

## Physiological responses of a black spruce forest to weather

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**Abstract.** We used eddy covariance to measure the net exchange of CO<sub>2</sub> between the atmosphere and a black spruce (*Picea mariana*) forest in Manitoba for 16,500 hours from March 16, 1994 to October 31, 1996. We then partitioned net exchange into gross photosynthesis and respiration by estimating daytime respiration as a function of temperature, and used these data to define the physiological responses of the forest to weather. The annual rates of gross production and respiration by the forest were both around 8 t C ha<sup>-1</sup> yr<sup>-1</sup>. Both photosynthetic and respiratory response were reduced in winter, recovered with warming in spring, and varied little in summer. Respiration in mid summer increased with air temperature ( $T_{\text{air}}$ ) at a  $Q_{10}$  of around 2 to a rate of 2–8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 15°C. Gross photosynthesis at high light (photon flux density (PPFD) greater than 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was negligible at  $T_{\text{air}} < 0^\circ\text{C}$ , increased linearly with  $T_{\text{air}}$  from 0° to 14°C, and was relatively insensitive to  $T_{\text{air}} > 14^\circ\text{C}$ . Gross CO<sub>2</sub> uptake at  $T_{\text{air}} > 14^\circ\text{C}$  increased with increasing light at an ecosystem-level quantum yield of 0.05 mol CO<sub>2</sub> mol<sup>-1</sup> photons before saturating at an uptake rate of 8–18  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at PPFDs greater than 500–700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Photosynthesis in summer did not appear limited by high evaporative demand or soil water depletion.

### Introduction

Boreal forests cover ~8% of the Earth's land surface and contain ~13% of the carbon in the terrestrial biosphere [Whittaker, 1975; Schlesinger, 1977]. Increasing concentrations of CO<sub>2</sub> and other trace gases in the atmosphere are expected to impact the climate of the boreal zone over the next century [Mitchell *et al.*, 1990] and, as a result, to alter the rates of photosynthesis and respiration by boreal forests [Bonan and Shugart, 1989; Oechel and Billings, 1992; Oechel *et al.*, 1993]. To the extent that these changes in activity translate into changes in carbon balance, a positive or negative feedback to the concentration of atmospheric CO<sub>2</sub> may result. However, an improved understanding of the physiological sensitivity of boreal forest CO<sub>2</sub> exchange to weather is required before the effects of climate change on carbon balance can be predicted reliably.

Most investigations of forest CO<sub>2</sub> exchange have relied on models to extrapolate short-term gas-exchange measurements made with small chambers. This approach has contributed greatly to understanding, but uncertainties are inevitable when small-scale observations are aggregated to whole ecosystems, and short-term data to annual balances [Whittaker and Marks, 1975]. An alternative approach is to use the eddy covariance technique over a complete growing season to directly measure the net exchange of CO<sub>2</sub> between the atmosphere and a several-hectare patch of forest [Wofsy *et al.*, 1993; Hollinger *et al.*, 1994; Fan *et al.*, 1995; Black *et al.*, 1996; Greco and Baldocchi, 1996].

We used eddy covariance to measure the net exchange of

CO<sub>2</sub> between the atmosphere and a black spruce (*Picea mariana* (Mill.) BSP) forest in Manitoba from March 1994 to October 1996 as part of NASA's Boreal Ecosystem-Atmosphere Study (BOREAS). Forests of this type are prevalent throughout much of the North American boreal zone [Larson, 1980; VanCleve *et al.*, 1983; Oechel and Lawrence, 1985]. We then partitioned net exchange into gross photosynthesis and respiration by estimating daytime respiration as a function of temperature. In this paper we analyze the responses of whole-forest photosynthesis and respiration to the physical environment from an ecophysiological perspective. We (1) introduce the site, experimental design, and data set, (2) discuss the accuracy of the measurements, (3) describe the seasonal changes in photosynthetic and respiratory response, (4) quantify the direct effects of physical environment on mid summer photosynthesis, and (5) assess the direct sensitivity of gross production to climate variability. A companion paper [Goulden *et al.*, 1997] discusses the current carbon balance of the site.

### Methods

#### Site

The measurements were made at the BOREAS northern study area—old black spruce site (NSA-OBS) in central Manitoba (55.879°N, 98.484°W [Sellers *et al.*, 1995]). The site was remote, with the nearest towns 40 km east (Thompson) and 25 km west (Nelson House) and the nearest road 4 km north (Route 391). Access from the road was by foot, all-terrain vehicle, or snowmobile. The initial installation of equipment was facilitated by helicopter.

The site was very level, with black spruce forest of varying stature for several kilometers in all directions. The vegetation immediately around the site differed markedly with small changes in elevation. Upland areas were dominated by dense, 10-m-tall 120-year-old black spruce, with a minor shrub layer

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and continuous feather moss. Low-lying areas were dominated by sparse, 1-to-6-m-tall, chlorotic spruce and continuous sphagnum moss. Approximately 45% of the area within 500 m of the tower was feather moss, 45% sphagnum moss, and 10% fen [*Harden et al.*, this issue].

The flux measurements were made from a 31-m-tall, 30-cm-cross-section tower (Rohn 25G, Peoria, Illinois). The data acquisition equipment and some of the instruments were housed in a climate-controlled hut 20 m northeast of the tower base. Power was provided by a diesel generator which operated continuously 300 m east. A network of boardwalks around the site minimized disturbance, and access to areas south, west, and north of the tower was strictly limited.

The data acquisition and control systems were fully automated, allowing extended periods of unattended operation. The raw digitized signals were stored on a hard drive and transferred by a local employee to a removable cartridge every 3–7 days for immediate shipment to our laboratory. The site was visited by science personnel every 5 weeks for maintenance and as needed for repairs.

### Measurements

The turbulent fluxes of sensible heat, latent heat, CO<sub>2</sub>, and momentum at 29 m were determined following *Wofsy et al.* [1993] and *Goulden et al.* [1996b]. The signals directly associated with the flux calculations were digitized and recorded at 4 Hz. Wind and temperature were measured with a three-axis sonic anemometer (Applied Technologies, Boulder, Colorado) pointed due west (270°). The anemometer incorporated on-line corrections for flow distortion [*Kaimal et al.*, 1990], and the effect of crosswind on the calculation of temperature [*Kaimal and Gaynor*, 1991].

The mixing ratios of CO<sub>2</sub> and H<sub>2</sub>O were monitored by sampling 16–18 standard liter min<sup>-1</sup> (slpm) from 0.5 m east of the vertical axis of the anemometer through four Teflon filters (3- $\mu$ m pore size, 50 mm diameter) configured in parallel. The inlet filters were changed at least once every 5 weeks. Sample air was drawn into the instrument hut through a 50-m-long, 0.64-cm inner diameter (id) high-density polyethylene tube. A subsample was drawn through a thermostated block to stabilize temperature [*Webb et al.*, 1980] and then through a CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer (IRGA; Model 6262, LI-COR, Lincoln, Nebraska) at 4 slpm. The main sample tube was replaced with Teflon PFA in May 1996, resulting in an improved response for fluctuations in water vapor. The pressures in the main sample line and immediately after the IRGA were monitored and controlled, maintaining the IRGA cell at 53 kPa (MKS Instruments, Andover, Massachusetts). The gain of the IRGA was determined every 3 hours by addition of 4% CO<sub>2</sub> at 40 and 80 standard mL min<sup>-1</sup> to the main sample stream. The IRGA zero was determined every 3 hours by passing sample air through a series of soda line and Mg(ClO<sub>4</sub>)<sub>2</sub> traps.

