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Agricultural and Forest Meteorology 90 (1998) 291–306

AGRICULTURAL
AND
FOREST
METEOROLOGY

Forest–atmosphere carbon dioxide exchange in eastern Siberia

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Received 12 June 1997; received in revised form 5 January 1998; accepted 14 January 1998

Abstract

We investigated the daily exchange of CO_2 between undisturbed *Larix gmelinii* (Rupr.) Rupr. forest and the atmosphere at a remote Siberian site during July and August of 1993. Our goal was to measure and partition total CO_2 exchanges into aboveground and belowground components by measuring forest and understory eddy and storage fluxes and then to determine the relationships between the environmental factors and these observations of ecosystem metabolism. Maximum net CO_2 uptake of the forest ecosystem was extremely low compared to the forests elsewhere, reaching a peak of only $\sim 5\ \mu mol\ m^{-2}\ s^{-1}$ late in the morning. Net ecosystem CO_2 uptake increased with increasing photosynthetically active photon flux density (PPFD) and decreased as the atmospheric water vapor saturation deficit (D) increased. Daytime ecosystem CO_2 uptake increased immediately after rain and declined sharply after about six days of drought. Ecosystem respiration at night averaged $\sim 2.4\ \mu mol\ m^{-2}\ s^{-1}$ with about 40% of this coming from the forest floor (roots and heterotrophs). The relationship between the understory eddy flux and soil temperature at 5 cm followed an Arrhenius model, increasing exponentially with temperature ($Q_{10} \sim 2.3$) so that on hot summer afternoons the ecosystem became a source of CO_2. Tree canopy CO_2 exchange was calculated as the difference between above and below canopy eddy flux. Canopy uptake saturated at $\sim 6\ \mu mol\ CO_2\ m^{-2}\ s^{-1}$ for a PPFD above $500\ \mu mol\ m^{-2}\ s^{-1}$ and decreased with increasing D. The optimal stomatal control model of Mäkelä et al. (1996) was used as a 'big leaf' canopy model with parameter values determined by the non-linear least squares. The model accurately simulated the response of the forest to light, saturation deficit and drought. The precision of the model was such that the daily pattern of residuals between modeled and measured forest exchange reproduced the component storage flux. The model and independent leaf-level measurements suggest that the marginal water cost of plant C gain in *Larix gmelinii* is more similar to values from deciduous or desert species than other boreal forests. During the middle of the summer, the *L. gmelinii* forest ecosystem is generally a net sink for CO_2, storing $\sim 0.75\ g\ C\ m^{-2}\ d^{-1}$. Published by Elsevier Science B.V.

Keywords: CO_2; Eddy correlation; *Larix*; Stomatal control; Carbon balance; Boreal forest

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PII S0168-1923(98)00057-4

1. Introduction

Recent studies suggest that boreal forests may play a major role in regulating the climate of the northern hemisphere and in global carbon cycling (e.g. Bonan et al., 1992; Tans et al., 1990; Ciais et al., 1995; Otto-Bliesner and Upchurch, 1997). In North America, the BOREAS program (Sellers et al., 1995) has investigated carbon and energy exchange in two regions of Canada. We carried out similar studies prior to BOREAS using the eddy-correlation technique to make area-averaged measurements of net CO_2 exchange between the atmosphere and the dry boreal forest of eastern Siberia in July 1993. The Siberian eastern boreal forest (taiga) is dominated by the deciduous conifer tree *Larix gmelinii* (Rupr.) Rupr. It is the most extensive coniferous forest in the world, covering approximately $205 \cdot 10^6$ ha (7% of the total world closed forest), an area larger than the North American boreal forest (Faladeev, 1985; Gower and Richards, 1990).

Our goals were to determine how environmental variables regulate ecosystem C exchange and how carbon storage in this ecosystem might change with a changing climate. In this paper, we examine a set of half-hourly measurements of the forest floor and whole ecosystem carbon exchange and environmental variables made on 14 summer days with different weather conditions in a *Larix gmelinii* forest. Total ecosystem and canopy exchange rates are interpreted using an optimal stomatal control model of photosynthesis and transpiration.

2. Methods

2.1. Experimental site

Data were collected from 12–27 July 1993 at a remote site in undisturbed *Larix gmelinii* forest in the eastern Siberian Republic of Sakha (Yakutia), Russia. The study region is on the Aldan plateau, a limestone plate covered by alluvium south of the bow of the Lena river. Shallow valleys, mostly running north–south, dissect the region. Slopes and hilltops (~90% of the landscape) are covered by almost pure Larch forest; the cooler valley bottoms are covered by *Betula exilis* Sukatschev and various grass and sedge species (Schulze et al., 1995). Our measurement site (60°51.59424′N latitude, 128°16.04004′E longitude; 348 m a.s.l.) was located about midway up a gently sloping (~3°) hill facing the southwest. Yakutsk, the nearest major city, was about 155 km to the northeast and the nearest human settlement was more than 60 km distant. The vegetation, nutrient status, physiology, energy balance and other features of this forest have been described previously (Schulze et al., 1995; Hollinger et al., 1995; Arneth et al., 1996; Vygodskaya et al., 1997; Kelliher et al., 1997).

Eastern Siberia experiences a continental, boreal climate characterized by long, extremely cold winters and short, dry summers. For the 10-year period between 1980 and 1990, the mean annual air temperature at Yakutsk averaged −9.6°C and annual precipitation averaged only 233 mm (213 mm as a long-term average), about one-half of that at the BOREAS sites in western Canada (Table 1) and less than one-third that of the eastern Canadian boreal forest (Vose et al., 1992). Summers are warm with a June–August average temperature at Yakutsk of 16.5°C, similar to that at the southern BOREAS site (Table 1). About 52% of the annual precipitation in Yakutsk falls in the summer, mostly from convective storms.

Vegetation at the measurement site was dominated by *Larix gmelinii* with a subcanopy of *Alnaster fruticosa* Rupr. and scattered *Betula platyphylla* Sukatschev. The understory was dominated by evergreen shrubs (*Vaccinium vitis-idaea* L. and *Arctosta-*

Table 1
Comparison of eastern Siberian climate to that at the BOREAS sites (1981–1991)

Site	Location	Annual T_{air}(°C)	June–August T_{air}(°C)	July T_{air}(°C)	Annual PPT(mm)
Yakutsk	60°52′N, 128°16′E	−9.6	16.5	19.0	233 [a]
BOREAS (N)	55°53′N, 98°29′W	−2.9	14.4	16.2	534
BOREAS (S)	53°55′N, 104°41′W	1.0	16.6	17.7	403

[a] long-term average=213 mm (Müller, 1982).

phylos uva-ursi (L.) Spreng.) and lichens (*Cetraria laevigata* Rassad. and *Cladina rangiferina* (L.) Nyl.). This site regenerated following a fire ∼125 years ago.

Trees in a 0.5 ha plot surrounding the tower were about 15–18 m tall with a dbh of <30 cm, typical of other Siberian, North American and European *Larix* sites (Schulze et al., 1995). Tree age averaged 125 years and the plot basal area was 23.5 $m^2\ ha^{-1}$. The projected area of *L. gmelinii* foliage per unit ground area (LAI) was estimated as 1.4 from biomass harvests (Schulze et al., 1995), giving the stand an open, park-like appearance. The forest floor vegetation of height ∼15 cm had a combined LAI of 1.0 (Kelliher et al., 1997).

