Carbon sequestration in a high-elevation, subalpine forest

R. K. MONSON*†, A. A. TURNIPSEED*, J. P. SPARKS*, P. C. HARLEY*,‡, L. E. SCOTT-DENTON*, K. SPARKS* and T. E. HUXMAN*
*Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado, 80309–0334, USA, †Cooperative Institute for Research in Environmental Science, University of Colorado, Boulder, Colorado, 80309–0334, USA, ‡Atmospheric Chemistry Division, National Center for Atmospheric Research, Boulder, Colorado, 80301, USA

Abstract

We studied net ecosystem CO_2 exchange (NEE) dynamics in a high-elevation, subalpine forest in Colorado, USA, over a two-year period. Annual carbon sequestration for the forest was 6.71 mol C m^{-2} (80.5 g C m^{-2}) for the year between November 1, 1998 and October 31, 1999, and 4.80 mol C m^{-2} (57.6 g C m^{-2}) for the year between November 1, 1999 and October 31, 2000. Despite its evergreen nature, the forest did not exhibit net CO_2 uptake during the winter, even during periods of favourable weather. The largest fraction of annual carbon sequestration occurred in the early growing-season; during the first 30 days of both years. Reductions in the rate of carbon sequestration after the first 30 days were due to higher ecosystem respiration rates when mid-summer moisture was adequate (as in the first year of the study) or lower mid-day photosynthesis rates when mid-summer moisture was not adequate (as in the second year of the study). The lower annual rate of carbon sequestration during the second year of the study was due to lower rates of CO_2 uptake during both the first 30 days of the growing season and the mid-summer months. The reduction in CO_2 uptake during the first 30 days of the second year was due to an earlier-than-normal spring warm-up, which caused snow melt during a period when air temperatures were lower and atmospheric vapour pressure deficits were higher, compared to the first 30 days of the first year. The reduction in CO_2 uptake during the mid-summer of the second year was due to an extended drought, which was accompanied by reduced latent heat exchange and increased sensible heat exchange. Day-to-day variation in the daily integrated NEE during the summers of both years was high, and was correlated with frequent convective storm clouds and concomitant variation in the photosynthetic photon flux density (PPFD). Carbon sequestration rates were highest when some cloud cover was present, which tended to diffuse the photosynthetic photon flux, compared to periods with completely clear weather.

The results of this study are in contrast to those of other studies that have reported increased annual NEE during years with earlier-than-normal spring warming. In the current study, the lower annual NEE during 2000, the year with the earlier spring warm-up, was due to (1) coupling of the highest seasonal rates of carbon sequestration to the spring climate, rather than the summer climate as in other forest ecosystems that have been studied, and (2) delivery of snow melt water to the soil when the spring climate was cooler and the atmosphere drier than in years with a later spring warm-up. Furthermore, the strong influence of mid-summer precipitation on CO_2 uptake rates make it clear that water supplied by the spring snow melt is a seasonally limited resource, and summer rains are critical for sustaining high rates of annual carbon sequestration.

Correspondence: Russell Monson, fax (303) 492–8699, e-mail Russell.Monson@colorado.edu

Introduction

Two of the primary aims of carbon cycle research are to quantify the long-term rate of carbon sequestration or losses for various ecosystems and to determine the primary environmental controls over diurnal, seasonal and interannual carbon exchange dynamics. Control of net ecosystem CO_2 exchange (NEE) is complex, often involving phenological variability, temporal variation in moisture availability, seasonal and interannual temperature variation, and forest structure and variation in light intensity. Two of the more important controls over NEE dynamics in forest ecosystems include soil moisture, which tends to be most important at lower latitudes (Goulden *et al.* 1996b; Greco & Baldocchi 1996; Malhi *et al.* 1998; Anthoni *et al.* 1999; Goldstein *et al.* 2000; Granier *et al.* 2000), and soil temperature which is more important at higher latitudes (Jarvis *et al.* 1997; Baldocchi *et al.* 1997; Goulden *et al.* 1998; Hollinger *et al.* 1998; although see Valentini *et al.* 2000).

In montane forest ecosystems of the western United States, both soil moisture and soil temperature are likely to affect NEE (Smith & Knapp 1990). Years with persistent climatic perturbations (e.g. La Niña years), can produce shallow snowpacks, and warm, dry summers. Dry climatic conditions can combine with shallow, rocky soils, to force these high elevation forests into a state of strong moisture limitation (Pataki *et al.* 2000). Furthermore, winter temperatures can be extremely cold, limiting aboveground metabolism to relatively low rates, and preventing water transport through frozen soils and xylem conduits. The interaction between moisture availability and temperature can be complex, and only a few studies have investigated these interactions as controls over forest NEE (Goulden *et al.* 1996b, 1998; Bubier *et al.* 1998; Granier *et al.* 2000).

In this report, we describe recent studies at the Niwot Ridge Ameriflux site in the Front Range of the Rocky Mountains of Colorado. Forests in the mountains of the western United States provide recreational opportunities, maintain biodiversity across sharp climatic gradients, and ensure the availability of water resources for one of the fastest growing components of the US population. The potential for these forests to sequester carbon, and play a role in national efforts to reduce the US contribution to rising atmospheric carbon dioxide concentrations is currently unknown. Our studies focused on quantifying the potential for carbon sequestration, and determining the effects of soil moisture and temperature on seasonal and annual patterns of NEE.

Materials and methods

The study site

The studies were conducted at the Niwot Ridge Ameriflux site located in a subalpine forest ecosystem just below the Continental Divide near Nederland, Colorado (40°1′ 58″N; 105°32′ 47″W). The site is located at 3050 m elevation, within 600 m of the NOAA C1 long-term monitoring station, approximately 8 km east of the Continental Divide. The surrounding subalpine forest is ∼97-year-old and in a state of aggradation, having recovered from early twentieth century logging. Flux measurements were conducted using a 26-m walk-up, scaffolding-type tower. The forest, west of the tower (within the fetch of the prevailing wind) is composed of subalpine fir (*Abies lasiocarpa*, 16 trees 100 m²), Engelmann spruce (*Picea engelmannii*, 10 trees 100 m²), and lodgepole pine (*Pinus contorta*, 9 trees 100 m²). The understorey is relatively sparse, containing tree seedlings from all three species and patches of *Vaccinium myrtillus* (25% average coverage). The forest slopes gently (6–7%) and uniformly, decreasing from west to east. Midsummer leaf area index for the forest west of the tower is 4.2 m² m⁻², canopy gap fraction is 17%, canopy height is 11.4 m, displacement height is 7.6 m, and roughness length is 1.79 m. Subalpine forest extends to 2 km west of the tower, where it forms a Krumholz, treeline ecotone that ultimately blends into alpine tundra. Annual precipitation for the site averages 800 mm and the mean annual temperature is 4 °C.

A climate-controlled trailer is located 600 m from the measurement tower and houses a Sun Microsystems (Sparc 5) workstation with an Ethernet connection to laboratories at the University of Colorado, approximately 25 km away. This connection allows instantaneous monitoring of instrument status from the university campus. Line power is supplied to the tower and trailer by two 17 kW power transformers.

Eddy covariance measurements

All CO_2 fluxes were calculated according to Goulden *et al.* (1996a). Net ecosystem CO_2 exchange (NEE) was defined as:

$$\text{NEE} = \underbrace{\overline{w'c'}}_{\text{I}} + \underbrace{\int_0^z \frac{dc}{dt} dz}_{\text{II}} \qquad (1)$$

where Term I is the time-averaged eddy flux for CO_2 [covariance between the turbulent fluctuations for vertical wind speed (w') and scalar concentration (c')] and

Term II is the beneath canopy storage of scalar [the time-dependent change in scalar concentration (dc/dt) as a function of vertical height (z)]. The eddy covariance method was used to measure the eddy flux for CO_2, H_2O and temperature. All flux measurements reported in this study were made at 21.5 m, approximately 10 m above the canopy. Wind velocity was measured with a Campbell Scientific Inc. (model CSAT-3) sonic anemometer and CO_2 concentration was measured with a Licor Inc. (model 6262) closed-path infrared analyser. The CO_2 analyser was kept on a platform near the base of the tower in an insulated box containing a small fan that mixed the air to maintain a homogenous operating temperature. Air was carried to the CO_2 analyser through 18 m of 5-mm (I.D) Dekabon tubing, filtered at the inlet with a 2-µm stainless steel filter. The air flow rate was maintained at 8.5 L min^{-1}. A 1-m coil of copper tubing was used as a heat exchanger to remove temperature fluctuations within the insulated box, and a second 2-µm stainless steel filter and flow meter (MKS, model 259 C) were attached to the inlet of the CO_2 analyser. The CO_2 analyser was operated in the absolute mode with Ultra High Purity (UHP) nitrogen flowing through the reference cell. Automated calibrations consisting of 20 s of zero gas followed by 20 s of span gas were conducted every 4 h, and controlled with a Campbell Scientific (model 21x) datalogger. Needle valves were adjusted such that the pressure within the CO_2 analyser during span calibration was the same as during sampling (typically 49–50 kPa). Span calibrations were conducted with secondary standards of CO_2 in air (N_2 and O_2), at concentrations between 370 and 400 µmol mol^{-1} as determined by comparison to a National Oceanic and Atmospheric Administration (NOAA) primary standard. Lag times due to transit for the CO_2 sample in the inlet tubing were periodically calculated using cross-correlation of the w-wind axis with CO_2 concentration. The lag was found to vary linearly with flow rate, which we constantly measured. On average the lag was found to be 1.6 s. Density corrections due to changes in H_2O vapour concentrations were made according to Webb et al. (1980). Wind coordinates were rotated according to Kaimal & Finnigan (1994) to force $\bar{v}$ and $\bar{w}$ (the mean crosswind and vertical wind speeds, respectively) to zero.

Post-processing of the eddy covariance data included screening for spikes in the anemometer and CO_2 concentration data and identification of data gaps due to loss of line power, sensor malfunction or inclement weather. The method of substitution for CO_2 flux data depended on the number of missing values. For three or fewer consecutive missing values, a spline fit to remaining values was used. For longer gaps, empirical regressions of CO_2 flux vs. PPFD at different air temperatures were used for daytime data if PPFD data was available

(otherwise 10-day averages for the period preceding and following the gap were used), and CO_2 flux vs. air temperature alone was used for nighttime data. Data were also screened to identify periods of nonstationarity and failure to comply with integral statistics (Foken & Wichura 1995). If both of these conditions were violated, the data were rejected and replaced as described above. Otherwise data were retained. Overall, less than 20% of the data record required filling or replacement.

The storage of CO_2 within the canopy was measured using a vertical profile system of six separate 21.8-m Dekabon lines (each 8 mm I.D) with a 1-µm Teflon filter at the intake. Tubing inlets were positioned 0.5, 1, 2, 5, 10 and 21.5 m above the ground. The lowest three inlets were attached to a short mast located 7 m from the tower base to avoid influences from the small clearing that surrounds the tower. Higher inlets were extended horizontally approximately 1 m from the tower. A sampling manifold consisting of a series of electrically activated solenoid valves (controlled with a Campbell Scientific 23x datalogger) were used to cycle among the inlets every 10 min. Air from each inlet was pulled through the tubing to a magnesium perchlorate desiccant trap to remove water vapour, through a second 1-µm filter, to a CO_2 analyser (model 6251, Licor Inc.). The sampling flow rate was maintained at 0.43 L min^{-1}. Data for the first 50 s of each sample was discarded to achieve complete flushing of the desiccant trap. Calibration of the zero and span for the CO_2 analyser was conducted automatically every 4 h as described above. The CO_2 concentration recorded for each level was averaged over a 30-min time interval, multiplied by vertical distance (taken with the inlet as midpoint), and used to compile the total CO_2 stored beneath 21.5 m.

