

# Ecophysiological controls on the carbon balances of three southern boreal forests

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## Abstract

Continuous measurements of carbon exchange using the eddy covariance (EC) technique were made at three boreal forest mature sites including Southern Old Aspen (SOA), Southern Old Black Spruce (SOBS) and Southern Old Jack Pine (SOJP) in 2000. Climatic conditions were slightly warmer than normal with precipitation exceeding evapotranspiration at each site. Annual ecosystem respiration ( $R$ ) derived from daytime analyses of EC data was 1141, 815 and 521 g C m<sup>-2</sup> per year and was consistently lower than nighttime EC estimates of 1193, 897 and 578 g C m<sup>-2</sup> per year for SOA, SOBS and SOJP, respectively. The differences, however, were not statistically significant given the large uncertainty associated with each analytical technique. The uncertainty in annual net ecosystem productivity (NEP) was assessed by randomly simulating missing data and gap filling using simple biophysical algorithms. The uncertainty analysis supports the finding that each site was a net sink, and that differences in NEP were only significant between SOA and SOBS. The annual NEP and uncertainty for SOA, SOBS and SOJP was 122 (64–142), 35 (18–53) and 78 (61–91) g C m<sup>-2</sup> per year, respectively. These relatively old growth forests represent a weak to moderate carbon sink. Despite having the shortest growing period, carbon sequestration was greatest at SOA because of its relatively large photosynthetic capacity ( $A_{\max}$ ). At the evergreen sites,  $A_{\max}$  was marginally larger at SOBS; however, annual carbon sequestration was smaller as a result of greater  $R$ . The evergreen sites exhibited a pronounced mid-season reduction in NEP, which was attributed to a large increase in  $R$  while  $A_{\max}$  had not reached its full capacity. Non-growing season  $R$  resulted in a carbon loss of 285, 120 and 64 g C m<sup>-2</sup> and accounted for 70, 80 and 46% of the summertime NEP at SOA, SOBS and SOJP, respectively. Six years of EC data at SOA indicate that carbon sequestration at boreal aspen sites may benefit from warmer climatic conditions because  $R$  is relatively conservative and photosynthesis increases in response to a longer growing period.

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## 1. Introduction

Over the past decade, considerable progress has been achieved in measuring and modeling the carbon balance of temperate and northern boreal forest

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ecosystems (Sellers et al., 1997; Grant et al., 2001; Chen et al., 2000; Baldocchi et al., 2001). Interannual data sets from long-term research programs, such as AmeriFlux, Euroflux and the Boreal Ecosystem Research and Monitoring Sites (BERMS) Program, are providing new insight into the biophysical controls on ecosystem–atmosphere carbon exchange and the role that different forest types play in the global carbon cycle (Black et al., 2000; Law et al., 2000; Valentini et al., 2000; Barr et al., 2002). The major issues that have emerged from these studies include: (1) the importance of phenology and its impact on ecosystem carbon sequestration; (2) interannual variation in ecosystem respiration ( $R$ ) and its relative contribution to annual carbon exchange; (3) problems associated with eddy covariance (EC) measurements over tall vegetation; and (4) the significance of old growth forests as carbon sinks. Here, we examine the annual net ecosystem productivity (NEP) of three relatively old growth forests located near the southern boreal treeline in central Canada, treating each with a common methodological and analytical approach, to help address some of the above issues.

### 1.1. Phenology

In northern boreal ecosystems, phenology is especially sensitive to the timing of snowmelt and spring warming, which can have a significant impact on the annual and growing season carbon balance (Black et al., 2000; Griffis et al., 2000; Lafleur et al., 2001). In a Southern Old Aspen (SOA) (*Populus tremuloides* Michx) boreal forest located in Prince Albert National Park, Saskatchewan, Canada, Black et al. (2000) found that warm spring conditions enhanced annual carbon sequestration due to earlier leaf emergence. This phenological response was significant during the 1998 growing season as a consequence of El Niño and increased the carbon sink strength at SOA by about  $180 \text{ g C m}^{-2}$  per year. Warmer air and soil temperatures and the increase in productivity did not appear to increase  $R$  significantly. Saigusa et al. (2002) and Yamamoto et al. (1999) also reported earlier leaf emergence during 1998 for a cool temperate deciduous forest in central Japan and found phenology to be an important cause of the interannual variability in NEP and to be directly related to spring temperatures.

Frost and freeze events can also have a dramatic impact on physiology, phenology and therefore carbon exchange. Hollinger et al. (1994) found that the first autumn frost event ( $T_a < -1^\circ \text{C}$ ) significantly reduced the NEP of a boreal-northern hardwood transitional forest near Bangor, Maine, USA. It has been well documented that conifer photosynthetic rates decrease substantially after being exposed to subfreezing temperatures (Delucia and Smith, 1987; Hällgren et al., 1990). The impact of springtime freeze events, following leaf emergence, on NEP is not well known. Hogg et al. (2002) hypothesize that the increased frequency of late spring thaw/freeze events in Western Canada from 1984 to 1993 may partially explain the recent dieback of aspen stands in the region. To what extent spring freeze events influence the interannual variation in NEP remains poorly understood.

### 1.2. Ecosystem respiration

Considerable debate has focused on the role of plant and soil respiration in determining the carbon balance of forest ecosystems and how  $R$  will respond to future climate change (see Valentini et al., 2000; Giardina and Ryan, 2000; Grace and Rayment, 2000; Piovesan and Adams, 2001; Jarvis et al., 2001; Janssens et al., 2001). Valentini et al. (2000) concluded from EC experiments that  $R$  is the main determinant of the carbon balance, observing an increase in  $R$  with increasing latitude across the Euroflux study sites. Barr et al. (2002) argue that this trend is unusually strong in Europe because latitude integrates the main features of climate, which is not true for North America. Several studies have concluded that  $R$  controls the interannual variation in NEP. In a Southern Old Black Spruce (SOBS, *Picea mariana* Mill.) forest, located near Prince Albert, Arain et al. (2002) used EC measurements and the Canadian Land Surface Scheme (CLASS) with the carbon sub-model (C-CLASS) to argue that the interannual differences were due primarily to an increase in  $R$  and a small reduction in gross ecosystem photosynthesis ( $P$ ) at warmer temperatures. Morgenstern et al. (2002) reported similar findings for a West Coast Douglas-fir forest located near Campbell River, Vancouver Island, Canada. In their 4-year study, NEP was controlled by  $R$  and the carbon sink strength was reduced substantially due to a large  $R$  response to the warmer temperatures produced by the 1997–1998 El

Niño. Lee et al. (1999) reported large interannual differences in NEP for a mixed deciduous forest located at Camp Borden, in Southern Ontario, Canada. Greater sequestration was attributed to lower  $R$  induced by colder temperatures during spring and fall periods. Similar findings were reported by Pilegaard et al. (2001) for a beech (*Fagus sylvatica* L.) forest located in Denmark. Law et al. (2000) also observed greater variation in  $R$  than  $P$  for an old growth pine forest in the Pacific Northwest region of the US, which is frequently subject to water stress. Over longer time scales, predicting the response of  $R$  to climate change will prove more challenging. Recent evidence from plot-scale soil warming experiments indicate that soil respiration may acclimate to long-term warming (Liski et al., 1999) and there is also evidence that some plant species will also acclimate to long-term changes in temperature (Tjoelker et al., 1999). Furthermore, Janssens et al. (2001) showed that there is strong coupling between productivity and  $R$ , so that changes in  $P$  will likely limit  $R$ .

### 1.3. Eddy covariance fluxes above tall vegetation

There is substantive evidence to suggest that nighttime EC-derived fluxes underestimate the true biotic flux (ecosystem respiration) over tall vegetation. For example, Lavigne et al. (1997) who scaled up biotic chamber measurements to represent the forest ecosystem at six different boreal sites found that EC fluxes were on average 27% lower than the scaled sum of chamber fluxes. Law et al. (2000) also reported an underestimate of about 23% for a Pacific pine forest. Drewitt et al. (2002) measured continuous forest floor  $\text{CO}_2$  exchange with an automated six chamber system and found that the average soil efflux (heterotrophic plus autotrophic root respiration) was 17% greater than  $R$  derived from nighttime EC measurements above the forest. Recently, Wilson and Baldocchi (2001) showed that nighttime EC measurements over a deciduous forest near Oak Ridge, TN, USA, were susceptible to drainage flows, which resulted in a systematic underestimate of  $R$ . They replaced all of the nighttime data using either chamber data or the ecosystem model CANOAK. Their corrected annual NEP value was approximately  $300 \text{ g C m}^{-2}$  less than the estimate based primarily on EC measurements.

