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Agricultural and Forest Meteorology 95 (1999) 151–168

AGRICULTURAL
AND
FOREST
METEOROLOGY

Carbon and water vapor exchange of an open-canopied ponderosa pine ecosystem

Peter M. Anthoni[a,*], Beverly E. Law[b], Michael H. Unsworth[c]

[a]*College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA*
[b]*Department of Forest Science, Oregon State University, Corvallis, OR 97331, USA*
[c]*College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA*

Received 19 October 1998; received in revised form 10 March 1999; accepted 12 March 1999

Abstract

Eddy covariance measurements of carbon dioxide and water vapor exchange were made above a ponderosa pine (*Pinus ponderosa* Dougl. ex P. and C. Laws.) forest located in a semiarid environment in central Oregon. The stand is a mixture of old-growth and young trees. Annual net carbon gain by the ecosystem (NEE) was 320 ± 170 gC m^{-2} year^{-1} in 1996 and 270 ± 180 gC m^{-2} year^{-1} in 1997. Compared to boreal evergreen forest at higher latitudes, the pine forest has a substantial net carbon gain (150 ± 80 gC m^{-2} year^{-1} in 1996 and 180 ± 80 gC m^{-2} year^{-1} in 1997) outside the traditionally defined growing season (from bud swell in early May (Day 125) to partial leaf-off in late September (Day 275)). Carbon assimilation continued to occur in the relatively mild winters, though at a slower rate (April, maximum leaf level assimilation ($A_{\max}$) of 6–9.5 μmol m^{-2} leaf s^{-1}), and ecosystem respiration was relatively low (~1.6 ± 0.1 gC m^{-2} day^{-1}). In the growing season, although photosynthetic capacity was large (July, $A_{\max} = 16$–21 μmol m^{-2} leaf s^{-1}), carbon assimilation was constrained by partial stomatal closure to maintain a sustainable water flow through the soil-plant system, and ecosystem respiration was large (3.5 ± 0.1 and 4.3 ± 0.1 gC m^{-2} day^{-1} in growing season of 1996 and 1997, respectively) because of high air and soil temperatures. Despite large changes in evaporative demand over just a few days (VPD changing from 0.5 to 3.5 kPa), the ecosystem water use was remarkably constant in summer (~1.6–1.7 mm day^{-1}). Such homeostasis is most likely another result of stomatal control. Interannual variations in climate had a large influence on the ecosystem carbon balance. In summer 1997, an El Niño year, precipitation was more frequent (17 days with 33 mm of rain) than in summer 1996 (5 days with 5 mm of rain), and the net ecosystem exchange was substantially lower in July to September 1997 (10 ± 60 gC m^{-2}) than during the equivalent period in 1996 (100 ± 60 gC m^{-2}). Although temperatures between years were similar, the carbon assimilation in 1997 was offset by increased respiration, probably because soils were more frequently wet, encouraging microbial respiration.

Keywords: Eddy covariance; Evapotranspiration; Micrometeorology; Net primary production; Net ecosystem exchange; *Pinus ponderosa*

1. Introduction

As part of the National Aeronautics and Space Administration (NASA)-supported Cooperative Spatial Energy and Carbon Transfer (COSPECTRA)

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[*] Corresponding author. Tel.: +1-541-737-2996; fax: +1-541-737-2540; e-mail: panthoni@oce.orst.edu

PII: S0168-1923(99)00029-5

project, ecosystem carbon and water vapor flux and related biological and microclimate factors have been measured since March 1996 in a ponderosa pine (*Pinus ponderosa* Dougl. ex P. and C. Laws.) forest in central Oregon. Ponderosa pine is the most widely distributed and common pine in North America (Whitney, 1985). *P. ponderosa* ecosystems are generally open-canopied and have low leaf area index (LAI; m^2 half-surface leaf area per m^2 ground). The forest at our site has been managed by controlled understory burns, resulting in a sparse understory. For such open-canopied ecosystems, larger fractions of the whole ecosystem energy and carbon fluxes originate from the soil surface than in systems with high LAI (Baldocchi and Vogel, 1996). The processes controlling the energy and carbon exchange in open-canopied ecosystems must be understood, both to predict the influences of climate on hydrology and productivity, and to improve atmospheric models relating exchange to surface conditions (Huntingford et al., 1995; Sun and Mahrt, 1995).

Ponderosa pine forests in central Oregon experience wet, cold winters and dry, hot summers, so large seasonal differences in energy partitioning and water use are expected. Runyon et al. (1994) suggested that a *P. ponderosa* forest close to our site was potentially capable of gaining carbon throughout the year, but that net primary production was limited by periods of stomatal closure resulting from freezing, drought, or high vapor pressure deficits (VPD). Recently, Law et al. (1999b) reported that high temperatures in summer at our site resulted in large respiration rates from trees and soil. The combination of reduced carbon assimilation (because of stomatal closure) and increased respiration could lead to net ecosystem loss of carbon to the atmosphere in the dry season (July to September). Conditions for net carbon gain may be more favorable during the wetter spring and fall when soil temperatures and water stress are moderate.

P. ponderosa forests growing in semiarid environments are widely thought to use water efficiently. But in hot summer conditions, a delicate balance must be achieved between conserving water and avoiding damage from foliage overheating and xylem cavitation (Sperry, 1995; Mencuccini and Grace, 1996; Ryan and Yoder, 1997). Understanding how this balance is achieved at the ecosystem scale is important for improving models that link carbon and water relations.

The aims of this research were (1) to determine how net ecosystem exchange (NEE) of CO_2 and whole ecosystem water vapour exchange (LE) respond to environmental factors (e.g., radiation and VPD); (2) to compare the annual carbon balance derived from eddy covariance and associated measurements with values deduced from mensuration and respiration estimates; and (3) to improve understanding of factors controlling the long-term carbon and water vapor exchange of this semiarid ecosystem.

2. Methods

2.1. Site description

We made measurements above and below the canopy of an old-growth ponderosa pine forest located in a USDA Forest Service Research Natural Area (RNA) in the Metolius River basin, Oregon (44°29′ 56″ N, 121°37′ 25″ W, elevation 941 m). The fetch is uniform for several kilometers in the most common wind directions (south, west, and north). A forested north–south ridge lies about 1 km to the east of the site, with a rise in elevation of ~400 m. The forest has a very open canopy (LAI = 1.6; Law et al., 1999b), typical of this region. The stand includes areas with widely spaced old-growth trees (~250 years old and 33 m in height), patches of young trees (~45 years old and 9 m in height), and mixed-age stands (stand structural data are summarized in Table 1; Law et al., 1999b). The understory consists primarily of bitterbrush (*Purshia tridentata*), strawberry (*Fragaria vesca*) and patches of bracken fern (*Pteridium aquilinum*). The understory LAI was 0.16 in summer 1996 (Law et al., 1999a). The sandy loam soils are classified

Table 1
Mean characteristics of the dominant old trees and patches of young trees at the site (standard errors in parentheses)

	Old trees	Young trees
Age of trees (year)	250	45
Trees per hectare	70	550
Tree height (m)	33 (0.8)	9 (0.2)
Diameter at breast height (cm)	63 (2.7)	12 (0.2)
Sapwood volume (m^3 sapwood per hectare)	293 (3)	37 (0.1)

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2.2. *Eddy covariance measurements*

Carbon and energy flux measurements were made with the eddy covariance technique (Baldocchi et al., 1988) from a tower at a height of 47 m, about 14 m above the dominant trees. The exchange rates of carbon dioxide (F_c), latent heat (LE) and sensible heat (H) were estimated following methods by Baldocchi and Vogel (1996). Wind speed and virtual temperature were measured with a three-dimensional sonic anemometer (model 1012 R2, Gill Instruments, Lymington, England). An open-path, infrared gas analyzer (IRGA) (Auble and Meyers, 1992) measured CO_2 and water vapor fluctuations. Half-hour eddy covariances and statistics were computed online from ~10 Hz raw data, but these values were also stored for further analysis. Above-canopy fluxes were rotated to allow interpretation of the exchange rates normal to the streamlines following the local terrain. Appropriate corrections for cross-wind contamination of virtual temperature (Schotanus et al., 1983) and air density fluctuations (Webb et al., 1980) were applied. In the following sections, F_c, LE, and H are reported as positive if directed away from the surface. A positive value for net radiation (R_n) indicates a net flux of energy to the surface.