The soils consisted of a 3 cm deep L (litter) layer, a shallow, silt loam Ah horizon free from calcium and of depth 5 cm and a similar AB silt loam containing remnants of charcoal of depth 2 cm that graded into a Bw horizon of depth 15 cm. Roots penetrated through the Bw horizon. The C-horizon (35 cm thick) consisted of silt loam with pieces of limestone. Permafrost lay under the site in mid-July at an estimated depth of 80 cm.

2.2. Instrumentation

A guyed, 21 m tall prefabricated aluminum tower was erected against a large *L. gmelinii* tree trunk and instrumented for background micrometeorological and eddy flux measurements. Total and diffuse photosynthetically active photon flux density (PPFD), net radiation, rainfall, wind speed, wind direction, air temperature and humidity above the forest and forest floor and soil temperature at a variety of depths were measured at 3 s intervals and stored as 30 min averages on data loggers (models CR10 and 21X, Campbell Scientific, Logan, UT).

CO_2, H_2O and sensible heat exchange rates were measured at 22 m with the eddy covariance technique (Baldocchi et al., 1988; McMillen, 1988). A three-component sonic anemometer (model SWS-11/3KE, Applied Technology, Boulder, CO) and a Krypton-line U.V. hygrometer (model KH2O, Campbell Scientific) were mounted on a boom connected to an antenna rotator at the top of the tower and were remotely pointed into the prevailing wind (Hollinger et al., 1994). The intake of a polypropylene tube (i.d.=4 mm) was located approximately 0.2 m from the 3-D anemometer and was used to duct a sample of air to a closed-path nondispersive infrared CO_2 analyzer (model 225 Mk3, Analytical Development Company, Hoddesdon, UK) located in a tent at the base of the tower. Air was drawn through 30 m of tubing to the tent, then through an 8 μm filter, a heat exchanger consisting of 5 m coiled copper tubing immersed in water, the analysis cell of the gas analyzer and then a flow meter at a rate of 4 l min^{-1}. The gas analyzer was operated in differential mode, with a trapped sample of ambient air in the reference cell. All connections were gas tight and a vacuum gauge was used to read the gas pressure in the IRGA analysis cell (typical pressure drop of ∼3 kPa). In this configuration, the analyzer 1-1/e time constant was 2.2 s, as measured by rapidly switching between two airstreams of different CO_2 concentration with a high-speed solenoid valve. Additional eddy flux measurements of sensible heat and CO_2 exchange were made at a height of 1.8 m above the forest floor. These data were obtained with a single-axis sonic anemometer and fine-wire thermocouple (model CA-27, Campbell Scientific) and by ducting a sample of air from near the anemometer to a second infrared gas analyzer (model LI-6252, Licor, Lincoln, NE) through 20 m of tubing, an 8 μm filter and coiled copper heat exchanger. The flow rate and pressure drop in this system was similar to that used for above canopy measurements but the 1-1/e time constant of 0.8 s was shorter. Because we lacked below canopy H_2O flux and net radiation measurements, we could not assess the energy balance of this system.

The instruments were read by a data acquisition system consisting of a 16 bit analog to digital board (model DAS HRES, Metrabyte, Taunton, MA) and a microcomputer. Raw data values were sampled at 10 Hz and recorded on disk and half-hourly fluxes were calculated with a computer program written by McMillen (1988). All raw data were retained and archived on optical disks (model PC-800, Storage Dimensions, San Jose, CA).

The CO_2 and H_2O flux data were corrected for density and spectral effects (Webb et al., 1980; Moore, 1986; Businger and Delany, 1990). We also corrected the hygrometer measurements for the effects of oxygen density fluctuations owing to the sensible heat flux (Tanner et al., 1993; Kelliher et al., 1997). The ecosystem energy balance was examined for ‘closure’ by checking the equality of the sum of the latent heat (λE, H_2O) and sensible heat (H) fluxes ($\lambda E + H$) to the available energy (R_a)($R_a = \lambda E + H$). Half-hourly values of R_a were determined by the difference between the measurements of above-forest net all-wave radiation (R_n), canopy and air column heat storage (S) and soil heat flux (G)($R_a = R_n - S - G$) according to Kelliher et al. (1992). Agreement of the turbulent fluxes H and λE with the available energy R_a was generally fair to good such that $(H+\lambda E) = 0.83R_a + 9\ \mathrm{W m^{-2}}$ ($r^2 = 0.92$) for 364 half-hourly periods (Kelliher et al., 1997).

We calculated half-hourly changes in CO_2 storage in the forest air column below our 22 m flux measurement height by measuring the CO_2 concentration at heights of 1, 5, 9, 13, 17 and 21 m with a system consisting of a non-dispersive infrared gas analyzer (model BINOS 1, Leybold-Heraeus, Hanau, Germany), pumps, switching manifold, PTFE inlet tubes and data logger (model DL2, Delta-T Devices, Cambridge, UK).

We followed stringent editing criteria to insure the quality of the eddy flux data. Data were rejected when winds dropped below 0.5 m s^{-1}, sensor variance was high, when the wind direction differed by >90° from the direction of the instrument array, or when the wind was blowing from the area of our camp (Hollinger et al., 1995).

All analyzers were calibrated daily with the same two reference bottles of CO_2 in air that were calibrated with a two-stage cascade of gas mixing pumps (model SA27/3F, Wösthoff, Bochum, Germany) which combined CO_2-free air and pure (>99.9%) CO_2.

2.3. Calculation of CO_2 exchange rates

We measured three components of CO_2 exchange between the forest ecosystem and the atmosphere; the turbulent eddy flux transported across the plane of instrumentation 22 m above the forest floor (F_e), an eddy flux at 1.8 m above the forest floor (F_f) and exchange below 22 m which is manifested as a change in the storage of CO_2 in the forest air column ($F_{\Delta S}$). The net flux of CO_2 crossing the planes at our instrumentation heights was calculated as the mean covariance between fluctuations in vertical wind velocity (w) and the density of CO_2 (c) (Baldocchi et al., 1988):

$$F_e = \rho(\overline{w'c'})$$

where ρ is the density of air, the primes denote deviations from the mean and the overbar signifies a time average. We use a meteorological convention for our CO_2 measurements where carbon flux out of the ecosystem is defined as positive. The flux associated with a change in storage ($F_{\Delta S}$) is calculated by integrating the change in CO_2 concentration, c, through the air column as a function of height (z) up to the instrumentation plane (H):

$$F_{\Delta S} = \int_0^H \frac{\mathrm{d}c}{\mathrm{d}t}\mathrm{d}z$$

In the absence of advection, the daily net storage of CO_2 in the air column should be approximately zero. We integrated the half-hourly change in CO_2 concentration up to $H = 22$ m for our estimates of $F_{\Delta S}$. The net flux between the ecosystem and atmosphere or net ecosystem exchange (F_n) over any time interval is the sum of the eddy and the Δ-storage fluxes:

$$F_n = F_e + F_{\Delta S} \tag{3}$$

Over 24 h $F_{\Delta S} = 0$ so $F_n = F_e$. The net flux between the tree canopy and atmosphere (F_c) is the sum of the eddy and the Δ-storage fluxes less the forest floor flux (F_f):

$$F_c = F_e + F_{\Delta S} - F_f \tag{4}$$

There are several potential problems that can arise when calculating a storage flux, however. The first is a problem of scale (Ruimy et al., 1996). It is assumed that the change in atmospheric CO_2 level in the forest air column is caused by vegetation representative of the measurement site. Change in the background CO_2 concentration is a regional-scale phenomena, although one in which the size of the 'region' changes during the day. For this study it is reasonable to assume that the vegetation at our study site was representative of the region. In other sites where the vegetation under study might have quite different exchange characteristics from those of the region, the calculation of the storage flux would be more problematic. The second potential problem relates to advection; a newly arriving air mass may contain CO_2 concentrations different from the previous air mass which will be incorrectly treated as a $F_{\Delta S}$ value. Careful measurement of the CO_2 concentration above the ecosystem in the early afternoon when the lower troposphere is well-mixed may allow the identification of such an occurrence.