The raw IRGA signals were recorded (CO<sub>2</sub> 1S, H<sub>2</sub>O 1S), and the effects of water vapor on CO<sub>2</sub> measurements removed and the signals linearized during subsequent processing [*LI-COR*, 1991]. The CO<sub>2</sub> flux was calculated as the 30-min covariance of the vertical wind velocity  $w'$  and the CO<sub>2</sub> concentration after subtracting the linear least squares regression  $c'$ . The time lag (typically, 6 s) was determined by maximizing the correlation between  $w'$  and  $c'$ . The flux was rotated to the plane with zero mean vertical wind [*McMillen*, 1988].

We used a second H<sub>2</sub>O/CO<sub>2</sub> IRGA to sequentially measure the mixing ratios at six levels through the canopy (0.3, 1.5, 4.6,

8.4, 12.9, and 28.8 m) every 12 mins. The profile IRGA was calibrated every 3 hours using a pair of CO<sub>2</sub> mixtures traceable to the 1993 Scripps–World Meteorological Organization (WMO) standard. The hourly change in CO<sub>2</sub> beneath 29 m (storage [*Wofsy et al.*, 1993]) was calculated by interpolation. The eddy flux and storage observations were summed to calculate the hourly net ecosystem exchange (NEE [*Wofsy et al.*, 1993]), except for a few intervals when storage data were unavailable and just eddy flux was used (less than 2% of the growing season).

The data required to characterize the physical environment were recorded at 0.5 Hz. The photosynthetically active photon flux density (PPFD) above the forest was measured with a silicon quantum sensor (LI-COR, Lincoln, Nebraska). Moss-surface PPFD was measured at eight locations along a topographic gradient with quantum sensors. The net radiation at 29 m was measured with a thermopile net radiometer (REBS Q\*6, Seattle, Washington). Air temperatures at 1, 8, and 28 m altitude were measured with ventilated thermistors. Soil temperatures at 5, 10, 20, 50, and 100 cm beneath the moss surface were measured at five sites along a topographic gradient with precision thermistors.

### Analysis

Our analysis proceeded by (1) examining the raw flux data for errors associated with wind from behind the tower, calm conditions, and the damping of high-frequency fluctuations and for intervals with malfunctioning instruments, and then excluding these periods or correcting for these errors in subsequent analyses; (2) separating the observed net CO<sub>2</sub> exchange into whole-ecosystem respiration and gross uptake by estimating daytime respiration as a function of temperature; and (3) using the large sample of observations to isolate the environmental factors controlling photosynthesis and respiration. We describe the first and fourth aspects of step 1 and all of step 2 here. The second and third aspects of step 1 are discussed in the Results, and step 3 is implicit in the Discussion.

We rejected flux data when the sonic anemometer or IRGA malfunctioned or when background CO<sub>2</sub> changed rapidly. Problems with the IRGA were identified by monitoring the flow and pressure at the instrument and by comparing the signals with simultaneous measurements made with the profile instrument. Additional problems with the IRGA were identified with an automated calibration every 3 hours. The sonic anemometer developed problems with spiking occasionally due either to precipitation or malfunctioning transducers. (Spikes are step changes in wind or temperature signal that occur when the instrument misidentifies the return pulse [*Kaimal and Finnigan*, 1994].) We therefore adapted the processing code to determine the number of spikes in each interval and to recalculate the turbulent fluxes after filtering out spikes. We subsequently discarded the sensible heat and momentum fluxes when the spike rate was greater than 5% and water vapor and CO<sub>2</sub> fluxes when the spike rate was greater than 20%. We also rejected periods with unreasonable means or variances in the temperature measured by the sonic based on comparison with an adjacent thermistor, and unreasonable horizontal wind based on comparison with an adjacent cup anemometer.

An analysis of turbulence statistics as a function of wind direction revealed anomalies such as a systematic decrease in  $\sigma w/u^*$  during neutral and unstable periods from a mean of

1.25 when the wind came from in front of the tower (135°–45°) to 1.1 when the wind came from behind the tower (45°–135°). Similarly, an analysis of energy exchange revealed anomalously poor closure of the energy budget during periods with wind from behind the tower, a sector that included the generator, instrument hut, and access trail. We therefore excluded from subsequent analyses observations with wind from 45° to 135°.

Net exchange can be separated into respiratory and photosynthetic fluxes by several approaches: an independent set of eddy covariance instruments may be deployed beneath the canopy to measure forest floor respiration [Baldocchi and Meyers, 1991], a series of automated chambers may be deployed to continuously measure soil and stem respiration, as was done at the site by Gouliden and Crill [1997] and Lavigne *et al.* [this issue], or day respiration  $R$  may be estimated from night measurements of NEE and the diel course of temperature [Gouliden *et al.*, 1996b]. We used the third method in conjunction with information on the diel variation in respiration from the second approach, since this approach provides the greatest likelihood that similar footprints are considered and minimizes biases between methods.

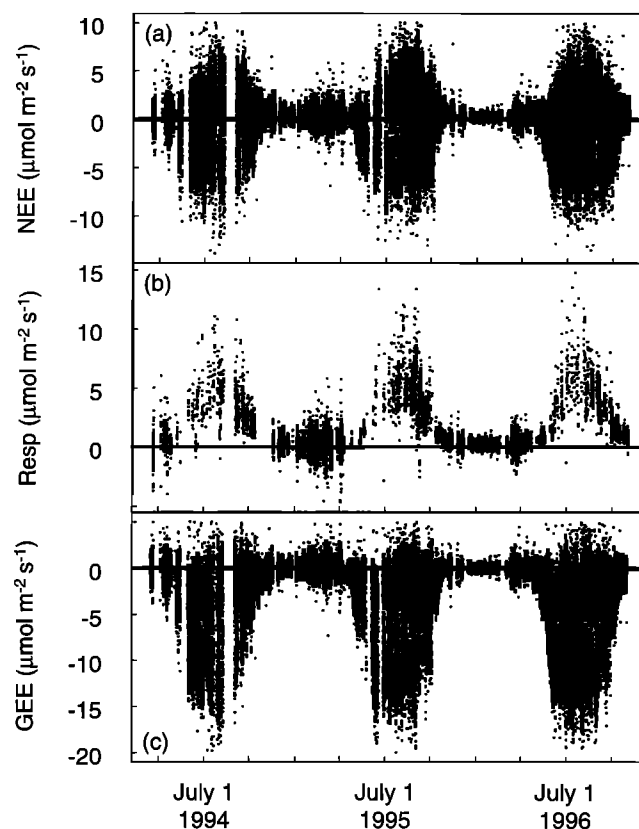
Forest respiration  $R$  was calculated assuming an exponential dependence on air temperature at 28 m altitude with a  $Q_{10}$  of 2.0. We determined the fit between the NEE during windy nights and air temperature at 28 m altitude for a series of intervals:

$$R = R_0 \exp(T_{\text{air}} 0.0693) \quad (1)$$

where 0.0693 results in a  $Q_{10}$  of 2.0 and  $R_0$  is the basal respiration for each interval. The intervals in late fall, winter, and early spring each contained 100 half-hour observations (~1 week). The growing season intervals were demarcated on May 30, August 3, and September 7 in 1994; on May 30, July 14, and September 5 in 1995; and on June 4, August 3 and September 2 in 1996 to account for observed changes in respiratory response (see Discussion for further information).