Flux measurements started on 23 March 1996. Data acquisition during winter was limited to two campaigns (Days 9–37 and 74–114) in 1997, because power supplied from solar panels was low. Data acquisition was generally continuous from April to November in both years, with a few data gaps caused by instrument problems.

2.3. *Climate measurements*

Fig. 1 shows daily aggregated weather variables for 1996 and 1997. Above-canopy meteorological measurements were recorded at the top of the tower, using a Campbell Scientific Inc. (CSI) datalogger (model CR10X, CSI, Logan, UT). Above-canopy R_n was measured with a net radiometer (model Q7, REBS, Seattle, WA), deployed from the south side of the tower. Downward global solar (S_r) and photosynthetically active radiation (PAR) were measured with radiation sensors (model LI-200SZ and LI-190SZ, respectively, LI-COR Inc, Lincoln, NE). Air temperature (T_a) and relative humidity (RH) were measured with a thermistor and capacitive RH sensor probe (model HMP35C, Vaisala, Helsinki, Finland). Wind speed and direction were monitored with a Wind Sentry set (model 03001, RM Young, Traverse City, MI).

Various other measurements were recorded below the canopy using CSI dataloggers (models CR10 and 21X, CSI, Logan, UT). T_a and RH were measured at 1 and 8 m with HMP35C sensors (Vaisala, Helsinki, Finland). Soil heat flux was measured at 0.02 m depth with four heat flux plates (model HFT-3, REBS, Seattle, WA). Spatial variation of soil temperature was measured at 18 locations with thermocouple probes at depths of 15 cm. Sapwood temperatures were measured in six trees with thermocouples placed about 2 cm into the sapwood at 1.5 m height. The rate of change in T_a, water vapor density, and sapwood temperature in the canopy layer was used to calculate change in energy storage (S).

Rainfall was measured with tipping-bucket rain gauges (model TE525MM, CSI, Logan, UT), above and below the canopy. Soil water content (SWC) was monitored continuously in the upper 30 cm of soil with two soil water content sensors (model CS615, CSI, Logan, UT). The spatial variation of SWC was measured periodically (at 15 locations in 1996 and 3–5 locations in 1997) using time-domain reflectometry (TDR) (model 1502, Tektronix, Beaverton, OR). The TDR sampling rods were placed vertically in the soil to depths of 30 and 100 cm.

2.4. *Carbon dioxide storage and vertical mass-flow term*

The rate of change in carbon dioxide (F_{stor}) stored in the canopy air-layer was calculated from CO_2 profile measurements. Half-hour mean CO_2 concentrations at four heights (1, 8, 31, and 46 m) were measured with a IRGA (model LI-6262, LI-COR, Lincoln, NE). The trend in the CO_2 concentration at each height over time was computed with a smoothing algorithm using running medians (S-PLUS, Mathsoft, Seattle, WA; Tukey, 1977). The value of F_{stor} below the eddy covariance system was then calculated by

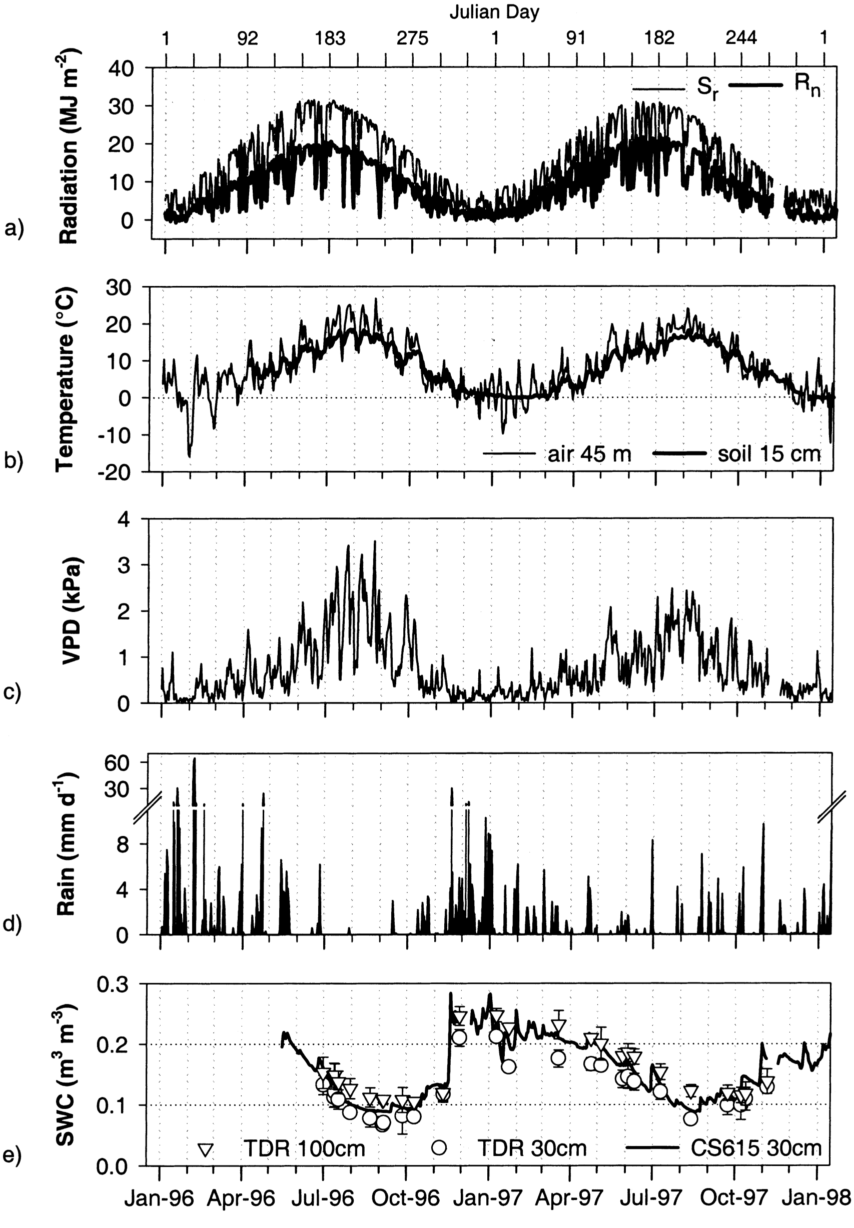

Fig. 1. (a) Daily above-canopy global solar (S_r) and net radiation (R_n), (b) mean daily above-canopy air temperature and soil temperature at 15 cm, (c) mean daylight above-canopy vapor pressure deficit (VPD), (d) daily total rainfall, and (e) mean soil water content (SWC) measured by TDR and CS615 sensor systems of the upper 30 and 100 cm soil layer for 1996 and 1997.

interpolating the CO_2 concentration trends in 1 m intervals and summing the change with time over all layers. During periods when the CO_2 profile system was not operational, the rate of change of the CO_2 signal of the eddy covariance IRGA, located above the canopy, was used to estimate F_{stor}.

