 1919, then the net carbon accumulation in OA forest ecosystem



**Fig. 13** Distributions of daily mean incident PPFD corresponding to the growing season in 1994 and 1996 at the OA forest site. The dashed lines mark the beginning and end of the growing seasons.



**Fig. 14** Differences in monthly integrated respiration rate  $R$  and photosynthetic rate  $P$  between 1994 and 1996 at the OA forest site.



**Fig. 15** Trends of annual mean air temperature and cumulative precipitation from 1943 to 1996 at the Prince Albert Airport. Dashed lines are linear regressions (see also Table 2).

was  $17.8 \text{ kg C m}^{-2}$  over the last 75 years. Due to climatic variability, the annual carbon sequestration by the forest must have fluctuated significantly over the last 75 years, as in the 1994 and 1996 measurements. Furthermore, the annual carbon sequestration has also varied with stage of growth of the forest over the last 75 years (Larcher 1975). Consequently, the annual carbon sequestration for a particular year cannot be estimated from the stand carbon inventory. Nevertheless, we can calculate the mean increment of forest carbon stock during the last 75 years, which is about  $240 \text{ g C m}^{-2} \text{ y}^{-1}$ . This result is 16–45% larger than the eddy covariance measurements of  $200 \text{ g C m}^{-2} \text{ y}^{-1}$  in 1994 and 130 in 1996. The lower values obtained by the eddy covariance technique probably reflect the old age of the forest stand at the time of measurement, although it is very likely that some forest-floor material remained following the forest fire in 1919.

The total area of the world's boreal forests is about  $15 \times 10^6 \text{ km}^2$  (Whittaker & Likens 1975; Bonan & Shugart 1989), while that of broadleaf deciduous forests in Canada's boreal region is about  $2 \times 10^5 \text{ km}^2$  (Porkland *et al.* 1991). If the annual carbon sequestration of the OA forest is representative of the latter forests, then they alone may fix about  $40\text{--}60 \text{ Tg C y}^{-1}$  ( $1 \text{ Tg} = 10^{12} \text{ g}$ ), which is about 2–3% of the missing carbon sink in the global carbon budget.

## Summary and conclusions

An eddy covariance system, which can make long-term (i.e. year-round) measurements of  $\text{CO}_2$  and water vapour fluxes at remote forest sites, has been developed and tested at the OA forest site in Prince Albert National Park, Saskatchewan, Canada, in 1994 and 1996. The system is currently being used in a long-term  $\text{CO}_2$  flux monitoring program at the site. Every night the system automatically calibrates the gas analyser, and all half-hourly flux data are automatically transferred to our laboratory at UBC through a modem-cellular phone communication system. The communication system also allows us to monitor system performance and to make changes to the operating program if necessary.

The respiration rate of the OA forest ecosystem was controlled mainly by temperature. Soil temperature alone explained 67–84% of the variance of daily (leafless period) and night-time mean (growing season)  $R$ , and 94% of monthly mean  $R$ . By including the effect of soil moisture, the explained variance during the growing season increased slightly (by about 6%). The photosynthetic rate of the OA forest was controlled largely by the absorbed photosynthetic photon flux density. Air temperatures less than  $10^\circ\text{C}$ , which generally occurred near the beginning and end of the growing season, decreased photosynthesis. Low saturation deficit enhanced photosynthesis probably by increasing stomatal conductance, resulting in a higher photosynthetic energy-use efficiency during cloudy days and

early mornings than during clear days. On the basis of absorbed PPFD, the photosynthetic energy-use efficiency was 5.6–6% on clear days and increased to 12.5% on cloudy days. Annually, the photosynthetic energy-use efficiency on the basis of incident PPFD was 2.3–2.5%, which is about twice that of boreal coniferous forests but is only about half that of the tropical forests. About 70% of the variance of daily mean photosynthetic rate was explained by the combination of  $Q_a$ ,  $T_a$  and  $D$ .

The OA forest sequestered  $200 \pm 30$  and  $130 \pm 30 \text{ g C m}^{-2} \text{ y}^{-1}$ , respectively, in 1994 and 1996. These rates were 16–45% lower than the mean carbon increment of about  $240 \text{ g C m}^{-2} \text{ y}^{-1}$  between 1919 and 1994 estimated by assessing the 1994 carbon stock of the forest. The difference was partly due to the old age of the forest at the time of the eddy covariance measurements. If these rates of carbon sequestration are representative of all Canadian boreal deciduous forests, which occupy about  $2 \times 10^5 \text{ km}^2$ , then these forests alone may fix  $40\text{--}60 \text{ Tg C y}^{-1}$ , which is 2–3% of the current global missing carbon sink (about  $1.9 \text{ Pg C y}^{-1}$ ).

The difference in carbon sequestration by the OA forest between 1994 and 1996 was mainly caused by the difference in leaf emergence date. The mean air temperature in the spring (March–May) of 1994 was  $4.8^\circ\text{C}$  higher than in 1996, resulting in the leaf emergence being 18–24 days earlier in 1994 than in 1996. The distribution of solar radiation over the OA forest growing season was highly asymmetrical, especially in 1996 when there were only 32 days before the summer solstice and 110 days after. The earlier leaf emergence in 1994, when the LAI was higher and the growing season longer than in 1996, resulted in 16% more absorbed PPFD and the annual photosynthesis being  $90 \text{ g C m}^{-2} \text{ y}^{-1}$  higher in 1994. The higher temperature in 1994 increased respiration by  $20 \text{ g C m}^{-2} \text{ y}^{-1}$ , or only 22% of the increase in photosynthesis. The increase in carbon sequestration by undisturbed terrestrial ecosystems due to rising air temperature and atmospheric  $\text{CO}_2$  concentration has usually been attributed to  $\text{CO}_2$  fertilization and an increase in soil nutrients. This analysis shows that increased spring temperature caused earlier leaf emergence which in turn caused the boreal OA forest to absorb more PPFD and sequester more carbon. This mechanism should be taken into account in future studies of the effects of global warming on boreal deciduous forests and their role in the global carbon budget.

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