The use of air temperature with a fixed  $Q_{10}$  to derive  $R$  was supported by stem [Lavigne *et al.*, this issue] and moss-surface [Gouliden and Crill, 1997] respiration measurements made at the site over diel courses. The key assumptions in the approach are (1) that the eddy flux measurements after removal of periods with  $u^* < 0.2 \text{ m s}^{-1}$  are not biased from day to night as discussed in the Results, and (2) that the temperature measured at 28 m is closely related to the activity-weighted temperature of the forest. The second assumption is most likely to fail if appreciable biomass is colder than the temperature at 28 m during the day due to storage, leading to an overestimation of daytime respiration, or colder than the temperature at 28 m during the night due to atmospheric inversion, leading to an underestimation of daytime respiration.

We checked for the sensitivity of calculated  $R$  to our selection of 28 m temperature by recalculating the regressions and daytime rates of  $R$  using the temperatures at 1 m elevation and also at 5 cm depth in the moss layer. The runs calculated with 1 m temperatures indicate the errors if respiration from boles and leaves dominates whole-forest respiration, providing an upper bound on the estimates of daytime  $R$ . The runs calculated with 5-cm-deep temperatures indicate the errors if respiration from moss and soil dominates whole-forest respiration, providing a lower bound. We found that calculated daytime  $R$  was not biased at or below 20°C by our choice of temperature location. At 30°C the rates of daytime  $R$  calculated using the 28 m temperature were  $2 \mu\text{mol m}^{-2} \text{ s}^{-1}$  less



**Figure 1.** (a) Net ecosystem exchange of CO<sub>2</sub> (NEE), (b) nocturnal efflux of CO<sub>2</sub> during windy periods (Resp), and (c) gross exchange of CO<sub>2</sub> (GEE) above the northern study area—old black spruce site at half-hour intervals from March 16, 1994 to October 31, 1996. Gross exchange was calculated as the difference between measured net exchange and the rate of respiration estimated from temperature. Positive exchange indicates a net input of CO<sub>2</sub> to the atmosphere.

than those calculated using the 1 m air temperature, and  $2 \mu\text{mol m}^{-2} \text{ s}^{-1}$  greater than those calculated using the 5 cm moss temperature.

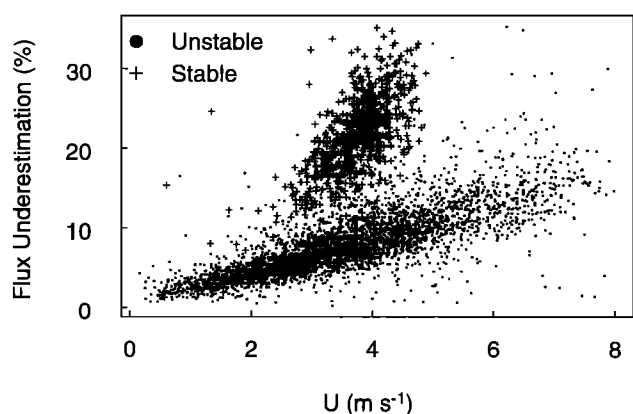
Gross ecosystem exchange (GEE) was calculated as the difference between NEE and estimated respiration:

$$\text{GEE} = \text{NEE} - R \quad (2)$$

Gross ecosystem exchange should equal the net rate of carboxylation and oxygenation by ribulose-1,5-bisphosphate carboxylase. Gross exchange does not include dark respiration and is not equivalent to measurements of net assimilation made with leaf or canopy chambers. Net or gross “exchange” of CO<sub>2</sub> into the forest was considered negative, and “exchange” out of the forest positive. However, we discuss “photosynthesis,” “uptake,” and “ecosystem production” as processes with positive signs.

## Results

We installed the instruments in October 1993 and began routine observations in March 1994. Valid measurements of CO<sub>2</sub> exchange were obtained for 33,000 half-hour intervals from March 16, 1994 to October 31, 1996, or 72% of the time, and 14,100 half-hour intervals from November 1, 1995 to October 31, 1996, or 80% of the time (Figure 1). Notable gaps



**Figure 2.** Underestimation of CO<sub>2</sub> flux due to damping of high-frequency fluctuations ( $\text{Loss}_{\text{smear}}$ ) for stable ( $0 \text{ m} < L < 100 \text{ m}$ ; crosses,  $n = 650$ ) and unstable ( $L < 0 \text{ m}$ ; points,  $n = 3700$ ) half-hour periods throughout 1995. The underestimation of flux was determined by recalculating the sensible heat flux after numerically slowing the response of the temperature detector with a low-pass analog of a  $R$ - $C$  filter to simulate the response of the CO<sub>2</sub> measurement (time constant of 0.6 s). The flux underestimation during near-neutral periods ( $L > 100 \text{ m}$ ) formed a series of curves of decreasing slope with increasing  $L$ .

occurred in May 1994 when an error was introduced into the data acquisition code, August 1994 when the sonic anemometer was damaged twice by lightning, fall 1994 when the generator failed repeatedly, June 1995 when computer disks failed twice, and November 1995 when the sonic anemometer failed with the onset of cold temperatures. The greatest challenges to maintaining measurement continuity were the remoteness of the site and the reliability of the sonic anemometer in extreme cold.

The seasonal trends of net exchange (NEE; Figure 1a), nocturnal efflux (respiration; Figure 1b), and gross exchange (GEE (NEE minus estimated respiration); Figure 1c) were consistent from year to year. The fluxes measured in winter 1994–1995 were more variable than those in winter 1995–1996. The greater variability in 1994–1995 was related to higher variance in the CO<sub>2</sub> measurements within 30-min intervals, which appears to have resulted from a slightly less stable temperature in the instrument hut. The rates of respiration in summer 1995 were approximately  $1 \mu\text{mol m}^{-2} \text{ s}^{-1}$  higher than in summer 1994 (Figure 1b [Goulden *et al.*, 1997]). The peak rates of photosynthesis were nearly identical from year to year (Figure 1c), and observations from all three years were pooled in subsequent analyses.

#### Accuracy of Flux Measurements: Underestimation of High-Frequency Fluctuations

The closed-path IRGA and long sampling tube resulted in an underestimation of water vapor and CO<sub>2</sub> flux due to the damping of high-frequency fluctuations [Moore, 1986]. The time constant for the damping of CO<sub>2</sub> fluctuations, as determined by analyses of cospectra, was 0.6 s, and the time constant for the damping of water vapor fluctuations was 1.25 s. We simulated the loss of flux ( $\text{Loss}_{\text{smear}}$ ) associated with these responses for each 30 min run by recalculating the sensible heat flux after numerically slowing the response of the temperature detector with a low-pass analog of a  $R$ - $C$  filter, and adjusting for the lag introduced between  $w'$  and  $T'$ .

The damping of CO<sub>2</sub> fluctuations caused a 2–10% underestimation of flux during daylight, which increased to 15–30% at night with the cospectral shift toward higher frequencies (Figure 2). The underestimation increased linearly with wind  $U$  during unstable and neutral periods (Obukhov length  $L < 0 \text{ m}$  or  $L > 1000 \text{ m}$ ):

$$\text{Loss}_{\text{smear}}(\%) = 1.9 + U(\text{m s}^{-1})1.67 \quad (3)$$

and with both  $U$  and  $1/L$  during stable and near-neutral periods ( $0 < L < 1000 \text{ m}$ ):

$$\text{Loss}_{\text{smear}}(\%) = 12.1 + (U/L)(136.9) \quad (4)$$

for  $U/L < 0.1 \text{ s}^{-1}$  and

$$\text{Loss}_{\text{smear}}(\%) = 24.6 \quad (5)$$

for  $U/L > 0.1 \text{ s}^{-1}$ . The effects of  $U$  and  $L$  on  $\text{Loss}_{\text{smear}}$  were qualitatively similar to the expected responses of the  $w'T'$  cospectral maximum [Kaival and Finnigan, 1994]. We therefore increased our raw CO<sub>2</sub> and water vapor fluxes during periods with positive or negative sensible heat fluxes greater than  $20 \text{ W m}^{-2}$  by the  $\text{Loss}_{\text{smear}}$  simulated for the interval, and during other periods by the  $\text{Loss}_{\text{smear}}$  calculated from (3)–(5). We expect this approach can be used elsewhere to correct  $\text{Loss}_{\text{smear}}$ , but caution that the coefficients reported are unique to this experiment.