The influence of vertical mass flow term (F_v) arising from horizontal flow divergence/convergence, resulting in a non-zero mean vertical velocity at the height of the flux observation was assessed following methods presented by Lee (1998). The mass-flow term was then added to the carbon dioxide flux, which was rotated to be normal to the plane defined by the horizontal velocity vector and the predicted mean vertical velocity.

2.5. Data screening

A data-screening procedure was used to remove possible eddy covariance instrumentation and sampling problems. The screening consisted of removal of periods with (1) kurtosis greater than 10 for wind speeds, IRGA CO_2 and H_2O signal, and virtual temperature; (2) excessive spikes in the sonic and IRGA data (due to precipitation, moisture or rime-frost on the sensors); (3) rainfall; (4) signals outside specified instrument limits; and (5) incomplete sampling over the entire half hour. Fluxes were also rejected when unreasonably large CO_2 fluxes ($|F_c| > 25\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$) were observed. After screening, about 75% of the above-canopy carbon fluxes and 85% of the energy fluxes remained available for further analysis.

2.6. Ecosystem respiration calculated from scaled-up chamber measurements

Ecosystem respiration (R_e) of CO_2 was estimated from scaled-up chamber measurements of fluxes from the soil surface, tree stems and foliage. Temperature response equations were developed for soil surface CO_2 flux (F_s), wood (F_w), and foliage (F_f) respiration (Law et al., 1999b). We extended the analysis for 1997 by determining separate F_s equations for 1996 and 1997 from soil chamber measurements in each year, because F_s accounted for 75% of R_e, and different environmental conditions in the two years may have influenced root phenology and microbial activity. Good agreement was found between F_s and CO_2 flux measurements made seasonally in 1996 and 1997 with an eddy covariance system set up above the forest floor (Law et al., 1999a). The temperature response equations for F_w and F_f from 1996 were used in 1997. Half-hourly respiration rates were calculated from continuously measured temperature data and R_e was calculated by summing the respiration rates from soil, wood, and foliage.

2.7. Net ecosystem exchange from eddy covariance

Daytime (sunrise until sunset) NEE was calculated from eddy covariance measurements. At night, the sum $F_c + F_{stor}$ did not compare well to independent R_e estimates from scaled-up chamber measurements for calm (friction velocity, $u_* \leq 0.25\ \text{m s}^{-1}$) and more turbulent ($u_* > 0.25\ \text{m s}^{-1}$) wind conditions (Law et al., 1999b). Under calm conditions, change in CO_2 storage alone compared well with R_e, probably because F_c is negligible (Law et al., 1999a). At sufficiently high wind speeds, the above-canopy F_c may be expected to give a good estimate of the night-time CO_2 exchange (Grelle, 1997), but these conditions seldom occur at our site. As an alternative to $F_c + F_{stor}$, we used night-time ecosystem respiration calculated from the scaled-up chamber measurements to estimate night-time NEE. Apparently, our night-time $F_c + F_{stor}$ would probably lead to an underestimation of night-time NEE during more turbulent conditions. During calm conditions F_{stor} could be used as an estimator for R_e at our site, but the CO_2 profile system was operated only occasionally from fall through spring, because of its high power consumption. The NEE calculated by micrometeorological methods and scaled-up chamber respiration will be referred to as NEE_m. An ecological sign convention is used for NEE, where positive NEE signifies a net gain of carbon by the ecosystem and negative NEE indicates that carbon is being lost to the atmosphere (Note: this is the reverse of the sign convention used for F_c).

For estimating annual NEE_m, missing days and screened-out data were filled in according to an empirical relationship, based on the light response of carbon assimilation (A_c), estimated by the difference between measured F_c and R_e from scaled-up chamber data, versus PAR of ∼±20 surrounding days for times with low VPD. The reduction of A_c at high VPD was estimated by linear regression of the residual of A_c after accounting for the radiation dependence. Predicted net carbon flux (F_{cp}) was then calculated as

$$F_{cp} = \left(\frac{P_{max} \cdot \text{PAR}}{K_m + \text{PAR}}\right) + (a_0 + a_1 \cdot \text{VPD}) + R_e \quad (1)$$

where P_{max} and K_m are empirically determined light-response parameters, and a_0 and a_1 are the VPD regression coefficients. The methods used to determine the model parameters are described in more detail in Appendix A. During the growing season, about 11% and 39% of missing $\mathrm{NEE_m}$ values were filled-in with F_{cp} in 1996 and 1997, respectively. About 65% and 60% of $\mathrm{NEE_m}$ values during the dormant season in 1996 and 1997, respectively, had to be filled-in using the empirical relationship.

2.8. Uncertainty assessment

Moncrieff et al. (1996) discussed random and systematic sources of errors in long term flux measurements. We evaluated possible systematic errors in our flux measurements. Uncertainties in the calibration of the gas analyzer due to calibration gases, which were compared to a NIST traceable calibration gas, were estimated to be about ±3%. Uncertainties from changes in the analyzer calibration due to dirt and residue build up on the IRGA optics was estimated as ∼±5–10% by the relative change in the calibration coefficients from one calibration to the next. Instabilities in calibration coefficients due to diurnal variation in temperature and pressure are difficult to quantify, but are assumed to be less than 5%. Uncertainties in wind speed and virtual temperature measured by the sonic anemometer result in ∼±2% uncertainty in scalar fluxes (Grelle, 1997). Combining all of the systematic errors geometrically, the overall uncertainty of the daytime carbon dioxide flux was ∼±12%.

The systematic error in R_{e} estimated by the chamber method includes uncertainties in respiration measurements and in biomass estimates used for scaling respiration to the stand level. The uncertainty in R_{e} was estimated as ∼±20% of the mean R_{e} (Law et al., 1999b) by recalculating respiration rates with the upper and lower confidence intervals (95%) for respiration rates, biomass and LAI.

2.9. Net ecosystem exchange from mensuration measurements

Net ecosystem exchange ($\mathrm{NEE_p}$) can be calculated from net primary production (NPP) and heterotrophic respiration (R_{h}),

$$\mathrm{NEE_p} = \mathrm{NPP} + R_{\mathrm{h}} \tag{2}$$

with the sign convention that positive NPP indicates net production of carbon and negative R_{h} means a loss of carbon by the ecosystem. NPP was estimated from aboveground wood and foliage production, and belowground root production. Aboveground stemwood production was calculated as the mean annual wood increment estimated from the last 5 years growth rings in wood cores. Foliage production was calculated from the fraction of total foliage biomass that was newly expanded foliage. Details of methods and estimates are given by Law et al. (1999b).

Belowground root production was estimated as 50% of belowground carbon allocation (B) (Ryan, 1991a, b; Law et al., 1999b). According to Raich and Nadelhoffer (1989), B can be calculated from annual soil respiration minus annual litterfall, assuming that soil carbon storage is near steady state. Heterotrophic respiration (R_{h}) was estimated as 50% of B plus surface litter decomposition, calculate from the mean residence time of litter (∼30 years) (Law et al., 1999c).

