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ORIGINAL PAPER

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Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation

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Abstract Measurements of net ecosystem CO₂ exchange by eddy correlation, incident photosynthetically active photon flux density (PPFD), soil temperature, air temperature, and air humidity were made in a black spruce (*Picea mariana*) boreal woodland near Schefferville, Quebec, Canada, from June through August 1990. Nighttime respiration was between 0.5 and 1.5 kg C ha⁻¹ h⁻¹, increasing with temperature. Net uptake of carbon during the day peaked at 3 kg C ha⁻¹ h⁻¹, and the daily net uptake over the experiment was 12 kg C ha⁻¹ day⁻¹. Photosynthesis dropped substantially at leaf-to-air vapor pressure deficit (VPD) greater than 7 mb, presumably as a result of stomatal closure. The response of ecosystem photosynthesis to incident PPFD was markedly non-linear, with an abrupt saturation at 600 μmol m⁻² s⁻¹. This sharp saturation reflected the geometry of the spruce canopy (isolated conical crowns), the frequently overcast conditions, and an increase in VPD coincident with high radiation. The ecosystem light-use efficiency increased markedly during overcast periods as a result of a more even distribution of light across the forest surface. A mechanistic model of forest photosynthesis, parameterized with observations of leaf density and nitrogen con-

tent from a nearby stand, provided accurate predictions of forest photosynthesis. The observations and model results indicated that ecosystem carbon balance at the site is highly sensitive to temperature, and relatively insensitive to cloudiness.

Key words Boreal woodland · Ecosystem physiology · Photosynthesis model · Biosphere-atmosphere exchange · *Picea mariana*

Introduction

Boreal forests cover approximately 8% of the earth's land surface, and store about 10% of the total carbon in terrestrial ecosystems (Bonan and Shugart 1989; Schlesinger 1991). The climate of the boreal zone is extreme with severe winters and a short growing season. The boreal environment exerts a strong and presumably direct control on photosynthesis and decomposition, resulting in significant accumulation of soil carbon, detritus, and living biomass (Bonan and Shugart 1989; Schlesinger 1991). Climatologists project that the build-up of greenhouse gases in the earth's atmosphere may lead to particularly dramatic shifts in temperature, cloudiness, and water balance at high latitudes (Mitchell et al. 1990). Since the carbon balance of boreal forests may be sensitive to climate change, this raises the possibility of a significant feedback on the future rate of change of atmospheric CO₂ (e.g., Oechel et al. 1993). Efforts to predict the response of boreal ecosystem CO₂ exchange to perturbation must rely on an understanding of the processes controlling photosynthesis and respiration (Pastor and Post 1988; Bonan 1991; Melillo et al. 1993), but the development, parameterization, and validation of mechanistic boreal ecosystem models have been impeded by the paucity of field observations.

Whole-stand observations of photosynthesis and respiration made using micro-meteorological techniques provide a powerful tool for understanding the carbon balance of terrestrial ecosystems (Wofsy et al. 1993).

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The eddy-correlation method relies on fast-response sensors to monitor the concentration of a trace gas and the vertical wind speed above a canopy (Baldocchi et al. 1988). The covariance of these observations provides a measure of the turbulent flux of the trace gas between the atmosphere and an area of forest approximately 10^4 m² centered about 10^2 m upwind of the sensor array (Baldocchi et al. 1988; Fan et al. 1992). Eddy correlation is suitable for long-term measurements of energy and CO₂ fluxes, but observations of this type have not been reported for a boreal forest.

Recently, Wofsy et al. (1993) presented an extended (2-year) record of the CO₂ eddy-flux by a deciduous forest, which included continuous observations over a range of conditions, and allowed an assessment of the physical and phenological controls on whole-forest assimilation and respiration. Amthor et al. (1994) subsequently used these data to test a biochemically based model of forest CO₂ assimilation, demonstrating both the utility of long-term flux measurements for model testing and refinement, and the usefulness of a mechanistic model for exploring the processes underlying whole-ecosystem exchange.

We report here whole-ecosystem CO₂ exchange observations made over a boreal woodland in Northern Labrador for 53 days during the summer 1990. Our principal objectives in this paper are to: (1) describe the diurnal and day-to-day variation of whole-ecosystem respiration and photosynthesis, (2) relate the patterns of CO₂ exchange to the physical environment, and (3) explore the environmental limitations on carbon assimilation. We address these goals by analyzing the eddy-flux observations using a mechanistic model of ecosystem carbon uptake.

Methods

Site description

This paper is a component of the NASA Arctic Boundary Layer Expedition (ABLE-3B; Harriss et al. 1994). The observations were made in a black spruce-lichen woodland located 13 km northeast of Schefferville, Province Quebec, Canada (54.83°N, 66.67°W, 500 m above sea level). The meteorological tower was 31 m tall, and situated on gently sloping terrain with lichen woodland extending for at least 1 km in all directions (Fitzjarrald and Moore 1994). A lightly traveled dirt road was located 300 m to the south-east of the site. Power to the site was supplied by a continuously-operated diesel generator located at the road. The wind during the study was predominantly from the north and north-west, and from the south-east less than 5% of the time (Fitzjarrald and Moore 1994). Disturbance to the south, west, and north of the tower was minimized during set-up. The data acquisition system and trace-gas instrumentation were operated in an all-weather tent 20 m south-east of the tower base.

Ecological background

The growing season at Schefferville is short (100–120 days; Vowinckel et al. 1975), with frequent cloud cover (Jackson 1959). The vegetation at the site was dominated by widely-spaced black spruce (*Picea mariana* BSP), with scattered white spruce (*P.*

glauca Moench) and tamarack (*Larix laricina* Koch). A patchy shrub understory was composed of birch, labrador tea and blueberry (*Betula glandulosa* Michx., *Ledum groenlandicum* Oeder, and *Vaccinium* sp.). The ground was covered with a nearly continuous mat of lichen (*Cladina stellaris* Brodo), with moss (*Dicranum fuscescens* Turn.) dominating low-lying poorly drained areas. The spruce were approximately 6.5 m tall, with a crown basal diameter of about 2 m. The living biomass at a nearby site (200 m south-west of the tower) was 21 tonnes C ha⁻¹ during the mid-1970s (60% in trees, the rest in shrubs, lichens and moss; Rencz 1976). The stem density of black spruce was 500–600 ha⁻¹ (Rencz and Auclair 1978; R. Downs, McGill University, personal communication). The forest around the tower was unevenly aged, with trees as old as 200 years. A detailed record of disturbance at the site is not available, although evidence suggests that the site had not burned for at least 250 years (Sharpe 1986).

The response of leaf photosynthesis to the physical environment has been characterized at several lichen woodland sites around Schefferville. Vowinckel et al. (1975) observed a maximum photosynthetic rate of 2.8 mg CO₂ h⁻¹ g⁻¹ dry needle for branches of *P. mariana* in ambient CO₂. Branch photosynthesis gradually saturated around 1000 μmol m⁻² s⁻¹, and the light compensation point was about 30 μmol m⁻² s⁻¹. Maximum photosynthesis occurred from 9 to 23°C, with no strong depression in carbon assimilation during the afternoon. Leaf respiration was closely correlated with temperature. Black spruce needles may be maintained for 10–15 years; photosynthetic activity of the aged needles can still be 40% of the maximum rate (Hom and Oechel 1983).