Night-time, cold-air drainage could result from the sloped topography of the site. In the presence of a downslope CO_2 concentration gradient, downslope flow would cause a net CO_2 flux which would go undetected in both the eddy covariance and storage measurements. Such advective CO_2 losses would violate the assumption of mass balance in the horizontal coordinates, and cause an overestimate of the true NEE. This issue would only be relevant during stable night-time periods when turbulent mixing is too weak to maintain good coupling between soil respiratory fluxes and the eddy covariance measurement. We dealt with this issue by replacing the measured NEE during night-time stable periods (u* < 0.2 m s^{-1}) with data from regressions of CO_2 flux vs. temperature observed during turbulent periods (u* > 0.2 m s^{-1}) (Goulden et al. 1996a). The regressions were derived from data collected during the months between May–September of each respective year. The u* threshold of 0.2 m s^{-1} was chosen according to the method recommended by Goulden et al. (1996a). Briefly,

the empirical function of night-time NEE vs. soil temperature (i.e. Fig. 12) was used to calculate a corrected NEE for u* increments of 0.1 m s^{-1} for the data pooled from both years. The ratio of the 'actual NEE' (NEE$_a$) to 'corrected NEE' (NEE$_c$) at each respective u* increment was determined. The u* threshold (depicted in Fig. 2) was chosen as the point where NEE$_a$/NEE$_c$ exceeds 0.7. This corresponds to a value of 0.2 m s^{-1} at our site. The ratio drops rapidly below 0.7 at u* < 0.2 m s^{-1}. At 0.2 m s^{-1} < u* > 0.3 m s^{-1} the ratio ranges from 0.71 to 0.76. Above 0.3 m s^{-1} the ratio fluctuates between 0.8 and 1.1.

Sensible and latent heat fluxes were also measured with the eddy covariance technique using the same sonic anemometer described above. Water vapour fluctuations were measured with an open-path Kr hygrometer (KH20, Campbell Scientific) mounted approximately 19 cm to the east of the sonic anemometer. Sensible heat flux was measured using temperature fluctuations obtained from the sonic anemometer. The sonic temperature flux was converted to real temperature flux using the correction described by Schotanus *et al.* (1983).

Canopy displacement height and roughness length were determined from vertical profiles of wind velocity during neutral conditions. A total of 314 profiles were analysed under these conditions for the period between November 1, 1998 and October 31, 1999. The measured displacement height was 7.6 ± 0.2 m, which is 67% of the average canopy height (11.4 ± 0.5 m). The measured roughness length was 1.79 ± 0.07 m, which is 16% of the average canopy height.

Footprint analysis was conducted using measured variables of canopy height, displacement height and roughness length in combination with the model of Schuepp *et al.* (1990). In unstable conditions (L = − 10 m, where L is the Obukhov length), it is estimated that 95% of the measured flux (at 21.5 m) comes from a 1.23-km fetch west of the tower. Under neutral conditions (L = −10 km), the westward fetch is predicted to expand to 3.2 km. A detailed analysis of the forest energy budget and turbulence structure has been conducted and is reported in a separate manuscript (Turnipseed, Blanken, Anderson & Monson, submitted). Briefly, the surface energy budget can be balanced (incident net radiation balanced by sensible, latent and soil conductive heat fluxes) to within 12% during the winter and 16% during the summer. The balance is equally effective irrespective of whether the wind originates from the west or east. During daytime summer periods when wind speeds were high (e.g. u* was greater than 1.2 m s^{-1}), the energy budget could be completely closed, and the dominant turbulence frequency was shifted to higher values. This suggests that the failure of complete closure at lower wind speeds was not due to inadequacies in measuring the high frequency flux component, but rather the low frequency flux component.

Statistical methods

For the data concerning the response of net ecosystem CO_2 exchange (NEE) to photosynthetic photon flux density (PPFD) nonlinear regression was used to compare the two study years (1999 and 2000), and differing environmental conditions. F-statistics were constructed from the residual sum of squares from each regression line following Potvin *et al.* (1990).

Results

Co-spectral analysis of sensible heat and CO_2 fluxes revealed that most of the power for both fluxes occurred at turbulent frequencies less than 1 Hz (Fig. 1). Sensible heat fluxes were measured to a frequency of 10 Hz, and it is assumed that the entire flux was measured. The upper limit to the resolution of the CO_2 flux is assumed to be 1–2 Hz, with the primary limitation resulting from the closed path CO_2 sensor, electrical noise which precludes the high frequency flux signal, and attenuation of flux in the tubing. Co-spectral analysis indicated that 99% of the total sensible heat flux occurred at turbulent frequencies less than 1 Hz. By superimposing cospectra of the sensible heat and CO_2 fluxes, it is concluded that 91% of the CO_2 flux below 1 Hz was actually measured (i.e. approximately 9% of the flux was lost due to inadequacies in the CO_2 measurement system).

The study site is regularly characterized by stable, night-time conditions, especially during the late summer and early autumn, which can confound the accurate determination of eddy fluxes. This is exemplified in the reduction of CO_2 flux as the surface friction velocity (u*) dropped below 0.2 m s^{-1} (Fig. 2). This analysis represents the basis for the u* filter; i.e. invoking replacement of fluxes when u* < 0.2 m s^{-1}.

The CO_2 flux data were collected across two sequential years that exhibited markedly different climatic conditions. Both 1999 and 2000 have been characterized as La Niña years, though 2000 was considerably drier and warmer than 1999 (Table 1). As an example, consider the months of April and May; two critical months with regard to snow melt dynamics and the initiation of net ecosystem CO_2 uptake. The average temperature of April and May, 2000 was 3–5 °C warmer and precipitation was 57% lower than in 1999. This was due primarily to an earlier spring warm-up, with April temperatures being significantly warmer in 2000. The average temperature during July and August, two months that support high summertime net CO_2 uptake rates, was 1–2 °C warmer and precipitation was 47% lower in 2000 compared to
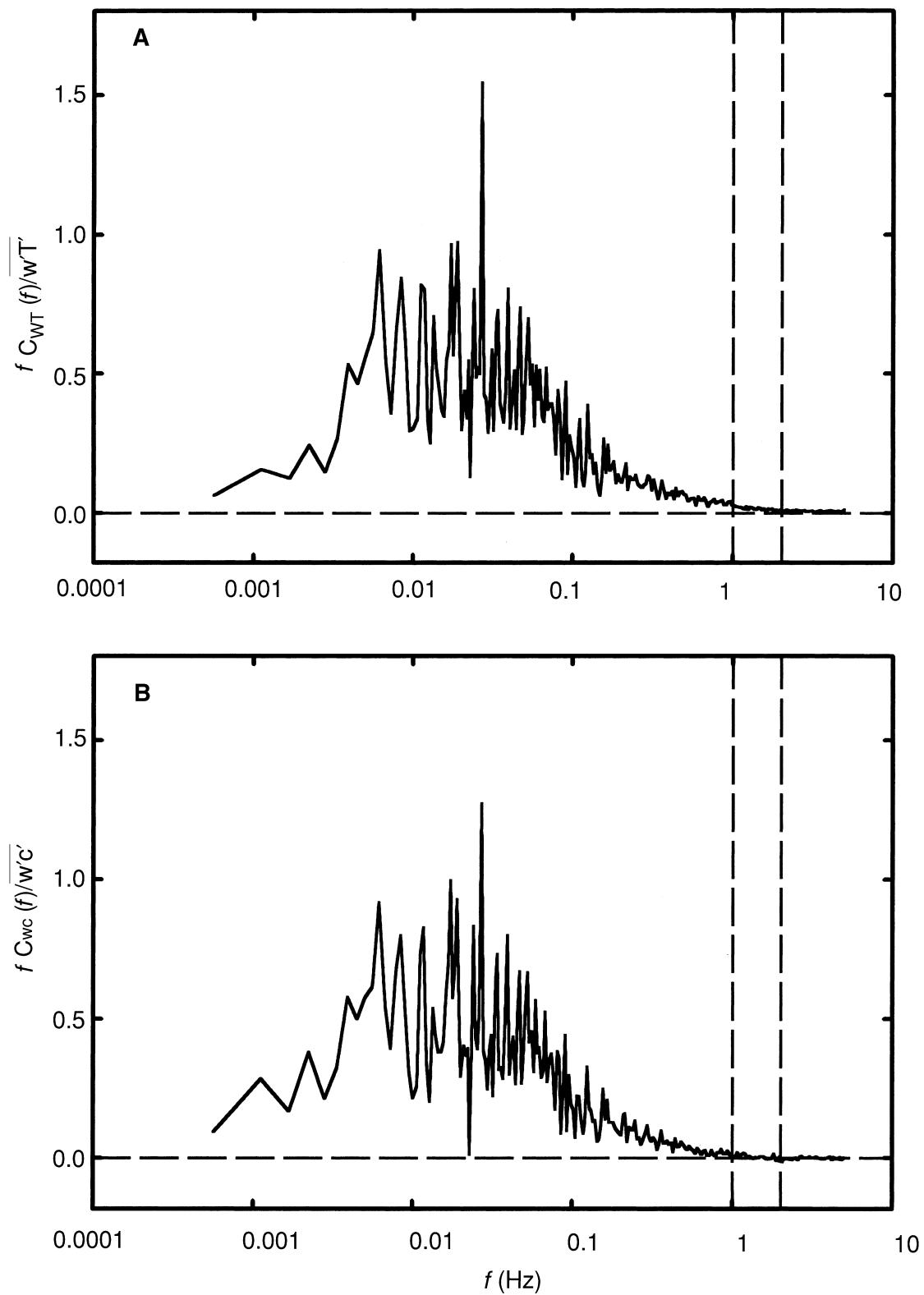
Fig. 1 Co-spectra of the sensible heat and CO_2 fluxes expressed as semilogarithmic plots. Data are derived from typical fluxes measured at mid-day during clear weather on July 23, 1999. Vertical reference lines are added to mark the 1 and 2 Hz frequencies.
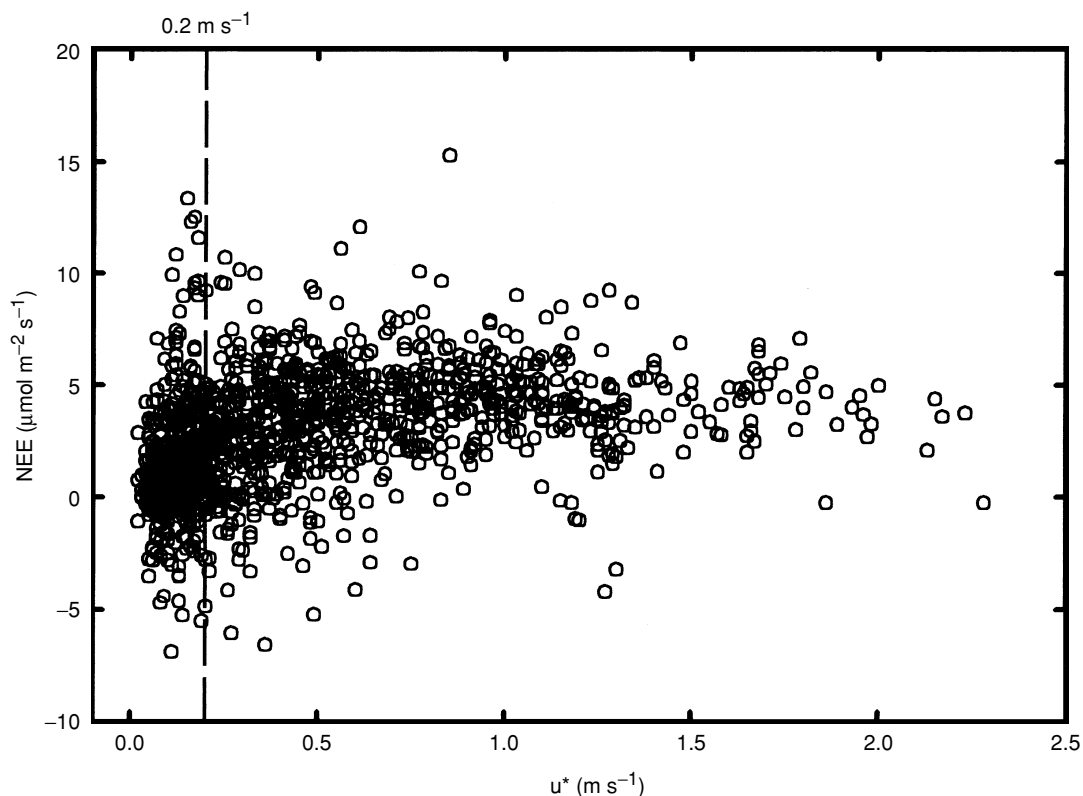
Fig. 2 NEE as a function of surface friction velocity (u*) using 30-min average fluxes from the entire 1999 growing season May–November. It is clear that fluxes decrease below a threshold of approximately 0.2 m s^{-1}.