Ignoring $F_{\triangle S}$ will not affect 24-hour flux estimates but may lead to under or over-estimates of assimilation at certain times of the day. In the early morning, for example, ignoring the contribution of $F_{\triangle S}$ to F_c would result in erroneously low values of F_c. Because of the large variability of $F_{\triangle S}$, however, we exclude the storage term from the estimate of canopy flux used to evaluate the MBH photosynthesis model and calculate $F_{c'} = F_{\mathrm{e}} - F_{\mathrm{f}}$ (e.g. $F_{c'} = F_c - F_{\triangle S}$).

We explored the relationship between environmental variables and components of *L. gmelinii* forest CO_2 exchange using an exponential (Arrhenius) model to relate forest and soil respiration to temperature and the optimal stomatal regulation model of Mäkelä et al. (1996) to estimate canopy photosynthesis. The Mäkelä et al. model, henceforth termed the 'MBH model', builds on earlier work by Cowan (1982) and Hari et al. (1986) and is based on the idea that stomata function so as to maximize the expected photosynthate production over a drought period. The frequent drought and high summer evaporative demand of the eastern Siberian forest argue for such an approach (Kelliher et al., 1997). The MBH model realistically captures the PPFD and VPD response of leaf-scale photosynthesis (Mäkelä et al., 1996). We use it as a 'big leaf' canopy model here. The model has been successfully tested against leaf-scale photosynthesis and transpiration data from Scots pine growing in central Finland (Berninger et al., 1996).

The instantaneous rates of photosynthesis, $A(t)$, and transpiration, $E(t)$, are functions of plant physiological and environmental driving variables as:

$$A(t) = \frac{g(t)c_a}{g(t) + f[I(t)]} f[I(t)] \tag{5}$$

$$E(t) = ag(t)[w_i(t) - w_a(t)] \tag{6}$$

where $g(t)$ is stomatal conductance to CO_2, $I(t)$ is PPFD, $f(I)$ is dependence of net CO_2 exchange assimilation on PPFD, c_a is the molar fraction of CO_2 in ambient air, $w_i(t)$ and $w_a(t)$ are intercellular and ambient molar fractions of water vapor and a (=1.6) is a constant for converting the stomatal conductance of CO_2 to water vapor. We use the standard Michaelis–Menten relationship for $f(I)$;

$$f(I) = \frac{\alpha \cdot I}{\gamma + I} \tag{7}$$

where α is the maximum rate of assimilation and γ is the PPFD at which assimilation reaches one-half of α. The water vapor gradient (w_i–w_a) is simulated by the saturation deficit, D, assuming the *L. gmelinii* foliage is at T_{air} and the intercellular air spaces are saturated with water vapor. Mäkelä et al. solved Eqs. (5) and (6) with the additional consideration that the availability of water during a drought period declined exponentially. The optimal stomatal control strategy over the course of a drought was;

$$g(t) = \begin{cases} 0 & \mathit{if}\ \tilde{g}(t) < 0 \\ g_0 & \mathit{if}\ \tilde{g}(t) > g_0 \\ \tilde{g}(t) & \text{otherwise} \end{cases} \tag{8}$$

where

$$\tilde{g}(t) = \left(\sqrt{\frac{c_a}{va[w_i(t) - w_a(t)]}} - 1 \right) f[I(t)] \tag{9}$$

where $v = p_0 e^{kt}$. The constant p_0 relates to the 'sensitivity' of stomata to drought and the atmospheric water vapor gradient and k is the probability of rain per unit time (d^{-1}). The constant p_0 must fulfill the integral constraint:

$$\int_0^\infty E(t)\mathrm{d}t \le W_{so} \tag{10}$$

where W_{so} is the initial soil water supply (per unit area) at the beginning of the drought. Mäkelä et al. (1996) point out that the term v can be interpreted as the 'cost of water' and that v=1/λ where (Cowan, 1977),

$$\lambda = \frac{\partial E}{\partial A} \tag{11}$$

In a solution which depends on the time since the last rainfall, the time varying rate of assimilation is:

$$A(t) = \left[c_a(t) - \sqrt{c_a(t) a p_0 e^{kt} [w_i(t) - w_a(t)]} \right] \times \frac{\alpha \cdot I(t)}{I(t) + \gamma} - R(t) \tag{12}$$

where $R(t)$ is the time varying canopy respiration (set to a constant as discussed below). The term in the large brackets represents the internal concentration of CO_2 and its regulation by drought and the atmospheric water vapor gradient. Parameters in the open solution (p_0, k, α, γ and R) were estimated using non-linear regression techniques (minimizing the sum of squares of the differences between measured and modeled C flux using the 'solver' add-in of Excel version 7.0). We optimized the model based on carbon rather than water flux because we were able to separate canopy carbon fluxes from total ecosystem fluxes (but not variations in storage) by subtracting the flux measured at 1.8 m (F_f) from F_e as described previously.

3. Results

3.1. Forest micro-environment

Days in Siberia during our studies tended to be either cloudy and cool (five days) or mostly sunny and hot (nine days). On sunny days during mid-day (10.00–14.00 h), ~32% of the incoming PPFD was diffuse and on overcast days the mid-day PPFD was ~93% diffuse. On perfectly clear days the diffuse PPFD dropped to as low as 17% of the total PPFD.

On sunny summer days, the daily range of temperatures is large and depends strongly on the topographic position. During our field measurements the mean daily minimum and maximum half-hourly temperatures at 21 m above the ground at mid-slope averaged at 11.9 and 26.9°C with 6.7 and 32.2°C as the overall range (Fig. 1(B)). Less than 0.5 km away, near the valley floor, maximum temperatures were similar but minimum temperatures routinely dropped below 0°C. On cloudy days the temperature at 21 m ranged between an average minimum of 9.6 and maximum of 16.3°C.

The sparse canopy resulted in large variations in soil surface temperatures (Fig. 1(B)). On sunny days, the amplitude of variations in forest floor surface temperature (1 cm depth) exceeded that of air temperature, ranging between 4 and 36°C. The permafrost led to a strong gradient in soil temperature; at 20 cm diurnal soil temperature varied by less than 0.5°C around a mean of 7.1°C, the mean daily soil temperature dropped to ~3.3°C at 50 cm and ~1.7°C at 70 cm. On cloudy days forest floor surface temperatures were more constant (averaging between 10 and 19°C).