#### Accuracy of Flux Measurements: Nocturnal Measurements During Calm Periods

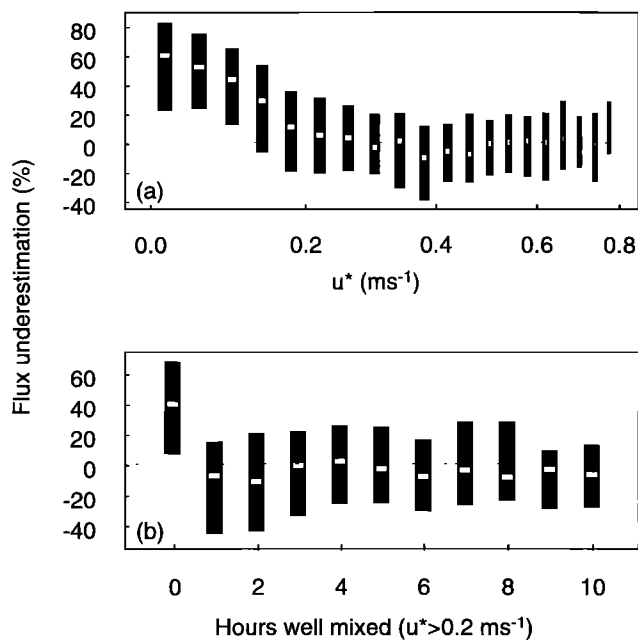
A selective measurement bias between day and night can also result if CO<sub>2</sub> “leaks” from the site during calm nocturnal periods [Goulden *et al.*, 1996b]. In principle, NEE (eddy flux plus directly measured storage) should be insensitive to reduced turbulence, since storage increases to offset any reduction in turbulent flux (as reported by Grace *et al.* [1996]). However, an analysis of nocturnal CO<sub>2</sub> exchange at NSA-OBS revealed that decreased eddy CO<sub>2</sub> flux at  $u^* < 0.2 \text{ m s}^{-1}$  was offset only partially by increased storage, resulting in a reduction in NEE (Figure 3a). Simultaneous measurements with chambers indicated that the CO<sub>2</sub> efflux at the moss surface was not similarly affected by turbulence [Goulden and Crill, 1997] and hence that the decline in NEE was a measurement artifact. The efflux of CO<sub>2</sub> immediately following resumption of mixing was not unusually high (Figure 3b), supporting the hypothesis that CO<sub>2</sub> escaped undetected during calm periods. We therefore excluded all periods with  $u^* < 0.2 \text{ m s}^{-1}$  from subsequent analyses.

The turbulent efflux of CO<sub>2</sub> at night became insensitive to increasing wind at  $u^* > 0.2 \text{ m s}^{-1}$  (Figure 3a). The observations during these periods presumably provide a reliable measure of ecosystem respiration. The efflux during cold, windy periods in January and February 1996 (air temperature  $< -10^\circ\text{C}$ ,  $u^* > 0.2 \text{ m s}^{-1}$ ) was  $0.16 \mu\text{mol m}^{-2} \text{ s}^{-1}$  ( $\sigma = 0.22$ ,  $n = 300$ ) when the sensible heat flux was out of the forest (unstable periods) and  $0.18 \mu\text{mol m}^{-2} \text{ s}^{-1}$  ( $\sigma = 0.16$ ,  $n = 440$ ) when  $H$  was in. The measurements during near-neutral periods ( $L > 25 \text{ m}$ ) were not systematically lower than those during unstable periods. Furthermore, the NEE during windy summer nights was  $\sim 20\%$  less than the respiration estimated from aggregated chambers [Lavigne *et al.*, this issue; Goulden and Crill, 1997], a pattern consistent with the measurement bias in turbulent exchange indicated by the energy budget as discussed in the next section.

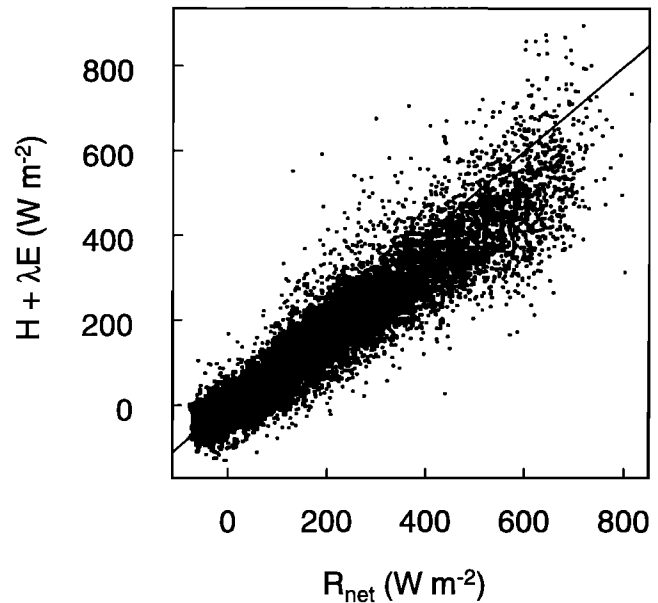
### Accuracy of Flux Measurements: Closure of the Surface Energy Budget

The turbulent flux of sensible ( $H$ ) plus latent ( $\lambda E$ ) heat was strongly correlated ( $r^2 = 0.90$ ) with the net radiation ( $R_{\text{net}}$ ) above the forest (Figure 4). The coherence was especially impressive considering that we did not account for heat storage and also that scatter is inevitable due to sampling uncertainty. Unfortunately, the absolute agreement between measurements was less gratifying with an 18% disparity between  $H + \lambda E$  and  $R_{\text{net}}$ . The inequality varied through the year, reaching a maximum in spring when energy was used during melt, a minimum in summer, and increasing again in fall despite energy release by freezing. A comparable 5–15% discrepancy between measured turbulent exchange and net radiation has been observed above other [Lee and Black, 1993; Fitzjarrald and Moore, 1994; Barr et al., 1994; Foken and Oncley, 1995; Goulden et al., 1996b], though not all [Denmead and Bradley, 1985; Verma et al., 1986; Kelliher et al., 1992], forested sites.

We examined our measurements in detail but were unable to account for the disparity. The apparent underestimation of  $H + \lambda E$  was not caused by the detrending algorithm or averaging interval, since the flux calculated was insensitive to the



**Figure 3.** (a) Nocturnal underestimation of flux (the difference between NEE observed and respiration predicted from temperature (e.g., Figure 7) normalized by respiration predicted) as a function of friction velocity  $u^*$ . (b) Flux underestimation as a function of recent mixing history (hours since  $u^*$  exceeded  $0.20 \text{ m s}^{-1}$ , with zero corresponding to periods that remain poorly mixed). Boxes encompass the 25th and 75th percentiles with a white line at the median. Data are for half-hour nocturnal intervals with wind from a suitable direction and predicted respiration greater than  $1 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Box widths in Figure 1a are proportional to sample sizes with 500 observations, out of 4400, in the first bin ( $0 \text{ m s}^{-1} < u^* < 0.04 \text{ m s}^{-1}$ ) and 20 observations in the last bin ( $0.76 \text{ m s}^{-1} < u^* < 0.8 \text{ m s}^{-1}$ ). Box widths in Figure 1b are invariant of sample size, with 2100 observations in the first bin ( $u^* < 0.2 \text{ m s}^{-1}$ ), 220 observations in the second bin (first hour after mixing resumes), and 36 observations in the last bin (the 10 preceding hours were windy).