A number of other researchers have demonstrated the strong sensitivity of estimating annual  $R$  to EC measurements below a critical friction velocity ( $u_*$ ,  $\text{m s}^{-1}$ ) threshold (Wofsy et al., 1993; Goulden et al., 1997; Jarvis et al., 1997; Black et al., 2000; Barr et al., 2002). Barr et al. (2002) demonstrated that increasing  $u_*$  from 0.15 to  $0.35 \text{ m s}^{-1}$  caused  $R$  to increase from 940 to  $1210 \text{ g C m}^{-2}$  at a temperate mixed wood forest near Camp Borden, Ont., and  $910\text{--}1020 \text{ g C m}^{-2}$  at SOA. However, Barford et al. (2001) have shown that the sensitivity of annual NEP is very small above the critical friction velocity threshold. Lee (1998) argued that the nighttime EC measurements could underestimate the true biotic flux under weak synoptic mixing conditions as a consequence of subsidence, vertical advection, and the development of thermal circulation, which are all interrelated. Although there has been considerable debate over this hypothesis, and the ability to measure and quantify such effects (Finnigan, 1999), Lee's analysis indicates that additional carbon loss at SOA could be as large as  $260 \text{ g C m}^{-2}$  per year causing the measured sink strength to nearly vanish.

### 1.4. Old growth forest carbon dynamics

For years, the carbon balance of mature forests has been considered to be in equilibrium, reaching a maximum capacity for a given climate and physiographic setting. Current research, however, suggests that mature forest carbon sequestration is underestimated in global carbon balance studies (Carey et al., 2001). Studies by Carey et al. (1997) and Lavigne and Ryan (1997) indicate that autotrophic respiration decreases with increasing age, allowing mature forests to maintain a carbon sink status. Entry and Emmingham (1998) showed that mature Douglas-fir forest soils contained greater carbon content and higher percentages of recalcitrant compounds than young forests, and that soil carbon recycling rates decreased with age. The accumulation of recalcitrant compounds may be key in maintaining the long-term sink strength of old forests (Schulze et al., 2000).

In this paper, we make use of daytime and nighttime half-hour EC measurements and a form of the Michaelis–Menten light-response equation to better understand the ecophysiological controls on the annual carbon balances of three old forests located at

the southern boreal treeline. The three forest types chosen for this investigation include aspen (*Populus tremuloides* Michx.), black spruce (*Picea mariana* Mill. BSP) and jack pine (*Pinus banksiana* Lamb.). These three forest types dominate the boreal biome (Sellers et al., 1997) and we hypothesize that they will each exhibit a unique response to climate variation. In order to assess these potential differences and improve our understanding of boreal forest carbon cycling, it is critical to obtain reliable estimates of NEP,  $P$ ,  $R$  and key ecophysiological parameters. Here, we report on measurements made during the year 2000 and present the first annual comparison of carbon fluxes and annual carbon balances for these three boreal forest types. The objectives of this paper are to:

- (i) estimate  $R$  using independent analyses of nighttime and daytime EC data;
- (ii) contrast the seasonal changes in the ecophysiological characteristics of deciduous and evergreen boreal forests;
- (iii) compare the seasonal and annual NEP values among these forest types and interpret these differences by partitioning NEP into  $P$  and  $R$ .

## 2. Methods

### 2.1. Study sites

The study sites were established in 1993 as part of the Boreal Ecosystem–Atmosphere Study (BOREAS) and are referred to as Southern Old Aspen (SOA), Southern Old Black Spruce (SOBS) and Southern Old Jack Pine (SOJP). The sites are located near the southern boreal treeline and are subject to the same synoptic meteorological forcing. SOA is located in Prince Albert National Park, Saskatchewan, Canada, approximately 80 km west–southwest of SOBS. SOJP is located about 30 km east–southeast of SOBS (Table 1). Detailed descriptions of the sites (vegetation, soil, etc.) can be found in Blanken et al. (1997), Jarvis et al. (1997) and Baldocchi et al. (1997a). Under the Boreal Ecosystem Research and Monitoring Sites Program, flux measurements at SOA have continued since 1996 and at SOBS and SOJP since 1999.

### 2.2. Eddy covariance flux measurements

Wind velocity and temperature fluctuations were measured with a three-dimensional sonic anemo-

Table 1  
Physical and historical features of the southern boreal forest study sites

Site <sup>a</sup>	Location	Elevation (m)	Slope (%)	Depth of organic (cm)	Soil carbon (kg C m <sup>-2</sup> )	Mean annual air temperature (°C) <sup>b</sup>	Annual precipitation (mm) <sup>b</sup>
(a) Location, physiography and climate							
SOA	53.629°N, 106.200°W	600.6	~1	5–10	6.7	1.3 (–0.2)	484 (463)
SOBS	53.987°N, 105.117°W	628.9	~1	20–30	39.2	1.1 (–0.2)	484 (463)
SOJP	53.916°N, 104.69°W	579.3	2–5	0–5	3.4	1.3 (–0.2)	379 (463)
Site	Stand age (years) <sup>c</sup>	Canopy height (m) <sup>d</sup>	EC height (m)	LAI	Stand density (stems ha <sup>-1</sup> ) <sup>d</sup>	Understory	Life history
(b) Stand characteristics and life history							
SOA	73	20.1	33.0	5.8	980	Dense hazelnut	Wildfire 1919 and natural regeneration
SOBS	121	7.2	25.0	4.2	5900	Dense moss cover with shrubs	Uniform age structure suggesting regeneration following wildfire
SOJP	71	12.7	28.0	2.5	1190	Dense lichen cover with herb species	Uniform age structure, regeneration from wildfire

<sup>a</sup> SOA is located in Prince Albert National Park, Saskatchewan, Canada, approximately 80 km west–southwest of SOBS and SOJP. SOJP is located about 30 km east–southeast of SOBS.

<sup>b</sup> Bracketed term is the climate normal based on the 30-year record 1951–1980 at Waskesiu Lake (53.917°N, 106.083°W) from Environment Canada.

<sup>c</sup> Age of stand as of year 2000 from Gower et al. (1997).

<sup>d</sup> Characteristics measured by Gower et al. (1997).

meter–thermometer (model R3, Gill Instruments, Lymington, UK at SOA and SOBS; model CSAT3, Campbell Scientific, Inc., Utah, USA at SOJP) mounted above the forest (Table 1) on scaffold towers. CO<sub>2</sub> and water vapour fluctuations were measured with a closed-path infrared gas analyzer (IRGA, model 6262, LI-COR, Inc., Lincoln, NE, USA). The IRGA was located in a temperature-controlled enclosure and mounted on the canopy tower within 3 m of the sonic anemometer. A heated tube, 4 m in length, was connected to the IRGA, which sampled air from within 30 cm of the sonic anemometer. A diaphragm pump (model DOA-V191-AA, Gast, Inc., Dayton, OH) pulled the air through the IRGA at a flow rate of 101 min<sup>-1</sup>. The tube intake was positioned below the sonic array to reduce flux loss (Kristensen et al., 1997). The IRGA was automatically calibrated daily using CO<sub>2</sub> standards from the Canadian Greenhouse Gases Measurement Laboratory (GGML) of the Meteorological Service of Canada in Downsview, ON. The analogue EC signals were measured by a data acquisition system (model DAQBook/200, IOTech, Inc.) at a sampling rate of 125 Hz, digitally filtered and down-sampled at 20.8 Hz to a computer for on-line flux calculations (see Chen et al. (1999) for a detailed description of the EC system). Half-hour block averaged carbon flux calculations were computed using

$$F_c = \frac{\bar{\rho}_a}{M_a} \overline{w's'_c} \quad (1)$$

where  $F_c$  is the eddy flux of CO<sub>2</sub> above the forest,  $\rho_a$  the density of dry air,  $M_a$  the molecular weight of dry air,  $w$  the vertical velocity,  $s_c$  the CO<sub>2</sub> mole mixing ratio, the primes indicate the differences between instantaneous and mean values and the over bar indicates an averaging operation.  $\overline{w's'_c}$  is the covariance of  $w$  and  $s_c$ . The averaging interval was 30 min.  $F_c$  values were corrected for daytime and nighttime energy balance closure (EBC) at each of the sites. The correction was derived from the linear regression analysis of annual half-hour turbulent fluxes ( $H + \lambda E$ ) versus available energy (net radiation ( $R_n$ ) – soil heat flux ( $G$ ) – change in air column and biomass heat storage ( $S$ )). The linear regression equation was applied to the half-hour fluxes of  $F_c$ . Energy balance closure at SOA, SOBS and SOJP was 88, 89 and 85%, respectively. CO<sub>2</sub> fluxes were storage corrected using an eight-level CO<sub>2</sub> concentration profile sys-

tem at SOA and SOBS. At SOJP, the storage correction was computed using the change in CO<sub>2</sub> concentration at the EC level following Hollinger et al. (1994). This procedure was validated following Yang et al. (1999) by comparing differences between the one-level correction and eight-level correction at SOA. In each case the annual cumulative storage was less than 1 g C m<sup>-2</sup> per year with half-hour fluctuations as large as 25 μmol m<sup>-2</sup> s<sup>-1</sup>. NEP was approximated by –NEE, the net ecosystem exchange, and computed from

$$\text{NEP} = -(F_{cc} + S_c) \quad (2)$$

where  $F_{cc}$  is the EBC corrected CO<sub>2</sub> flux and  $S_c$  is the change in air column CO<sub>2</sub> storage between the forest floor and the sonic anemometer. Missing  $F_c$  observations at SOA, SOBS and SOJP in 2000 accounted for 9.3, 9.5 and 8.2% of the half-hour flux measurements, respectively. Approximately 2% of the missing observations resulted from system calibration. The remaining missing data were most often caused by frost accretion on the sonic anemometer transducers.