Subsequent investigators have examined lichen, moss, and shrub photosynthesis (Smith and Hadley 1974; Hicklenton and Oechel 1976, 1977a,b; Carstairs and Oechel 1978; Bigger and Oechel 1982). Soil respiration, measured using the soda-lime technique in an Alaska black spruce stand, was 0.8–1.4 kg C ha⁻¹ h⁻¹ at surface temperatures around 10°C (Schlentner and Van Cleve 1985). Soil respiration peaked in June, and over the season was not well correlated with soil moisture.

Eddy-flux measurements

Measurements of the fluxes of CO₂, sensible heat, and momentum between the forest and the atmosphere were made using the eddy-correlation technique. Wind and temperature were monitored at the top of a 31-m triangular-cross-section tower (Rohn 25G, Peoria, Ill.), 20–25 m above the canopy, using a three-axis sonic anemometer (model SWS 211/3 Applied Technologies, Inc., Boulder, Colo.). The sonic anemometer was mounted on a rotating boom which was periodically turned into the wind to reduce errors associated with flow distortion and shadowing by the tower. The mixing ratio of CO₂ at 31 m was continuously monitored by drawing 6–7 standard l min⁻¹ of air down a 50-m-long 0.4-cm inner diameter Teflon tube and through a nondispersive infrared gas analyzer (IRGA; model LI-6251, LiCor, Lincoln, Neb.). The air stream passed through a Nafion dryer (Perma Pure, Toms River, N.J.) and reached an equilibrium temperature before entering the CO₂ analyzer, removing the effects of coincident latent and sensible heat flux (e.g., Webb et al. 1980). The gain of the IRGA was automatically determined every 4 h by addition of a 1% CO₂ gas mixture at 10 standard ml min⁻¹ to the main sample stream. Ozone was measured at the top of the tower using an ethylene chemiluminescence sensor (J.W. Munger, personal communication); the deposition velocity of ozone provides an indicator for stomatal conductance (Fan et al. 1990). The incident photosynthetically active radiation above the forest was measured using a silicon quantum sensor (model LI-190SA, LiCor, Lincoln, Neb.). Air temperature and water vapor content at 31 m were measured using a thermistor and solid-state humidity probe (Vaisala, Helsinki, Finland). Soil temperature was monitored at 5 cm depth using a thermistor inserted into the organic layer underneath the lichen mat.

The data acquisition and control systems were fully automated, providing frequent calibrations and extended periods of unattended operation. The system recorded outputs from the sonic anemometer, CO₂ analyzer, and ozone detector at 4 Hz. The ancillary

sensors, including those responsible for monitoring the physical environment, and a suite of pressure and flow sensors, were either logged at 0.5 Hz or recorded by Fitzjarrald and Moore (1994). The raw data was stored on a disk at the site, and subsequently transferred to tape every 2 days. Eddy CO₂ flux was calculated as the 30-min covariance of the fluctuations in vertical wind velocity (w') and CO₂ concentration (c'). Prior to the flux calculation, the linear trend in CO₂ was subtracted from each 30-min time series, and a time lag introduced into the record of CO₂ to account for the delay in drawing air down the tower. The time lag was fairly constant, 7–8 s, as determined from peaks in the cross correlation functions between w' and c' (Fan et al. 1990). The flux was corrected for the orientation of the sonic anemometer relative to the streamlines by rotating the flux tensor to the plane where the mean of $w'=0$ (McMillen 1988). Additionally, we corrected for the limited high-frequency band-pass of the CO₂ sampling assembly by simulating the loss of sensible heat flux for a temperature detector with a response time of 0.3 s. We subsequently checked the flux computations by cross-comparison with other research groups using simultaneously-collected raw data. Throughout the study, we calculated the total CO₂ stored in the airspace from the ground to the sensor array, and the hourly change in storage, based on sequential measurements of CO₂ at seven levels (0.05, 0.85, 2.8, 6.2, 9.5, 18.2, and 30.8 m) completed every 40 min using an IRGA (Binos, Leybold-Heraeus, Hanau, Germany).

Data quality

We began observations on 11 June, but a data-acquisition problem during the early phase of the experiment forced us to discard the CO₂ flux data prior to 26 June. From 26 June to 17 August the system was operated nearly continuously, providing CO₂ fluxes for 1120 h, or 90% of the interval. We eliminated all eddy flux observations during periods when the output from the sonic anemometer indicated water on the transducers (i.e., output signals saturated at full scale or spiking in the temperature signal). We confirmed the normal operation of the fast-response sensors by spectral and co-spectral analysis for a large number of data intervals. Measurements of sensible and latent heat fluxes, and net radiation above the canopy, are reported in Fitzjarrald and Moore (1994). The closure of the energy budget showed a marked diel variability due to unaccounted storage. When integrated over 24 h, the summed sensible and latent heat fluxes were on average 10% lower than net radiation.

Derived variables

The eddy-correlation method measures the net exchange of CO₂ above the forest. This flux is similar to the total ecosystem respiration during the night, and the sum of photosynthesis and respiration during the day. Respiration from soil heterotrophs and plant maintenance is strongly controlled by temperature (Jarvis and Leverenz 1983). We estimated the respiration during daylight periods using a linear relationship between the nighttime eddy-flux during well-mixed periods (see below) and the soil temperature at 5 cm depth. We then subtracted this calculated respiration from the daytime eddy flux to calculate the gross CO₂ assimilation. We also derived a number of meteorological values that we could not measure directly, but expected to correlate closely with physiological activity. These included aerodynamic leaf temperature (Baldocchi et al. 1991), which we calculated from air temperature assuming similarity in the fluxes of sensible heat and momentum, and leaf vapor pressure deficit (VPD), which we calculated from leaf temperature and air humidity at 31 m.

Model of carbon assimilation

We developed a mechanistic model of forest carbon assimilation following the approach outlined by Amthor et al. (1994). We pa-

rameterized the carbon assimilation module of the Amthor model for the Schefferville site using field observations from a nearby stand, and compared model results with the eddy flux measurements. Our modeling goals in this study were to (1) test the model of canopy CO₂ assimilation (Amthor 1994) at the Schefferville site, (2) determine the physiological and environmental factors regulating CO₂ exchange, and (3) assess the sensitivity of gross ecosystem productivity to cloudiness and temperature.

We modeled the CO₂ assimilation separately for four canopy layers (black spruce, evergreen shrub, deciduous shrub and lichens) by treating each stratum as a big leaf. The principal environmental inputs used in the model are incident photosynthetically active photon flux density (PPFD), air temperature, leaf temperature, specific humidity, and momentum and heat fluxes. The CO₂ assimilation module is based on the biochemical treatment of photosynthesis described by Farquhar et al. (1980), Sharkey (1985), and Collatz et al. (1991). The model relates CO₂ assimilation to light absorption, ribulose-1,5-bisphosphate carboxylase (Rubisco) capacity, and potential triose-phosphate turnover, as well as the supply of CO₂ from the atmosphere to chloroplasts. Carbon dioxide transport in the model is governed by the rate of chloroplast metabolism and by intracellular, stomatal, and leaf boundary-layer conductances. We modified the stomatal conductance (g_s) treatment described in Amthor (1994) for the present application, by relating g_s to the leaf-air vapor pressure difference (VPD):

$$g_s = g_s^{\circ} (1 - k_{VPD} \text{VPD}) \quad (1)$$

where g_s° is stomatal conductance at VPD=0 mb, and k_{VPD} (=0.02 mb⁻¹) is an empirical coefficient. Because photosynthesis, conductance, and intercellular CO₂ partial pressure (c_i) are interdependent in the model, we solved for photosynthesis, g_s , and c_i iteratively for each stratum. Since lichen lack stomata, we eliminated g_s and included only leaf boundary-layer and intracellular conductances for the ground layer. We expect that the CO₂ uptake by the lichen layer may be overestimated since the model did not incorporate the direct effect of desiccation on photosynthesis (Carstairs and Oechel 1978).