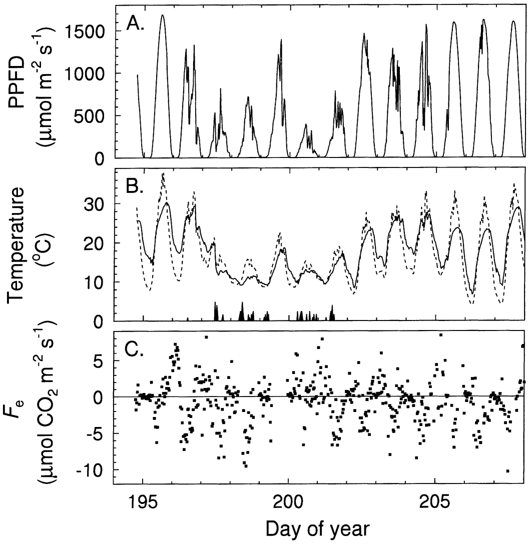

Fig. 1. Daily patterns of the environmental variables and net ecosystem carbon exchange in an eastern Siberian *Larix gmelinii* forest, 13–27 July, 1993. (A) Daily pattern of photosynthetically active photon flux density measured above the forest. (B). Daily pattern of air temperature measured above the forest (solid line) and at 1 cm soil depth (dashed line). The vertical lines on the 'X'-axis represent measurable rainfall with the tallest lines equivalent to a half-hourly rainfall of 1.2 mm. (C). Net ecosystem CO_2 exchange; positive values represent carbon lost by the ecosystem.

Humidities were low, leading to clear day saturation deficits (D) that routinely exceeded 2.7 kPa and reached a maximum of 3.8 kPa. On cloudy days D was generally <0.5 kPa. Winds above the forest (21 m) were light-moderate, averaging 1.7 m s^{-1}. During our studies 20 mm of rain fell.

On clear nights, radiational cooling led to a strong surface temperature inversion as evidenced by mean soil temperatures (1 cm depth) that averaged 6.5°C below air temperature (Fig. 1(B)). These inversions trapped respired CO_2 close to the surface (Fig. 2(A)). CO_2 concentration within the forest dropped rapidly after sunrise as the forest air mixed with air from above (note the 'chimney' of elevated CO_2 through the profile from ~06.00–08.00). The forest air column remained well mixed throughout the middle of the day but concentrations increased again below the canopy as net radiation (R_n) became negative just before sunset. Less CO_2 appeared to be trapped below the canopy on overcast nights (Fig. 2(B)) than on clear nights, probably because of reduced radiational cool-

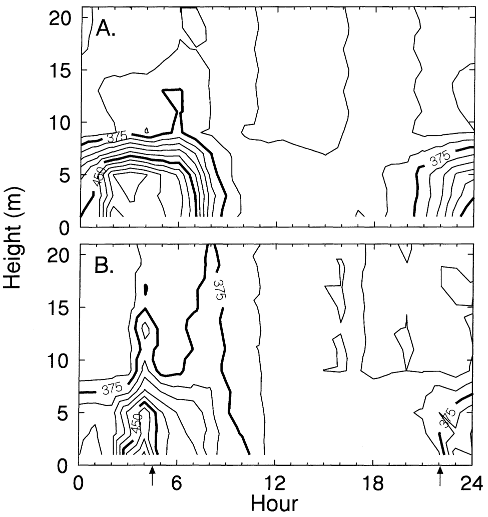

Fig. 2. Average daily pattern of CO_2 concentration in the *L. gmelinii* forest. The arrows on the 'X' axis represent the approximate times of sunrise and sunset during the study. (A) Average pattern on clear days (DOY 194, 195, 205, 206 and 207). (B) Average pattern on overcast days (DOY 196–201).

ing. Net radiation averaged −30.4±3.1 W m^{-2} (mean and 95% confidence level) on overcast nights compared with −64.1±3.4 W m^{-2} on clear nights. Overcast conditions also appeared to slow the morning breakup of the inversion so that high CO_2 surface air was not exported from the forest until ~07.00–09.00. As on clear days, the forest air column remained well-mixed from late morning until sunset. On all days the CO_2 concentration in the air trapped near the forest floor remained well above the midday values recorded above the forest (~345 ppm) for several hours after sunrise, creating an environment highly favorable for photosynthetic carbon fixation.

3.2. Diurnal CO_2 exchange

Half-hourly CO_2 eddy fluxes between the *L. gmelinii* forest and the atmosphere were low, ranging between a maximum daytime uptake rate of less than 10 μmol m^{-2} s^{-1} (uptake shown as negative values in Fig. 1(C)) and a night-time respiratory loss of up to 8 μmol m^{-2} s^{-1}. Maximum CO_2 uptake occurred on the cooler, cloudy days after rain and maximum respiration rates were associated with warm nights (Fig. 1(C)).

The CO_2 fluxes at 22 m, storage flux and flux at 1.8 m were ensemble averaged over the 14-day measurement period to obtain diurnal forest carbon exchange rates (Fig. 3). The average flux at 22 m (Fig. 3(A)) remained positive at ~1 μmol m^{-2} s^{-1} through the night and early morning to about 08:00, indicating that carbon was leaving the forest system. By noon, the net flow of carbon at 22 m peaked at ~−4 μmol m^{-2} s^{-1} and then declined to zero about an hour before sundown. Integrated over 24 h, the forest ecosystem was on average, a net sink of 0.72 ± 0.25 (mean and 95% confidence interval) μmol CO_2 m^{-2} s^{-1} (7.5 kg C ha^{-1} d^{-1}).

On average, the storage flux (ΔCO_2 in the forest air column below 22 m over time) was positive throughout the night (Fig. 3(B)) as CO_2 built up near the surface (Fig. 2). After sunrise, the storage flux became negative as the CO_2 in the air column decreased. Some of this decrease resulted from mixing with air from above the forest as indicated by the positive eddy flux at 22 m (Fig. 3(A)), while the rest was presumably consumed by photosynthetic uptake. Over 24 h, the

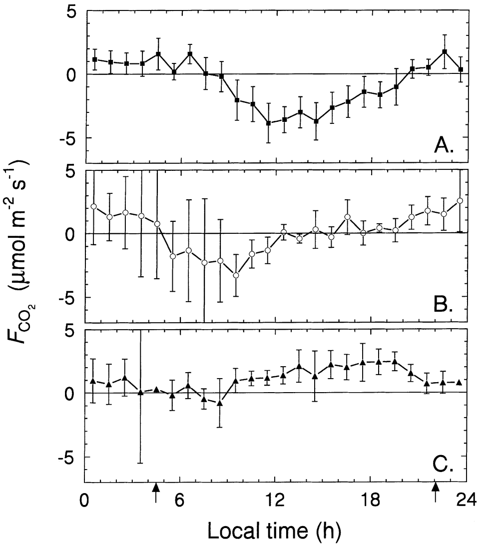

Fig. 3. Ensemble averages of daily component CO_2 fluxes in a *Larix gmelinii* forest, Yakutsk, Siberia, Russia, 13–27 July, 1993. Positive values signify carbon loss by the ecosystem. The arrows on the 'X' axis represent the approximate times of sunrise and sunset during the study, the error bars indicate ±1 standard deviation. (A). Eddy flux (F_e) measured at 22 m. (B). Storage flux ($F_{\Delta S}$) measured between the ground and 22 m. (C). Understory and forest floor eddy flux (F_f) measured at 1.8 m.

average storage flux was 0.02±0.50 µmol CO_2 m^{-2} s^{-1}, not significantly different from the expected value of 0. The storage flux was more variable than the eddy flux at 22 m between adjacent sampling periods and between days, especially in the morning.