### 2.3. Climate measurements

Supporting measurements included air and soil temperature, measured using a platinum resistance thermometer and copper–constantan thermocouples, respectively. Atmospheric humidity was measured using humidity sensors (model HMP-35C, Vaisala, Inc., Oy, Finland). Incident photosynthetic photon flux density (PAR), was measured above the canopy ( $Q_0$ ) with a quantum sensor (model 190-SB, LI-COR, Inc., Lincoln, NE, USA). Net radiation was measured above each canopy with a net radiometer (model CN1-R, Middleton Instruments, Melbourne, Australia). Precipitation was measured with a weighing gauge (Belfort Instruments, Baltimore, MD, USA) at each site. Volumetric soil water content was measured using soil water reflectometers (model CS 615, Campbell Scientific, Inc.).

### 2.4. Canopy PAR absorption

Following Chen et al. (1999) we estimated the fraction of incident PAR absorbed by the canopy foliage ( $Q_a$ ) for each of the forests. For SOA PAR absorption



was calculated from

$$Q_a = Q_0[1 - e^{-k_a A_{La}} + e^{-k_a(A_{La} + A_{wa})}(1 - e^{-k_h A_{Lh}})] \times (1 - \alpha) \quad (3a)$$

where  $k_a$  and  $k_h$  are extinction coefficients for the aspen and hazel nut (0.540 and 0.756, respectively),  $A_{La}$  and  $A_{Lh}$  the effective leaf area index (LAI), corrected for clumping, for aspen and hazelnut (Table 1),  $A_{wa}$  the wood area index for aspen (0.96), and  $\alpha$  the PAR albedo (0.03) of the aspen forest canopy. For SOBS and SOJP,  $Q_a$  was calculated from

$$Q_a = Q_0(1 - e^{-k A_L})(1 - \alpha) \quad (3b)$$

where  $k$  is the extinction coefficient (0.430 and 0.523, respectively)  $A_L$  the effective LAI (4.2 and 2.5), and  $\alpha$  the PAR albedo (0.035 and 0.04, respectively).

## 2.5. Canopy-scale light-response analysis

Light-response functions have been used extensively in the literature to characterize the photosynthetic and respiratory characteristics of a variety of ecosystems (Ruimy et al., 1995; Landsberg and Gower, 1997; Frolking et al., 1998). We analyzed the daytime only ( $Q_a > 0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) EC half-hour fluxes, using a minimum friction velocity threshold of  $u_* = 0.35 \text{ m s}^{-1}$ . This quality control criterion was used to ensure turbulent conditions during periods of low light and low available energy during the early morning and late afternoon hours and to reduce the run-to-run variability in half-hour EC fluxes caused by changes in  $\text{CO}_2$  storage. The photosynthetic and respiratory parameters were obtained daily and monthly during the growing period using a non-linear least squares optimization of the light-response function from Landsberg and Gower (1997)

$$\text{NEP} = \frac{\alpha_p A_{\max} Q_a}{\alpha_p Q_a + A_{\max}} - R_d \quad (4)$$

where  $A_{\max}$  is the canopy-scale photosynthetic capacity,  $\alpha_p$  the quantum yield and  $R_d$  the daytime ecosystem respiration. The sensitivity of the light-response parameters to a simultaneous 10% change in each of the  $Q_a$  parameters was less than 0.5% for  $A_{\max}$  and  $R_d$  and 13% for  $\alpha_p$ . The daily estimates of  $R_d$  were used to develop an annual respiration–temperature

function independent of nighttime EC measurements (discussed below).

## 2.6. Annual ecosystem respiration and photosynthesis

We estimated annual  $R$  using empirical functions to fill gaps in  $R$  at night and to estimate  $R$  during the day. We compared two empirical approaches based on nighttime and daytime EC measurements of NEP. In both cases, measured NEP was excluded when  $u_*$  was less than  $0.35 \text{ m s}^{-1}$ . The first approach used the nighttime measurements of NEP to estimate  $R$  as a function of soil temperature at the 2 cm depth:

$$R = d_1 e^{d_2 T_s} \quad (5)$$

where  $d_1$  and  $d_2$  are the fitted parameters obtained from the regression of nighttime NEP versus the 2 cm soil temperature ( $T_s$ ). We refer to this as the nighttime  $R$  function ( $R_{\text{nf}}$ ). Barr et al. (2002) demonstrated that  $R$  is not sensitive to  $u_*$  above  $0.35 \text{ m s}^{-1}$  at SOA, which was also the case for SOBS and SOJP. A bin width of  $2^\circ\text{C}$  with a minimum bin size of  $n = 10$  was used in the fitting procedure to reduce the effects of heteroscedasticity and to provide equal weighting in the parameter estimates. For comparative analysis, the daily estimates of  $R_d$  and the non-growing season daytime carbon fluxes satisfying the  $u_*$  threshold criterion,  $u_* > 0.35 \text{ m s}^{-1}$ , were used to develop an annual daytime  $R$  function ( $R_{\text{df}}$ ) dependent on the mean daytime soil temperature measured at the 2 cm depth.  $R_d$  values were included in the annual analysis for cases with a regression coefficient of determination ( $r^2$ ) greater than 0.70 for the daily fitting procedure. The partitioning of daytime NEP into  $P$  and  $R$  using the daily light-response analysis is shown in Fig. 1 for each site during three different growing periods. The agreement between the light-response estimate and measured NEP on a daily basis illustrates that this method can be used to estimate  $R$  independently of nighttime EC measurements. Each of the light-response parameters was successfully obtained (i.e.  $r^2 > 0.70$  and excluding unrealistic values of  $A_{\max}$  and  $R_d$ ) for greater than 60% of the growing period days for each of the sites. The annual  $R$  function derived from this daytime EC analysis ( $R_{\text{df}}$ ) was described using the exponential function (Eq. (5)). For consistency, bin widths of  $2^\circ\text{C}$  with a minimum