The photosynthetic capacity of a leaf is a function of leaf nitrogen (N_{leaf}) and the fraction of leaf N in Rubisco (f_{Rubisco} ; Amthor 1994). In a similar woodland stand near Schefferville, ground-area-based foliar nitrogen contents were 0.20 mol N m⁻² for black spruce, 0.066 mol N m⁻² for deciduous shrubs, 0.026 mol N m⁻² for evergreen shrubs, and 0.42 mol N m⁻² for lichens (Rencz and Auclair 1978; Auclair and Rencz 1982). Within the lichen layer, 16% of the nitrogen (0.07 mol N m⁻²) was found in the upper algae-rich region that dominates lichen photosynthesis (Carstairs and Oechel 1978). We are unaware of any measurements of f_{Rubisco} for boreal vegetation. We used the photosynthesis model to solve for the f_{Rubisco} that was consistent with literature reports of N_{leaf} and leaf CO₂ assimilation near 12°C (2.8 mg CO₂ g⁻¹ h⁻¹ for *P. mariana*, Vowinckel et al. 1975; 19 mg CO₂ g⁻¹ h⁻¹ for deciduous shrubs, Bigger and Oechel 1982; 4.7 mg CO₂ g⁻¹ h⁻¹ for evergreen shrubs, Bigger and Oechel 1982; 2 mg CO₂ g⁻¹ h⁻¹ for *Cladina stellaris*, Carstairs and Oechel 1978). Area-based rates from the model were converted to a mass basis using area densities of leaf dry mass from a nearby stand (Rencz and Auclair 1978). The observed levels of CO₂ assimilation were reproduced at f_{Rubisco} =0.06 for spruce, 0.14 for deciduous shrubs, 0.06 for evergreen shrubs, and 0.06 for lichens.

We constructed a simple sub-model that accounts for the three-dimensional structure of the canopy to predict the fraction of incident PPFD intercepted by each plant stratum. In this model, the projection area of a conical crown is formulated following Oker-Blom and Kellomaki (1982). PPFD interception under clear skies was calculated assuming 100% direct-beam radiation and evenly spaced, uniform cone-shaped trees (stem density $Y=600$ stems ha⁻¹; height $H=6.5$ m; basal radius $R=1$ m):

$$I_{\text{tree}} = I_0 \{ R(H^2 \tan^2 \theta - R^2)^{1/2} + R^2 [\pi - \arccos(R/H \tan \theta)] \} 10^{-4} Y \quad (2)$$

where I_{tree} is the PPFD intercepted by trees, I_0 is the measured PPFD incident on the forest, and θ is the solar zenith angle. The

PPFD intercepted by the shrubs and lichen was calculated from the area covered by each layer and the fraction of ground that was not shaded by the trees, using observations of ground cover at a nearby site by Rencz and Auclair (1978; deciduous shrubs 10%; evergreen shrubs 7%; lichens 97%). We assumed a photon absorption coefficient of 0.9 for all plant surfaces.

For overcast periods we calculated light absorption from the area covered by each stratum, assuming uniform (i.e., isotropic) irradiance from the sky. We defined overcast periods as those with PPFD below 50% of that expected for clear-sky conditions (Tenhunen et al. 1990). During overcast periods the model distributed the intercepted PPFD evenly over the entire surface of each tree. During clear sky conditions 50% of each tree was fully illuminated, while the other side of a plant was illuminated at 10% of incident PPFD. The model assumed a uniform azimuthal distribution of nitrogen throughout the crown of each tree, although in practice a differential allocation of nitrogen by direction could improve a plant's carbon gain (Field 1983).

Results and discussion

Physical environment

Detailed information on the climatic conditions at Schefferville during the study is available from Fitzjarrald and Moore (1994) and Mortsch (1994). The summer of 1990 was characteristic, with monthly air temperatures during June and July within 1°C, and rainfall within 10%, of the 35-year mean. The median PPFD was only half that expected for clear-sky conditions (Fig. 1). The soil temperature at 5 cm depth rose rapidly in the morning and peaked several hours before the maximum air temperature. The diurnal amplitude of soil temperature exceeded that of air temperature (Fig. 1). This wide swing in soil temperature was consistent with the sparse canopy, and presumably resulted from direct radiative heating and cooling at the soil surface. The leaf to air VPD increased through the day, reflecting the course of leaf temperature. The specific humidity at the site was generally constant over a day, indicating that land-surface evaporation did not substantially increase the water-vapor content of the air over a diurnal cycle. There was substantial day-to-day variation in peak air temperature and VPD. Periods between the 25th and 75th percentiles had maximum temperatures of 10–20°C, and VPDs of 4–12 mb (Fig. 1).

Night-time observations and CO₂ storage beneath the sensor array

The eddy-correlation system measured the transfer of CO₂ through a plane 31 m above the ground. Figure 2 displays the diel courses of eddy-flux and air-column storage averaged from days 177–229 (26 June–17 August). During nocturnal stable periods an appreciable fraction of respired CO₂ was stored in the air column, and the eddy-flux observations were systematically lower than the total CO₂ respired (i.e., the net ecosystem exchange). Conversely, CO₂ was depleted from the air column during the morning, causing the eddy-flux obser-

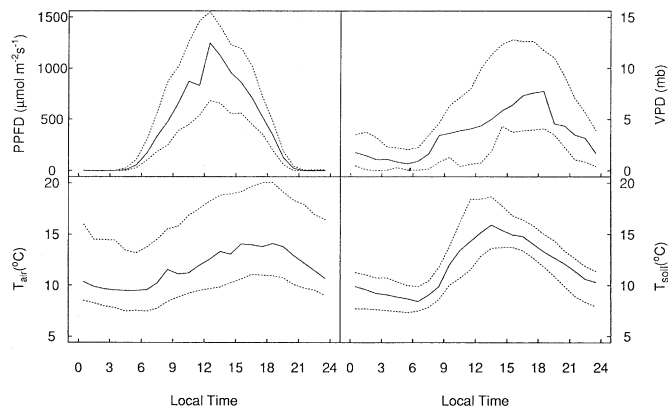


Fig. 1 Climatic conditions at the Schefferville site from 26 June through 17 August 1990. *Solid lines* are medians, *dashed lines* are 25th and 75th percentiles (PPFD photosynthetically active photon flux density, T_{air} air temperature)

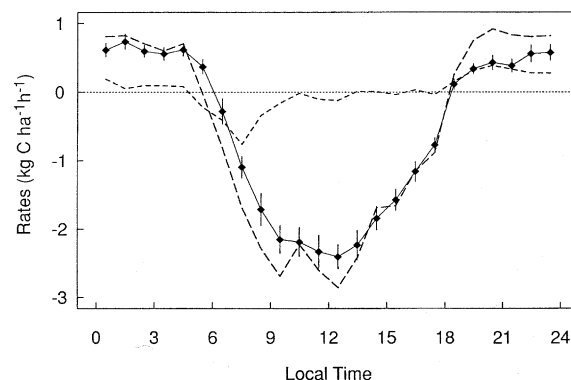


Fig. 2 Mean diel courses of eddy flux (*solid line*), air-column storage (*short dashes*), and net ecosystem exchange (*long dashes*) from 26 June through 17 August 1990. *Bars* are SEs

vations to underestimate photosynthesis during that period.