1999. Most of the difference in July and August precipitation between the two years was due to weather patterns during the first two weeks of August.

Cumulative carbon sequestration for the period between November 1, 1998 and October 31, 1999 was 6.71 mol C m^{-2} (80.5 g C m^{-2}), and for the period between November 1, 1999 and October 31, 2000 it was 4.80 mol C m^{-2} (57.6 g C m^{-2}) (Fig. 3). These values represent cumulative sums obtained from the data subjected to the postprocessing u* filter and gap filling. The respective unfiltered sums for these periods were 13.82 mol C m^{-2} (165.9 g C m^{-2}) and 10.51 mol C m^{-2} (126.2 g C m^{-2}). Cumulative losses of carbon by ecosystem respiration during the winter (i.e. the time between growing seasons) were 12.13 mol C m^{-2} for 1999 and 11.84 mol C m^{-2} for 2000. Growing-season cumulative carbon sequestration was 18.84 mol C m^{-2} during 1999 and 16.64 mol C m^{-2} during 2000. The cumulative carbon sequestration rate during the first 30 days of the growing season was 6.01 mol C m^{-2} for 1999 and 3.36 mol C m^{-2} for 2000. Most of the difference between the two years was due to consistently lower net CO_2 uptake rates beginning after the first week of carbon sequestration in the spring of 2000, compared to 1999 (Fig. 4A). The lower rates of NEE during the beginning

of the 2000 growing season were due to lower rates of daytime CO_2 uptake, not higher rates of night-time respiration (Fig. 4B). Air temperatures during the first 30 days of the 2000 season (which occurred in late April and early May) were 3–5 °C lower, and daytime atmospheric vapour pressure deficits were 0.2–0.3 kPa higher, compared to the first 30 days of the 1999 season (which occurred in mid May and early June) (Fig. 4C). Snow depth dynamics were markedly different during the spring months of the two years. At the beginning of April 1999, the average snow depth was 64 cm (57% of the average snow depth at the beginning of April for the previous 17 years). By the end of April 1999, the snow depth had increased to 113 cm (103% of the average snow depth at the end of April for the previous 17 years). At the beginning of April 2000, the average snow depth was 131 cm (116% of the average snow depth at the beginning of April for the previous 17 years). By the end of April 2000, the snow depth had decreased to 59 cm (54% of the average snow depth at the end of April for the previous 17 years). The liquid water equivalent of the measured snowpack was not different between the two years, being 33% in both cases (indicating that differences in snow depth were not due to differences in compaction). [Snow data were obtained from the Niwot Ridge

Table 1 Climatic parameters for the Niwot Ridge Ameriflux site during the 24-month period from November 1, 1998 – October 31, 2000, the same analysis period used in the measurements of net ecosystem CO_2 exchange rate. Seasonal values were calculated as the average of the monthly means (for T_a, PPFD and VPD) or the sum of the monthly totals (for Ppt). Note that values for the Autumn 2000 only include two months since the measurement period began on November 1, 1998. T_a = average air temperature, Ppt = precipitation, PPFD = average daytime photosynthetic photon flux density, VPD = average atmospheric vapour pressure deficit ($e_{sat} - e$, where e is H_2O vapour pressure)

Season	T_a (°C)	Ppt (mm)	PPFD (µmol m^{-2} s^{-1})	VPD (kPa)
Winter 98–99 (Dec, Jan, Feb)	− 6.51	105	507	0.28
Spring 99 (Mar, Apr, May)	− 0.84	313	804	0.36
Summer 99 (Jun, Jul, Aug)	11.42	250	847	0.71
Autumn 99 (Sep, Oct, Nov)	4.65	89	754	0.67
Winter 99–00 (Dec, Jan, Feb)	− 5.19	179	591	0.50
Spring 00 (Mar, Apr, May)	1.59	186	900	0.89
Summer 00 (Jun, Jul, Aug)	12.86	181	924	1.45
Autumn 00) (Sep, Oct)	6.05	88	819	1.05

Long-Term Ecological Research (LTER) Climate Database recorded for the C-1 site, which is approximately 600 m from the flux tower.]

A second period of significant deviation in the cumulative NEE patterns for the two years occurred during the late summer and early autumn. In 1999, heavy convective rain storms occurred during the first 10 days of August, keeping the soil relatively moist during the late-summer weeks. In 2000, late-summer drought occurred particularly during early August. The contrast between years is evident in the lower NEE rates observed in early August 2000, compared to 1999 (Fig. 5). NEE rates during both years recovered from the summer drought and increased again during October, in response to more frequent precipitation events (primarily as snow) and cooling of the soil with concomitant reductions in respiration.

Daily integrated NEE during the winter remained positive, indicating a persistent phase of respiration (Fig. 6). Even when the daily average air temperature increased above 0 °C, photosynthetic carbon uptake was not significant during the winter (Fig. 7). In early May 1999 and

mid April 2000, NEE for the forest switched sharply from net CO_2 emission to net CO_2 uptake, and reached maximum rates of CO_2 uptake within a few days of the switch (Fig. 6). As the growing season progressed, carbon uptake rates decreased, though there was considerable day-to-day variation. Much of the variation in NEE was correlated with variation in daily integrated PPFD. In this mountain environment, clouds form on a near-daily basis. Depending on when during the day the clouds form, the daily integrated NEE can swing from strongly negative (CO_2 uptake) to strongly positive (CO_2 loss). Summertime days with the most positive NEE (e.g. the two dates marked by the ellipse in Fig. 6) had cool, cloudy weather for the entire day. On June 16, for example, the first day of those marked by the ellipse, night-time air temperatures plunged to −2 °C, the subsequent daytime temperature did not rise above 5 °C, and PPFD averaged 212 µmol m^{-2} s^{-1}. Soil temperatures (upper 10 cm) remained relatively high at 4–7 °C (soil temperatures immediately before and after this anomalous cold event ranged between 6 and 11 °C).

Carbon sequestration rates progressively decreased from the beginning of June through the beginning of August 1999, and the decrease was correlated with increases in night-time respiration, not decreases in daytime CO_2 uptake (Fig. 8). Net radiation and sensible heat exchange were generally higher during the first 10 days of July, compared to the same period during June, and August Latent heat exchange was similar during June and July, but increased slightly during early August in response to precipitation events (the average Bowen ratio, or ratio of sensible to latent heat exchange, during the first 10 days of August 1999 was 0.77). Night-time respiration rates were higher during the first 10 days of July and August, compared to the first 10 days of June (a period in which snow continued to cover the ground), although daytime net CO_2 uptake rates were similar. A substantially different pattern emerged during the summer of 2000. The summer drought developed early in the season, as evidenced by the high rates of sensible heat exchange and low rates of latent heat exchange during the first 10 days of August (Fig. 9) (the average Bowen ratio during this time was 2.86). Night-time respiration rates during the first 10 days of July and August were not significantly different from those during the first 10 days of June (a period when snow did not cover the ground). Daytime net CO_2 uptake rates during August were lower compared to those during June and July.