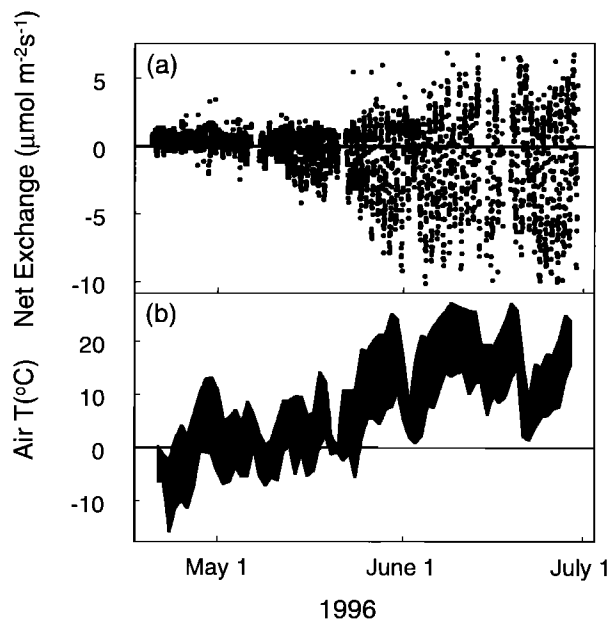
**Figure 4.** Sensible ( $H$ ) plus latent ( $\lambda E$ ) heat flux above the forest as a function of net radiation ( $R_{\text{net}}$ ). Points are half-hour intervals for all 3 years when the net radiometer was not obscured by snow and the wind was from a suitable direction ( $135^\circ$ – $45^\circ$ ). The mean sensible heat flux was  $59.7 \text{ W m}^{-2}$ , the latent heat flux was  $29.1 \text{ W m}^{-2}$ , and the net radiation was  $108.3 \text{ W m}^{-2}$ . Plot shows 1:1 line; the least squares fit was  $R_{\text{net}} 0.81 + 1.6$  with  $r^2 = 0.90$  and  $n = 17,200$ .

algorithm used and to changes in the averaging interval between 15 and 60 min. We found no major errors in the calibration of the net radiometer or sonic anemometer during comparisons with nearby, independent instruments. The horizontal wind measured with the sonic anemometer was consistently within 10% of that measured with an adjacent cup anemometer, and consequently,  $w'$  was judged reliable since  $\sigma w$  and  $u^*$  were linearly related during neutral and stable periods with the expected ratio of 1.25 [Kaimal and Finnigan, 1994]. The disparity continued year-round, and was reduced but not eliminated in late afternoon, implying that it was not caused entirely by changes in storage. Similarly, the discrepancy was independent of Bowen ratio, implying that it was not caused by a bias peculiar to one of the turbulent exchange measurements.

Energy closure did improve with increasing  $u^*$ , a trend that could indicate stationary circulation patterns during calm periods which transport flux that is not included in the detrended covariance [Barr et al., 1994; Lee and Black, 1993]. We also observed a systematic difference in closure as a function of wind direction, a pattern that could indicate spatial heterogeneity in albedo and net radiation. However, we are unable to account fully for the bias between measurements and must conclude that our turbulent exchange measurements may underestimate both day and night surface activity by 10–20%. Nonetheless, the strength of the correlation between  $H + \lambda E$  and  $R_{\text{net}}$ , establishes the integrity of the measurements and their usefulness for characterizing the proportional responses of exchange to the physical environment.

### Annual Integrated Activity

We integrated the observations of NEE, GEE, and  $R$  to calculate the annual net ecosystem production (NEP), gross



**Figure 5.** (a) Net CO<sub>2</sub> exchange and (b) daily maximum and minimum air temperature at the northern old jack pine Saskatchewan Research Council site (approximately 10 km northwest of NSA-OBS) during the start of the 1996 growing season. The CO<sub>2</sub> exchange observations are for periods with  $u^* > 0.20 \text{ m s}^{-1}$  and all wind directions.

ecosystem production (GEP), and respiration ( $R_{\text{annual}}$ ) of the forest [Goulden *et al.*, 1996a, b]. The NEP of the forest was 0 to  $-500 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ , indicating the forest lost carbon at a modest rate over the study (Goulden *et al.*, [1997]; we discuss NEP and GEP from the perspective of the forest with a positive NEP indicating forest growth). The GEP and  $R_{\text{annual}}$  were both around  $8000 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ , rates that are nearly as large as we observed at Harvard Forest, an aggrading deciduous forest in Massachusetts [Goulden *et al.*, 1996a]. The forest at NSA-OBS was quite active, but the high integrated rate of respiration canceled the high rate of photosynthesis, resulting in low rates of net uptake at both daily and annual time steps.

The NEP represents the small residual of  $\sim 4000 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  gained during daylight and  $\sim 4000 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  lost at night. A seemingly minor systematic bias of 20% in the measurements from day to night will cause an error in the calculated NEP of  $800 \text{ kg C ha}^{-1} \text{ yr}^{-1}$  [Goulden *et al.*, 1996b]. We assume that our correction for the damping of high-frequency fluctuations and our exclusion of calm periods remove any day-to-night bias from the measurements. Each of these corrections decreased the calculated NEP by  $\sim 500 \text{ kg C ha}^{-1} \text{ yr}^{-1}$ , underscoring the need to pursue these biases aggressively when integrating eddy flux. We emphasize that the reliability of eddy covariance at night requires further investigation and that day-to-night biases represent the greatest uncertainty in the use of eddy covariance to calculate NEP. In contrast, the bias of 10–20% in turbulent flux indicated by the energy budget (Figure 4), assuming it was consistent from day to night, would have a small effect on the assessment of NEP.

## Discussion

### Seasonal Changes in Activity

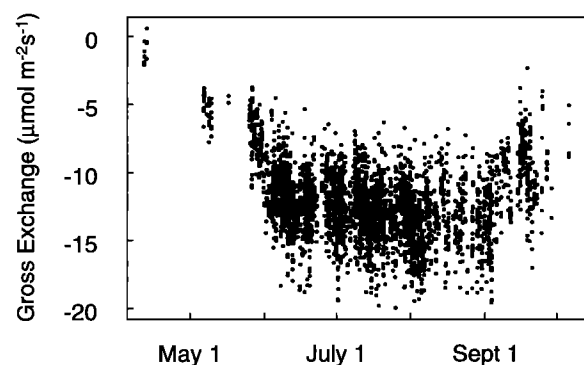
Photosynthesis at high PPFD was negligible in winter, increased with warming in late May, decreased moderately in

early September, and ceased with freezing in late October (Figure 1c). Respiration was low, but not negligible, in winter, increased a few weeks after warming in early June, decreased moderately in early September, and decreased considerably with freezing in late October (Figure 1b). The annual cycles of respiration and photosynthesis reflected the direct effects of temperature on metabolism and also changes in the physiological responses of the forest to weather.