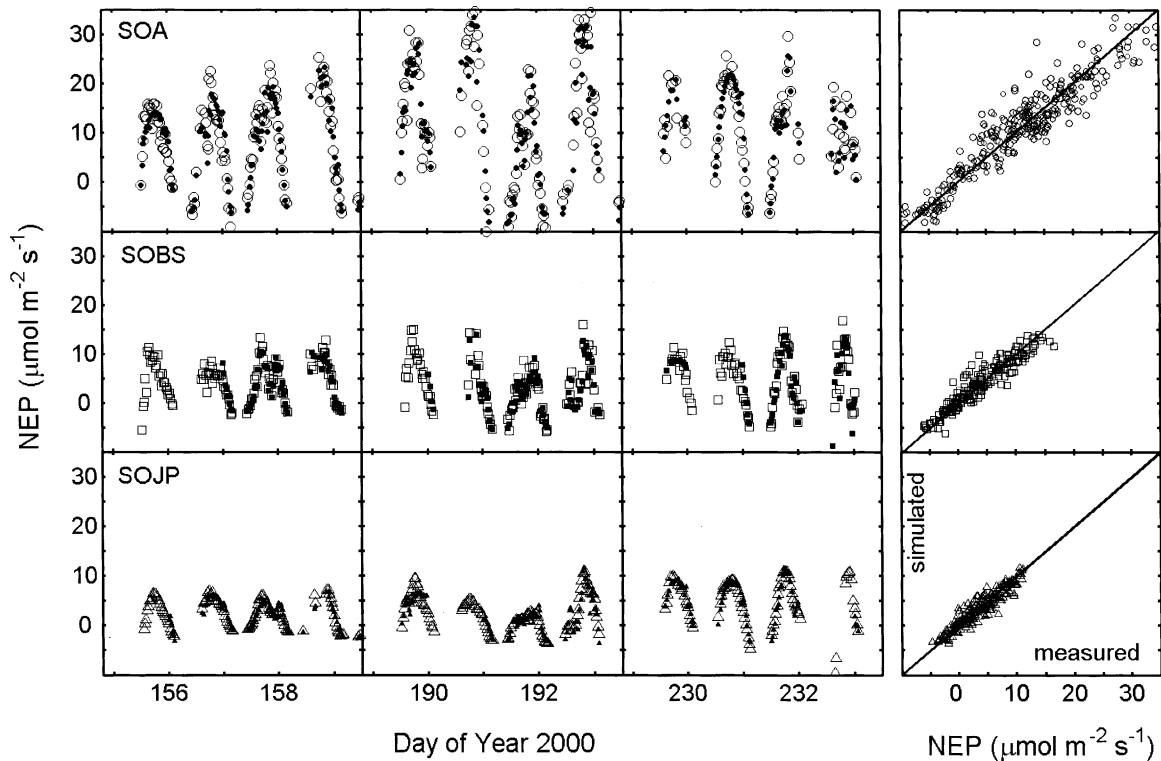


Fig. 1. Daily light-response analysis showing the agreement between diurnal half-hour estimates (closed symbols) and measured NEP values (open symbols) for three different growing periods (left panels) and the 1:1 plot of the half-hour estimates of NEP versus measured NEP for the three periods (far right panel). The non-linear fitting procedure was based on daytime eddy covariance data with  $u_* > 0.35 \text{ m s}^{-1}$ . The Michaelis–Menten light-response parameter,  $R_d$ , was accepted for cases when the coefficient of determination ( $r^2$ ) was greater than 0.70.

bin size of  $n = 10$  were used in the fitting procedure. Finally, annual  $P$  was estimated from  $P = \text{NEP} + R$ .

### 3. Results

#### 3.1. Forest climate

Climatic conditions during 2000 were warmer and wetter at SOA and SOBS and warmer and drier at SOJP than the 30-year normal recorded at Waskesiu Lake (Table 1 and Fig. 2). Daily average air temperature and  $Q_0$  was similar among the sites. The warmest air temperatures were observed during late July, with maximum half-hour air temperatures exceeding  $30^\circ\text{C}$ . For the three sites, average annual mean air temperature was  $1.2^\circ\text{C}$  and average annual precipitation was 449 mm. SOJP received significantly less summertime

precipitation than SOA and SOBS. The majority of the precipitation, 81%, was received during the period of 1 May (DOY 120) to 31 August (DOY 242). Annual evapotranspiration measured using EC was 399, 346 and 283 mm at SOA, SOBS and SOJP, respectively. The corresponding sum of precipitation minus evapotranspiration was 85, 138 and 96 mm indicating that water was not limiting during this year. The summertime volumetric soil water content at a depth of  $\sim 10$  cm ranged from 20 to 33% at SOA, 9 to 15% at SOBS and 4 to 10% at SOJP.

SOA absorbed  $\sim 56\%$  of the annual  $Q_0$  ( $Q_0$  in Eq. (3)) with maximum absorption occurring between leaf emergence (24 April, DOY 115) and the beginning of leaf senescence (15 September, DOY 260). PAR reaching the forest floor was substantial prior to hazelnut leaf emergence. This observation is in good agreement with Blanken et al. (1997) who measured

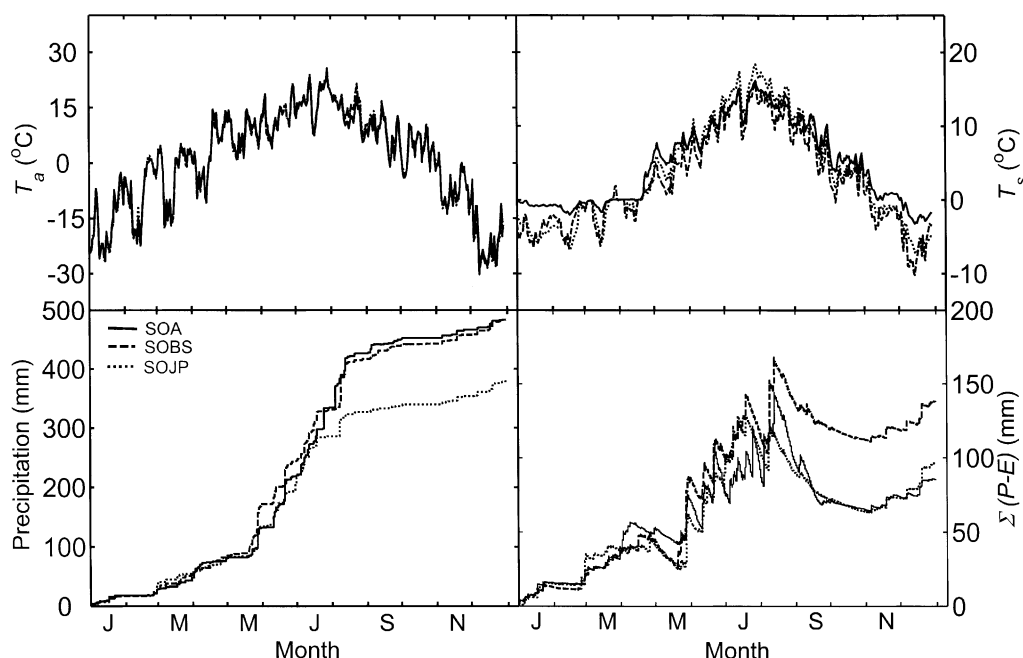


Fig. 2. Comparison of forest climate at the Southern Old Aspen (SOA), Southern Old Black Spruce (SOBS) and Southern Old Jack Pine (SOJP) sites during 2000. Each site is subjected to the same synoptic meteorological forcing. Air temperature ( $T_a$ ) was measured at each site at the height of the sonic anemometer; soil temperature ( $T_s$ ) was measured at a depth of 2 cm; cumulative water balance,  $\Sigma(P - E)$ , was estimated by subtracting the eddy covariance estimate of evapotranspiration from precipitation.

the spatial variability in PAR below the aspen canopy using a tram system. By May 29 (DOY 150), the SOA canopy absorbed nearly 90% of  $Q_0$ . The SOBS overstory absorbed 81% of annual  $Q_0$ . About 19% penetrated to the forest floor and was available for driving the photosynthetic activity of the dense surface cover of mosses and shrubs. Roujean (1999) estimated that only 10% of  $Q_0$  reached the SOBS forest floor but acknowledged this could be an underestimate due to the placement of sensors within a relatively dense sample plot. The SOJP canopy absorbed  $\sim 70\%$  of annual  $Q_0$  and was substantially lower compared to SOBS. This value is in excellent agreement with measured observations at SOJP (Baldocchi et al., 1997a; Roujean, 1999). A small fraction of radiation reaching the lichen surface is absorbed and used for photosynthesis (Baldocchi and Vogel, 1996).

Canopy structure and phenological changes affect radiation absorption, transmission, and energy exchange with the atmosphere and, thereby, influence the thermal regime of the underlying soil and

soil respiration rates. Differences in soil temperature between the sites and through the season were substantial. From May to August, SOJP had the highest soil temperature followed by SOA and SOBS. High soil temperature at SOJP was due to the relatively large transmission of radiation to the soil surface and the high thermal conductivity of its sandy soil. During September to December the soil at SOA was relatively warm. From January to April the lowest soil temperatures were observed at SOJP and SOBS, while soil temperature at SOA remained near  $0^\circ\text{C}$ . The upper soil layer was frozen at SOBS and SOJP from approximately November to May and at SOA from December to May.