Uncertainty in $\mathrm{NEE_p}$ arises from uncertainties in: (1) estimates and scaling of production and respiration measurements to the stand level; (2) calculation of belowground root production and R_{h} as a fraction of B; and (3) estimates of wood production for the current year as the mean wood increment of the last 5 years.

2.10. Water vapor exchange

Daily total ecosystem water vapor exchange (LE) was calculated from the measured above-canopy eddy covariance water vapor flux and the change in water vapor concentration in the canopy air-layer, which was estimated from half-hour changes in water vapor concentrations measured within the canopy. Screened-out data during the day were filled in by linear interpolation between neighboring data points.

For estimating an annual water budget, missing days were filled in according to an empirical relationship, based on the Penman–Monteith equation (Monteith and Unsworth, 1990), in which whole ecosystem bulk surface conductance was estimated seasonally (from 6–7 $\mathrm{mm\,s^{-1}}$ in the wet season down to 2–3 $\mathrm{mm\,s^{-1}}$ in the dry season) from measured LE. The IRGA was calibrated periodically with a dew-point generator (LI-610, LI-COR, Lincoln, NE), and instrument performance was checked against measured water vapor density. The overall error in the latent heat exchange due to calibration uncertainties and systematic sonic anemometer errors was estimated to be ∼±15%.

3. Results and discussions

3.1. Energy closure and spectral analysis

Daily energy closure, evaluated as $(H+\mathrm{LE})/(R_n-G-S)$, was usually about 70% ($H+\mathrm{LE}=0.69(R_n-G-S)+0.35\ \mathrm{MJ\ m^{-2}\ day^{-1}}$, $r^2=0.88$, $n=426$), and was relatively independent of wind direction for winds from the most common directions. Closure was lower for winds from the south-east or north and it was generally lower than values reported for other forest ecosystems (∼80–100%; Kelliher et al., 1992; Lee and Black, 1993; Laubach et al., 1994; Fan et al., 1995; Goulden et al., 1996; Blanken et al., 1997; Grelle, 1997; McCaughey et al., 1997). Possible causes of incomplete energy closure are errors and uncertainties in the spatial characterization of net radiation and soil heat flux, or in the detection and measurement of all turbulent and advective energy fluxes. All of these sources of error are likely to occur in open-canopied ecosystems. Large gaps in the canopy result in large spatial variations in soil heat flux and upwelling radiation. At a nearby juniper/sagebrush site with a more open-canopy structure, we estimated the uncertainty in the upwelling radiation due to net radiometer placement above the canopy (Anthoni et al., 1998). We found a spatial range of $\sim 60\ \mathrm{W\ m^{-2}}$ in the upwelling radiation (unpublished data). Because of the differences in tree height and net radiometer placement, the amount of soil or understory 'seen' by the radiometer at the pine site is less than at the juniper site, but differences in the surface properties of the over- and understory cause uncertainty in measurements of net radiation from towers. Above a deciduous forest, Droppo and Hamilton (1973) detected up to 13% difference in midday net radiation when measured simultaneously from towers just 15 m apart. There is also large uncertainty in the absolute calibration of net radiometers. Smith et al. (1997) found a ∼16% range of variation in measured R_n from different net radiometer models.

Blanken et al. (1997) found low values of fractional energy closure over their boreal aspen forest at low wind speeds. Closure increased linearly with u_*, reaching within 20% of unity (perfect closure) when u_* exceeded $0.35\ \mathrm{m\ s^{-1}}$. They suggested that lack of fully developed turbulence at low u_* was partly responsible for lack of closure. A similar problem may occur at our site, where energy closure was better at higher wind speeds (Mahrt, 1998). Horizontal advection of energy seems unlikely to be a significant source of lack of closure, because (a) closure was relatively independent of wind direction and (b) assuming a relatively large horizontal temperature gradient of $1\ \mathrm{K\ km^{-1}}$ and moisture gradient of $1\ \mathrm{g\ kg^{-1}\ km^{-1}}$ with a mean midday wind speed of $2\ \mathrm{m\ s^{-1}}$ would result in an energy transport of less than $10\ \mathrm{W\ m^{-2}}$.

Considering the possible large uncertainties in the estimation of the available energy, we conclude that it is very difficult to judge the validity of eddy covariance measurements in open-canopy ecosystems by testing the energy budget closure.

Spectral analyses of measured turbulent fluctuations were used to determine the reliability of our flux measurements. We generated power and co-spectra of measured fluctuations in vertical wind speed (w), CO_2, H_2O, and virtual temperature (T_v) by averaging the spectral coefficients from eight data segments, each with 4096 data points. The power spectra of w, T_v and H_2O exhibited an inertial subrange with the expected slope of $-2/3$ to about 5 Hz. The inertial subrange with a $-2/3$ slope of the CO_2 power spectra reached about 1 Hz, with higher frequencies showing some random noise. The cospectra between vertical wind speed and T_v, CO_2, and H_2O were nearly identical, indicating similarity of the turbulent transport of these entities. Main contributions to the fluxes were from frequencies less then 1 Hz. Auble and Meyers (1992) used an open-path IRGA of the same design over a fully leafed deciduous forest and found very similar spectra. We conclude that the eddy covariance system recorded nearly all turbulent fluctuations, with only fluctuations of CO_2 and H_2O with frequencies higher than 1 Hz attenuated, most likely as a result of sensor separation between the IRGA and the sonic anemometer.

3.2. Storage and mass-flow corrections of daily NEE

It is common practice to assume horizontal homogeneity in the calculation of NEE by the eddy covariance method. Consequently NEE is the sum of measured eddy CO_2 flux (F_c) and the change in CO_2 concentration below the measurement level (F_{stor}). Lee (1998) pointed out that analysis should also usually include a vertical mass-flow term, F_v, that accounts for possible vertical advection due to a non-zero mean vertical wind component. The often-seen early-morning change in CO_2 concentration has to be accounted for by net plant uptake plus any exchange of CO_2 with the atmosphere, due to either a flush-out event (Grace et al., 1996), a vertical mass-flow F_v, or entrainment of CO_2 from above the boundary layer.

Fig. 3 shows measured and modeled carbon flux components during late summer 1997 for groups of days when especially high or low CO_2 concentrations were encountered at night. For about 40% of the year, relatively turbulent conditions suppressed the build up of respired CO_2 at night (Fig. 2(a)). The rest of the time, calm conditions at night led to a build up of CO_2, and concentrations exceeding 400 ppm were observed within and above the canopy air layer (Fig. 2(b)). Concentrations decreased in the early daylight hours, as was also observed with chamber measurements at the soil surface (425 ppm–350 ppm between 7.30 and 10 am). This decline led to large values of F_{stor} (Fig. 2(d)). To determine whether the estimation of NEE_m as $F_c + F_v + F_{stor}$ is reasonable at our site, we compared NEE_m estimates with potential net plant CO_2 uptake (F_{cp}). F_{cp} was calculated from an empirical model incorporating light and VPD responses (see Eq. (1)), with model parameters determined from $F_c + F_v + F_{stor}$, using only periods when F_{stor} was small ($|F_{stor}| < 2\ \mu mol\ m^{-2}\ s^{-1}$). At night, F_{cp} was assumed equal to the R_e value from the scaled up chamber measurements. On days following nights of a build up of CO_2 in the canopy air space, F_{cp} was substantially more positive than $F_c + F_v + F_{stor}$ for