Moderate rates of uptake in 1996 were first observed a few weeks after above-freezing maximum temperatures became common, but before snow melt was complete (Figure 5). Photosynthetic uptake increased through May, with the largest rises following nights with above-freezing air temperatures (e.g., May 11 and 24). The spring increase in respiration was delayed at least 1 week relative to the increase in photosynthesis during each of the 3 years (Figures 5 and 1a). High rates of respiration were not consistently observed until the second week of June 1996, despite warm temperatures and high rates of photosynthesis in late May.

The rate of photosynthesis at PPFDs greater than  $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and air temperatures greater than  $14^\circ\text{C}$  varied through the year (Figure 6). Photosynthetic uptake was not observed under favorable conditions during a brief thaw in early April 1994. Gross uptake increased to around  $5 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in May of each year before reaching a peak of around  $12 \mu\text{mol m}^{-2} \text{ s}^{-1}$  that lasted from June to August and declining to around  $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the first week of September (Figures 6, 1c, and 5). These trends were not correlated with any contemporaneous aspects of the physical environment that we could discern and appear to reflect changes in the physiological state of the forest.

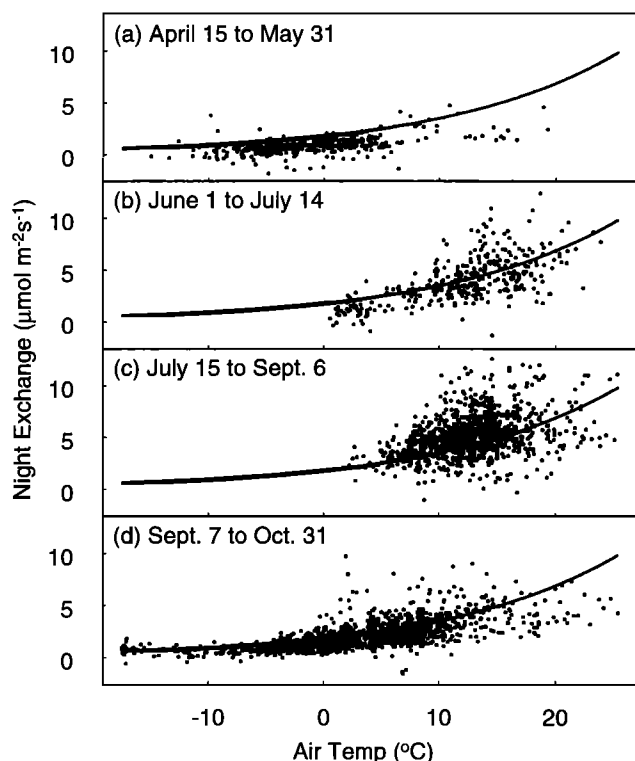
The relationship between nocturnal respiration and air temperature also changed through the season. Respiration was low and insensitive to air temperature in spring (Figure 7a) and high and uniformly sensitive to air temperature in summer (Figures 7b and 7c). Late summer respiration (Figure 7c) was about  $1 \mu\text{mol m}^{-2} \text{ s}^{-1}$  higher than early summer respiration (Figure 7b) over a range of temperatures. Autumn respiration (Figure 7d) increased with temperature at a lower rate than in summer (Figures 7b and 7c), and was about  $1 \mu\text{mol m}^{-2} \text{ s}^{-1}$  higher over a range of temperatures than in spring (Figure 7a). The shifts in sensitivity to air temperature indicate that the increases in respiration observed in early June (Figure 5) and subsequent decreases in early September (Figure 1b) reflect



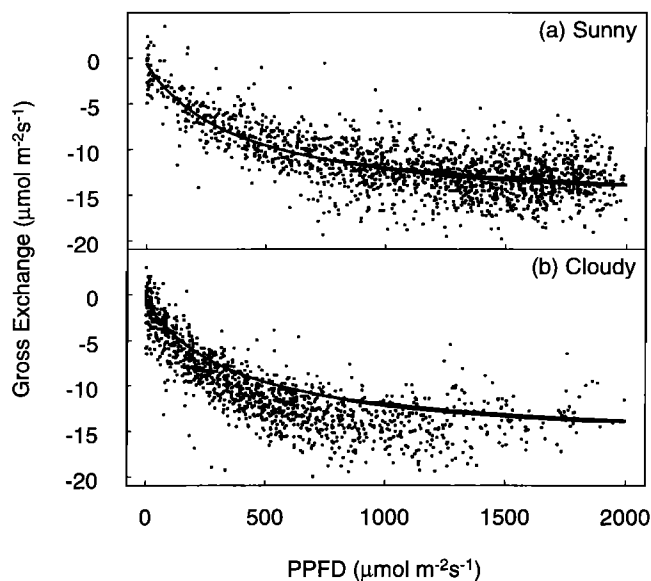
**Figure 6.** Seasonal change in gross exchange during favorable environmental conditions. Points are half-hour intervals from all three years with PPFD  $> 600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ,  $T_{\text{air}} > 14^\circ\text{C}$ , and all wind directions ( $n = 2900$ ).

changes in above-ground spruce or moss basal metabolism. The  $1 \mu\text{mol m}^{-2} \text{s}^{-1}$  rise from early to late summer that was insensitive to diel and synoptic changes in temperature suggests increased emissions from a region of stable temperature such as deep in the soil [Goulden *et al.*, 1997]. Nocturnal eddy flux measurements are noisy, and we were unable to find consistent relationships between respiration and aspects of the physical environment other than temperature.

The lack of uptake during periods with favorable conditions in early spring (Figures 5 and 6) may be a direct effect of soil and stem frost or, alternatively, of changes in leaf biochemistry associated with dormancy [Larcher, 1995]. Photosynthetic capacity appeared to increase with the onset of above-freezing nights, allowing uptake in mid-May that was approximately 60% of the mid summer rate. The photosynthetic response then increased gradually, and the respiratory response increased rapidly, to reach maxima in early June (Figures 5, 6, and 7). The comparatively low rates of respiration in late May (Figure 5), despite moderate rates of photosynthesis, may reflect the need for carbohydrate replenishment prior to growth resumption. Both respiratory and photosynthetic response decreased in the first week of September (Figures 6 and 7), possibly due to changes in allocation or shifts in biochemistry in preparation for winter. The timing of this reduction was remarkably consistent from year to year. The increases in response around June 1 and decreases in the first week of Sep-



**Figure 7.** Nocturnal CO<sub>2</sub> exchange as a function of air temperature at 28 m for (a) April 15 to May 31,  $n = 350$ , (b) June 1 to July 14,  $n = 340$ , (c) July 15 to September 6,  $n = 875$ , and (d) September 7 to October 31,  $n = 1300$ . Points are half-hour intervals from all 3 years with  $u^* > 0.20 \text{ m s}^{-1}$  and wind from a suitable direction. The best fit for all observations from April 15 to October 31 is replicated on each panel to allow comparison (night exchange ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) =  $\exp(0.576 + 0.0676 T_{\text{air}})$ ;  $n = 2900$ ).