The effects of variations in PPFD on NEE are evident in the short term flux data. The relationship between NEE, calculated from the 30-min averages, and PPFD was nonlinear, although considerable scatter in the data was observed (Fig. 10). Data trends for the two years were
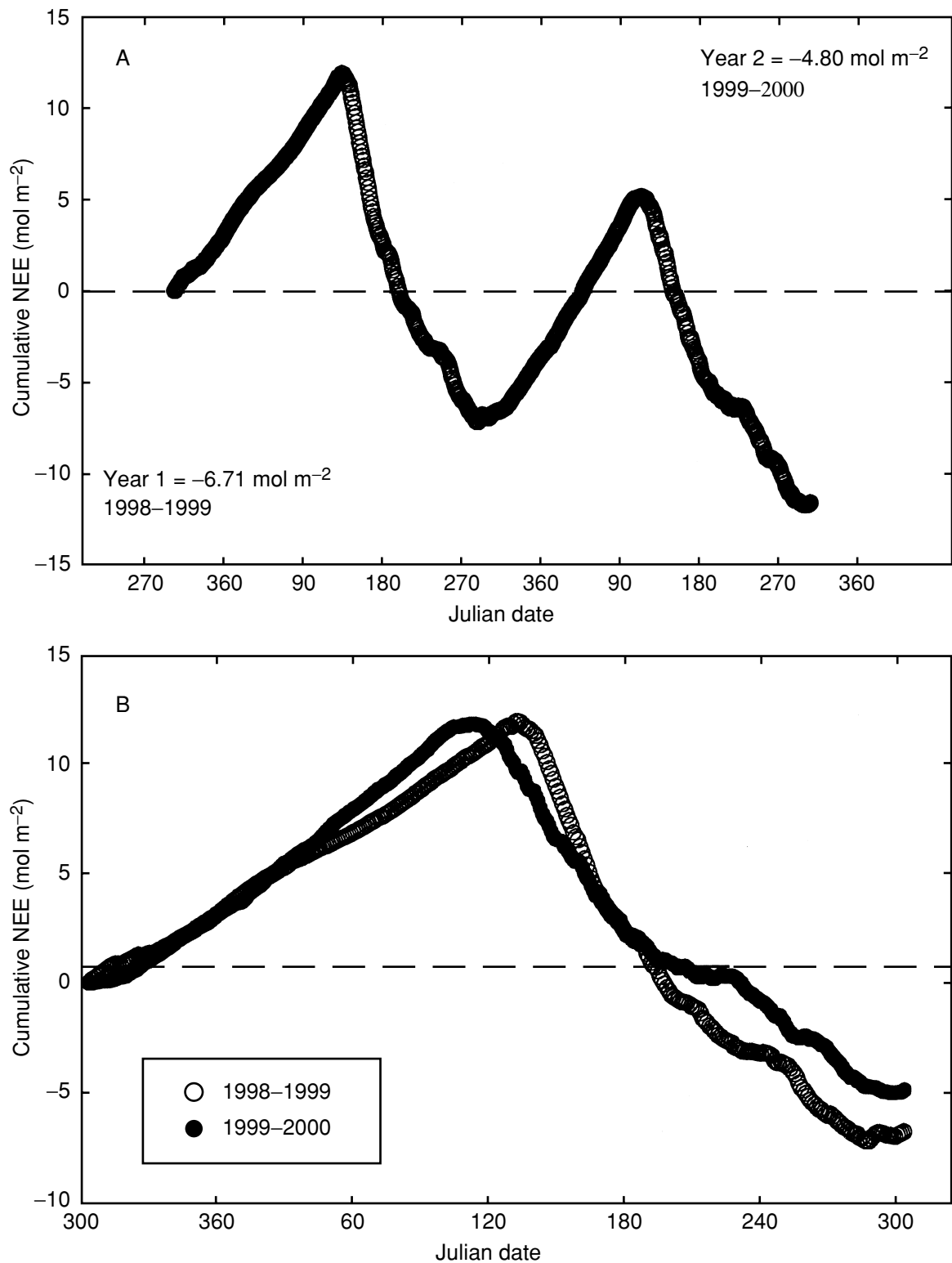
Fig. 3 (A) Cumulative net ecosystem CO_2 exchange (NEE) as a function of Julian date for the Niwot Ridge subalpine forest during two sequential years. Standard convention is used to indicate the direction of the CO_2 flux, with positive NEE indicating net respiratory CO_2 emission and negative NEE indicating net photosynthetic CO_2 uptake. (B) The same data from A, but presented in overlapping fashion to make clear the earlier initiation of net CO_2 uptake, and the slower rate of carbon sequestration in the growing season of the second year (1999–2000), compared to the first (1998–99). Also note, the similar magnitude of winter respiration for the two years.
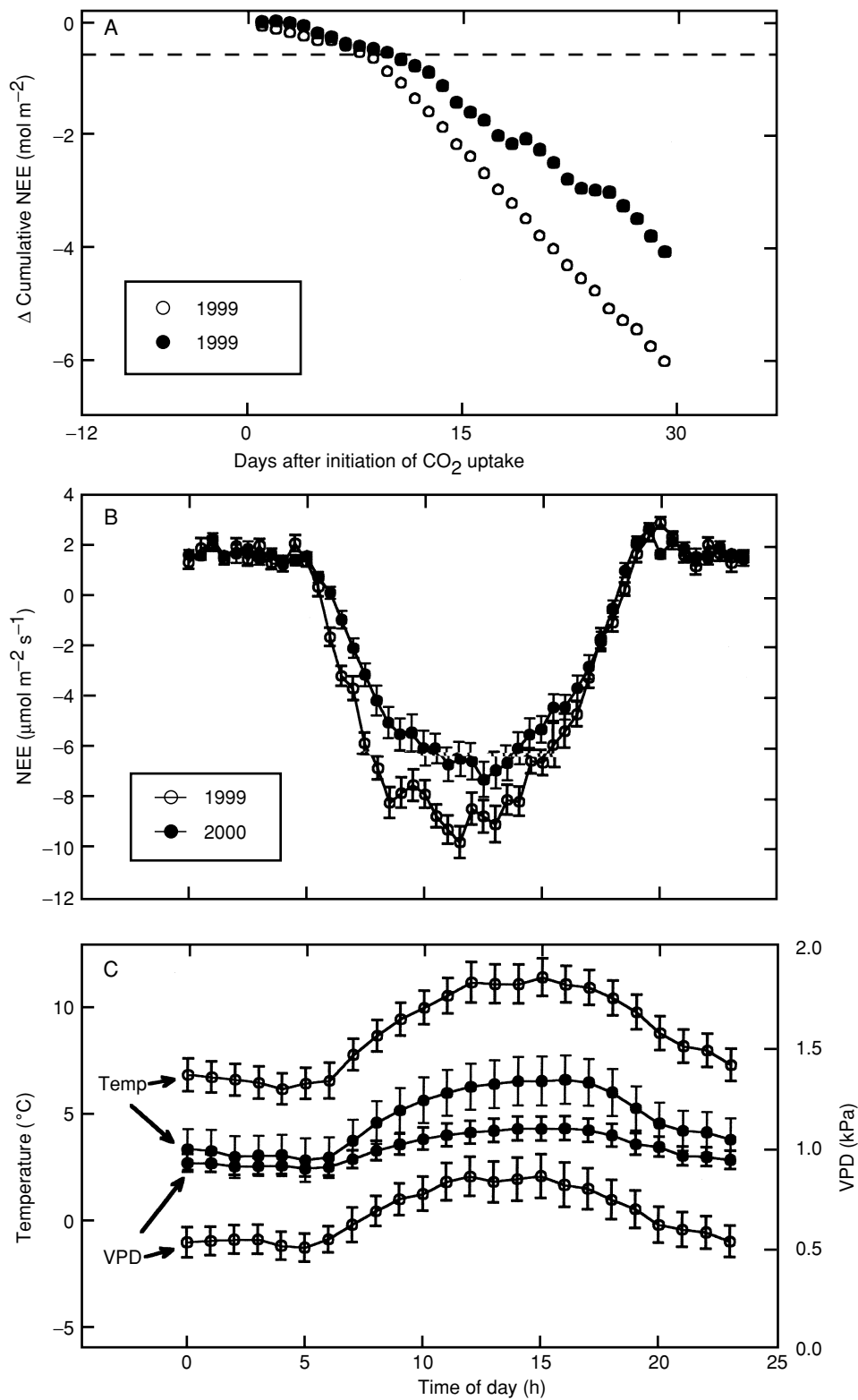
Fig. 4 (A) The change in cumulative NEE during the first 30 days of the growing season (here defined as the time after the switch from positive daily integrated NEE to negative daily integrated NEE), for the 1999 and 2000 seasons. (B) The mean ($\pm$SE) of NEE as a function of time of day for the first 30 days of the growing season of 1999 (Julian dates 134–163) and 2000 (Julian dates 114–143). (C) The mean ($\pm$SE) of air temperature and atmospheric vapour pressure deficit (the difference between saturation and actual vapour pressure of the air), both measured at 21 m above the ground, for the first 30 days of the 1999 and 2000 growing seasons.
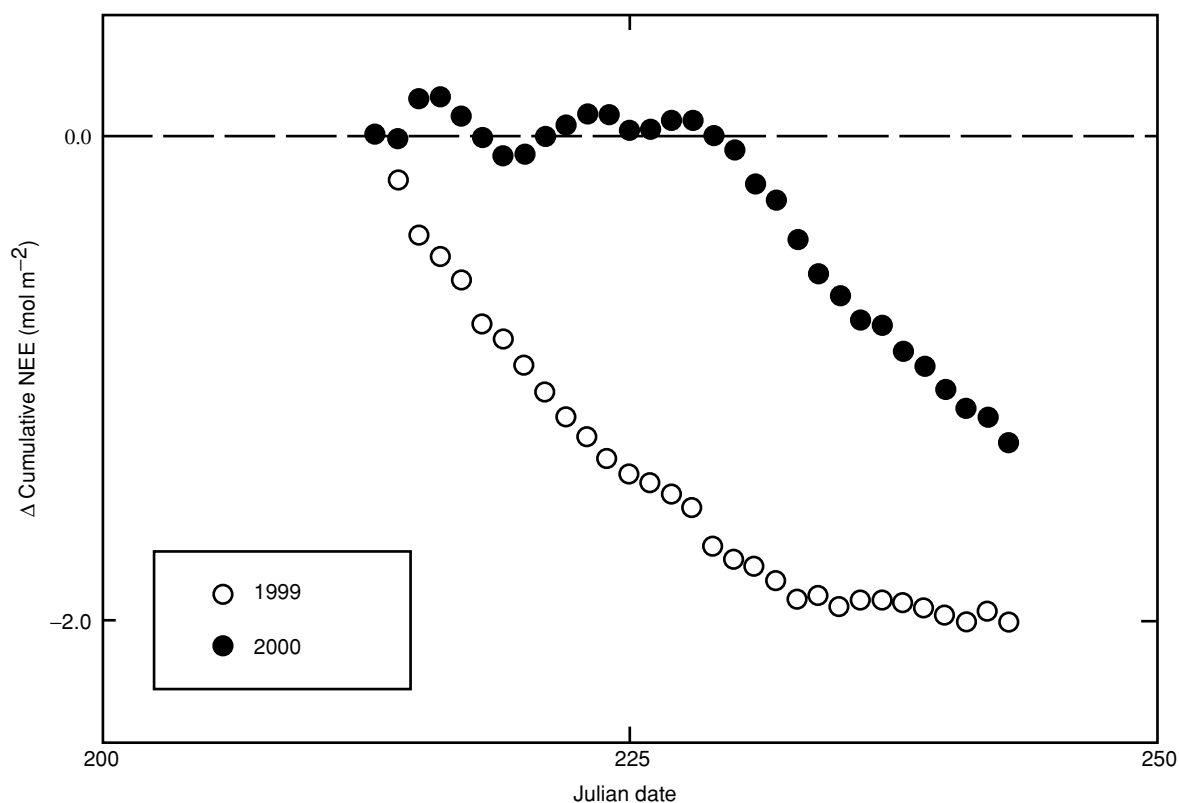
Fig. 5 The change in cumulative NEE during the first few days of August 1999 or 2000. During 1999, this period was characterized by heavy convective rain showers. During 2000, the period was characterized by an extended mid-summer drought.

different, with generally smaller fluxes in response to increasing PPFD in 2000 ($F = 89.1$, $p < 0.001$, d.f. = 3637). The maximum observed NEE in 1999 and 2000 was approximately 19 µmol CO_2 m^{-2} s^{-1}. Regression analysis revealed that the maximum mean NEE (obtained as the predicted asymptote of the regression) was -15.5 µmol CO_2 m^{-2} s^{-1} for 1999 and -13.8 µmol CO_2 m^{-2} s^{-1} for 2000. The observed mean NEE appeared to reach a maximum in the range 8–9 µmol CO_2 m^{-2} s^{-1} for both years, although the mean observed NEE was slightly lower for 2000 compared to 1999. In 1999, the apparent quantum yield (initial slope of the response) was -0.038 mol CO_2 mol^{-1} photons, and the ecosystem respiration rate (*y*-intercept) was 3.57 µmol CO_2 m^{-2} s^{-1}. For 2000, the apparent quantum yield was -0.030 mol CO_2 mol^{-1} photons and the ecosystem respiration rate was 2.92 µmol CO_2 m^{-2} s^{-1}. During cloudy periods, NEE was slightly higher than during clear, sunny periods (Fig. 11). The predicted maximum NEE during cloudy periods (from regression analysis) was -18.5 µmol CO_2 m^{-2} s^{-1}, the apparent quantum yield was -0.042 mol CO_2 mol^{-1} photons, and the ecosystem respiration rate was 4.37 µmol CO_2 m^{-2} s^{-1}. The predicted maximum NEE

during sunny periods was -16.7 µmol CO_2 m^{-2} s^{-1}, the apparent quantum yield was -0.030 mol CO_2 mol^{-1} photons, and the ecosystem respiration rate was 4.39 µmol CO_2 m^{-2} s^{-1}. The sunny and cloudy relationships are significantly different ($F = 16.2$, d.f. = 4.182, $p < 0.0001$).