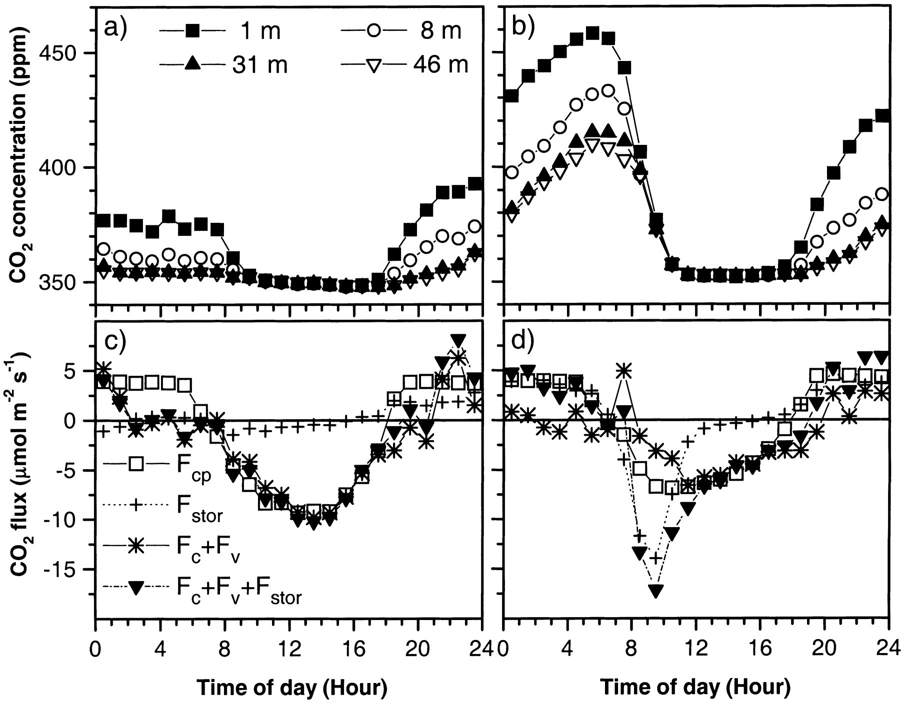

Fig. 2. Mean diurnal CO_2 concentration within (1, 8, and 31 m) and above the canopy (46 m) and measured carbon flux components (F_c, F_v, F_{stor}) and potential net plant CO_2 uptake (F_{cp}; Eq. (1)) during 38 days in late summer 1997. Shown are the average diurnal trends (a, c) for 10 days with more turbulent conditions at night ($u_* \geq 0.175$ m s^{-1}) and (b, d) for 28 days with calm conditions at night ($u_* < 0.175$ m s^{-1}). The carbon flux components are eddy CO_2 flux (F_c), vertical mass flow correction (F_v), and correction for change in CO_2 storage (F_{stor}). F_{cp} was calculated with model parameters determined from $F_c + F_v + F_{stor}$, using only periods when F_{stor} was small ($|F_{stor}| < 2\ \mu mol\ m^{-2}\ s^{-1}$) during the 38 days.

Table 2
Daytime, night-time, and daily total of carbon flux components (F_c, F_v, F_{stor}) and potential net CO_2 uptake (F_{cp}; Eq. (1)) during 38 days in late summer 1997 with and without night-time build up of CO_2 in the canopy air layer[a]

	$F_c + F_v + F_{stor}$ (gC m^{-2})	F_{cp} (gC m^{-2})	F_v (gC m^{-2})	F_{stor} (gC m^{-2})
(a) 10 Days without build up of night-time CO_2 (night-time $CO_2 < 400$ ppm, $u_* \geq 0.175$ m s^{-1})				
Day	−3.2	−3.1	−0.1	−0.3
Night	0.9	1.9	0.3	0.5
Daily total	−2.3	−1.2	0.2	0.2
(b) 28 Days with buildup of night-time CO_2 (night-time $CO_2 \geq 400$ ppm, $u_* < 0.175$ m s^{-1})				
Day	−3.4	−2.1	−0.1	−1.6
Night	1.8	1.8	0.4	1.5
Daily total	−1.6	−0.3	0.3	−0.1

[a] The R_e value calculated from the scaled-up chamber measurements was used to estimate night-time F_{cp}. F_c is eddy CO_2 flux, F_v is vertical mass flow correction, and F_{stor} is correction for change in CO_2 storage. Positive values indicate a net carbon loss and negative values a net carbon gain by the ecosystem.

several hours in the morning (Fig. 2(d)). Night-time values of $F_c + F_v + F_{stor}$ underestimated the scaled-up chamber respiration estimate of R_e for more turbulent nights (Fig. 2(c)), but there was agreement for calm nights (Fig. 2(d)). Daily total, daytime and night-time sums of carbon flux components (F_c, F_v, F_{stor}) and potential net CO_2 uptake (F_{cp}) during days with and without night-time build up of CO_2 in the canopy air layer are shown in Table 2. Using the night-time $F_c + F_v + F_{stor}$ instead of R_e to estimate night-time ecosystem respiration would lead to a substantial overestimation (~1 gC m^{-2} day^{-1}) of daily NEE_m on more turbulent nights. However, incorporating F_v improved the disagreement reported earlier between $F_c + F_{stor}$ and the scaled-up ecosystem respiration estimate R_e at night (Law et al., 1999b). During daytime, the mass-flow term F_v was small (less than 2% of daytime NEE_m) and continuous information for the vertical CO_2 gradient was not available. Therefore, we choose not to apply the mass-flow correction to the daytime eddy CO_2 flux in calculating daily NEE_m.

An unusual feature of our results is the high concentration of CO_2 that built up over substantial depth on calm nights (Fig. 2). Most other sites observe less storage of CO_2. For an Amazonian rain forest Grace et al. (1995a, b, 1996) reported high night-time CO_2 concentrations similar to our observations. After calm nights at their site, there was a consistent morning flush out in the eddy CO_2 flux, which accounted for part of the change in the CO_2 concentration in the canopy air-layer. Consequently the net effect of storage on daily NEE at their site was relatively small. After calm nights at our site, we seldom observed a consistent flush out in the eddy CO_2 flux (Fig. 2(d)). This may be because the vertical CO_2 concentration became well mixed within and above the canopy (Fig. 2(b)) shortly after sunrise. If we assume that the total amount of stored CO_2 is assimilated by the vegetation in the first few hours of the day, our daily estimates of NEE are implausibly large on calm days and disagree both with measured NEE on windier days and with the simple model (F_{cp}).

Other processes (e.g., horizontal advection or entrainment of air from above the boundary layer) could be responsible for the depletion of CO_2 during the early morning hours. In complex terrain, considerable differences in horizontal CO_2 concentrations can be expected. Large spatial variations in the night-time CO_2 concentrations were observed in boreal forests (Baldocchi), which can lead to horizontal advection effects (Sun et al., 1997). A north–south ridge to the east of our site shields the forest around the flux tower from direct radiation for 1–2 h after sunrise, but areas farther west are sunlit earlier. This could lead to localized convective circulation as well as spatial variation in CO_2 exchange; these differences may result in a horizontal gradient in the CO_2 concentration in the early morning hours, but we do not yet have measurements to confirm this.