Unfortunately, the horizontally patchy distribution of CO₂ in the air column at night caused appreciable noise in the measurement of storage. While the seasonally-averaged diurnal course of air-column CO₂ clearly established the significance of flux divergence (Fig. 2), individual hourly measurements proved unreliable. As a result we relied on a second approach to reduce the impact of storage changes on our determination of net ecosystem CO₂ exchange. The relationship between hourly mean friction velocity (u^* ; a measure of atmospheric mixing) and the rate of nighttime eddy CO₂ exchange (ϕ_{31}) is shown in Fig. 3. The eddy CO₂ flux was suppressed during calm periods ($u^* < 0.2 \text{ m s}^{-1}$), apparently reflecting the buildup of CO₂ beneath the sensor array. During windy periods ($u^* > 0.2 \text{ m s}^{-1}$), ϕ_{31} was independent of turbulence, establishing that the surface layer was well mixed and CO₂ accumulation was less important. These observations did not reflect a change in biotic activity since there was no evident relationship between u^* and soil temperature. We therefore choose to use eddy-flux data during nocturnal periods with $u^* > 0.2 \text{ m s}^{-1}$ for our analysis of ecosystem respiration.

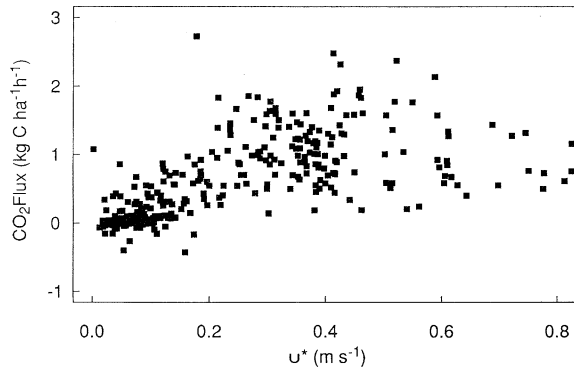


Fig. 3 Hourly mean nighttime CO₂ flux as a function of turbulent mixing (u^*)

Temporal patterns of carbon dioxide exchange

Net CO₂ uptake occurred between 6 a.m. and 6 p.m. local time, with a maximum rate of 3 kg C ha⁻¹ h⁻¹ around noon (Fig. 2). Respiration at night was around 0.8 kg C ha⁻¹ h⁻¹. These levels of metabolic activity are below those reported for temperate and tropical forests (Baldocchi et al. 1986, 1987; Fan et al. 1990; Wofsy et al. 1993; Hollinger et al. 1994). The daytime fluxes were about 75%, and the nighttime fluxes 60%, lower than those observed in mid-latitude deciduous forests.

The diurnal course of net carbon exchange, averaged over 10-day intervals, was relatively consistent throughout the study (Fig. 4). The net carbon uptake from 27 July to 6 August, a warm, dry, sunny period, was lower than during other intervals. This pattern is evident also in the seasonal course of 10-day mean gross assimilation, respiration, and net CO₂ uptake (Fig. 5). High rates of carbon accumulation (20 kg C ha⁻¹ day⁻¹) occurred during the early part of July and again during the middle of August. The net carbon gain during early August was only 8 kg C ha⁻¹ day⁻¹. The daily gross uptake of carbon increased slightly over the study, while there was considerable variation between periods in net carbon gain. The rate of ecosystem-level carbon storage was closely related to temperature and respiration. The maximum rate of ecosystem carbon storage coincided with reduced respiration during cool periods at the beginning and end of the study.

When summed over the 53-day period, the gross assimilation by the forest was 2450 kg C ha⁻¹, the total respiration was 1660 kg C ha⁻¹, and the net storage was 790 kg C ha⁻¹. Extrapolation of these observations to a growing season of 100 days yields a net carbon uptake of approximately 1500 kg C ha⁻¹. This compares with a total biomass of about 20 000 kg C ha⁻¹ at a nearby site (Rencz and Auclair 1978), and implies that the forest could double its biomass in 15 years. This rate of carbon storage is unlikely to be realized since a substantial amount of carbon is lost during fall, winter, and spring respiration (Moore 1983). Additionally, the carbon uptake during the early and late periods of the growing season may be lower than that observed in July and August.

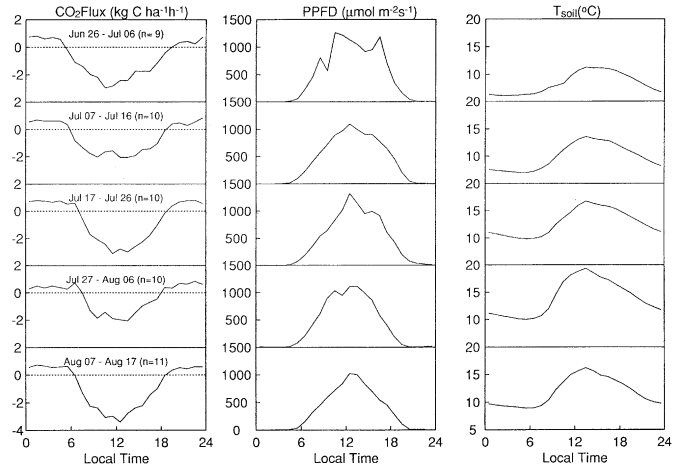


Fig. 4 Diel courses of CO₂ flux, PPFD, and soil temperature (at 5 cm depth) averaged over the indicated time intervals

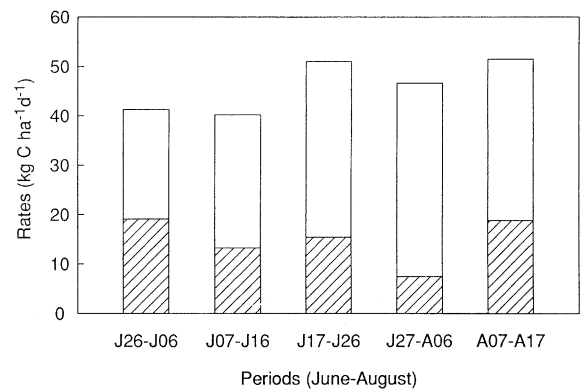


Fig. 5 Seasonal course of daily net CO₂ uptake (shaded areas), respiration (unshaded areas), and gross CO₂ assimilation (sum of the two areas) averaged over the indicated time intervals

Nonetheless, these observations establish that a boreal forest can act as a considerable short-term, and possibly long-term, sink for atmospheric carbon dioxide as suggested by D'Arrigo et al. (1987).