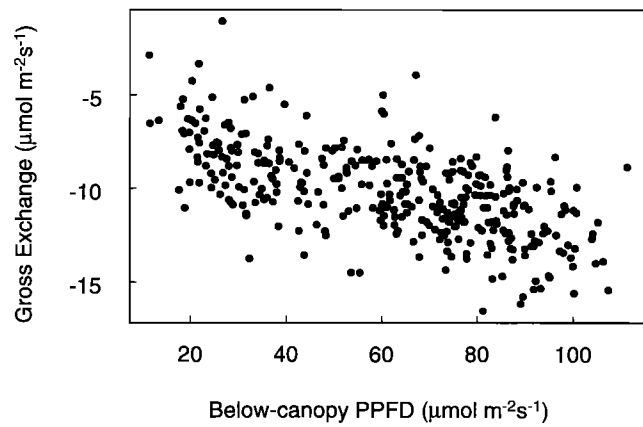
**Figure 8.** Gross CO<sub>2</sub> exchange as a function of incident photon flux density (PPFD) for (a) sunny periods (below-canopy PPFD/above-canopy PPFD < 0.12) and (b) cloudy periods (below/above > 0.12). Points are half-hour intervals from June 9 to September 17 of all 3 years when the air temperature was greater than 14°C,  $u^* > 0.20 \text{ m s}^{-1}$ , and wind from a suitable direction. The best fit for the sunny periods is replicated on each panel to allow comparison (GEE ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) =  $-0.8 + (-15.7 \text{ PPFD})/(389.9 + \text{PPFD})$ ;  $n = 1650$ , quantum yield as PPFD approaches 0 is  $0.040 \text{ mol CO}_2 \text{ mol}^{-1} \text{ photons}$ ). The best fit line (not shown on plots) for cloudy periods was GEE ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) =  $-0.4 + (-16.9 \text{ PPFD})/(258.0 + \text{PPFD})$ ;  $n = 1250$ .

tember coincide with the typical ending and beginning of frost. More detailed and longer-term investigations of phenology are needed to reliably predict the responses of boreal forest photosynthesis and respiration to climate variation.

#### Controls on Photosynthesis Within the Growing Season

Incident light was the dominant controller of instantaneous photosynthesis within the growing season. Photosynthesis increased with increasing light at an ecosystem-level quantum yield of  $0.05 \text{ mol CO}_2 \text{ mol}^{-1} \text{ photons}$  before saturating at an uptake rate of  $8\text{--}18 \mu\text{mol m}^{-2} \text{s}^{-1}$  and a light level of  $500\text{--}700 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 8). The ecosystem-level quantum yield at low light is comparable to or higher than that observed for individual black spruce branches [Dang *et al.*, 1997] and also for Harvard Forest [Wofsy *et al.*, 1993], indicating that most of the incident light at NSA-OBS was absorbed by photosynthesizing surfaces. The peak rate of photosynthesis and the level of light required for saturation are consistent with the leaf area index of the site ( $4 \text{ m}^2 \text{ m}^{-2}$  [Gower *et al.*, this issue]), and the response of individual black spruce branches, which saturate at an uptake rate of  $4 \mu\text{mol m}^{-2} \text{s}^{-1}$  and a light level of  $400\text{--}600 \mu\text{mol m}^{-2} \text{s}^{-1}$  [Dang *et al.*, 1997; Vowinckle *et al.*, 1975].

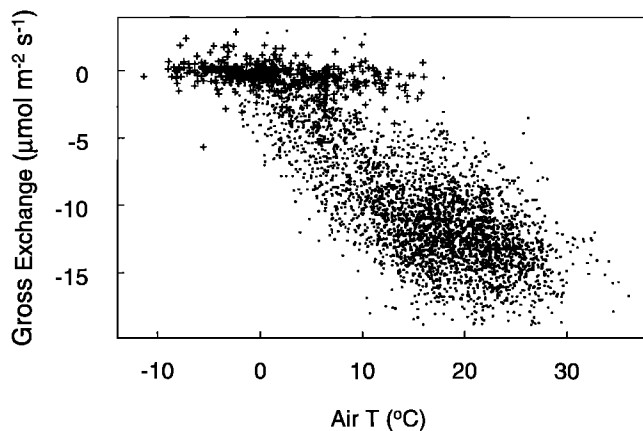
Photosynthesis was consistently higher during cloudy periods than during sunny periods with the same PPFD (Figure 8; [Fan *et al.*, 1995; Hollinger *et al.*, 1994]). Cloud cover increases the proportion of diffuse light and hence the fraction of light penetrating to lower branches and the forest floor [Oechel and Lawrence, 1985]. The light at the moss surface was  $20\text{--}40 \mu\text{mol m}^{-2} \text{s}^{-1}$  during clear-sky periods with incident light from  $350\text{--}$



**Figure 9.** Whole-forest gross exchange as a function of below-canopy PPFD. Observations are for half-hour intervals from June 9 to September 17 of all 3 years when the above-canopy PPFD was 350–550  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , air temperature greater than 14°C,  $u^* > 0.20 \text{ m s}^{-1}$ , and wind from a suitable direction. Below-canopy PPFD was the median of eight quantum sensors at the moss surface. The least squares fit was flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) =  $-6.6 - 0.059$  (below-canopy PPFD),  $r^2 = 0.38$ ,  $n = 343$ .

550  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and 60–100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  during cloudy periods with the same incident light. The increase in below-canopy irradiance was correlated with an increase in forest photosynthesis from 8 to 12  $\mu\text{mol m}^{-2} \text{s}^{-1}$  (Figure 9). This variation in photosynthesis was not associated with other aspects of the physical environment such as evaporative demand. Rather, the relationship between below-canopy PPFD and photosynthesis appears to reflect variation in the contribution of shaded surfaces to whole-forest photosynthesis [Fan *et al.*, 1995].

The regression between below-canopy light and photosynthesis indicates that one-third to two-thirds of forest photosynthesis occurs on shaded surfaces with a bulk quantum yield of around 0.05 mol CO<sub>2</sub> mol<sup>-1</sup> photons (Figure 9). Chamber



**Figure 10.** Gross exchange as a function of air temperature at 28 m during bright periods. Crosses are from April 10–30 (before the start of the active season) and dots are from May 1 to October 31. Observations are for half-hour intervals with PPFD > 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $u^* > 0.20 \text{ m s}^{-1}$ , and wind from a suitable direction. The sample size was 390 for April and 3900 for the remaining interval.

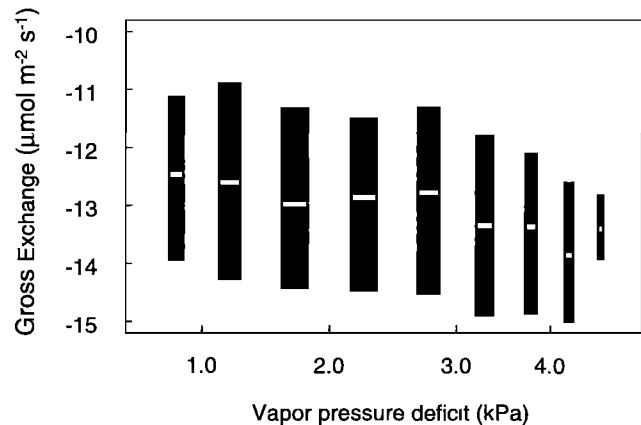
measurements of moss photosynthesis indicate that vascular plants must dominate this flux [Goulden and Crill, 1997]. The whole-forest photosynthesis by shaded surfaces at a below-canopy PPFD of 80  $\mu\text{mol m}^{-2} \text{s}^{-1}$  was about 4  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , or 4 times the gross uptake observed by feather moss surfaces at the site in summer 1996. Similarly, the quantum yield for shaded surfaces was several times that observed for feather moss surfaces (0.01 mol CO<sub>2</sub> mol<sup>-1</sup> photons).

Hourly photosynthesis under bright light was negligible at air temperatures below 0°C, increased linearly with air temperatures from 0°C to 14°C, and was relatively insensitive to temperatures above 14°C (Figure 10). Gross photosynthesis was not obviously reduced at high temperature, though we cannot eliminate the possibility of a modest (1–2  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) depression at air temperatures of 25–30°C, since our estimation of respiration during these periods is uncertain (see Methods). Our measurements do not exclude the possibility of decreased leaf net photosynthesis with warming, since GEE does not include dark leaf respiration (see Methods).