When calculated as 30-min averages, night-time NEE (i.e. ecosystem respiration rate) was sensitive to soil surface temperature, and an exponential function best described the relationship (Fig. 12). Respiration rates were lower during 2000 at any given temperature, compared to 1999. Considerable scatter occurred within the relationships between night-time NEE and temperature.

Discussion

The annual rate of C sequestration measured for the Niwot Ridge forest is low compared to most other forest ecosystems that have been studied. The annual rate of NEE is 23% of that reported for a coastal, temperate coniferous forest (Anthoni *et al.* 1999), 19% that of a wet tropical forest in Brazil (Grace *et al.* 1995), 20–101% that of a boreal aspen forest (Chen *et al.* 1999; Black *et al.* 2000), and 29–33% that of temperate, northern hemisphere
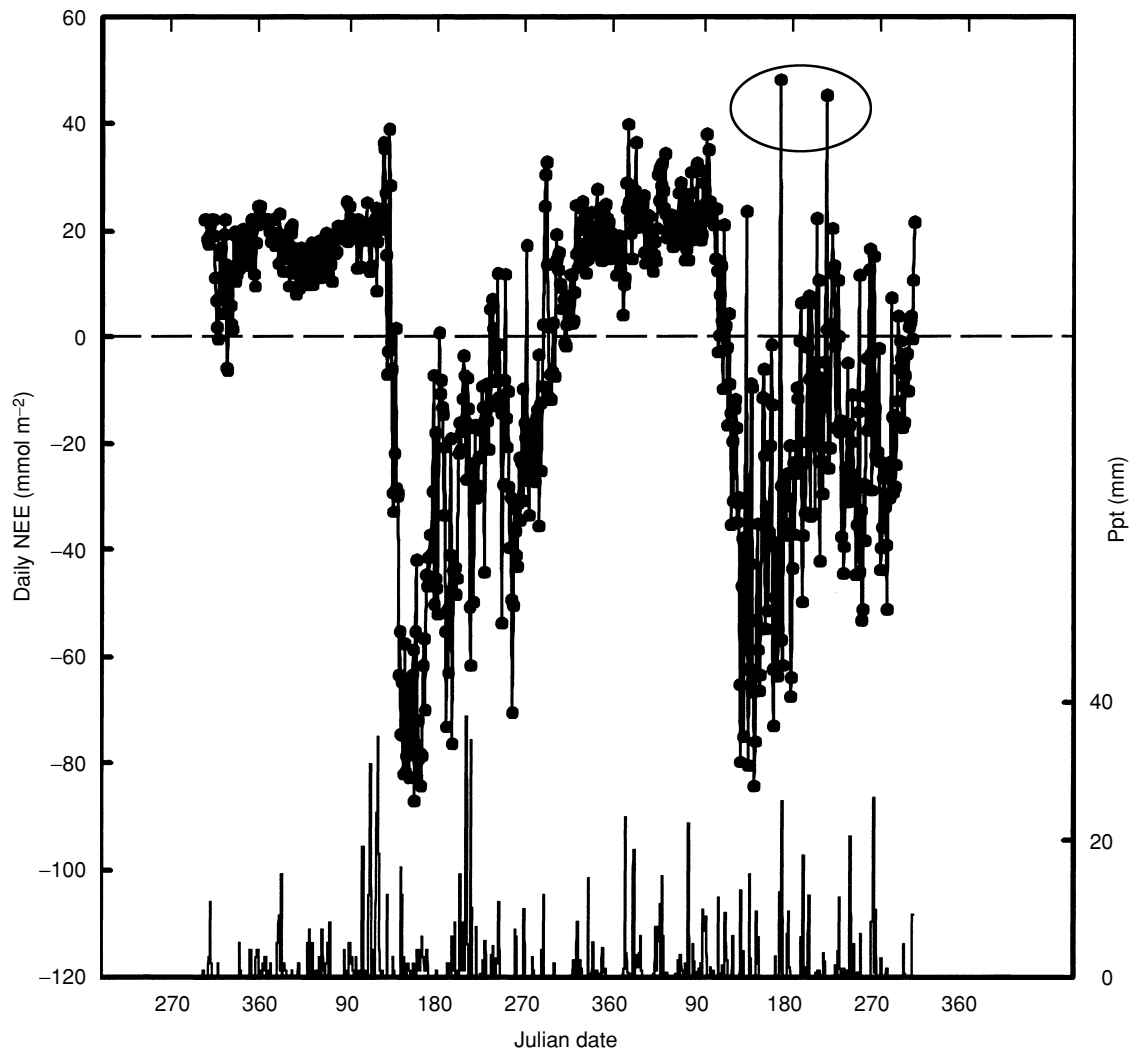
Fig. 6 Daily integrated NEE for the 24-month period between November 1998 and October 31, 2000 as a function of Julian date. Positive values indicate net respiratory CO_2 loss and negative values indicate net photosynthetic CO_2 uptake. Individual precipitation events are represented by the vertical bars across the bottom of the panel. The two values encircled with the ellipse indicate two days during the summer when the weather was cool and dark due to thick cloud cover, but soil temperatures remained relatively high; the daily net CO_2 flux was respiratory for these dates.

deciduous forests (Goulden *et al.* 1996b; Granier *et al.* 2000). In a thorough study of annual NEE in forest ecosystems across a latitudinal transect in Europe, Valentini *et al.* (2000) reported values ranging from -470 to -660 g C m^{-2} at the lowest latitudes and 80 to -245 g C m^{-2} at the highest latitudes. The Niwot Ridge forest exhibited annual NEE of -58 to -81 g m^{-2}, which is considerably less than that reported along the entire transect, except for some of the most northerly boreal sites. The low rate of C sequestration for the Niwot Ridge forest is presumably due to the harsh, high-elevation climate that characterizes the site, and the constraints that such a harsh climate place on soil miner-alization, plant growth, and the recruitment of new trees.

The cold winters of the Niwot Ridge site are particularly effective in reducing the potential for carbon uptake. Unlike a more productive ponderosa pine stand in old-growth forest of central Oregon, which gains 50% of its annual carbon uptake during the relatively mild winters (Anthoni *et al.* 1999), the forest of Niwot Ridge exhibits consistent wintertime respiration, losing 60% of its annual carbon uptake as winter CO_2 emissions.

In a recent analysis of carbon gain in a high-elevation subalpine forest in Montana, Carey *et al.* (2001) presented the case that old forests may be larger C sinks than previously realized. Through destructive harvests and allometric scaling they estimated that annual net primary productivity (ANPP = annual NEE plus the microbial
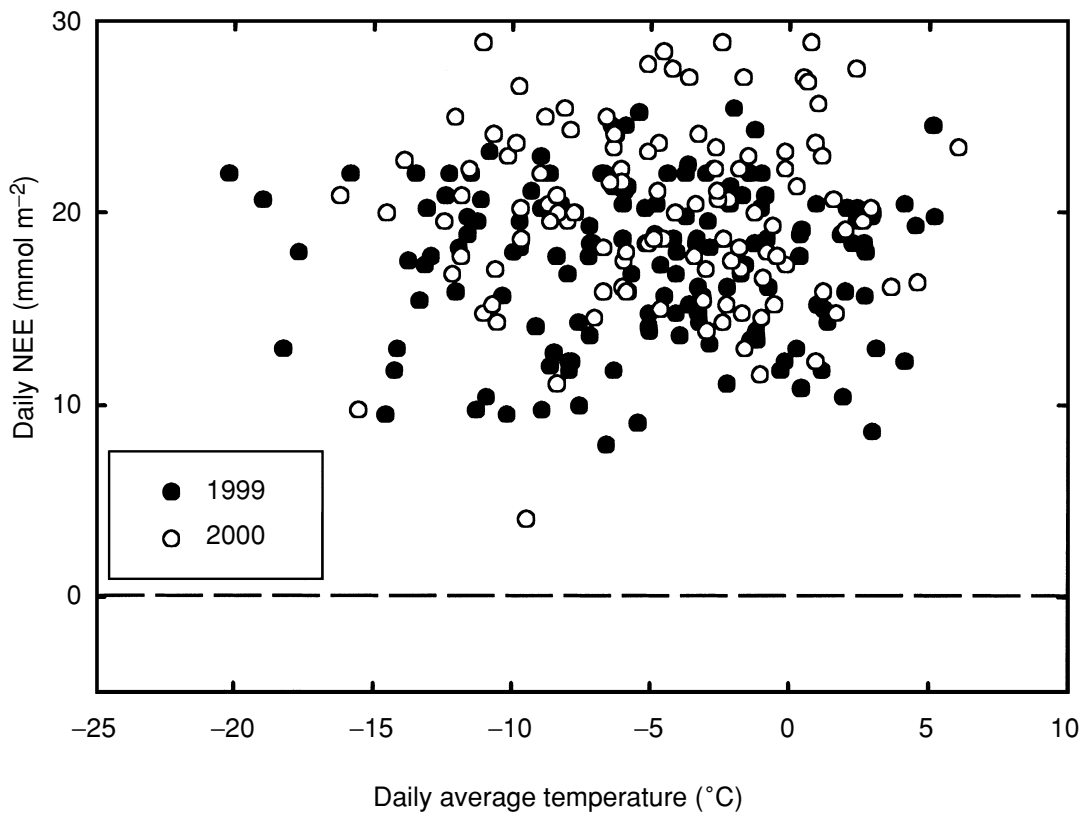
Fig. 7 The relationship between wintertime daily integrated NEE and average daily temperature for both 1999 and 2000.

component of soil respiration) of a 100-year-old-subalpine forest was approximately 250 g m^{-2}, and that by 500 years annual NPP could average 500 g m^{-2}. These estimates are considerably higher than those generated from forest-growth models, and the authors used this fact to argue that old forests, and in this case old subalpine forests, may contribute significantly to global CO_2 sinks. Using harvest techniques, as well as determination of NPP from NEE plus soil chamber measurements of respiration, we have derived an estimate of NPP for the 100-year old Niwot Ridge forest that is between 250 and 500 g m^{-2} (data not shown), similar to the estimate of Carey *et al.* (2001). However, the large gap between the estimated NPP and the measured NEE (i.e. from 250–500 g m^{-2} 56–81 g m^{-2}) demonstrates that when soil respiration is added into the calculation, the potential for the forest to be a significant CO_2 sink is greatly diminished.