The CO_2 flux at 1.8 m was dominated by forest floor respiration and increased through the late morning and afternoon, reaching a maximum of ~3 µmol m^{-2} s^{-1} around 18.00 (Fig. 3(C)). In the morning between about 06.00 and 09.00, the flux at 1.8 m sometimes became negative, suggesting that understory photosynthetic uptake dominated over forest floor and understory respiration. However, background CO_2 levels were changing rapidly at this time making the flux measurements less reliable. Over 24 h, the below canopy flux averaged 1.22±0.22 µmol CO_2 m^{-2} s^{-1}, meaning that canopy uptake, F_c, averaged ~1.9 µmol CO_2 m^{-2} s^{-1}.

3.3. Influence of environmental factors on forest CO_2 exchange

3.3.1. Forest floor CO_2 exchange

The CO_2 flux at 1.8 m (F_f) consists of a combination of understory photosynthesis and respiration, soil heterotroph respiration and root respiration. Generally, this flux increased strongly with increasing 5 cm soil temperature (Fig. 4). We used soil temperature at 5 cm depth rather than 'surface' (1 cm) values because most roots and soil C were located in the top 10 cm (Schulze et al., 1995). The activation energy of an Arrhenius function that best fits the data is −51 KJ mol^{-1} equivalent to a Q_{10} of ~2.3.

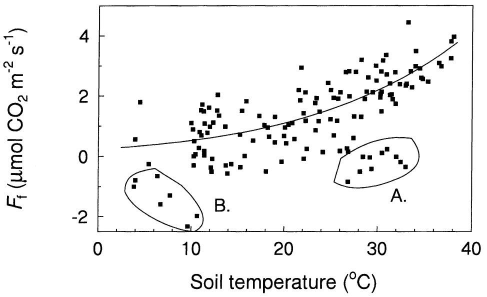

Fig. 4. The relationship between the eddy flux at 1.8 m (F_f) and soil temperature at 5 cm depth contains two clusters of outliers associated with recent precipitation ('A') and early morning hours ('B'). The line signifies the best-fit Arrhenius model: $F_f = 1.39E09e^{(51000/(8.3(T_s+273.1)))}$, r^2=0.60.

The exponential relationship between temperature and daytime CO_2 flux at 1.8 m does not include 2 clusters of outliers (Fig. 4). The first cluster ('A' in Fig. 4) is associated with the first few hours after rainfall. At this time the forest floor is often a photosynthetic sink for CO_2. Assuming that the forest floor is continuing to respire at the expected rate, the understory at this time would have a photosynthetic uptake of ~2 µmol m^{-2} s^{-1}. The forest floor was also generally a CO_2 sink for a few hours each morning (cluster 'B') when light levels were moderate, forest floor temperatures cool, dew was present and the saturation deficit low. This may have been associated with hydration and photosynthetic activation of forest floor mosses and lichens.

3.3.2. Night-time ecosystem CO_2 exchange

The relative magnitude of night-time F_e and $F_{\Delta S}$, the component fluxes of net ecosystem exchange, depended upon atmospheric stability (Table 2). The stability of the nocturnal atmosphere was classified according to the Monin–Obukhov length (L) with $L = -u^{*3}/[k(g/T_a)\overline{w'T_a'}]$ where k is the von Karman constant, g is the acceleration due to gravity and T_a is air temperature in K (Stull, 1988). Under near neutral conditions ($L<-200$ m), F_e averaged ~1.8 µmol m^{-2} s^{-1}. Under stable conditions ($L>0$), however, CO_2 released in the lower forest was trapped by the temperature inversion and isolated below the plane of measurement at 22 m. At these times F_e averaged ~0.3 µmol m^{-2} s^{-1}. The nocturnal CO_2 storage flux behaved in an opposite manner, increasing from ~1.2 µmol m^{-2} s^{-1} under near neutral or unstable conditions to ~2.6 µmol m^{-2} s^{-1} when the atmosphere was stable. The effect of atmospheric stability on atmospheric transport was thus the dominating influence on our half-hourly measurements of

Table 2
Components of nocturnal CO_2 flux as a function of the atmospheric stability class (mean and 95% confidence intervals)

L (m)	Stability class	Storage flux ($F_{\Delta S}$)	Eddy flux (F_e)
<−200	Near neutral	1.11±0.77	1.76±1.19
−20<L<0	Unstable	1.18±0.87	0.80±0.34
L>0	Stable	2.58±1.10	0.28±1.23

F_e and $F_{\Delta S}$, overriding the short-term influence of other factors such as air or soil temperature. The sum of nocturnal F_e and $F_{\Delta S}$ did not vary systematically with windspeed or u^* (e.g., $F_e+F_{\Delta S}=2.85-0.76u^*$, $r^2<0.01$, $p=0.24$) suggesting that these fluxes adequately accounted for total night-time ecosystem respiration.

3.3.3. Net ecosystem and canopy CO_2 exchange

Net ecosystem exchange F_n, is affected by environmental factors which influence soil and aboveground respiration as well as photosynthesis of the tree canopy and understory. For example, a significant amount ($P<0.001$, $r^2=0.31$) of the variation in F_n can be accounted for with a saturating function of light Eq. (7). Although such simple relationships between F_n and environmental variables can be derived, they tend to obscure the fundamental component fluxes of F_n, especially in the daytime when respiratory fluxes offset photosynthetic uptake. An alternate approach favored here is to separately model and evaluate the canopy and below canopy fluxes.

Canopy CO_2 uptake, $F_{c'}$, behaved in a manner similar to F_n, initially increasing rapidly with increasing PPFD and then reaching a plateau (Fig. 5(A)). Canopy uptake saturated at ~−6 μmol CO_2 m^{-2} s^{-1} compared to ~−4 μmol CO_2 m^{-2} s^{-1} for the whole ecosystem. The quantum yield or initial efficiency of photon usage of the canopy was ~0.0103 μmol CO_2 μmol^{-1} photosynthetically active photons and the light compensation point for canopy CO_2 uptake was ~180 μmol m^{-2} s^{-1}. Dark respiration of the whole canopy at ~1.2 μmol CO_2 m^{-2} s^{-1} was similar to that of the soil and understory at ~0.9 μmol CO_2 m^{-2} s^{-1}.

An examination of the residual canopy CO_2 flux after accounting for the effects of the PPFD suggests that $F_{c'}$ is depressed at higher air saturation deficits, high air temperatures, or after several days of drought (Fig. 5(B)–(D)). These factors are all somewhat correlated (especially air temperature and D where the correlation coefficient exceeds 0.9) and after incorporating the next most important variable (D), the r^2 improves from 0.55 to 0.64 (Table 3). With this preliminary analysis in hand, we next turn to an examination of the optimal stomatal control model of Mäkelä et al. (1996).