To avoid the uncertainties in daily NEE_m, when early morning periods included a large F_{stor} ($F_{stor} \leq -2$ μmol m^{-2} s^{-1}), we replaced $F_c + F_v + F_{stor}$ with the predicted F_{cp}. Because model parameters for F_{cp} were determined mainly from periods with low F_{stor}, which are biased toward low CO_2 concentrations, the model may not account for increased assimilation as a consequence of CO_2 'fertilization'. However, a sensitivity analysis conducted using a process-based soil-plant-atmosphere model that incorporates Farquhar's equations (Williams et al., 1996) indicated that F_{cp} might underestimate the true net plant uptake by only about 0.5 μmol m^{-2} s^{-1} during conditions of high CO_2 concentrations (Williams, pers. comm.).

3.3. Environmental constraints on carbon and water vapor exchange

Fig. 3 shows day-to-day variation in NEE, ecosystem respiration, whole ecosystem latent heat exchange, and environmental drivers over a period of 40 days in the summer of 1996. On several occasions during the summer (i.e., Day 201 and 220), weather systems moving over the region from the Pacific Ocean resulted in overcast conditions, cooler air temperatures and lower VPD (Fig. 3((a)–(c)). During those conditions, ecosystem respiration (Fig. 3(d)) decreased because of lower temperatures, and carbon assimilation was high due to less stomatal constraint, resulting in relatively large NEE$_m$ (Fig. 3(e)) by the ecosystem (up to 4 gC m^{-2} day^{-1}). After each weather system passed, T_a and VPD gradually increased, resulting in higher ecosystem respiration and lower carbon assimilation. In consequence, NEE$_m$ declined steadily on successive days, particularly in the afternoon, and after a few days the ecosystem switched from gaining carbon to losing carbon, until the next weather system moved in. During the whole period, LE remained relatively constant at 4–5 MJ m^{-2} day^{-1} (1.6–2.0 mm day^{-1}); only on days with variable radiation did LE show larger variations (Fig. 3(f)).

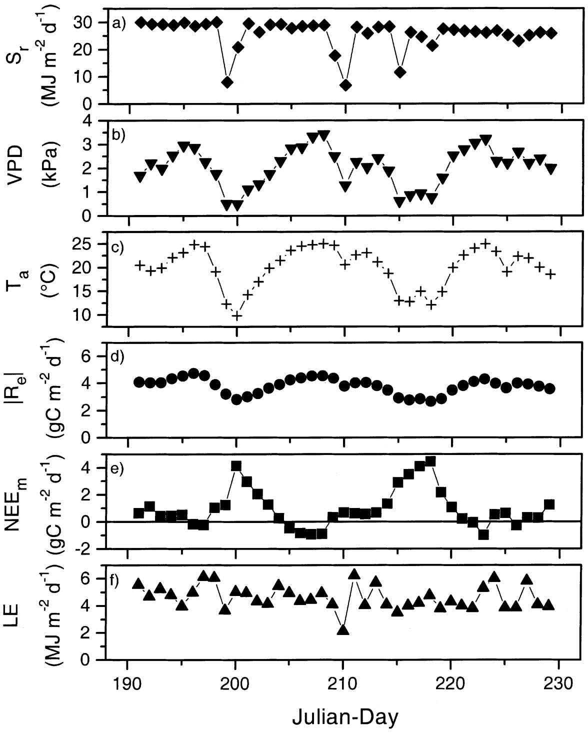

Fig. 3. Day-to-day variations in (a) daily total global solar radiation (S_r), (b) mean daylight vapor pressure deficit (VPD), (c) mean daily air temperature (T_a), and daily total (d) ecosystem respiration (R_e; absolute value of R_e is shown), (e) net ecosystem exchange (NEE$_m$), and (f) whole ecosystem latent heat exchange (LE) during 40 days in summer 1996.

Fig. 4(a) shows the variation of daily NEE$_m$ with VPD for three classes of solar radiation levels. For days with high radiation ($S_r > 20$ MJ m^{-2} day^{-1}), daily NEE$_m$ declined at a rate of 1.5 gC m^{-2} day^{-1} per 1 kPa increase in VPD. Because VPD is positively correlated with temperature, Fig. 4(a) confounds the effects of partial stomatal closure and increased respiration. For example, on high-radiation days, daily R_e (modeled as a function of temperature) increased by about −0.5 gC m^{-2} day^{-1} as VPD increased by 1 kPa, simply due to the accompanying higher temperatures. To remove this respiration response, Fig. 4(b) shows the variation of daily gross ecosystem production GEP (= NEE$_m$ − R_e) with VPD. On days with high radiation, there was a 1 gC m^{-2} day^{-1} decline in GEP per 1 kPa VPD increase. Thus the variation in NEE with increasing VPD was dominated by variation in gross carbon uptake rather than R_e, unlike findings of Jarvis et al. (1997).

Carbon assimilation did not halt at high VPD (>2 kPa), though NEE$_m$ was occasionally negative (indicating that the system was a source of carbon to the atmosphere, Fig. 3(e) and Fig. 4(a)). Fig. 4(b) suggests that on the sunniest days, daily gross carbon exchange was about twice as large when VPD was low (0.5–1 kPa) as it was when VPD was high (>2 kPa). As an exception, there were a few days with high

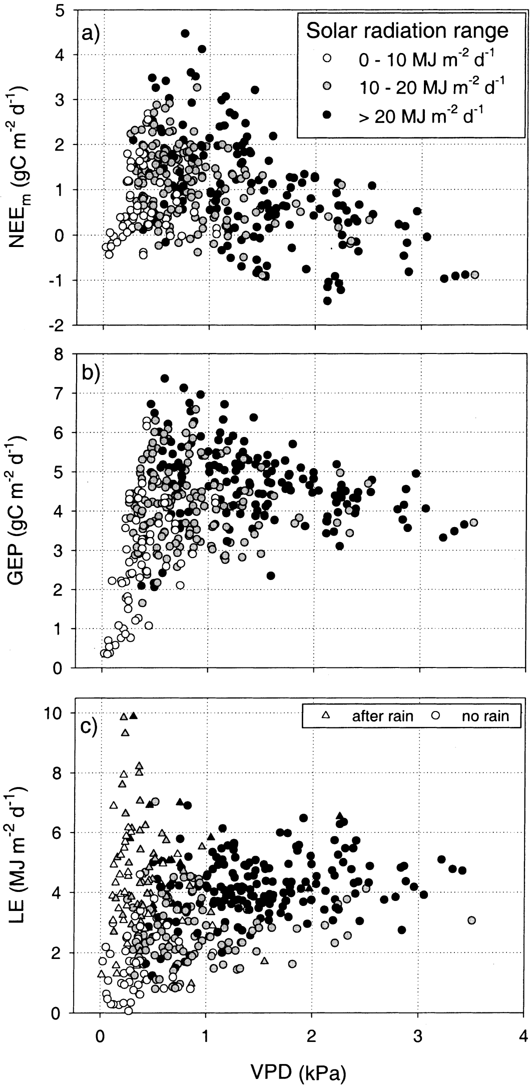

Fig. 4. Daily total (a) net ecosystem exchange ($\mathrm{NEE_m}$) and (b) gross ecosystem production ($\mathrm{GEP} = \mathrm{NEE_m} - R_e$), and (c) whole ecosystem latent heat exchange versus mean daylight above-canopy vapor pressure deficit (VPD) for differing conditions of global solar radiation (symbol shading). (c) Symbol form indicates days with and without rain occurrence.

radiation and low VPD (<1 kPa) when GEP was low. On most of those days, near-freezing night-time temperatures followed by clear sky conditions may have led to photoinhibition, limiting carbon uptake.