For the two years studied, NEE in the Niwot Ridge forest was sensitive to interannual variation in precipitation and temperature. The wetter, cooler climate of 1999 resulted in higher rates of carbon sequestration compared to the drier, warmer climate of 2000 (Fig. 3). Most of the difference was due to growing-season CO_2 uptake, rather than winter respiration. Cumulative winter respiration was only 2% higher during 1999–2000, compared to

1998–99, whereas cumulative growing-season CO_2 uptake was 14% lower. Much of the year-to-year difference in CO_2 uptake was due to the first 30 days of the growing season. Cumulative NEE for the first 30 days of the 2000 growing season was only 56% the rate during the first 30 days of the 1999 season (Fig. 4A). These early season patterns were, once again, due to differences in the daytime CO_2 uptake rate, not night-time respiration rates (Fig. 4B). The most obvious springtime environmental difference between the two years involved the timing of the snow melt and the climate during the snow melt. The spring warm-up in 2000 resulted in an abnormally early loss of snow, compared to the spring warm-up of 1999. The differences in spring snow melt dynamics between the two years were equivalent to a loss of 12 cm of liquid precipitation (taken from the snowpack) in April 2000 and a gain of 13 cm of liquid precipitation (stored in the snowpack) in April 1999. The water from the 2000 snow melt was supplied to the soil during a period when daytime air temperatures were 4–5 °C lower and daytime atmospheric vapour pressure deficits were 0.2–0.3 kPa higher, compared to when water was supplied to the soil during the 1999 snow melt (Fig. 4C). In both cases, the snow depth at the beginning of the melt period was similar (in fact, it was
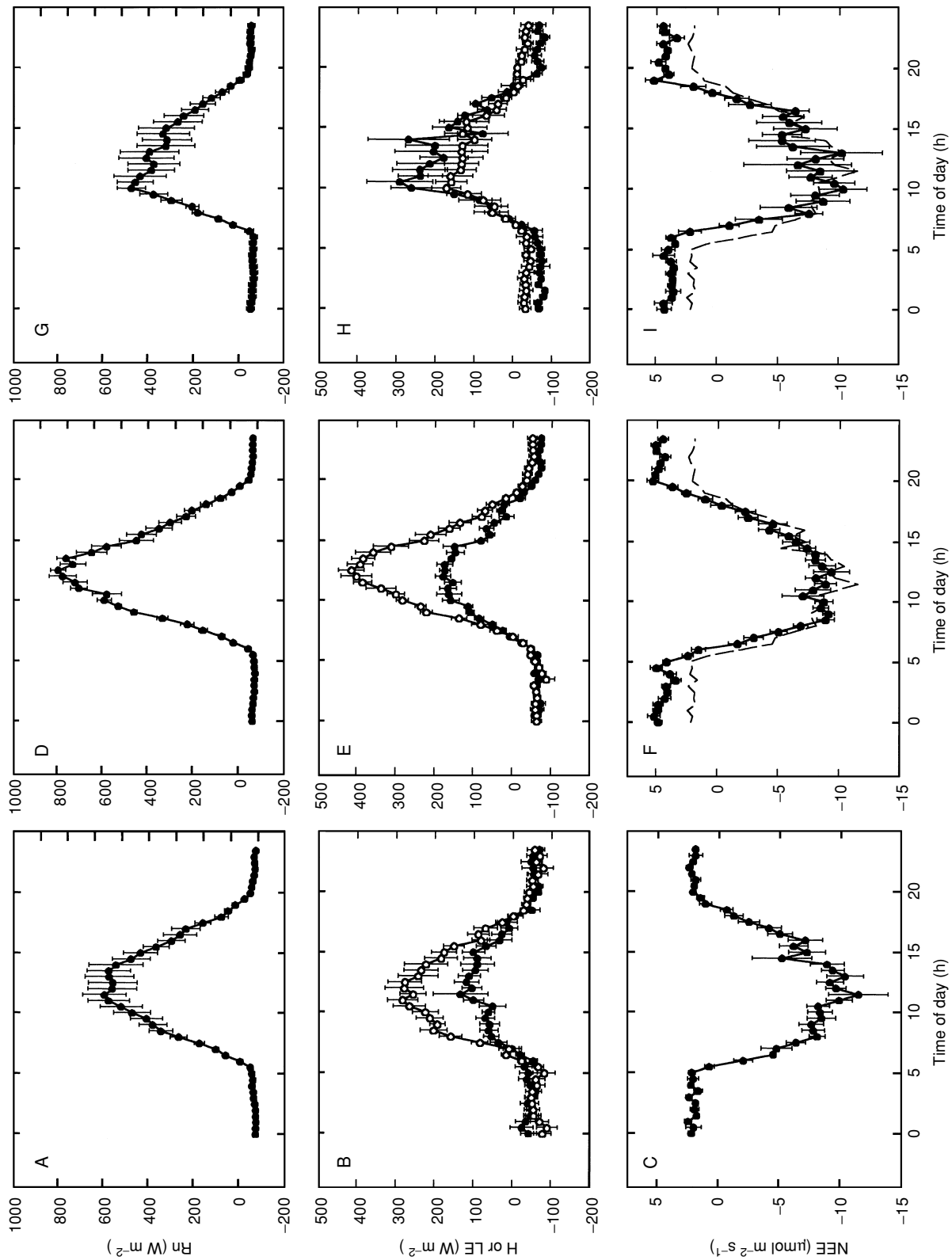
Fig. 8 Ten-day averages for 1999 of net radiation (Rn), sensible heat exchange (H; open symbols), latent heat exchange (LE; closed symbols), and NEE as a function of hour of day for the first 10 days of June (panels A–C), July (panels D–F), and August (panels G–I). Vertical bars represent ±SE. The dashed lines in panels F and I represent the mean NEE pattern for the first 10 days of June (panel C) presented again for purposes of comparison.
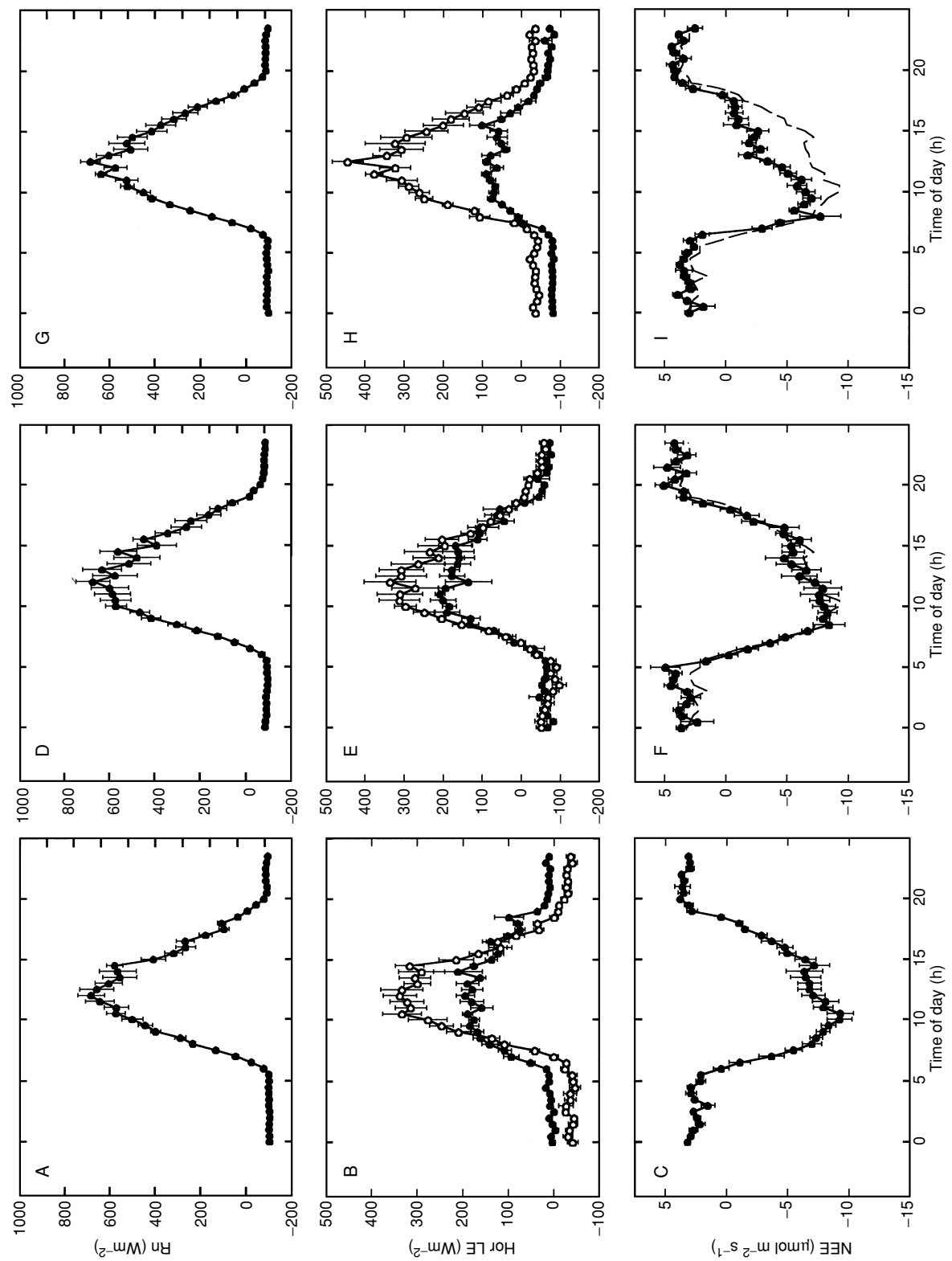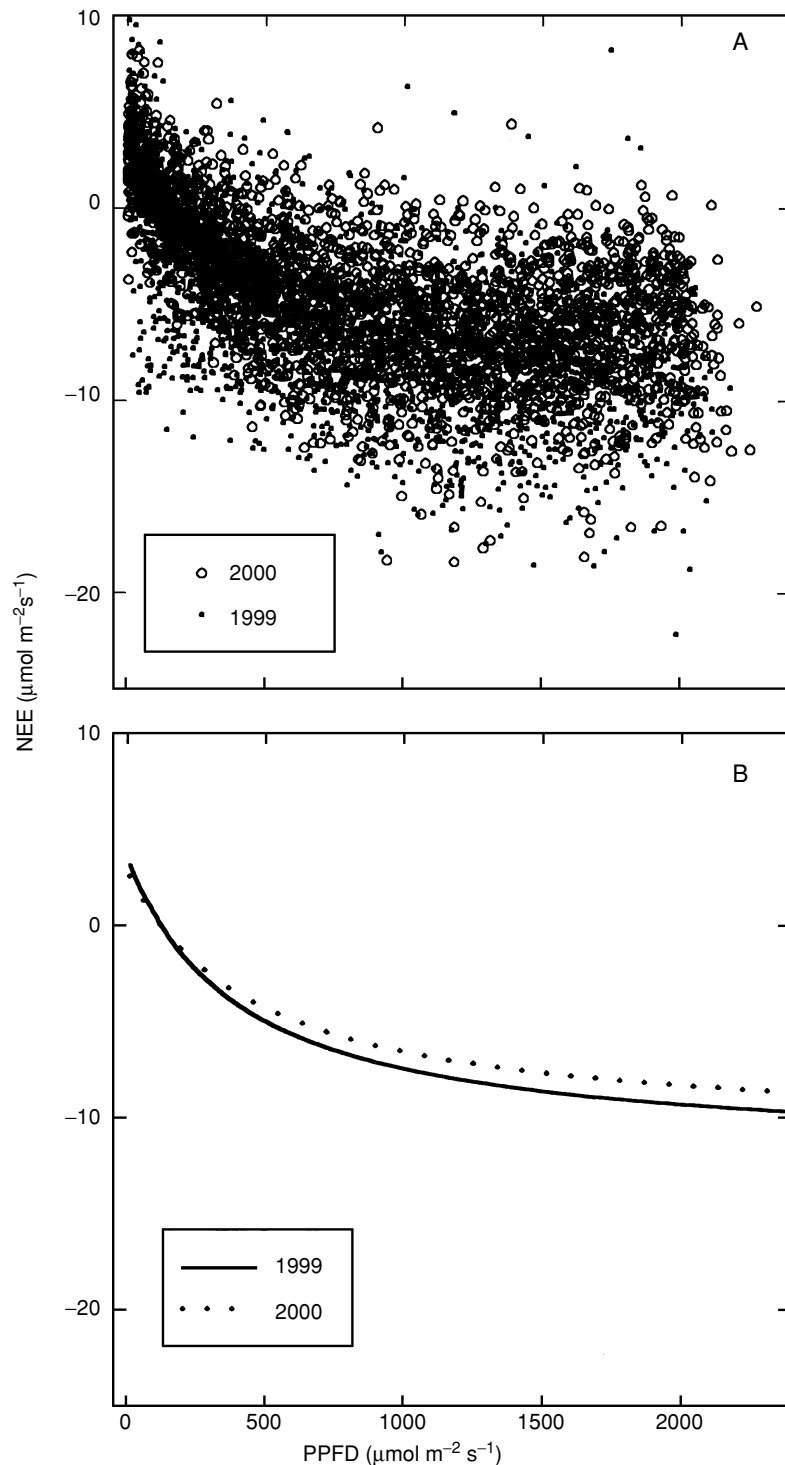
Fig. 9 Ten-day averages for 2000 of net radiation (Rn), sensible heat exchange (H; open symbols), latent heat exchange (LE; closed symbols), and NEE as a function of hour of day for the first 10 days of June (panels A–C), July (panels D–F), and August (panels G–I).
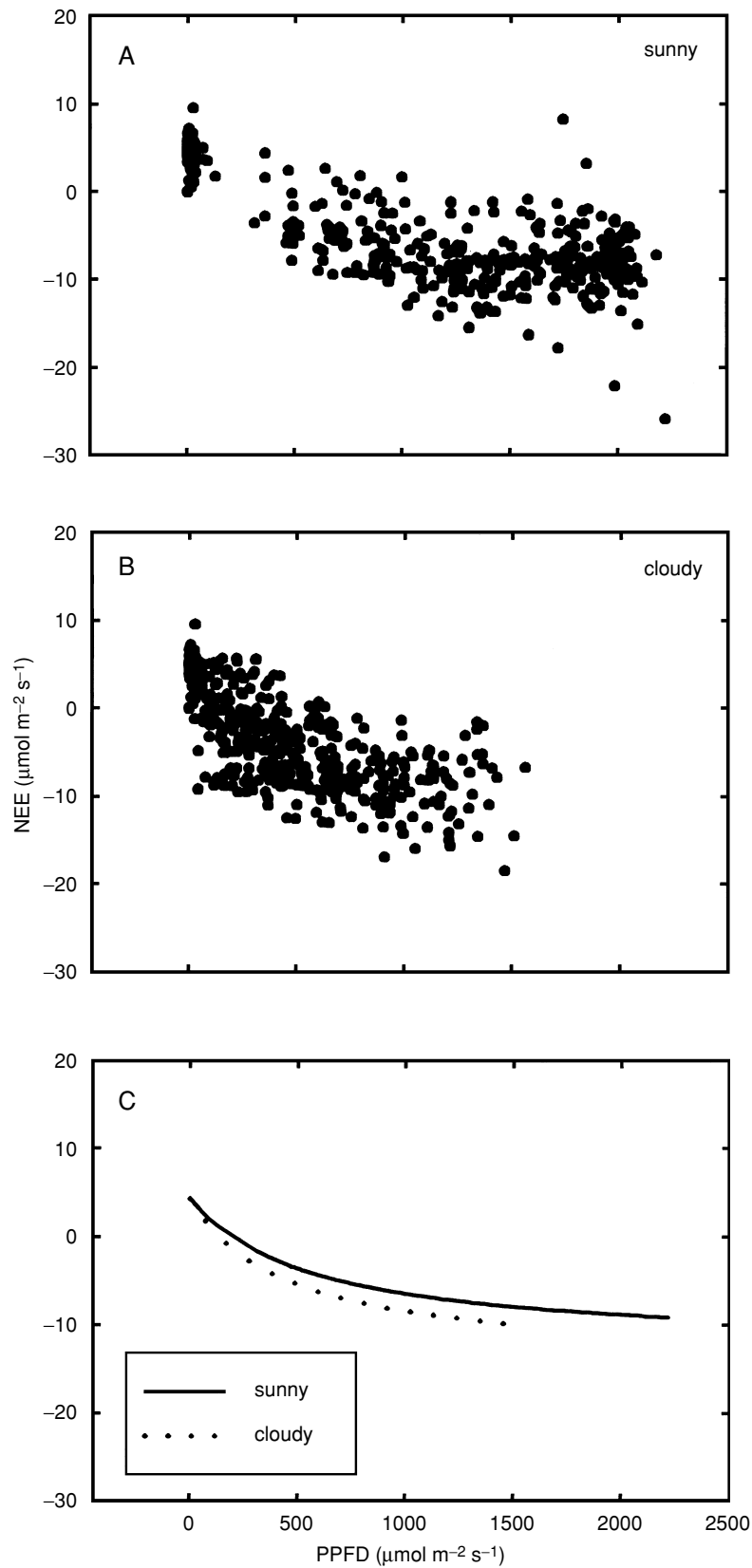
Fig. 10 (A) The dependence of 30-min averages for NEE on the 30-min averages for photosynthetic photon flux density (PPFD) during the growing season (days with daily integrated negative NEE values) for both years of the study. B. The best-fit nonlinear relationships for the data presented in the upper panel for both years of the study. The equation describing the 1999 relationship is NEE = [(− 0.038 PPFD 15.5)/(15.5 + 0.038 PPFD)] + 3.57, with an associated $r^2 = 0.79$; and the equation describing the 2000 relationship is NEE = [(− 0.030 PPFD 13.8)/ (13.8 + 0.030 PPFD)] + 2.9, with an associated $r^2 = 0.81$.