Forest respiration

The hourly nighttime eddy flux of CO₂ during well-mixed periods ($u^* > 0.2$ m s⁻¹) was positively correlated with soil temperature (Fig. 6). The levels of respiratory activity (0.5–2 kg C ha⁻¹ h⁻¹) were consistent with the component fluxes that have been measured in black spruce northern forests (Schlentner and Van Cleve 1985). The bulk ecosystem Q_{10} of ≈ 3 is slightly higher than has been reported for soil (Raich and Schlesinger 1992), and also for whole forests (Wofsy et al. 1993), a pattern that may reflect our reliance on a single set of temperature observations at 5 cm depth. Q_{10} should be measured in thermally homogeneous systems, and the diurnal amplitude of temperature at 5 cm may have been less than for the ecosystem as a whole. The simple linear model we use to derive the ecosystem respiration may introduce bi-

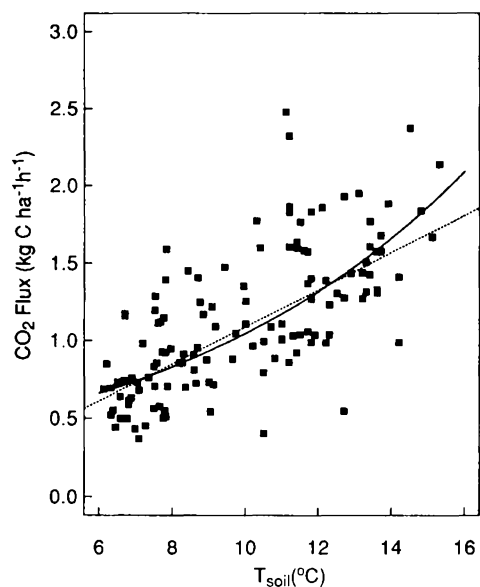


Fig. 6 Hourly average nighttime CO_2 flux (respiration) during well-mixed periods ($u^* > 0.2 \text{ m s}^{-1}$) as a function of soil temperature (5 cm depth). The dotted line is a linear fit ($\text{flux} = -0.11 + 0.12T_{\text{soil}}$); the solid line is an exponential fit [$\text{flux} = 0.33 \exp(0.1167T_{\text{soil}})$]

ases in the daytime, but a mechanistic respiration model cannot be constrained with available measurements. There was considerable scatter in the temperature-respiration relationship, a pattern similar to that observed in other forests (Wofsy et al. 1993; Hollinger et al. 1994). This variation reflects the combined effects of change in storage, measurement noise, spatial heterogeneity in physiological activity and temperature, and perhaps additional unknown controls on respiration. We were unable to account for any residual variance in nighttime CO_2 exchange by considering wind direction, soil water balance, or air temperature.

Carbon assimilation

Hourly photosynthesis (gross assimilation) was calculated from the estimated ecosystem respiration and measured CO_2 flux. The rate of gross assimilation was strongly dependent on the incident PPFD (Fig. 7). The maximum photosynthesis was 4–5 $\text{kg C ha}^{-1} \text{ h}^{-1}$. At low PPFD ($< 600 \mu\text{mol m}^{-2} \text{ s}^{-1}$) photosynthesis was nearly linearly related to light. Above $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$, ecosystem photosynthesis was light saturated, becoming insensitive to PPFD. The slope of the light response at low PPFD indicates an ecosystem-level quantum yield of $0.017 \text{ mol CO}_2 \text{ mol}^{-1} \text{ photon}$. This is 25% of the leaf-level quantum yield of C_3 plants (Farquhar and von Caemmerer 1982; Walker 1992), a pattern that presumably reflects the fraction of PPFD absorbed by foliage. The sharp transition to light saturation contrasts with the comparatively smooth, non-saturating response of most temperate and tropical forest canopies (Jarvis and Leve-

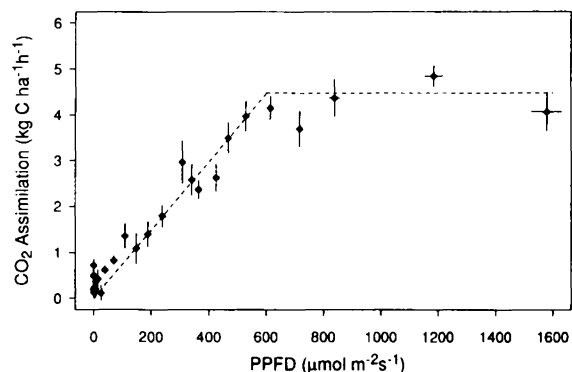


Fig. 7 Ecosystem photosynthesis as a function of incident PPFD. Points are averages within PPFD intervals, bars are SEMs. The dashed line illustrates the sharp light saturation at $600 \mu\text{mol m}^{-2} \text{ s}^{-1}$

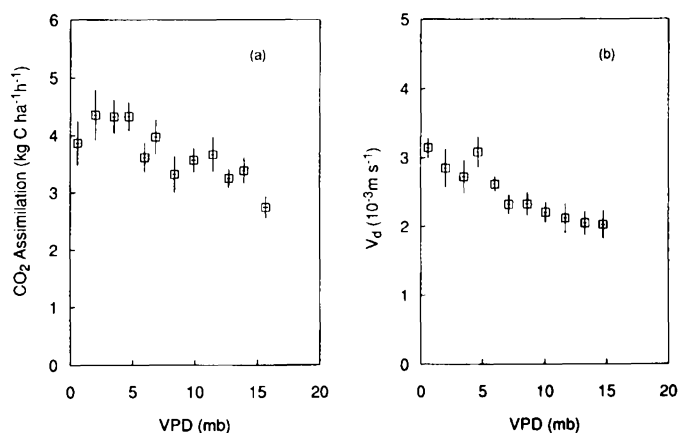


Fig. 8 a Ecosystem photosynthesis at saturated light ($\text{PPFD} > 800 \mu\text{mol m}^{-2} \text{ s}^{-1}$) as a function of leaf-to-air vapor pressure deficit (VPD). b Ozone deposition velocity during the same periods as a function of leaf-to-air VPD. Points are averages for binned VPD intervals, bars are SEMs

renz 1983; Baldocchi et al. 1987; Fan et al. 1990; Wofsy et al. 1993; Hollinger et al. 1994).

Light-saturated photosynthesis was negatively correlated with leaf VPD; a 30% reduction in gross assimilation was observed during periods of high evaporative demand ($\text{VPD} > 7 \text{ mb}$; Fig. 8a). A similar trend was noted for ozone deposition velocity (V_d ; Fig. 8b). Since ozone deposits to terrestrial ecosystems primarily through leaf stomata (Rich et al. 1970), the reduction in V_d at high VPD presumably reflected a decrease in leaf-surface conductance. Light-saturated photosynthesis during periods of low evaporative demand ($\text{VPD} < 6 \text{ mb}$, $\text{PPFD} > 800 \mu\text{mol m}^{-2} \text{ s}^{-1}$) was unrelated to air temperature (Fig. 9), a behavior similar to that of individual black spruce branches (Vowinckel et al. 1975). The reduction in photosynthesis during high-VPD periods likely involved a stomatal response to evaporative demand and a subsequent decline in supply of CO_2 to chloroplasts, rather than a direct effect of temperature on leaf biochemical activity. The reduction in V_d and presumably stomatal conductance on hot days (air temperature=

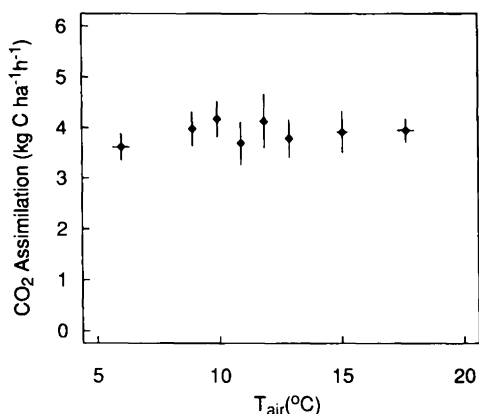


Fig. 9 Light-saturated photosynthesis during periods of low evaporative demand ($VPD < 6$ mb, $PPFD > 800 \mu\text{mol m}^{-2} \text{s}^{-1}$) as a function of air temperature. Points are averages for binned temperature intervals, bars are SEMs

20–25°C) was at least 25%. This stomatal response, coupled with the generally high aerodynamic conductances and Bowen ratios at the site (Fitzjarrald and Moore 1994), is presumably sufficient to limit stand and regional evaporation on days of high evaporative demand (Jarvis and McNaughton 1986).