3.4. Modeling canopy fluxes with an optimal control model

The low rainfall at the site and evidence of a decrease in surface conductance in the days following precipitation (Kelliher et al., 1997) suggested that

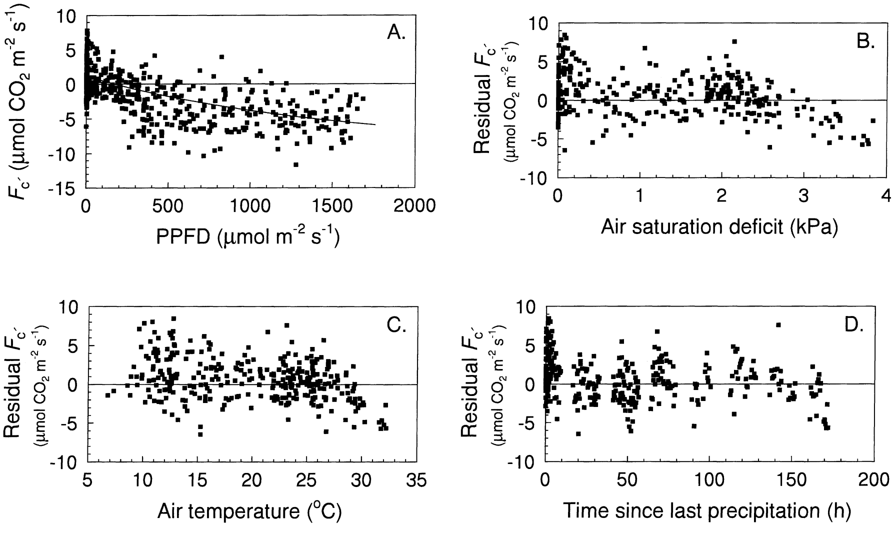

Fig. 5. Relationship between half-hourly canopy CO_2 exchange, $F_{c'}$ and environmental variables. (A) A saturating model with PPFD was associated with the largest percentage of the total variance (solid line: $F_{c'}=-15.6I/(I+2134)+1.16$, $r^2=0.55$). Examination of the residual variation (B)–(D) suggests that $F_{c'}$ is depressed at higher air saturation deficits, high air temperatures, or after several days of drought.

Table 3
Comparison of models of CO_2 exchange of a *Larix gmelinii* forest

Predicted variable	Model type	Equation	r^2
F_f	Arrhenius	$\omega e^{(E_a/(8.3(T_s+273.1)))}$	0.60
$F_{c'}$	Saturating in PPFD	$\frac{P_1 I}{I+K_1}+R_d$	0.55
$F_{c'}$	Saturating/linear	$\frac{P_2 I}{I+K_2}+\tau_D$	0.64
$F_{c'}$	MBH open solution	$\left[c_a-\sqrt{c_a a p_0 e^{kt} D}\right]\frac{\alpha I}{I+\gamma}-R$	0.67

Parameter	Value	Units
ω	−1.39E09	$\mu mol\ m^{-2}\ s^{-1}$
E_a	51000	$kJ\ mol^{-1}$
P_1	−15.6	$\mu mol\ m^{-2}\ s^{-1}$
K_1	2134	$\mu mol\ m^{-2}\ s^{-1}$
R_d	1.16	$\mu mol\ m^{-2}\ s^{-1}$
P_2	−21.9	$\mu mol\ m^{-2}\ s^{-1}$
K_2	2510	$\mu mol\ m^{-2}\ s^{-1}$
τ	1.13	$\mu mol\ m^{-2}\ s^{-1}\ kPa^{-1}$
a	1.6	Dimensionless
p_0	0.00097	Dimensionless
k	0.066	d^{-1}
α	0.050	$mol\ m^{-2}\ s^{-1}$
γ	994	$\mu mol\ m^{-2}\ s^{-1}$
R	1.45	$\mu mol\ m^{-2}\ s^{-1}$

Variables	Description	Units
T_s	Soil temperature	°C
I	PPFD	$\mu mol\ m^{-2}\ s^{-1}$
D	Saturation deficit	kPa
c_a	Ambient CO_2 molar fraction	
t	Time since last rain	d

drought would probably be an important regulator of *L. gmelinii* CO_2 exchange. The MBH model (Mäkelä et al., 1996) predicts the pattern of water use and CO_2 exchange based on PPFD, D and the time since last precipitation based on Cowan's theory of optimal water use (Cowan, 1977, 1982). It assumes that the probabilities of various lengths of rainfree periods P, can be approximated with a Poisson distribution $P=e^{-kt}$, where t is the length of the rainless period in days and k is the probability of rain per unit time. This appears to be a good assumption in Siberia (e.g. see Fig. 5; Kelliher et al., 1997). Daily meteorological data between May and September, 1961–1980, from Yakutsk (Razuvaev et al., 1993) were used to calculate probabilities based on thresholds of 10 and 20 mm to wet the soils.

The MBH model accounted for ~67% of the variance in canopy carbon exchange (Table 3) and yielded physiologically reasonable model coefficients. The slope of the measured to modeled C flux was not significantly different from 1 and the residuals were apparently evenly distributed (Fig. 6(A)). The fit to the data was thus superior to a saturating function with a linear effect of D (Table 3), although the MBH model does utilize an extra degree of freedom. An analysis of residuals (=measured C−modeled C)

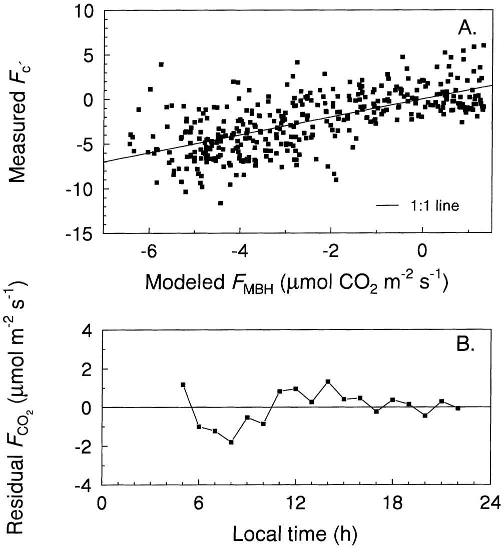

Fig. 6. (A) Comparison of modeled (F_{MBH}) and measured ($F_{c'}$) canopy CO$_2$ exchange. (B) The difference between the modeled and measured fluxes ($F_{MBH}-F_{c'}$) reproduces the daily pattern of the storage flux (Fig. 3(B)) which is the difference between F_c and $F_{c'}$.

indicated that there was no statistically significant relationship (in each case P >0.1) between the residuals and the environmental variables PPFD, D, T_{air}, or time since last rainfall. There was, however, a weak (r^2=0.05) but significant (P>0.001), relationship between the amount of diffuse light reaching the forest and the difference between measured and modeled C exchange. The model underpredicted photosynthetic C uptake under increasing diffuse PPFD. This is to be expected with a simple, ‘big leaf’ model. The value obtained for k was between that calculated from Yakutsk meteorological data for rainfall thresholds of 10 and 20 mm (0.088 and 0.053, respectively) and the value of the half saturation constant of the light function is similar to values derived from photosynthetic light curves of *L. gmelinii* (Vygodskaya et al., 1997).

An examination of Eq. (12) indicates that assimilation in the MBH model is directly proportional to the value of α. The effects of the other parameters, however, are nonlinear. We carried out a sensitivity analysis of model output to variation in the fitted parameters by normalizing the effects of a ±10% change of the parameters on the mean square of the residuals to the effect of a similar change in α (Table 4). This analysis shows that the variation in γ, the half-saturation parameter in the light response, has the next strongest effect on assimilation while variation in the probability of rainfall per unit time, k, has the least effect.