slightly greater in 2000 at 131 cm than in 1999 at 113 cm), it is the timing of the melt that most differed. It appears that total forest carbon sequestration is greater with a snowpack that lasts later into the growing season, rather than when a warm-up occurs that melts the snowpack earlier in the growing season.

It is clear that the timing of the spring warm-up will have a different impact on carbon gain by this subalpine forest ecosystem, compared to forest ecosystems that have been observed in past studies. Goulden *et al.* (1996b) observed that a 2-fold range in annual NEE by a north-eastern deciduous forest over a five-year period

Fig. 11 (A) The dependence of 30-min averages for NEE on the 30-min averages for photosynthetic photon flux density (PPFD) measured during the summer (Julian days 180–210) during sunny morning periods (defined as periods when average net radiation was greater than 70% the maximum recorded for the same time of day over the 30-day interval). (B) The same as panel A, but for cloudy morning periods (defined as periods when average net radiation was less than 70% the maximum recorded for the same time of day over the 30-day interval). (C) The best-fit nonlinear relationships for the data presented in the upper panels. The equation describing the relationship during sunny periods is NEE = [(− 0.030 PPFD 16.7)/ (16.7 + 0.030 PPFD)] + 4.39; and the equation describing the relationship during cloudy periods is NEE = [(− 0.042 PPFD 18.52)/(18.52 + 0.042 PPFD)] + 4.37.
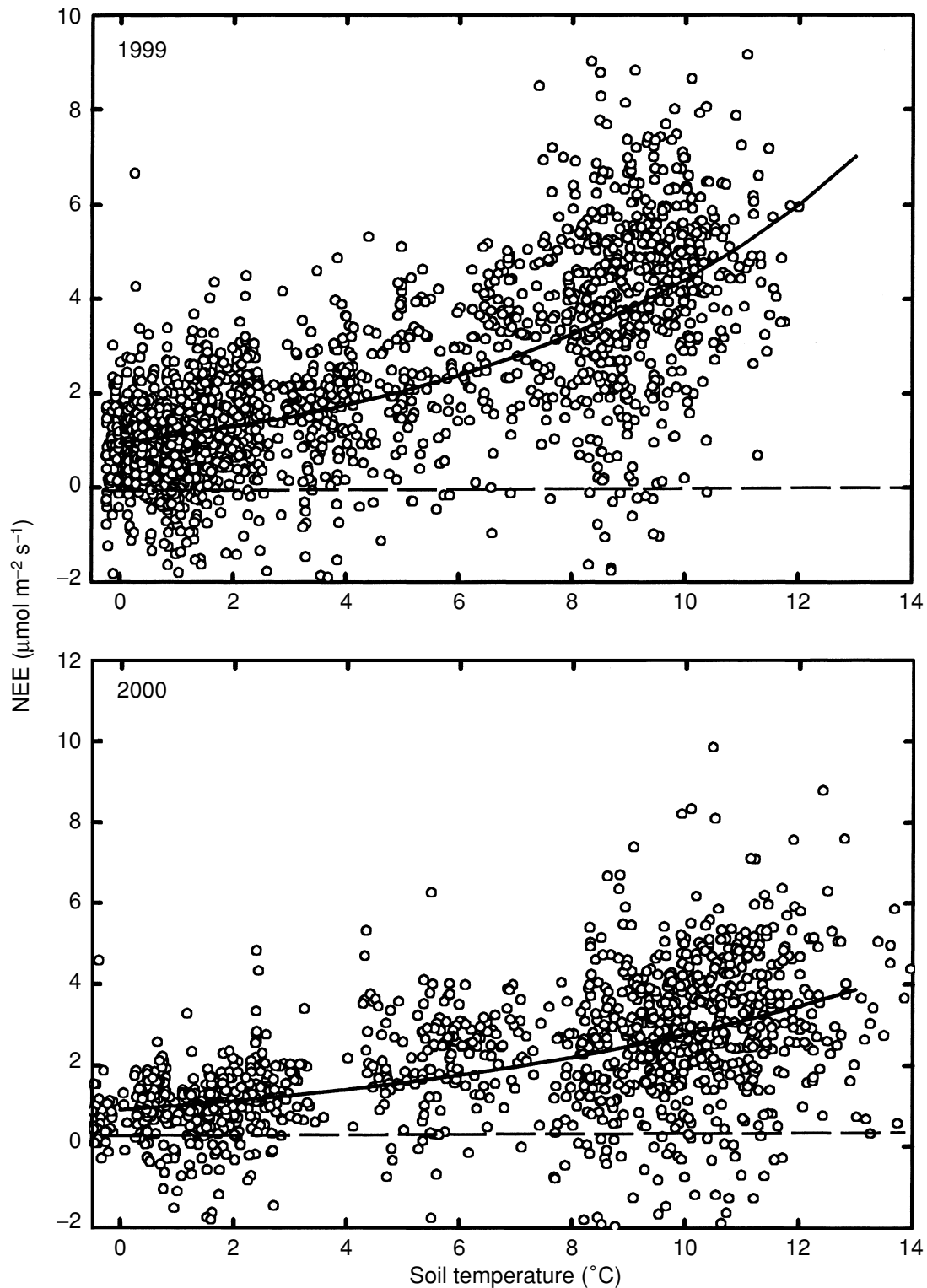
Fig. 12 The relationship between night-time, 30-min average NEE and soil temperature (T_s) (measured at 10 cm depth) observed for the period July–November during both study years. The best-fit functions for each year are NEE = 0.945 exp (0.154 T_s) for 1999 (r^2 = 0.48) and NEE = 0.889 exp (0.113 T_s) for 2000 (r^2 = 0.34).

could be explained in large part by the timing of the spring warm-up and its influence on bud-break and subsequent leaf expansion. As long as summer precipitation was adequate, an earlier warm-up led to earlier leaf expansion and higher rates of annual NEE. A hard summer drought could negate the effects of an early spring warm-up. Chen *et al.* (1999) observed an earlier-than-normal spring warm-up in a boreal, deciduous aspen forest, and documented a 54% increase in annual net carbon uptake. Several years of observations in the same boreal forest showed that those years with the highest annual NEE had the warmest springs with the earliest leaf emergence (Black *et al.* 2000). In these deciduous forest ecosystems, an early spring warm-up allows for large carbon assimilation in leaves that emerge a few weeks earlier-than-normal and which compound the growth they support over the entire season. For these forests, maximum growth and carbon uptake occur during the middle of the summer. Thus, the spring climate is only indirectly connected (through its influence on the timing of spring bud break) to the mid-summer processes that control maximum rates of NEE. In the Niwot Ridge forest, the period of maximum growth and carbon uptake occur during the spring. Thus, the physiological processes that control the maximum rate of NEE are directly coupled to the spring climate, and annual NEE is more dependent on springtime conditions.