Model predictions

Model simulations of ecosystem photosynthesis were carried out for 24 days with complete and continuous field measurements. The model provided generally accurate predictions of CO_2 assimilation, with discrepancies of $\pm 1 \text{ kg C ha}^{-1} \text{ h}^{-1}$ between predicted and observed fluxes, comparable to the statistical error of the flux measurement. The predicted rates of daily photosynthesis by the tree, shrub, and lichen layers were similar (Fig. 10a; black spruce $16.4 \text{ kg C ha}^{-1} \text{ day}^{-1}$; shrubs $12.4 \text{ kg C ha}^{-1} \text{ day}^{-1}$; lichen $13.2 \text{ kg C ha}^{-1} \text{ day}^{-1}$). This high rate of carbon uptake by the ground cover is consistent with the relative net production of trees and mosses at other black spruce sites (Van Cleve et al. 1983; Bonan and Shugart 1989). When averaged over the 24 days, the model predicted a daily gross whole-ecosystem uptake of $42 \text{ kg C ha}^{-1} \text{ day}^{-1}$, comparable to the observed flux of $40 \text{ kg C ha}^{-1} \text{ day}^{-1}$. The model also effectively simulated the diurnal course of photosynthesis (Fig. 10b). A slight systematic overestimation of photosynthesis in the morning presumably reflected the change in CO_2 storage following sunrise (Fig. 2). The model generally over-estimated photosynthesis during wet or misty periods when the sonic anemometer appeared to be in normal operation. This trend possibly reflected a change in surface conductance associated with leaf wetting, or more likely errors in some other measurement associated with wet instruments.

The modeled and observed rates for hourly photosynthesis are plotted against incident PPFD in Fig. 11, with overcast periods distinguished from sunnier intervals. At

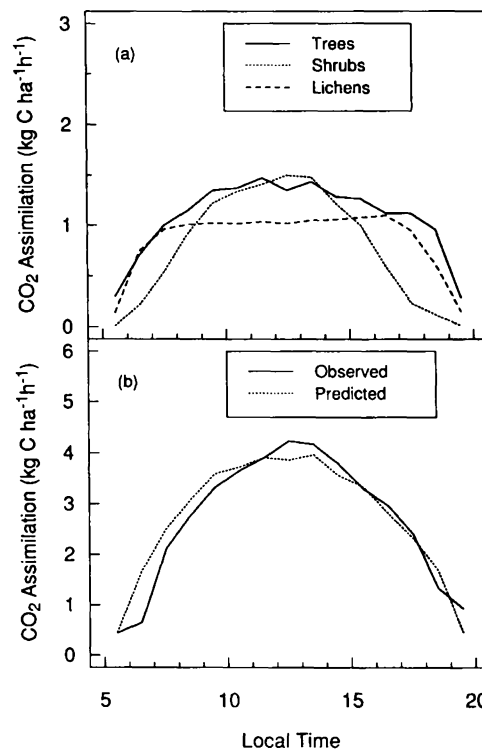
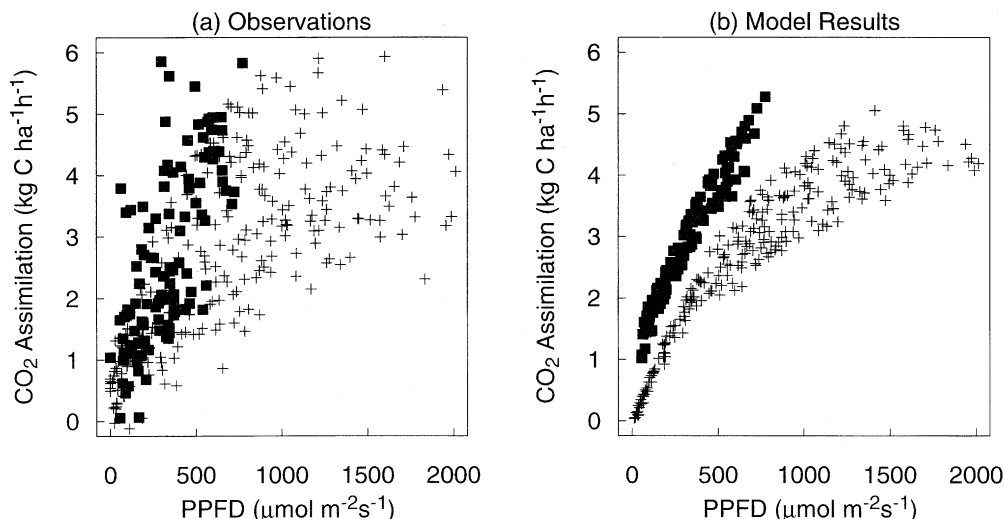


Fig. 10 a Simulated diurnal courses of photosynthesis by the tree, shrub, and lichen layers. b Comparison between predicted and observed ecosystem photosynthesis. Hourly means were averaged over the 24 days with complete observations from 5 a.m. to 8 p.m. local time

a given light intensity, the carbon uptake was at least 50% greater during cloudy intervals compared with clear-sky periods. This trend was primarily the result of the canopy geometry of the Schefferville site, although an associated increase in VPD may have played a role in decreasing the photosynthesis during sunny periods. The isolated conical crowns of *P. mariana* allowed an even distribution of light over the forest surface during cloudy intervals. The modeled intensity of light on shadowed surfaces was usually higher during overcast conditions compared with brighter cloud-free periods. A forest composed of conical trees is efficient at absorbing direct-beam light from a low elevation angle, a pattern that is especially beneficial at high latitude (Oker-Blom and Kellomaki 1982). The trees intercepted a larger fraction of light than lichens at low solar elevation under clear sky conditions, but less when the sun was high in the sky. Since the ground-area-based photosynthetic capacity of the trees was 3 times higher than that of the lichens, the three-dimensional structure of the forest, together with frequently overcast conditions, was largely responsible for the sharply non-linear response of photosynthesis to incident PPFD.

The comparatively efficient use of light by the forest during overcast periods limited the impact of cloudiness on the annual gross ecosystem-level production. Figure 12a shows the relative predicted change in gross photosynthesis during overcast periods for a series of different

Fig. 11 **a** Observed ecosystem photosynthesis as a function of PPFD. **b** Predicted ecosystem photosynthesis as a function of PPFD. For both plots, overcast periods are shown by *filled squares*, intervals with clear skies are shown by *crosses*



levels of light attenuation. At 50% light attenuation, the ecosystem assimilated more CO_2 on an overcast day than on a day with clear sky. On a day of heavier cloud cover with 70% light attenuation, gross CO_2 assimilation was reduced by ~15%. As expected, the predicted plant water use efficiency increased substantially during overcast conditions (data not shown). A limited impact of cloudiness on gross production has also been predicted in other ecosystems; Tenhunen et al. (1990) modeled a similar annual carbon gain but lower transpiration by Mediterranean-climate shrubs during an “overcast year” compared to a “clear year”.