Table 4
Sensitivity of model output for a 10% change in parameter values compared to the sensitivity of model output to a 10% change in α

Parameter	Relative sensitivity	
	+10%	−10%
P_0	0.22	0.23
k	0.07	0.17
α	1.00	1.00
γ	0.52	0.87
R	0.32	0.33

We conclude the analysis of the residuals by showing block averages of the difference between the measured and modeled values (residual F_{CO_2}) as a function of the time of day (Fig. 6(B)). This daily pattern of residual variation is similar to the storage flux (correlation coefficient=0.54, P<0.05) which is the unaccounted for component of the canopy flux, $F_{c'}$. This is a good but unanticipated test of the predictive power of the model.

Using the modeled values of g and the saturation deficit to calculate E, Eq. (6) provided a reasonable fit to the whole forest E(r^2=0.52), again with a slope not significantly different from 1. However, the measured values are for the whole forest water vapor exchange and our previous work has indicated that the canopy supplies only 50–62% of this flux with the rest coming from the understory (Kelliher et al., 1997; Arneth et al., 1996). Thus the model appears to overestimate canopy E by at least 50%. A similar order of overestimation of evaporation was seen in a previous test of the MBH model with leaf-level data (Berninger et al., 1996).

Comparing the modeled values for canopy conductance, g_s and evaporation with measured values during a drying cycle (Fig. 7) suggests that the model underestimates these values in the first few days after rain. This behavior of forest evaporation is consistent with our hypothesis that moss and lichens hydrated by precipitation events temporarily boost forest C uptake (e.g. Fig. 5(D)). Because these plants do not possess stomata, their rate of water loss would be high. This

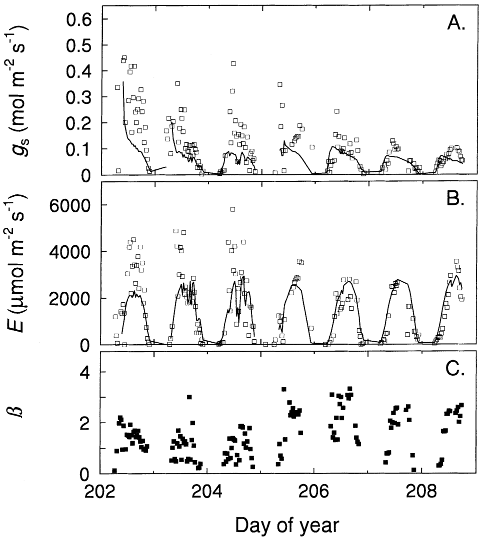

Fig. 7. (A) Measured (open symbols) and modeled surface conductance, g_s and (B) evaporation, E, on 7 days following rain. Rain fell on JD 201. The MBH model underestimates conductance and E early in the drying cycle. (C) Midday Bowen ratio, $\beta(=H/\lambda E)$ routinely exceeded 2

suggests that an improved model of forest evaporation might utilize both fast and slower exponential decreases in water use. We should also note these data in conjunction with the Bowen ratio, $\beta=H/\lambda E$, estimates presented by us in a companion paper (Kelliher et al., 1997); in our other work we calculate average daily values for β for days when rain fell and in the first few days after rain. These values were typically modest (<2). However, as Fig. 7 shows, midday values of β ranged between 2 and 3 after four or more days without rain, suggesting that the forest was strongly limiting water loss at these times.

4. Discussion

4.1. Comparison with other forest ecosystems

The net midday midsummer CO_2 exchange rate of the *Larix gmelinii* ecosystem at ∼−4 µmol m^{-2} s^{-1} is very low compared to values from studies of other forest types but consistent with results from leaf-level studies of this species (Vygodskaya et al., 1997). An undisturbed, old-growth broad-leaved forest measured with the same flux system had a typical midday summer CO_2 exchange rate in excess of −15 µmol m^{-2} s^{-1} (Hollinger et al., 1994). Midday summer CO_2 uptake rates in eastern U.S. deciduous forests typically exceed −20 to −25 µmol m^{-2} s^{-1} (Goulden et al., 1996a, b; Baldocchi and Vogel, 1996). However, gross uptake rates seen in other coniferous boreal forests are much more similar, although still higher, than those observed in *L. gmelinii*. The mean midday summer CO_2 uptake rate averaged ∼−12 µmol m^{-2} s^{-1} over black spruce at the northern BOREAS site (Goulden et al., 1997) and ∼−8 µmol m^{-2} s^{-1} over a black spruce-lichen woodland in Labrador (Fan et al., 1995). Mean midday summer CO_2 uptake by a jack pine canopy at the southern BOREAS site was similar at ∼−8 µmol m^{-2} s^{-1} (Baldocchi et al., 1997). Carbon uptake saturates at a PPFD of ∼500–700 µmol m^{-2} s^{-1} in all of these conifer forests. Although C-uptake declined with increasing saturation deficit in the *L. gmelinii* forest, this was not observed in the black spruce (Goulden et al., 1997). The role of isotropic diffuse light in increasing forest C-uptake (Hollinger et al., 1994) has been predicted (Jarvis et al., 1985) and more recently observed in other studies of boreal forest carbon exchange (Baldocchi et al., 1997; Goulden et al., 1997) and appears to be a common feature of forest C exchange. This provides support for the hypothesis that anthropogenically-induced increases in haze levels may have contributed to an enhanced global C sink (Hollinger et al., 1994).

The mean night-time CO_2 flux in the *L. gmelinii* forest (∼2.5 µmol m^{-2} s^{-1} at a mean air temperature of 15°C was similar to that measured in Jack Pine forest at ∼10°C (Baldocchi and Vogel, 1996; Baldocchi et al., 1997) and black-spruce forest also at ∼10°C (Goulden et al., 1997). At temperatures similar to those experienced by the *L. gmelinii* forest, respiration in the jack pine and black-spruce stands would probably be ∼4 µmol m^{-2} s^{-1} (e.g. Goulden et al., 1997 and Fig. 4). However, July temperatures are substantially higher at Yakutsk than at the BOREAS sites (Table 1) so midsummer night-time respiration rates at the 3 sites are similar.

Respiration in this and the other boreal sites is a very large fraction of maximum canopy photosynthesis. In the *L. gmelinii* forest, night-time respiration is ∼40% of maximum daily uptake, similar or slightly higher than at the jack pine site (Baldocchi et al., 1997).

4.2. Optimal stomatal control model and ecosystem fluxes

The MBH model has been tested previously with cuvette measurements of foliage transpiration and photosynthesis obtained in July from a scots pine tree growing in central Finland. The climate of this site is similar to that of Tampere, Finland (Müller, 1982) where the mean annual precipitation is 573 mm and July air temperature is 17.3°C. In Finland, the fitted value of p_0 yielded an initial value for the average marginal water cost of plant gain, of $\sim$350 compared to our value of $\sim$1000. In other words, water is relatively more valuable to Scots pine and carbon more valuable to *L. gmelinii*. The value for λ in Finland is similar to the value (250) estimated by Lloyd and Farquhar (1994) for cool/cold conifer forest, while the *L. gmelinii* value is more similar to values for deciduous forest or semi-desert. Our value of λ derived from the time varying course of canopy assimilation is consistent with a calculated value based on our leaf-level measurements (Vygodskaya et al., 1997) where we found the internal to ambient mole fraction of CO_2 to be about 0.71. Using an average D of 1.8 kPa and an average leaf temperature of 20°C, we calculate $\lambda \approx 900$ (see Lloyd and Farquhar, 1994 and Eq. (11)). This high value is also consistent with the value of Δ_A, the average discrimination against $^{13}CO_2$ during photosynthesis, we found for this forest of 19.5‰ (Schulze, unpublished data).