At the present time, the springtime cues that cause the forest to switch from the wintertime phase of respiration to the springtime phase of net carbon uptake are unclear. During the springs of 1999 and 2000, we observed that the initiation of springtime net carbon uptake occurred within one to three days of the night-time soil temperature within the first 10 cm rising above 0 °C (data not shown). It is not clear if this is due to a direct response of the trees to warmer soil temperatures, or a response to the seasonal availability of liquid water for night-time rehydration. In both years, carbon sequestration rates were highest during the early part of the growing season, compared to the middle or end of the growing season (Fig. 6). This is due to seasonal dynamics in soil respiration during years with adequate mid-summer moisture (e.g. 1999), and seasonal dynamics in photosynthetic CO_2 uptake during years with inadequate mid-summer moisture (e.g. 2000). During the first 30 days of the 1999 growing season, snow continued to cover the ground, and soil respiration rates were suppressed (Fig. 8). Following snow melt, ecosystem respiration rates increased and forest NEE declined. Daytime rates of CO_2 uptake were similar before and after snowmelt, leading to the conclusion that higher night-time respiration rates after snowmelt are responsible for the observed mid-summer reductions in NEE. In 2000, a pronounced mid-summer drought prohibited soil respiration rates

from increasing above early season values, but mid-day CO_2 uptake was reduced. Mid-day sap flow and stomatal conductance in *Abies lasiocarpa* and *Pinus contorta* have been observed to be significantly reduced during summer droughts in the subalpine forest of Wyoming (Pataki *et al.* 2000). Thus, two different mechanisms function to curtail the high rates of early season NEE as the growing season progresses. If mid-summer rains are adequate, night-time soil respiration rates increase after snow melt and drive down NEE; if mid-summer rains are inadequate, decreases in mid-day photosynthetic CO_2 uptake drive down NEE.

Once the forest begins sequestering carbon in the early summer, day-to-day variation in NEE can be substantial (Fig. 6). Much of the variation is due to the changeable weather typical of high elevation ecosystems. Convective, summertime thundercells develop on a routine basis in the late-morning and early afternoon, especially after cool, clear mornings. The timing of these convective events, which often bring darkened skies and rain, can significantly reduce NEE (Fig. 10). Additionally, during some midsummer periods synoptic, upslope storms affect the site for an entire day or more. These storms cause cool temperatures and are characterized by dark, thick clouds that persist throughout the day. During such periods, the cold air temperatures and low PPFD reduce daytime photosynthesis to a minimum; but relatively warm soil temperatures maintain soil respiration rates near maximum. The result is that the daily integrated NEE can be positive, indicative of a net carbon loss (see the dates encircled by the ellipse in Fig. 6). There were no significant correlations between the amount of daily precipitation and the magnitude of daily integrated NEE the following day (data not shown). It is likely that the observed day-to-day variation in NEE is more due to variation in air temperature and PPFD than variation in precipitation.

Though heavy clouds can reduce photosynthesis, and lead to overall lower rates of carbon sequestration, the diffuse photon flux that occurs during cloudy weather enhances the photon-utilization efficiency of CO_2 uptake (Fig. 11). This effect has been observed in past studies of coniferous forests (Goulden *et al.* 1997) and deciduous forests (Gu *et al.* 1999), and is presumably due to deeper penetration of PPFD into the canopy. In our study, the relationship between NEE and PPFD at the lowest portion of the response curve was derived from morning observations. Thus, a higher apparent quantum yield (initial slope) for cloudy mornings is indicative of greater dispersion of the photon flux, which is delivered to the forest from more angles than would occur with a collimated photon flux. This drives higher photosynthesis rates in west-facing portions of the trees that would normally be shaded on clear mornings. When NEE was

analysed as a function of all PPFD data (diffuse and direct; Fig. 10), there was some indication that residuals for data for the highest PPFD's fell below the regression lines more often than data for the moderately high PPFDs. This trend was apparently not strong enough to influence the overall shape of the regression. However, it does indicate some tendency toward decreases in NEE at the highest PPFDs compared to moderately high PPFDs. This may be due to covariance between temperature and PPFD, with the effects of high temperature on NEE being observed at the highest PPFDs.

The results of this study clearly identify dynamics in the timing of the spring snow melt as a primary control over the annual rate of carbon sequestration in this high-elevation subalpine forest. Additionally, the strong influence of mid-summer precipitation on CO_2 uptake rates make it clear that the water supplied by the spring snow melt is a limited seasonal resource, and summer rains are critical for sustaining high rates of annual carbon sequestration. At the present time, it is unclear how the timing of the spring warm-up and the intensity of summer droughts will respond to future climate change. Past experiments that relied on artificial warming in a montane meadow ecosystem demonstrated that climate warming could significantly change the timing of the spring snow melt, its interaction with summer moisture, and their effects on ecosystem carbon exchange (Saleska *et al.* 1999). The resolution of such responses would appear to be a crucial issue in understanding the response of ecosystems to future warming. Future research at the Niwot Ridge site will aim to better understand the physiological processes that are most affected by the timing of the spring warm-up, the interannual nature of the warm-up within the context of temperature–snowpack interactions, and the compensatory interactions of snow melt dynamics and mid-summer precipitation events.

References

Anthoni PM, Law BE, Unsworth MH (1999) Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem. *Agricultural and Forest Meteorology*, **95**, 151–168.

Baldocchi DD, Vogel CA, Hall B (1997) Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agricultural and Forest Meteorology*, **83**, 147–170.

Black TA, Chen WJ, Barr AG, Arain MA, Chen Z, Nesic Z, Hogg EH, Neumann HH, Yang PC (2000) Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters*, **27**, 1271–1274.

Bubier JL, Crill PM, Moore TR, Savage K, Varner RK (1998) Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex. *Global Biogeochemical Cycles*, **12**, 703–714.

Carey EV, Sala A, Keane R, Callaway RM (2001) Are old forests underestimated as global carbon sinks? *Global Change Biology*, **7**, 339–344.

Chen WJ, Black TA, Yang PC, Barr AG, Neumann HH, Nesic Z, Blanken PD, Novak MD, Eley J, Ketler RJ, Cuneca A (1999) Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. *Global Change Biology*, **5**, 41–53.

Foken Th, Wichura B (1995) Tools for quality assessment of surface-based flux measurements. *Agricultural and Forest Meteorology*, **78**, 83–105.

Goldstein AH, Hultman NE, Fracheboud JM, Bauer MR, Panek JA, Xu M, Qi Y, Guenther AB, Baugh W (2000) Effects of climate variability on the carbon dioxide, water and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA). *Agricultural and Forest Meteorology*, **101**, 113–129.

Goulden ML, Daube BC, Fan S-M, Sutton DJ, Bazzaz A, Munger JW, Wofsy SC (1997) Physiological responses of a black spruce forest to weather. *Journal of Geophysical Research*, **102**, 28,987–28,928,996.

Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC (1996a) Measurements of carbon sequestration by long-term eddy covariance: Methods and a critical evaluation of accuracy. *Global Change Biology*, **2**, 169–182.

Goulden ML, Munger JW, Fan S-M, Daube BC, Wofsy SC (1996b) Exchange of carbon dioxide by a deciduous forest: Response to interannual climate variability. *Science*, **271**, 1576–1578.

Goulden ML, Wofsy SC, Harden JW, Trumbore SE, Crill PM, Gower ST, Fries T, Daube BC, Fan S-M, Sutton DJ, Bazzaz FA, Munger JW (1998) Sensitivity of boreal forest carbon balance to soil thaw. *Science*, **279**, 214–217.

Grace J, Lloyd J, McIntyre J, Miranda AC, Meir P, Miranda HS, Nobre C, Moncrieff J, Massheder J, Malhi Y, Wright I, Gash J (1995) Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia, 1992–93. *Science*, **270**, 778–780.

Granier A, Ceschia E, Damesin C, Dufrene E, Epron D, (and 9 others) (2000) The carbon balance of a young beech forest. *Functional Ecology*, **14**, 312–325.

Greco S, Baldocchi DD (1996) Seasonal variations of CO_2 and water vapor exchange rates over a temperate deciduous forest. *Global Change Biology*, **2**, 183–197.

Gu LH, Fuentes JD, Shugart HH, Staebler RM, Black TA (1999) Responses of net ecosystem exchanges of carbon dioxide to changes in cloudiness: Results from two North American deciduous forests. *Journal of Geophysical Research*, **104**, 31,421–31,431,434.

Hollinger DY, Kelliher FM, Schulze ED, Bauer G, Arneth A, (and 10 others) (1998) Forest-atmosphere carbon dioxide exchange in eastern Siberia. *Agricultural and Forest Meteorology*, **90**, 291–306.

Jarvis PG, Massheder JM, Hale SE, Moncrieff JB, Rayment M, Scott SL (1997) Seasonal variation of carbon dioxide, water vapor and energy exchanges of a boreal black spruce forest. *Journal of Geophysical Research*, **102**, 28953–28966.

Kaimal JC, Finnigan JJ (1994) Atmospheric Boundary Flows: *Their Structure and Measurement*. Oxford University Press, New York.

Malhi Y, Nobre AD, Grace J, Kruijt B, Pereira MGP, Culf Scott S (1998) Carbon dioxide transfer over a central Amazonian rain forest. *Journal of Geophysical Research*, **103**, 31593–31612.

Pataki DE, Oren R, Smith WE (2000) Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology*, **81**, 2557–2566.

Potvin C, Lechowicz MJ, Tardif S (1990) The statistical analysis of ecophysiological response curves obtained from experiments involving repeated measures. *Ecology*, **71**, 1389–1400.

Saleska SR, Harte J, Torn MS (1999) The effect of experimental ecosystem warming on CO_2 fluxes in a montane meadow. *Global Change Biology*, **5**, 125–141.

Schotanus P, Nieuwstadt FTM, DeBruin HAR (1983) Temperature measurement with a sonic anemometer and its application to heat and moisture fluxes. *Boundary Layer Meteorology*, **26**, 81–93.

Schuepp PH, Leclerc MY, MacPherson JI, Desjardins RL (1990) Footprint predictions of scalar fluxes from analytical solutions of the diffusion equation. *Boundary Layer Meteorology*, **50**, 353–373.

Smith WK, Knapp AK (1990) Ecophysiology of high elevation forests. In: *Plant Biology of the Basin and Range, Ecological Studies*, Vol. 80. (eds Osmond CB, Pitelka LF, Hidy GM), pp. 87–142. Springer-Verlag, Berlin.

Valentini R, Matteucci G, Dolman AJ, Schulze E-D, Rebmann C, (and 25 others) (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

Webb EK, Pearman GI, Leuning R (1980) Correction of flux measurements for density effects due to heat and water vapor transfer. *Quarterly Journal of the Royal Meteorological Society*, **106**, 85–100.