The annual gross and net production of forested ecosystems may be tightly correlated with the cumulative intercepted photosynthetic photon flux (Monteith 1972; Jarvis and Leverenz 1983). This correlation reflects the conservative quantum yield of C_3 photosynthesis, and the comparatively linear light response of whole canopies. In turn, the fraction of light intercepted by a canopy during clear-sky conditions may be correlated with spectral reflectance (i.e., Normalized difference Vegetation index), opening the possibility of using satellite observations to estimate carbon uptake (Kumar and Monteith 1981; Potter et al. 1993). The eddy-flux observations at Schefferville indicate this approach may not be directly applicable to boreal woodlands. The sharply non-linear light response (Fig. 7), the substantial decrease in photosynthesis at moderate evaporative demand (Fig. 8), and the importance of diffuse solar radiation (Figs. 11 and 12a) may necessitate the use of short-time-step models, and high-resolution meteorological inputs, to accurately predict the carbon uptake of boreal forests.

Increases in temperature in the boreal zone are projected in the next few decades as a result of the continuing accumulation of “greenhouse” gases in the atmosphere (Manabe and Stouffer 1980). Figure 12b shows the predicted change in photosynthesis and respiration for a series of temperature shifts. A decrease in photosynthesis with warmer conditions is predicted to result from the increase in VPD and subsequent stomatal closure. Additionally, respiration increases with tempera-

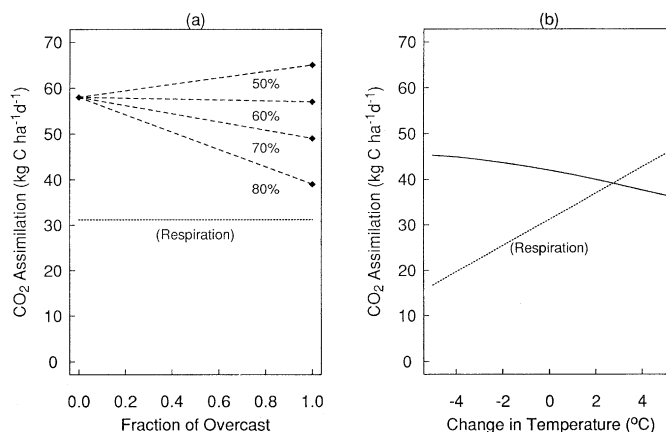


Fig. 12 Simulated ecosystem photosynthesis **a** as a function of overcast frequency, at 50%, 60%, 70% and 80% light attenuation, **b** at a series of shifts in air temperature. Other model inputs are for **a** median observations (see Fig.1) and **b** hourly observations over the 24 days with complete observations. Ecosystem respiration was calculated in **b** assuming the same temperature shifts in soil as in air

ture, resulting in a shift in the ecosystem carbon balance over the 24 modeled days from a net sink to a source of atmospheric CO_2 at a temperature increase of 3°C . This increase in temperature is within the range of most future-climate projections, and also within the range of interannual variability.

These findings suggest strong sensitivity of a boreal forest’s carbon balance to relatively small shifts in temperature. Oechel et al. (1993) reported a shift from CO_2 sink to source for an Alaskan tundra, as a result of a change in water table depth. In contrast, Pastor and Post (1988) predicted a substantial increase over time in forest biomass at Schefferville associated with CO_2 -induced climate change. Melillo et al. (1993) also estimated increases in net primary production in northern ecosystems in response to a warmer climate, reflecting an enhanced nitrogen availability.

Remaining gaps in our understanding of boreal forest carbon and nutrient cycles prevent a more quantitative

prediction of how the carbon balance of the Schefferville site would respond to a change in climate. In particular we lack long-term data to predict the CO₂ exchange during spring, fall, and winter. Additionally, we have only a limited understanding of the significance of extreme conditions such as drought that could subject the forest to physiological damage, or of the long-term changes in metabolism associated with a shifting climate. Finally, the effect of stand age and the fire-succession mosaic needs to be considered in efforts to predict how the carbon balance of the boreal forest as a whole will respond to climatic perturbation. Until the ecosystem-level feedbacks between the physical environment and the forest physiology are quantitatively understood, efforts to predict the future course of boreal forest carbon storage must be viewed as uncertain.

Conclusions

1. The maximum observed rates of respiration and photosynthesis by the black spruce boreal woodland were one-quarter to one-half of those observed in temperate-deciduous forests. Nonetheless, carbon gain by the forest was significant, totaling 790 kg C ha⁻¹ over a period of 53 days from the end of June to mid-August. Much of this carbon gain may be lost during fall, winter, and spring respiration; measurements of CO₂ fluxes during these periods are needed to estimate the annual carbon balance.
2. The forest showed a marked reduction in carbon uptake and ozone deposition conductance at modest VPDs (>7 mb). This response presumably is an important controller of ecosystem carbon uptake and transpiration.
3. The sparse-conical canopy of the forest and the degree of cloudiness play important roles in defining the short-term response of ecosystem photosynthesis to incident light. The field observations established that at a given light level carbon uptake was ~50% greater during overcast periods compared with periods when the sky was clear. The model indicated that increased light on shaded surfaces during overcast periods accounts for this observed increase in photosynthesis.
4. The mechanistic model provided an accurate prediction of forest photosynthesis once the effect of evaporative demand and light absorption were incorporated. The photosynthetic capacity of the woodland, incident PPF, specific humidity, temperature, and canopy structure were important factors regulating the observed CO₂ exchange. Each of these factors may change in the future, possibly shifting the carbon balance of boreal forests.