In contrast to the reduction of carbon assimilation that occurred when VPD exceeded 1.0 kPa (Fig. 4(b)), daily ecosystem latent heat exchange (LE) showed less response to high VPD (Fig. 3(f) and Fig. 4(c)). Daily summer water loss for high radiation days was remarkably similar throughout the summer season and between years. The mean was $4.0 \pm 0.2\ \mathrm{MJ\ m^{-2}\ day^{-1}}$ ($1.6\ \mathrm{mm\ day^{-1}}$) in summer 1996 and $4.1 \pm 0.2\ \mathrm{MJ\ m^{-2}\ day^{-1}}$ ($1.7\ \mathrm{mm\ day^{-1}}$) in summer 1997, even though the summer mean daylight VPD was significantly higher in 1996 (1.7 kPa) than in 1997 (1.3 kPa; $p >> 0.05$). High rates of LE up to $10\ \mathrm{MJ\ m^{-2}\ day^{-1}}$ ($4\ \mathrm{mm\ day^{-1}}$) were only observed after periods of rain (Fig. 4(c)) and were usually maintained for only one day.

Whole-ecosystem LE leveled out as VPD increased beyond ~1 kPa, suggesting that water flow may have been limited by the hydraulic capacity of the whole plant system (roots, stems, leaves). If this were the case, stomata would adjust to maintain a sustainable water flow and minimize the possibility of cavitation (Mencuccini and Grace, 1996). As a direct consequence of partial stomatal closure, the rate of CO_2 diffusion into the leaves becomes limited and assimilation is reduced. The large variations in $\mathrm{NEE_m}$ and relatively stable LE at our ponderosa pine site in summer were similar to the pattern of NEE and LE reported for a boreal black spruce forest by Jarvis et al. (1997).

3.4. Cumulative water vapor and net ecosystem carbon exchange

Cumulative whole ecosystem water vapor exchange, LE, and rainfall for the years 1996 and 1997 are shown in Fig. 5. Annual whole ecosystem LE was 430 ± 70 mm in 1996 and 400 ± 60 mm in 1997, relatively constant compared to annual precipitation of 595 mm in 1996 and 188 mm in 1997. The larger annual evapotranspiration compared to annual precipitation in 1997, could be partly due to the time mismatch between the water year (October to September) and the calendar year (January to December) used for summing LE. It is also very likely that there might be another water source besides local precipitation, possible drainage and run-off from the ridge east of the site, which consists of porous volcanic rock. The annual precipitation on the ridge may be twice that of our site (George Taylor, Oregon Climate Service).

Monthly estimates of NEE, R_e and GEP for 1996 and 1997 are shown in Fig. 6. The most striking

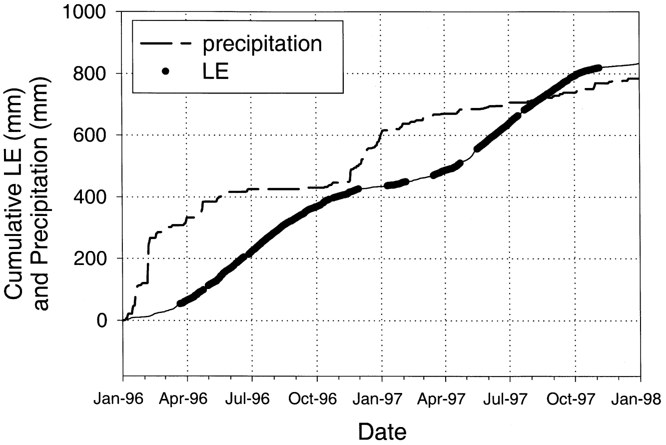

Fig. 5. Cumulative precipitation and ecosystem water vapor exchange (LE) during 1996 and 1997. Breaks in the cumulative LE indicate periods for which data are missing; daily LE was then modeled based on the Penman–Monteith equation.

difference between years are in summer values of R_e and NEE_m. The July–September mean daily T_a was slightly lower in 1997 than in 1996 (19.4°C versus 18.7°C). The soil temperature at 15 cm was also slightly lower in July–September 1997 than in 1996 (14.1°C versus 14.5°C). Interestingly, precipitation patterns were different from normal in summer 1997; precipitation was more frequent (17 days with a total of 33 mm) than in July–September 1996 (5 days with a total of 5 mm). Despite slightly cooler temperatures in 1997, the ecosystem respiration estimates for July–September were higher for 1997 (-410°gC m^{-2}) than for 1996 (-330 gC m^{-2}) (Fig. 6). The difference was mainly due to increased soil respiration. Because of higher respiration rates in summer 1997, the NEE_m was only 10 ± 60 gC m^{-2} between July and September 1997, much less than the value of 100 ± 60 gC m^{-2} for the same time period in 1996. Law et al. (1999a) examined the relationship of soil respiration with different environmental variables at our site in 1996, including soil moisture (0–30 cm, 0–100 cm), soil temperature and soil chemistry and

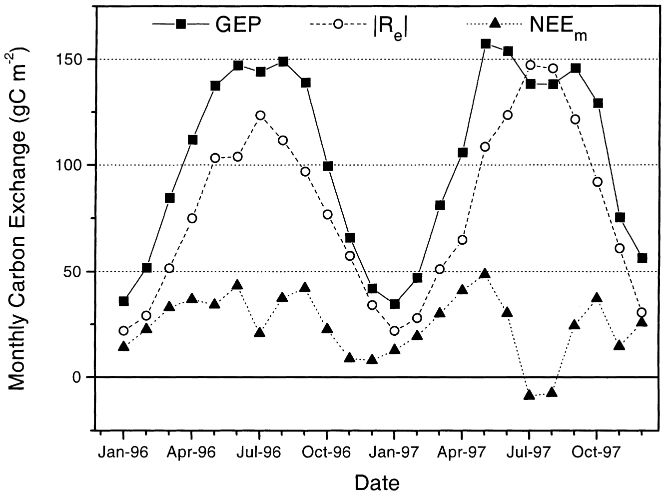

Fig. 6. Monthly sums of net ecosystem exchange (NEE_m), ecosystem respiration (R_e; absolute value of R_e is shown) and gross ecosystem exchange ($GEP = NEE_m - R_e$) for 1996 and 1997.

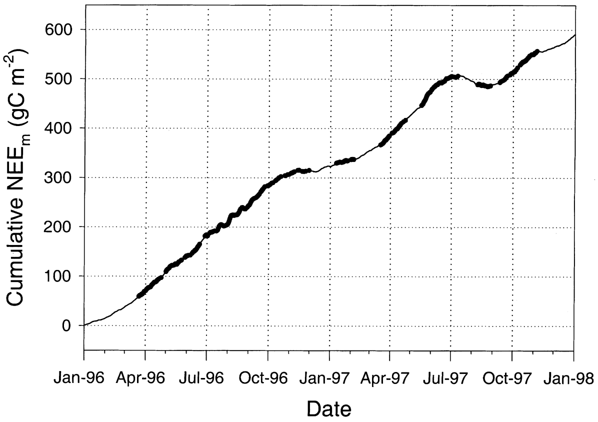

Fig. 7. Cumulative net ecosystem exchange (NEE$_m$) during 1996 and 1997. Breaks in the cumulative NEE$_m$ indicate periods for which data are missing; daily NEE$_m$ was then modeled based on Eq. (1).

found only a weak correlation with soil moisture; soil temperature explained ~60% of the variation in the soil CO_2 efflux. After accounting for the temperature effect, by normalizing to a common temperature (10°C), the normalized soil respiration rates in summer 1997 (2.3 μmol m^{-2} s^{-1}) are generally higher than in summer of 1996 (1.9 μmol m^{-2} s^{-1}). The more frequent rain in summer of 1997 than in summer of 1996 might have encouraged microbial respiration, offsetting the carbon gain in 1997 more than in 1996.