### 3.2. Comparing nighttime and daytime estimates of ecosystem respiration

Given the potential problems associated with nighttime EC measurements such as inadequate turbulent mixing, vertical advection, extended flux footprints,



and as well, the potential for differences in physiological behavior between daytime and nighttime, we compared the annual values of  $R$  estimated using the function derived from daytime EC measurements ( $R_{df}$ ) with those estimated using the nighttime function ( $R_{nf}$ ) derived from high  $u_*$  EC measurements. The annual  $R_{nf}$  and  $R_{df}$  functions computed for the three sites indicated that the daytime respiration values were within the uncertainty of the nighttime estimates (Fig. 3 and Table 2). Falge et al. (2002) also reported excellent agreement between daytime light-response estimates of  $R$  and nighttime  $R$  for a variety of ecosystem types. Studies have concluded that leaf respira-

tion is lower during the daytime than at night due to the Kok effect—the light inhibition of dark respiration (Brooks and Farquhar, 1985; Villar et al., 1994; Padmavathi and Raghavendra, 2001). Janssens et al. (2001) suggested that daytime  $R$  could be overestimated by as much as 15% when using nighttime functional relationships because they do not account for the Kok effect. However, it must be noted that the Kok effect only influences daytime leaf respiration, which is a relatively small component of total  $R$  (Ryan et al., 1997). Annual  $R_{df}$  for SOA, SOBS and SOJP were 1141, 815 and 521 g C m<sup>-2</sup> per year, respectively, and were slightly lower than the nighttime EC estimates,

Table 2  
Nighttime and daytime respiration algorithms and annual respiration estimates

Site and wind direction	$d_1$	$d_2$	$r^2$	$Q_{10}$	Mean $T_a$ (°C)	Mean $T_s$ (°C)	$x_{max}$ (m)	$n$	Annual $R$ (g C m <sup>-2</sup> per year)
SOA									
$R_{nf}$									
All directions	1.17	0.15	0.98	4.3	-1.6	3.4	153	3191	1193
NE	1.44	0.13	0.97	3.5	-5.2	2.9	114	571	1235
SE	1.14	0.13	0.95	3.7	2.9	4.8	132	670	1022
SW	1.16	0.16	0.99	5.0	-2.5	2.7	200	584	1364
NW	1.19	0.15	0.99	4.3	-2.3	3.1	156	1366	1229
$R_{df}$	1.37	0.12	0.91	3.3	4.4	5.7	78	5084	1141
SOBS									
$R_{nf}$									
All directions	1.26	0.12	0.98	3.5	-3.6	1.2	268	2437	897
NE	0.96	0.15	0.99	4.5	-3.7	1.6	249	418	852
SE	1.11	0.13	0.96	3.8	0.3	2.9	235	512	845
SW	1.09	0.15	0.96	4.6	-3.4	0.3	342	253	979
NW	1.28	0.13	0.97	3.7	-5.1	0.6	273	1254	951
$R_{df}$	1.38	0.10	0.92	2.7	4.9	4.2	114	4532	815
SOJP									
$R_{nf}$									
All directions	0.64	0.13	0.99	3.6	-4.3	1.6	171	2560	578
NE	0.53	0.14	0.99	4.0	-4.6	3.1	153	986	529
SE	0.70	0.12	0.95	3.2	-2.4	2.5	169	411	565
SW	0.57	0.17	0.94	5.6	-5.2	-0.9	223	311	832
NW	0.59	0.15	0.99	4.6	-4.6	0.3	174	852	680
$R_{df}$	0.76	0.10	0.91	2.7	4.9	5.1	86	4762	521

Nighttime respiration functions ( $R_{nf}$ ) were estimated using NEP data as a function of the 2 cm soil temperature for  $u_* > 0.35$  m s<sup>-1</sup>. Wind direction analysis for the nighttime data was used to examine the uncertainty caused by landscape heterogeneity on estimating respiration parameters and annual estimates of respiration. Daytime respiration functions ( $R_{df}$ ) were estimated using daytime only NEP data with  $u_* > 0.35$  m s<sup>-1</sup> derived from a light-response analysis. Bin widths of 2 °C with a minimum bin size of  $n = 10$  were used in the fitting procedure to reduce the effects of heteroscedasticity and to provide equal weighting in the parameter estimates. Peak flux footprint ( $x_{max}$ ) was used to examine the influence of extended flux footprints on estimating the daytime and nighttime respiration functions. The model proposed by Schuepp et al. (1990) was adapted to include stability corrections (Blanken et al., 2001) to estimate  $x_{max}$ . The energy balance closure correction was applied prior to calculating the respiration parameters.

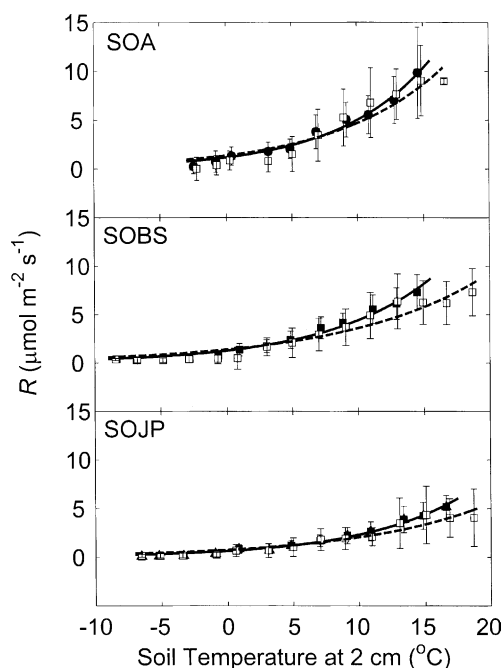


Fig. 3. Comparison of nighttime (closed symbols) and daytime (open symbols) derived respiration functions. Nighttime respiration functions were estimated from the relation between NEP data and the 2 cm soil temperature for  $u_* > 0.35 \text{ m s}^{-1}$ . Daytime respiration functions were estimated using daytime only NEP data with  $u_* > 0.35 \text{ m s}^{-1}$  with daily respiration values during the growing season estimated from the Michaelis–Menten light-response analysis. Bin widths of  $2^\circ\text{C}$  with a minimum bin size of  $n = 10$  were used in the fitting procedure to reduce the effects of heteroscedasticity and to provide equal weighting in the parameter estimates.

however, within the relative error of each analytical technique. The  $R_{\text{df}}$  estimates were also similar to the  $R_{\text{nf}}$  estimates based on a wind direction analysis. Although the nighttime-derived functions and annual  $R$  totals are associated with extended flux footprints (approximately double the daytime peak flux footprint estimated from the Schuepp et al. (1990) one-dimensional model) they generally agree with the daytime-derived estimates at each site. Furthermore, there was no evidence of a significant influence of landscape heterogeneity on the annual  $R$  estimates derived using the nighttime analysis. The use of  $R_{\text{nf}}$  may not be suitable at study sites where heterogeneity and fetch limitations are an issue. The agreement between  $R_{\text{nf}}$  and  $R_{\text{df}}$  in this analysis confirms that these study sites are not significantly affected by het-

erogeneity or fetch problems. These two independent approaches, therefore, suggest that they can be used reliably to partition daytime NEP into  $R$  and  $P$ .

### 3.3. Seasonal variation of net ecosystem productivity, respiration and photosynthesis

The daytime and nighttime values of NEP for the three stands are shown in Fig. 4 for the year 2000. Approximately 48, 56 and 61% of the nighttime observations at SOA, SOBS and SOJP, respectively, were excluded due to low friction velocity. The seasonal change in nighttime  $R$  (minus nighttime NEP) at each of the sites was strongly correlated with soil and air temperature. Maximum wintertime (November to March) nighttime  $R$  fluxes from SOA, SOBS

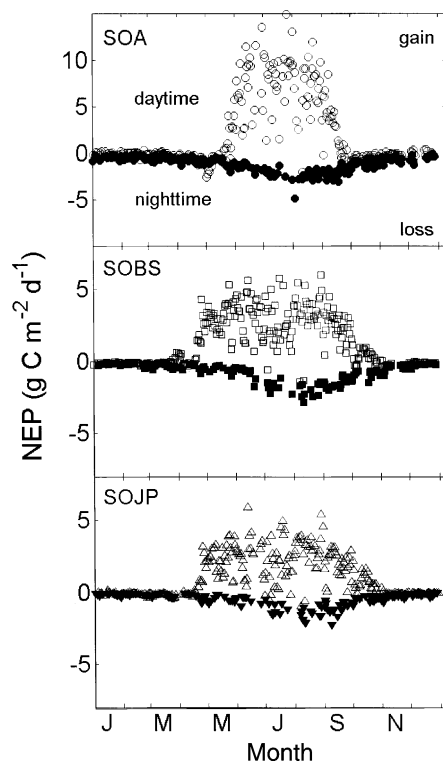


Fig. 4. Seasonal course of the total daytime (open symbols) and total nighttime (closed symbols) NEP measured with eddy covariance for  $u_* > 0.35 \text{ m s}^{-1}$  with number of acceptable half hours during a night,  $n > 5$  at SOA (circles), SOBS (squares) and SOJP (triangles). Note the large day-to-day variability in fluxes and the large number of missing observations at night resulting from low  $u_*$ .

and SOJP were 1.4, 1.0 and 0.7 g C m<sup>-2</sup> per day, respectively. Corresponding maximum growing season (May to September) nighttime  $R$  fluxes from SOA, SOBS and SOJP were 4.9, 2.9 and 2.3 g C m<sup>-2</sup> per day, respectively. The maximum daytime growing season NEP (i.e.  $P - R$ ) was 17.4, 6.0 and 5.9 g C m<sup>-2</sup> per day at SOA, SOBS and SOJP, respectively. There was considerable day-to-day variability in the daytime growing period NEP and a significant reduction was observed at both of the evergreen sites during July.