It is interesting to speculate why λ is higher in the Siberian *Larix* than might be expected based on other boreal studies. We concluded previously (Vygodskaya et al., 1997) that the water use characteristics of *L. gmelinii* were similar to those of *L. decidua*, despite the severe Siberian environment. It may be that the deciduous habit of *L. gmelinii* or needle morphology places limits on the range of physiological adaptation possible in this species. An alternative hypothesis is that a high value of λ befits the particular characteristics of the eastern Siberian taiga. We have documented severe N deficiency in this species (Schulze et al., 1995) which severely constrains leaf carbon gain (Vygodskaya et al., 1997). This N deficiency and short growing season place a premium on C uptake which can be addressed by increasing λ (e.g. when N or time is limiting, the marginal value of C is high relative to the cost of water). A unique aspect of northern climates, permafrost, can aid this strategy by providing a slow release of water as the melting front descends in the soil (Kelliher et al., 1997). The relatively high λ value for this large biome should be noted by those modeling isotopic discrimination by the biosphere.

4.3. The carbon balance of the Siberian forest

Averaging our net ecosystem exchange rates over the day, night and 24 h suggests that the average rate of *L. gmelinii* ecosystem CO_2 uptake in the daytime was only about two-thirds of the average rate of CO_2 loss at night. Because days are $\sim$18 h long at this latitude in mid-July, however, over the 24 h of all of our measurement days we measured an average net uptake of $\sim$0.72 μmol m^{-2} s^{-1}. Integrated daily C exchange by the *L. gmelinii* forest during our study ranged between an uptake of $\sim$1.9 g C m^{-2} d^{-1} and a loss of $\sim$0.4 g C m^{-2} d^{-1}. In general, daily uptake increased with increasing total daily quantum flux but declined at higher temperatures (Fig. 8). The lowest rates of uptake were on clear hot days after five or more days of drought or on the most heavily overcast days of rain. Based on our understanding of soil respiration and canopy photosynthesis, we conclude that the decline in uptake at elevated temperatures results from both an increase in soil respiration and a saturation deficit

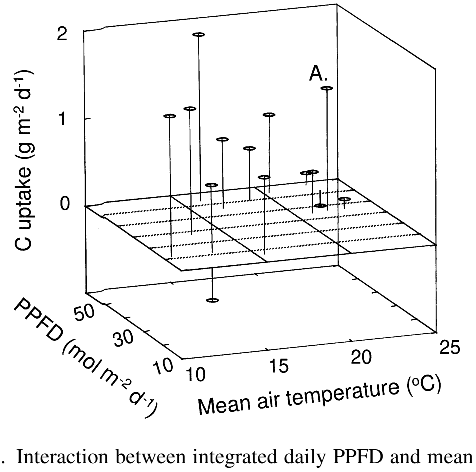

Fig. 8. Interaction between integrated daily PPFD and mean daily air temperature on integrated daily whole-ecosystem CO_2 exchange.

induced reduction in photosynthetic uptake. An exception was a warm and clear day after several days of rain ('A'in Fig. 8) which had a high rate of C uptake, presumably due to the contribution of moss and lichen photosynthesis. Several implications can be drawn from this complex interaction of light, temperature, drought and net daily C exchange. An increase in mean temperature would be expected to lead to lower daily rates of C uptake. However, an increase in the frequency of precipitation would likely lead to enhanced C storage in these forests. Simple extrapolation of these trends must be avoided, however, because although higher temperatures might lead to lower daily uptake rates, they would probably also lead to a longer growing season. Based on a 100 year record of the mean daily air temperatures (Razuvaev et al., 1993), a 3°C increase in mean daily temperature would increase the growing season (defined as mean daily temperature >5°C) from about 120 to 140 days. These results highlight the need for long-term, year-round flux measurements in this and other ecosystem types to understand the potential impacts of climatic change.

In their studies over boreal jack pine, Baldocchi et al. (1997) found little seasonal variation in daily net C uptake, but similar large variations in daily exchange. Carbon uptake in the jack pine forest varied between an uptake of $\sim$3 g C m^{-2} d^{-1} and a loss of almost 2 g C m^{-2} d^{-1}. Average mid-season C-uptake was similar to or slightly lower than the average over the whole growing season. Averaging our mid-season values over a 120-day season, suggests that net growing season C uptake is $\sim$0.9 t C ha^{-1}. Non-growing season respiration will reduce this rate, although a feature of the Siberian climate is solid freezing of the soils to the permafrost and an abrupt transition between the deep cold of winter and the warmth of the growing season. Both of these factors would limit winter respiratory loses.

Biomass estimates from the same 125-year-old stand (Schulze et al., 1995) can help place limits on the annual C uptake of the *L. gmelinii* forest. Schulze et al. (1995) found $\sim$47 t C ha^{-1} in the forest aboveground biomass, 5 t C ha^{-1} in the litter and $\sim$37 t C ha^{-1} in the top soil (Ah) horizon. To this we could add an estimated 5 t C ha^{-1} in coarse roots. It is unlikely that the previous fire would have burned all of the Ah horizon, so a reasonable estimate of C accumulation over 125 years would be $\sim$75 t C ha^{-1}, or $\sim$0.6 t C ha^{-1} y^{-1}. Our estimate of 0.9 t C ha^{-1} y^{-1} exclusive of winter respiration thus seems reasonable. When considering the annual C storage of the eastern Siberian boreal forest as a whole, changes in the standing stocks due to the possible changes in fire frequency could override any year-to-year variation in photosynthetic uptake. Efforts must thus also be made to understand the climatological, biological and social factors that influence fire frequency and burn area.

5. Conclusions

The key to modeling ecosystem fluxes is to identify a minimal set of environmental and biological variables that can be incorporated into the simplest-possible models that simulate ecosystem behavior. By combining the essence of leaf-level biochemistry with optimal water-use theory, the model of Mäkelä et al. (1996) is a substantial step forward in this respect. We found it suited for estimating canopy-level fluxes of an open forest, although deficiencies in its ability to explain all aspects of ecosystem C exchange are present and expected (specifically relating to the influence of diffuse light and nonvascular species). One reason that a 'big leaf' form of model worked so well here, however, may be because of the minimal self-shading involved with a LAI of 1.5. The values of the model coefficients are consistent with estimates based on leaf-level measurements and for λ, are substantially different from the values found in other boreal forests. The high ratio of night respiration to daytime C-uptake suggest that net exchange in the *L. gmelinii* forest would be especially sensitive to variations in the environment. Linking simple models of ecosystem C exchange (e.g. Table 3) to global climate models will be necessary to evaluate this sensitivity as will longer-term monitoring of the components of ecosystem carbon exchange.

Acknowledgements

This work was supported by funding from the New Zealand Foundation for Research, Science and Technology, New Zealand–Germany Scientific and Technical Cooperation Agreement, Bundesminister für Ernährung, Landwirtschaft und Forsten, the Humboldt

Foundation (Max-Planck Forschungspreis) and the USDA Northern Global Change Program. We wish to thank Inge and the rest of the Schulze family for their expert field assistance and support. We also acknowledge the valuable comments of two anonymous referees.

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