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References

- Amthor JS (1994) Scaling CO₂-photosynthesis relationships from the leaf to the canopy. *Photosynth Res* 39:321–350
- Amthor JS, Goulden ML, Munger JW, Wofsy SC (1994) Testing a mechanistic model of forest-canopy mass and energy exchange using eddy correlation: carbon dioxide and ozone uptake by a mixed oak-maple stand. *Aust J Plant Physiol* 21:623–651
- Auclair AND, Rencz AN (1982) Concentration, mass, and distribution of nutrients in a subarctic *Picea mariana-Cladonia alpestris* ecosystem. *Can J For Res* 12:947–968
- Baldocchi DD, Verma SB, Matt DR, Anderson DE (1986) Eddy correlation measurements of carbon dioxide efflux from the floor of a deciduous forest. *J Appl Ecol* 23:967–975
- Baldocchi DD, Verma SB, Anderson DE (1987) Canopy photosynthesis and water-use efficiency in a deciduous forest. *J Appl Ecol* 24:251–260
- Baldocchi DD, Hicks BB, Meyers TP (1988) Measuring biosphere-atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology* 69:1331–1340
- Baldocchi DD, Luxmore RJ, Hartfield JL (1991) Discerning the forest from trees: an essay on scaling canopy stomatal conductance. *Agric For Meteorol* 54:197–226
- Bigger M, Oechel WC (1982) Nutrient effect on maximum photosynthesis in arctic plants. *Holarct Ecol* 5:158–163
- Bonan GB (1991) Atmosphere-biosphere exchange of carbon dioxide in boreal forest. *J Geophys Res* 96:7301–7312
- Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. *Annu Rev Ecol Syst* 20:1–28
- Carstairs AG, Oechel WC (1978) Effects of several microclimatic factors and nutrients on net carbon dioxide exchange in *Cladonia alpestris*. *Arct Alp Res* 10:81–94
- Collatz GJ, Grivet C, Ball JT, Berry JA (1991) Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric For Meteorol* 54:107–136
- D'Arrigo R, Jacoby GC, Fung IY (1987) Boreal forests and atmosphere-biosphere exchange of carbon dioxide. *Nature* 329:321–323
- Fan S-M, Wofsy SC, Bakwin PS, Jacob DJ, Fitzjarrald DR (1990) Atmosphere-biosphere exchange of CO₂ and O₃ in the central Amazon forest. *J Geophys Res* 95:161851–161864
- Fan S-M, Wofsy SC, Bakwin PS, Jacob DJ, Anderson SM, Keenan PL, McManus JB, Kolb CE, Fitzjarrald DR (1992) Micrometeorological measurements of CH₄ and CO₂ exchange between the atmosphere and subarctic tundra. *J Geophys Res* 97:161627–161643
- Farquhar GD, Caemmerer S von (1982) Modeling of photosynthetic response to environmental conditions. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) *Physiological plant ecology II*. (Encyclopedia of plant physiology, NS, vol 12B). Springer, Berlin Heidelberg New York, pp 549–587
- Farquhar GD, Caemmerer S von, Berry JA (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149:78–90
- Field C (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56:341–347
- Fitzjarrald DR, Moore KE (1994) Growing season boundary layer climate and surface exchanges in a subarctic lichen woodland. *J Geophys Res* 99:1899–1917
- Harris RC, Wofsy SC, Hoell JM Jr, Bendura RJ, Drewry JW, McNeal RJ, Pierce D, Rabine V, Snell RL (1994) The Arctic boundary layer expedition (ABLE-3B): July-August 1990. *J Geophys Res* 99:1635–1643
- Hickleton PR, Oechel WC (1976) Physiological aspects of the ecology of *Dicranum fuscescens* in the subarctic. I. Acclimation and acclimation potential of CO₂ exchange in relation to habitat, light, and temperature. *Can J Bot* 54:1104–1119
- Hickleton PR, Oechel WC (1977a) Physiological aspects of the ecology of *Dicranum fuscescens* in the subarctic. II. Seasonal patterns of organic nutrient content. *Can J Bot* 55:2168–2177

- Hickleton PR, Oechel WC (1977b) The influence of light intensity and temperature on the field carbon dioxide exchange of *Dicranum fuscescens* in the subarctic. *Arct Alp Res* 9:407–419
- Hollinger DY, Kelliher FM, Byers JN, Hunt JE, McSeveny TM, Weir PL (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* 75:134–150
- Hom JL, Oechel WC (1983) Photosynthetic capacity, nutrient content and nutrient use efficiency of different needle age classes of black spruce (*Picea mariana*) found in interior Alaska. *Can J For Res* 13:834–839
- Jackson CI (1959) Insolation and albedo in Quebec-Labrador. *McGill Subarct Res Pap* 5:1–105
- Jarvis PG, Leverenz JW (1983) Productivity of temperate, deciduous and evergreen forests. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) *Physiological plant ecology IV*. (Encyclopedia of plant physiology, NS, vol 12D). Springer, Berlin Heidelberg New York, pp 233–280
- Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. *Adv Ecol Res* 15:1–49
- Kumar M, Monteith JL (1981) Remote sensing of crop growth. In: Smith H (ed) *Plants and the daylight spectrum*. Academic Press, San Diego, pp 133–144
- Manabe S, Stouffer RJ (1980) Sensitivity of a global climate model to an increase of CO₂ concentration in the atmosphere. *J Geophys Res* 85:5529–5554
- McMillen RT (1988) An eddy correlation technique with extended applicability to non-simple terrain. *Boundary-Layer Meteorol* 43:231–245
- Melillo J.M, McGuire AD, Kicklighter DW, Moore III B, Vorostarty CJ, Schloss AL (1993) Global climate change and terrestrial net primary production. *Nature* 363:234–240
- Mitchell JFB, Manabe S, Meleshko V, Tokiola T (1990) Equilibrium climate change – and its implications for the future. In Houghton JT, Jenkins GJ, Ephraums JJ (eds) *Climate change: the IPCC scientific assessment*. Cambridge University Press, Cambridge, pp 131–172
- Monteith JL (1972) Solar radiation and productivity in tropical ecosystems. *J Appl Ecol* 9:747–766
- Moore TR (1983) Winter-time litter decomposition in a subarctic woodland. *Arct Alp Res* 15:413–418
- Mortsch LD (1994) Assessment of the temperature and precipitation of 1990 during the Northern Wetlands Study (NOWES). *J Geophys Res* 99:1429–1438
- Oechel WC, Hastings SJ, Vourlitis G, Jenkins M, Riechers G, Grulke N (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* 361:520–523
- Oker-Blom P, Kellomaki S (1982) Theoretical computations on the role of crown shape in the absorption of light by forest trees. *Math BioSci* 59:291–311
- Pastor J, Post WM (1988) Response of northern forests to CO₂-induced climate change. *Nature* 334:55–58
- Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, Mooney HA, Klooster SA (1993) Terrestrial ecosystem production: a process model based on global satellite and surface data. *Global Biogeochem Cycles* 7:811–841
- Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus* 44B:81–99
- Rencz AN (1976) The level and distribution of biomass and nutrients in a subarctic lichen woodland. M.Sc. thesis, McGill University, Montreal
- Rencz AN, Auclair AND (1978) Biomass distribution in a subarctic *Picea mariana*-*Cladonia alpestris* woodland. *Can J For Res* 8:168–176
- Rich S, Waggoner PE, Tomlinson H (1970) Ozone uptake by bean leaves. *Science* 169:78–79
- Schlentner RE, Van Cleve K (1985) Relationships between CO₂ evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. *Can J For Res* 15:97–106
- Schlesinger WH (1991) *Biogeochemistry: an analysis of global change*. Academic Press, New York
- Sharkey TD (1985) Photosynthesis in intact leaves of C₃ plants: physics, physiology and limitations. *Bot Rev* 51:53–105
- Sharpe M (1986) Post-fire succession in the lichen woodlands of the Schefferville area, Quebec. Thesis, McGill University, Montreal
- Smith EM, Hadley EB (1974) Photosynthetic and respiratory acclimation to temperature in *Ledum groenlandicum* populations. *Arct Alp Res* 6:13–27
- Tenhunen JD, Sala Serra A, Harley PC, Dougherty RL, Reynolds JF (1990) Factors influencing carbon fixation and water use by mediterranean sclerophyll shrubs during summer drought. *Oecologia* 82:381–393
- Van Cleve K, Dyrness CT, Viereck LA, Fox J, Chapin FS III, Oechel WC (1983) Taiga ecosystems in interior Alaska. *BioScience* 33:39–44
- Vowinckel T, Oechel WC, Boll WG (1975) The effect of climate on the photosynthesis of *Picea mariana* at the subarctic tree-line. 1. Field measurements. *Can J Bot* 53:604–620
- Walker D (1992) Excited leaves. *New Phytol* 121:325–345
- Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapour transfer. *Q J R Meteorol Soc* 106:85–100
- Wofsy SC, Goulden ML, Munger JW, Fan S-M, Bakwin PS, Daube BC, Bassow SL, Bazzaz FA (1993) Net exchange of CO₂ in a mid-latitude forest. *Science* 260:1314–1317