Fig. 5 illustrates the differences in the canopy-scale,  $A_{\max}$ ,  $\alpha_p$  and  $R_d$ , among the sites for June, July and August. SOA showed the largest  $A_{\max}$ , reaching a maximum of 43.4  $\mu\text{mol m}^{-2} \text{s}^{-1}$  during July. SOBS and SOJP reached a maximum of 21.6 and 18.5  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively during August.  $\alpha_p$  reached a maximum during July for each of the sites and was greatest at SOA, followed by SOBS and SOJP. Our  $\alpha_p$  values are larger than previously pub-

lished values ranging from 0.04 to 0.06 for SOA (Chen et al., 1999; Hogg et al., 2000). This is largely related to the data screening procedure where  $u_* > 0.35 \text{ m s}^{-1}$ . Low  $u_*$  values are often experienced in the early morning when conditions are relatively stable and light-levels are low. Removal of these data from the analysis tends to increase the initial slope of the light-response curve and therefore  $\alpha_p$ .  $R_d$  progressively increased during the summer at SOA and SOBS reaching a maximum in August, while at SOJP it was greatest in July.

Daily average NEP,  $P$  and  $R$  are shown in Fig. 6. There were strong phenological differences between the evergreen and deciduous ecosystems and a high degree of similarity between the evergreen forests. Photosynthetic activity occurred 31 days earlier in spring and 25 days later in fall at SOBS and SOJP compared to SOA. At SOA,  $P$  was greatest during early summer when  $R$  was relatively small. Daily carbon

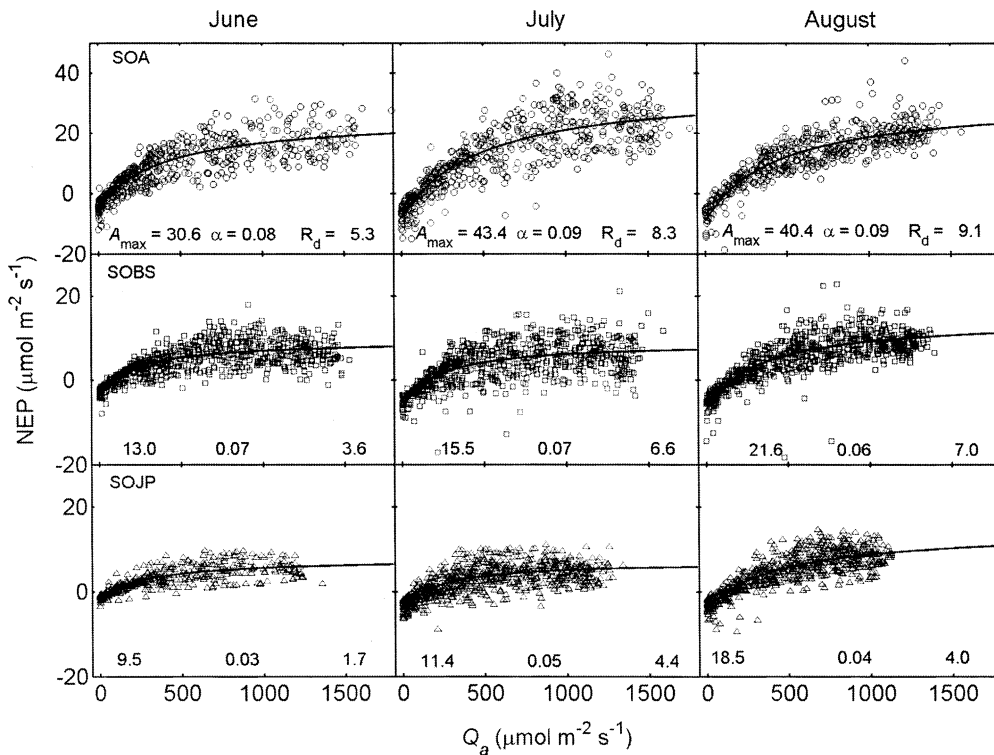


Fig. 5. Michaelis-Menten light-response analysis (see Eq. (4)) of daytime eddy covariance NEP data for the BERMS sites during June, July and August 2000 plotted as a function of absorbed photosynthetically active radiation ( $Q_a$ ). All eddy covariance data shown satisfy  $u_* > 0.35 \text{ m s}^{-1}$ .

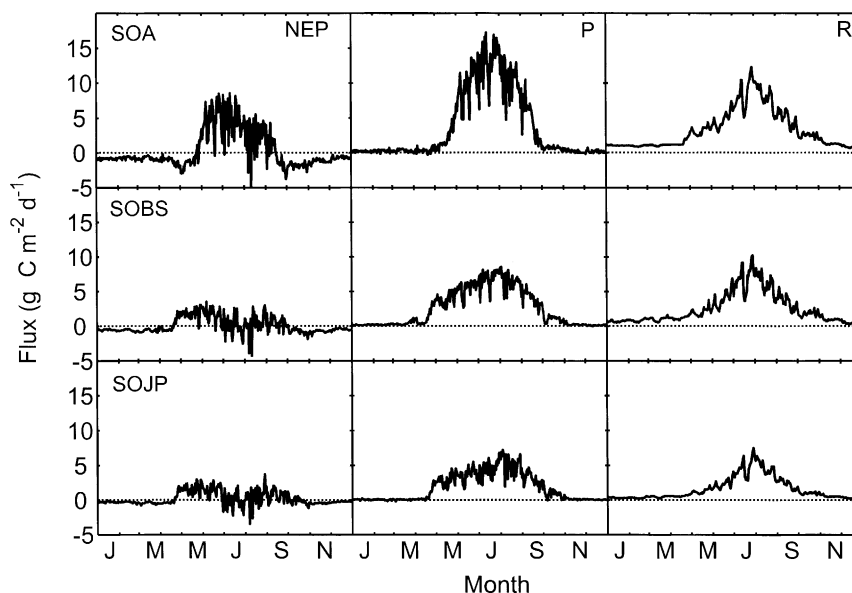


Fig. 6. Seasonal courses of daily values of net ecosystem production (NEP), gross ecosystem photosynthesis ( $P$ ) and ecosystem respiration ( $R$ ) for the BERMS sites. NEP was partitioned into  $R$  using the annual nighttime eddy covariance respiration–temperature function.  $P$  was estimated by adding  $R$  to the daytime NEP. All values are corrected for energy balance closure.

sequestration during the early summer period averaged  $\sim 8 \mu\text{mol m}^{-2} \text{s}^{-1}$  ( $\sim 8 \text{ g C m}^{-2}$  per day). NEP decreased as the summer season progressed due to increased  $R$  and a small reduction in  $A_{\text{max}}$  during August. No appreciable change was observed in  $\alpha$ . NEP was greatest at SOBS and SOJP during May, June and August.  $P$  was greatest during August and September due to a peak in  $A_{\text{max}}$  during this period. The strong mid-summer (July) decline in NEP at the evergreen sites was characterized by relatively low  $A_{\text{max}}$  and increasing  $R$ . A comparison of the light-response functions for SOBS and SOJP for June, July and August highlight these seasonal changes (Fig. 5).

### 3.4. Annual carbon balances

The annual cumulative carbon balance for each site was computed by replacing missing daytime growing season data with a 14-day moving window light-response estimate of NEP. Missing nighttime and non-growing season data were estimated from the  $R_{\text{nf}}$  function. The annual sum of raw and corrected fluxes is listed in Table 3. In each case, replacement of low  $u_*$  data at night reduced the raw flux totals

Table 3

Annual estimates of ecosystem respiration ( $R$ ), gross ecosystem photosynthesis ( $P$ ) and net ecosystem production (NEP)

Site	$R$		$P$		NEP		
	EBC	N-EBC	EBC	N-EBC	Raw	EBC	N-EBC
SOA							
Annual	1193	1081	1315	1188	187	122	107
Night	444	391					
Day	749	690					
SOBS							
Annual	897	800	932	830	142	35	30
Night	311	277					
Day	586	523					
SOJP							
Annual	578	491	656	557	104	78	66
Night	196	166					
Day	382	325					

EBC, energy balance closure corrected flux values; N-EBC, non-energy balance closure corrected flux values; Raw, non-energy balance closure corrected with low  $u_*$  nighttime observations included. Annual totals were obtained by replacing missing daytime growing season data with a 14-day moving window light-response estimate of NEP. All  $R$  totals were derived from the nighttime  $R$  function.  $P$  was estimated as  $\text{NEP} + R$ .

substantially. EBC and  $u_*$  corrected annual totals were 122, 35 and 78  $\text{g C m}^{-2}$  per year at SOA, SOBS and SOJP, respectively. Without EBC correction totals were 107, 30 and 66  $\text{g C m}^{-2}$  per year, respectively. The EBC correction increased daytime fluxes more than nighttime fluxes and resulted in greater NEP because  $P$  was significantly larger than daytime  $R$ . The replacement of low  $u_*$  data at night reduced the annual NEP at SOBS the most due to the large difference between fluxes during calm and turbulent conditions.