Photosynthesis was not reduced during periods of high evaporative demand (Figure 11), though, as with the analyses at high temperature (Figure 10), we cannot exclude a modest depression. Nonetheless, vapor pressure deficit (VPD) exceeded 4 kPa during only 4% of the daylight summer periods, and a reduction in gross exchange of 2  $\mu\text{mol m}^{-2} \text{s}^{-1}$  during these periods would have reduced annual gross production by less than 1%. Similarly, we did not observe obvious effects of soil drought during dry periods in August and September 1994 and June 1995 (Figure 1c), a pattern consistent with previous investigations of black spruce [Oechel and Lawrence, 1985].

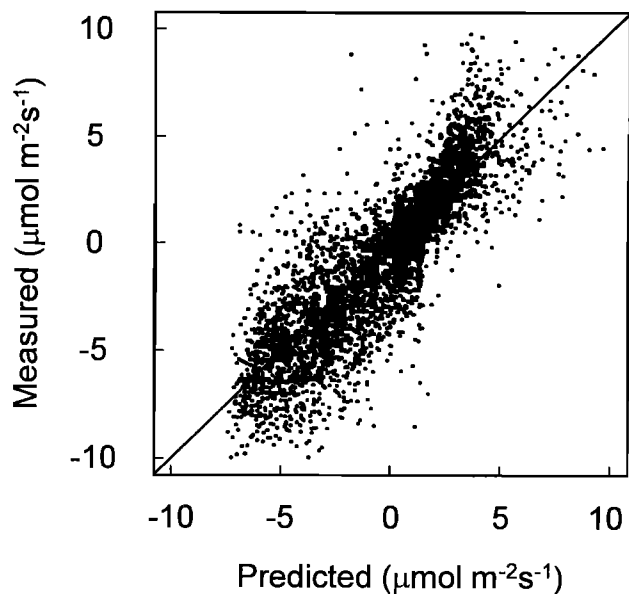
#### Empirical Model of CO<sub>2</sub> Exchange

The overall response of CO<sub>2</sub> exchange to the physical environment was remarkably simple [Sinclair *et al.*, 1976; Jarvis and



**Figure 11.** Gross exchange during favorable conditions as a function of leaf-to-air vapor pressure deficit (VPD). Boxes encompass 25th and 75th percentiles, with a white line at the median. Box widths are proportional to sample size with 380 observations, out of 1800, in the third bin (1.5 kPa < VPD < 2.0 kPa) and a total of 70 observations in the last two bins (4.0 kPa < VPD < 5.0 kPa). Observations are from June 1 to September 7 of all 3 years with PPFD > 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $T_{\text{air}} > 14^\circ\text{C}$ ,  $u^* > 0.20 \text{ m s}^{-1}$ , and wind from an appropriate direction. The leaf VPD was calculated from the aerodynamic leaf temperature and the air humidity measured at 28.8 m. The aerodynamic leaf temperature was calculated from air temperature assuming similarity in the fluxes of sensible heat and momentum [Baldocchi *et al.*, 1991; Fan *et al.* 1995].





**Figure 12.** Accuracy of a simple statistical model for predicting hourly net exchange. Gross exchange was calculated from regressions describing the mean responses of forest photosynthesis to light ( $GEE_{\text{light limit}} = (-12.97 \text{ PPF}) / (259 + \text{PPFD})$ ) and temperature ( $GEE_{\text{temp limit}} = 0$  for  $T_{\text{air}} < 0$ ;  $GEE_{\text{temp limit}} = T_{\text{air}} / 14$  for  $0^\circ\text{C} < T_{\text{air}} < 14^\circ\text{C}$ ;  $GEE_{\text{temp limit}} = 1$  for  $T_{\text{air}} > 14^\circ\text{C}$ ). Net exchange was calculated as respiration ( $R = \exp(0.324 + 0.075 T_{\text{air}})$ ) plus the product of  $GEE_{\text{light limit}}$  and  $GEE_{\text{temp limit}}$ . Predicted net exchange was compared to hourly observations from the first 2 years when  $u^* > 0.24 \text{ m s}^{-1}$  and wind was from an appropriate direction. Plot shows 1:1 line, the slope of the least squares fit was 1.03,  $r^2 = 0.72$ , and the sample size was 6400.

Leverenz, 1983]. A single set of regressions describing the average responses of forest photosynthesis to light (of the form in Figure 8) and temperature (Figure 10), and the response of respiration to temperature (of the form in Figure 7), accounted for 72% of the variation in hourly CO<sub>2</sub> exchange (Figure 12). Additional variation could be explained by the effect of light penetration on forest photosynthesis (Figure 9), and the phenological changes in photosynthetic (Figure 6) and respiratory (Figure 7) response. We have observed a similar pattern at Harvard Forest, where regressions describing the average effects of recent temperature on canopy development, light on photosynthesis, and temperature on respiration account for 78% of the variation in hourly exchange over a 5-year period [Goulden et al., 1996a, b].

The simplicity and consistency of CO<sub>2</sub> exchange at Harvard Forest and NSA-OBS arguably represent our most significant finding from eddy covariance to date. Nonlinear and spatially variable physiological responses coupled with spatial and temporal heterogeneity in the physical environment could have resulted in complex or seemingly random responses at the whole-forest level. Furthermore, heterogeneity in vegetation associated with local drainage or history could have caused marked variation in exchange as the region of forest sampled shifted with wind and atmospheric stability. However, we found that the physiological responses of leaves and soil microbes scale remarkably well to the stand at both sites and hence that models of CO<sub>2</sub> exchange that treat complex ecosystems as simple integrated units are justifiable. In fact, the

overall response of CO<sub>2</sub> exchange may be so simple that it creates a problem in the use of eddy flux data to validate models, since flawed algorithms may nonetheless match observations over certain ranges. Regression analysis provides a benchmark against which sophisticated models of ecosystem CO<sub>2</sub> exchange can be evaluated [Aber et al., 1996]. Complex models that have been tuned to NSA-OBS should explain more than 72% of the variation in hourly exchange. Models that have not been tuned, and therefore are presumably more general, should outperform the regression model from NSA-OBS when applied to other black spruce sites.

The physiological responses of the forest determine the direct sensitivity of gross production to climate. Photosynthesis was not limited markedly by high evaporative demand (Figure 11) or soil water depletion, and modest changes in either aspect of climate should not impact gross production appreciably. Similarly, increased cloudiness should have little effect, since the concomitant increase in diffuse light would largely offset the reduction in light (Figure 8). The limitations imposed by cold can be estimated with the photosynthetic components of the regression model, assuming the seasonal course of photosynthetic capacity (Figures 5 and 6) is linked to the occurrence of favorable temperatures (Figure 10) in a consistent manner. A 4°C warming from April 10 to June 9 would have extended the growing season and increased GEP by 500 kg C ha<sup>-1</sup> yr<sup>-1</sup>. Similarly, warming from September 7 to November 11 would have increased GEP by 350 kg C ha<sup>-1</sup> yr<sup>-1</sup>, and warming from June 29 to August 28 would have increased GEP by only 150 kg C ha<sup>-1</sup> yr<sup>-1</sup>. These changes of 2–6% in annual GEP are small compared to those observed at, and calculated for, Harvard Forest (10–20% [Goulden et al., 1996a]). The gross production of evergreen boreal forest therefore appears relatively insensitive to the direct effects of climate.

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