The uncertainty in the annual NEP estimates was assessed by randomly removing up to 30% of the annual data using a uniform discrete random number generator. The number of continuous missing observations was also randomly selected to range from one missing half-hour to 3 days. The daytime and nighttime  $R$  functions and the light-response estimates of NEP, used for gap filling, were then recomputed from the remaining data. The missing observations were replaced with the new gap filling function estimates (as described above) and the annual carbon balance was recomputed (see Falge et al., 2001; Goulden et al., 1996 for similar approaches). The experiment was repeated 100 times to produce the uncertainty range shown in Fig. 7. From this analysis we conclude that the annual carbon balance differences were only significant between SOA and SOBS. The annual uncertainty in NEP for SOA, SOBS and SOJP ranged from 64 to 142, 18 to 53 and 61 to 91  $\text{g C m}^{-2}$  per year, respectively. A large number of the uncertainty simulations indicated that NEP was substantially lower than our “best” annual estimate demonstrating that the gap filling procedure tends to increase  $R$  relative to  $P$ .

Annual  $R$ , based on corrected estimates from  $R_{\text{nf}}$ , were 1193, 897 and 578  $\text{g C m}^{-2}$  per year for SOA, SOBS and SOJP, respectively. Daytime  $R$  accounted for 59, 53 and 51% of the total  $R$  at SOA, SOBS and SOJP, respectively. Non-growing season carbon loss (or NEP) was about 285  $\text{g C m}^{-2}$  at SOA. A strong increase in  $R$  was observed in May and correlated with spring warming, an increase in soil temperature, and the onset of photosynthesis. Non-growing season carbon losses at SOBS and SOJP were 120 and 64  $\text{g C m}^{-2}$ , respectively. Thus, non-growing season carbon losses accounted for approximately 70, 80 and 46% of the summertime NEP at SOA, SOBS

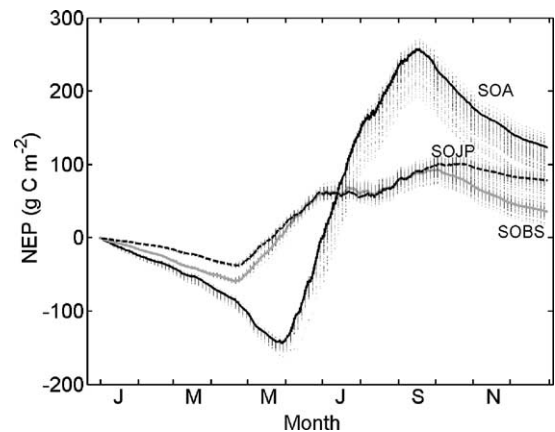


Fig. 7. Seasonal pattern of cumulative NEP in 2000. Missing daytime growing season data were estimated with a 14-day moving window light-response function. The non-growing season and nighttime missing data were replaced using the eddy covariance  $R$  functions. Nighttime observations with  $u_* < 0.35 \text{ m s}^{-1}$  were replaced with the nighttime eddy covariance  $R$  function. All half-hour fluxes were energy balance closure corrected. The solid line represents the best estimate of the cumulative NEP and the cloud of points represents the uncertainty of the estimate. The uncertainty was evaluated by (1) randomly removing up to 30% of the annual NEP data using a uniform discrete random number generator; (2) missing data were randomly selected in continuous blocks ranging from a single half-hour up to 3 days to simulate worst-case equipment failure; (3) new  $R$  and light-response functions were computed using the remaining data; (4) the missing data were gap filled using the new functions; and (5) the experiment was repeated 100 times to establish a range of annual NEP estimates.

and SOJP, respectively. The phenological difference between the deciduous and evergreen sites has a dominant influence on the shape of the seasonal variation in cumulative exchange. Although the growing period was 56 days longer for the evergreens, annual photosynthesis was greatest at SOA. Both evergreen sites experienced a mid-season decline in NEP resulting from an increase in  $R$  during a period when  $A_{\text{max}}$  had not reached its full capacity. Increased sequestration at SOBS and SOJP occurred during early fall when  $A_{\text{max}}$  reached its maximum and air temperature decreased. SOBS and SOJP showed markedly similar seasonal changes in ecophysiological characteristics and changes in  $P$  and  $R$ . The main difference between these sites was the larger  $R$  at SOBS, which is likely related to its greater soil carbon storage and biomass.



## 4. Discussion

### 4.1. Ecosystem respiration

One of the major uncertainties in estimating the annual carbon balance of forest ecosystems results from the transfer of carbon by non-turbulent exchange processes, which are not detected by the EC technique (Mahrt, 1998). These processes dominate under calm and stable atmospheric conditions and frequently occur at night. Since respiratory fluxes are relatively large at night, unlike the scalar fluxes of sensible and latent heat, methods must be developed to provide a best estimate of nighttime respiration. Furthermore, since micrometeorological methods measure the net ecosystem  $\text{CO}_2$  exchange, nighttime functions are often used to partition daytime NEP into  $P$  and  $R$ . However, daytime light-response analyses or stable isotope techniques (Bowling et al., 2001) may provide suitable alternative methods to obtain daytime  $R$  and  $P$ . Greater than 48% of the EC data were excluded from our nighttime analysis of  $R$  for each of the sites due to low friction velocity. Annual nighttime  $R$  algorithms, derived for different wind directions (source areas), showed little variation in parameter value and temperature sensitivity ( $Q_{10}$ ). The daytime estimate,  $R_{\text{df}}$ , was similar to the nighttime estimates and was associated with a  $Q_{10}$  closer to the accepted value of 2.0 (Ryan, 1991) often used in modeling studies. Furthermore, the lower daytime  $Q_{10}$  value supports the findings of Tjoelker et al. (2001) who demonstrated that the  $Q_{10}$  decreases at higher temperatures for boreal species. From this analysis we conclude that local-scale heterogeneity is not an important source of error in estimating  $R$  or extrapolating  $R$  to the daytime when the peak flux footprint is often half of the nighttime peak flux footprint value. A comparison of aircraft flux measurements with these micrometeorological tower-sites support that there is adequate fetch and that they are representative of the region (Desjardins et al., 1997). It is apparent that the light-response analysis of daytime EC data cannot resolve potential differences between nighttime and daytime  $R$  rates resulting from the Kok effect. Although the daytime  $R_{\text{df}}$  estimate was generally lower than the nighttime estimate we cannot conclude with certainty that it was related to the photoinhibition of leaf respiration. Together, however, the independent estimates of daytime and night-

time  $R$  help constrain the annual  $R$  budget of these forests.

Black et al. (2000) reported annual  $R$  estimates at SOA of 1140, 1101, 1096 and 1130  $\text{g C m}^{-2}$  per year, in 1994 and 1996–1998, respectively. Arain et al. (2002) estimated an annual  $R$  of 1127  $\text{g C m}^{-2}$  per year for 1999. Our nighttime- and daytime-derived annual  $R$  estimates of 1193 and 1141  $\text{g C m}^{-2}$  per year for 2000 are in good agreement with these previous values. These results highlight the fact that interannual variation in  $R$  is relatively conservative for the deciduous aspen forest despite significant variation in climate. Measured estimates of annual  $R$  are not available for SOBS or SOJP for the years prior to 2000. However, Grant et al. (2001) modeled annual  $R$  at SOBS using *ecosys* and reported an estimate of  $\sim 900 \text{ g C m}^{-2}$  per year. This value is in excellent agreement with our nighttime- and daytime-derived estimates of 897 and 815  $\text{g C m}^{-2}$  per year, respectively. Measured and modeled  $R$  values for partial years at SOBS (Jarvis et al., 1997; Arain et al., 2002) indicate greater interannual variability than is observed at SOA. Despite the relatively small soil organic carbon pool at SOJP (Table 1) annual  $R$  was relatively large (521–578  $\text{g C m}^{-2}$  per year). Baldocchi et al. (1997b) found similar growing season  $R$  rates (1–5  $\text{g C m}^{-2}$  per day) at this site in 1994 and hypothesized that the relatively large magnitude is caused by increased root respiration from rapidly growing roots and is stimulated by the dry soil conditions. Continuous multi-year datasets are needed to better quantify the interannual variation of  $R$  at the southern boreal conifer sites and to examine how it responds to varying climatic conditions.

### 4.2. Photosynthesis

The uncertainty in  $R$  ultimately limits our ability to accurately estimate  $P$  and understand how it responds to environmental conditions diurnally, seasonally and interannually. Our estimate of  $P$  for SOA was 40% larger than that for SOBS and 90% larger than that for SOJP. Black et al. (2000) reported annual  $P$  estimates at SOA of 1284, 1181, 1212 and 1420  $\text{g C m}^{-2}$  per year, in 1994 and 1996–1998, respectively. Arain et al. (2002) estimated an annual  $P$  of 1259  $\text{g C m}^{-2}$  per year for 1999. Our  $P$  estimate of 1315  $\text{g C m}^{-2}$  per year represents the second largest total in the 6

years of study. There is accumulating evidence that the southern aspen site increases productivity in warm years. The best direct evidence for this was observed in 1998 when warm conditions associated with El Niño increased  $P$  by approximately  $170 \text{ g C m}^{-2}$  per year relative to the average of the other 5 years. Annual estimates of  $P$  for SOBS and SOJP are not available for the years prior to 2000. However, Grant et al. (2001) simulate an annual  $P$  of  $\sim 950 \text{ g C m}^{-2}$  per year for SOBS in 1994. This value is in excellent agreement with our measured value of  $932 \text{ g C m}^{-2}$  per year for the year 2000. Simulations by Arain et al. (2002) using C-CLASS indicate that the interannual variation in  $P$  is more conservative relative to SOA. Daily measured values of  $P$  at SOJP in 1994 ranged from 1 to  $6 \text{ g C m}^{-2}$  per day and reached maximum values in spring (DOY 160) and mid to late summer (DOY 200 to DOY 240) (Baldocchi et al., 1997b). The magnitude, seasonal variability and large day-to-day variability of  $P$  observed at SOJP in 1994 are very similar to our observations in this study.

At the leaf level, Hogg et al. (2000) measured the net photosynthetic rate, based on the branch bag technique, and reported light-saturated half-hour values of  $12 \mu\text{mol m}^{-2} \text{ leaf s}^{-1}$  for aspen and  $4 \mu\text{mol m}^{-2} \text{ leaf s}^{-1}$  for the understory hazelnut at SOA. Scaling up the branch bag estimates using a linear function of LAI (following Dang et al., 1997) gave a canopy-scale  $A_{\text{max}}$  of  $46 \mu\text{mol m}^{-2} \text{ ground s}^{-1}$  and agrees favorably with our EC light-response analysis of  $45 \mu\text{mol m}^{-2} \text{ ground s}^{-1}$ . Leaf-level measurements of  $A_{\text{max}}$  for aspen leaves at SOA under saturated light and  $\text{CO}_2$  reached a maximum  $A_{\text{max}}$  of  $33\text{--}41 \mu\text{mol m}^{-2} \text{ leaf s}^{-1}$  in mid-summer (Middleton et al., 1997). These values are considerably higher than those obtained under natural conditions at SOA and indicate that the carboxylation capacity ( $V_{\text{cmax}}$ ) of aspen leaves is substantially higher than the  $A_{\text{max}}$  observed under ambient conditions at the canopy-scale. Middleton's analysis at SOBS and SOJP showed that maximum black spruce and jack pine  $A_{\text{max}}$  values for light and  $\text{CO}_2$  saturated ( $5\text{--}10\%$   $\text{CO}_2$  in air) needles were 19 and  $14 \mu\text{mol m}^{-2} \text{ leaf s}^{-1}$ , respectively. Their study also revealed that  $A_{\text{max}}$  peaked during late summer to early autumn, which supports our analysis at the canopy-scale. The difference in physiological behavior of  $A_{\text{max}}$  between the deciduous and evergreen sites may be related to seasonal changes in

leaf chlorophyll. Middleton et al. (1997) showed that chlorophyll content per leaf area in jack pine and black spruce needles reached a maximum ( $>25 \mu\text{g cm}^{-2}$ ) during late May and early June and again during mid September. A mid-season (July) minimum was also observed. A similar pattern was not observed for measured leaf nitrogen concentration. At SOA, Middleton et al. (1997) found the chlorophyll content to reach a maximum of  $30.6 \mu\text{g cm}^{-2}$  during late July to early August and to rapidly decline during September to  $8.5 \mu\text{g cm}^{-2}$ . These seasonal changes in chlorophyll content may partially explain the differences in the behavior of photosynthesis and cumulative NEP among the BERMS sites.

Precipitation frequency is likely an important control on the photosynthetic uptake of carbon at SOBS given the large component of mosses. Swanson and Flanagan (2001) showed that the mean  $A_{\text{max}}$  of feather moss and *Sphagnum* at SOBS was  $4.9 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and  $9.5 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , respectively during the 1996 summer period 12 July (DOY 193) to 1 August (DOY 213). They concluded that the understory mosses represented approximately 13% of  $P$ . Grant et al. (2001) used the model *ecosys* to show that values of  $P$  for the moss understory and the black spruce overstory were 288 and  $660 \text{ g C m}^{-2}$  per year, respectively. The annual partitioning of  $P$  at SOA into the aspen and hazelnut canopies was estimated by Grant et al. (1999) to be 811 and  $321 \text{ g C m}^{-2}$  per year, respectively. These model results are consistent with those obtained using above and below canopy EC measurements by Black et al. (1996) and further highlight the complexity of canopy architecture and its role in ecosystem carbon cycling.

#### 4.3. Ecological and climatic significance

Although the distribution of deciduous stands with in the southern boreal study area represent only 15% of the land cover (Hall et al., 1997), their evapotranspiration rates are relatively large compared to the wet evergreen sites that dominate the region (Blanken et al., 2001; Jarvis et al., 1997; Baldocchi et al., 1997a). The greater water loss from deciduous aspen stands in the southern boreal is thought to regulate the local climate by reducing the vapor pressure deficit and temperature of the convective boundary layer, and by promoting precipitation events during the growing season (Hogg et al., 2000a). These feedbacks likely have important

carbon cycling implications for the southern boreal region. Under drier climatic conditions it is likely that the photosynthetic efficiency and carbon fixation at SOA would decrease (see Arneth et al., 2002) appreciably due to the strong sensitivity of aspen and hazelnut stomatal conductance to atmospheric saturation deficits greater than 4 kPa and decreasing soil water content (Hogg et al., 1997, 2000b). To date, however, summer drought has not occurred during the period of ongoing carbon balance studies at BERMS. Drier climatic conditions at SOBS could have a significant impact on NEP by reducing the photosynthetic contribution of the mosses. Long-term measurement and modeling studies are needed to better understand how these stands will respond to warmer and drier climatic conditions and to explore the implications that this might have on the region's carbon balance. The potential for a change to net carbon loss is most likely at SOBS because of its large soil carbon pool (Table 1), relatively low photosynthetic capacity, and strong sensitivity of  $R$  to soil temperature. At present the annual  $R$  represents less than 3% of the soil carbon pool at SOBS. However, heterotrophic respiration could decrease substantially with drier conditions. Evidence is emerging that acclimation of respiration to warmer temperatures may result in lower soil respiration rates over the long-term (Luo et al., 2001; Giardina and Ryan, 2000; Liski et al., 1999). Furthermore, the dependence of  $R$  on  $P$  may limit the ability to predict  $R$  in a changing climate. The ratio  $R/P$ , based on the annual totals, for SOA, SOBS and SOJP was 0.91, 0.96 and 0.83, respectively, and further supports the hypothesis that  $R$  is proportional to productivity (Janssens et al., 2001). Future studies are needed to: (1) develop new methods to partition daytime NEP into  $P$  and  $R$  to help validate nighttime and daytime  $R$  and  $P$  estimates; (2) study the links between  $P$  and  $R$ ; (3) better understand how drought will impact carbon cycling in these forests; and (4) examine the amount of interannual variation in the  $R$  and  $P$  ecophysiological parameters and their sensitivity to environmental factors, which are needed in climate-carbon modeling studies.

## 5. Conclusions

1. Annual ecosystem respiration ( $R$ ) derived from daytime analyses of EC data were 1141, 815 and

521 g C m<sup>-2</sup> per year and were consistently lower than nighttime EC estimates of 1193, 897 and 578 g C m<sup>-2</sup> per year for SOA, SOBS and SOJP, respectively. The differences, however, were not statistically significant given the large uncertainty associated with each analytical technique.

2. The agreement between the annual  $R$  estimates derived from daytime and nighttime analyses of EC data indicate that these study sites are not significantly affected by heterogeneity or fetch problems.
3. Annual NEP at BERMS indicated that these relatively old growth forests are a weak to moderate sink of carbon ranging from 35 to 122 g C m<sup>-2</sup> per year. The uncertainty in the annual estimates, based on random simulations of missing data and gap filling with simple biophysical algorithms, suggests that the differences in NEP was only significant between SOA and SOBS.
4. Although the growing period was 56 days longer for the evergreen forests, NEP was greatest at the deciduous aspen forest due to its larger photosynthetic capacity ( $A_{\max}$ ).

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