Cumulative NEE$_m$ for 1996 and 1997 is shown in Fig. 7. Annual NEE$_m$ estimated by eddy covariance was 320 ± 170 gC m^{-2} year^{-1} in 1996 and 270 ± 180 gC m^{-2} year^{-1} in 1997. The uncertainty in the night-time respiration estimate based on chamber data led to uncertainties in the annual NEE$_m$ of 80 and 90 gC m^{-2} year^{-1} in 1996 and 1997, respectively. The uncertainty in the daytime NEE$_m$ from the eddy covariance flux resulted in uncertainties of 90 gC m^{-2} year^{-1} in both years. The NEE$_m$ in the 1996 growing season (Day 125–275) was 170 ± 90 gC m^{-2}. Thus, NEE$_m$ outside the growing season in 1996 was 150 ± 80 gC m^{-2} (47% of annual NEE$_m$). In 1997, NEE$_m$ was 80 ± 100 gC m^{-2} during the growing season and 180 ± 80 gC m^{-2} (67% of annual NEE$_m$) outside the growing season.

Annual net carbon gain by the *P. ponderosa* ecosystem is comparable to carbon gains of other temperate forests (ranging from 150 to 700 gC m^{-2} year^{-1}; Greco and Baldocchi, 1996). Compared to boreal evergreen forests at higher latitudes, the pine forest has a substantial net carbon gain outside the traditionally defined growing season. At a boreal black spruce site (Goulden et al., 1998) net carbon gain in the growing season of 1996 (~60 gC m^{-2} from May through September) was lower than at our site in 1996, but the net carbon gain of the spruce forest in the growing season of the El Niño year in 1997 (~70 gC m^{-2}) was higher than at our site during the same time period, probably because of the higher soil respiration at our site in 1997 than in 1996. From October 1996 through May 1997, our data indicate that the pine forest gained about 140 ± 80 gC m^{-2}. In contrast, the boreal spruce forest lost ~60 gC m^{-2} during the same time period (Goulden et al., 1998). The large carbon gain of the *P. ponderosa* ecosystem outside the growing season reflects the fact that carbon assimilation continues to occur in the relatively mild winters, though at a slower rate, and ecosystem respiration is relatively low (Fig. 6). Leaf photosynthesis measurements performed in 1996 indicated a maximum leaf level photosynthetic capacity (A_{max}) of 6–9.5 μmol m^{-2} leaf s^{-1} in April and 16–21 μmol m^{-2} leaf s^{-1} during July. In comparison, A_{max} at Harvard Forest was ~12 μmol m^{-2} leaf s^{-1} in August (Williams et al., 1996), which is lower than A_{max} at our site in July. In the growing season at our site, although the photosynthetic capacity is large, carbon assimilation is constrained by partial stomatal closure in response to high VPD, and ecosystem respiration is large because of high air and soil temperatures.

The annual estimate of NEE$_p$ in 1996 from net primary production and heterotrophic respiration (NEE$_p$ = NPP + R_h) was 130 ± 120 gC m^{-2} year^{-1}. R_h was −280 gC m^{-2} year^{-1} in 1996, estimated from root decomposition (−277 ± 50 gC m^{-2} year^{-1}) and litter decomposition (−3 gC m^{-2} year^{-1}). Total NPP was 410 ± 70 gC m^{-2} year^{-1} (Law et al., 1999b).

The mensuration estimate of NEE$_p$ in 1996 was lower than our micrometeorological estimate of NEE$_m$ (320 ± 170 gC m^{-2} year^{-1}). The disagreement could partly be due to the modeling of NEE$_m$ of missing days with an empirical derived model Eq. (1). About 65% of the days during the dormant season of 1996 were filled-in, if we assume that on all of the modeled days the predicted carbon assimilation was overestimated by 50% we would have to lower the annual $\mathrm{NEE_m}$ in 1996 by ~130 gC $\mathrm{m^{-2}}$.

Our data, and results from several other groups suggest that some of discrepancy between $\mathrm{NEE_p}$ and $\mathrm{NEE_m}$ arises because soil carbon processes are poorly understood (Landsberg and Gower, 1997). Greco and Baldocchi (1996) reported an aboveground NPP at the Walker Branch deciduous forest (Oak Ridge, TN) of 192–212 gC $\mathrm{m^{-2}}$ $\mathrm{year^{-1}}$. Their NEE estimate from eddy covariance data was 525 ± 100 gC $\mathrm{m^{-2}}$ $\mathrm{year^{-1}}$. They suggested that the low NPP compared to annual NEE was either because some fraction of aboveground carbon accumulation must be supported by an accumulation of carbon in the root system, or even a small systematic error in the nocturnal carbon flux could have resulted in a large biased estimate in the annual NEE. Valentini et al. (1996) reported an annual NEE of 472 gC $\mathrm{m^{-2}}$ $\mathrm{year^{-1}}$ and a total NPP of 802 gC $\mathrm{m^{-2}}$ $\mathrm{year^{-1}}$ for a temperate beech forest in Italy. They suggested that there should have been a net accumulation of organic matter in the soil or in living roots in the order of 234 gC $\mathrm{m^{-2}}$ $\mathrm{year^{-1}}$ (after taking into account annual litterfall of 107 gC $\mathrm{m^{-2}}$ $\mathrm{year^{-1}}$ and fine root production of 457 gC $\mathrm{m^{-2}}$ $\mathrm{year^{-1}}$). They surmised that the high ratio of below- to above-ground productivity of the actively regrowing beech forest was due to the high investment of carbon in roots to overcome periods of water stress, which are typical for the central-south region of Italy, as for ponderosa pine regions of the western US (Law and Waring, 1994). Old-growth stands are expected to be in equilibrium in terms of carbon uptake and release. However, our mixed-age forest, which has patches of young trees, may be in a non-steady state condition and accumulating carbon belowground, offsetting some of the discrepancy between $\mathrm{NEE_p}$ and $\mathrm{NEE_m}$. Thus, our estimate of annual $\mathrm{NEE_p}$ from NPP and R_h is probably low because (i) we did not include coarse root production, which can be assumed to be ~20% of above-ground wood production (Waring, pers. comm.) and (ii) we assumed steady-state conditions.

4. Conclusions

There have been few long-term studies of carbon and energy fluxes in open-canopied semiarid ecosystems such as the ponderosa pine forest. Challenges of such systems are in understanding and modeling the interactions between water use and carbon exchange when both vegetation and the soil surface are sources of significant fluxes.

Exchange at our site is influenced by the strong seasonal variation in rainfall and temperature, and by the local topography. The complex topography appears to limit the scope for micrometeorology and simple one-dimensional transfer models to estimate fluxes in stable conditions at night and in the early morning. Frequent low wind speeds make turbulent flux measurement difficult with current instrumentation, and drainage flows or advection limit the use of change in $\mathrm{CO_2}$ storage in the canopy air space in calculations of NEE. Measurement of horizontal gradients of $\mathrm{CO_2}$ and temperature may help in quantifying advective terms. These problems are likely to be encountered increasingly often as flux studies extend to sites that are not ideal micrometeorologically, but typical of the real world. Availability of independent measurements of respired carbon fluxes from the main sources in the ecosystem allowed us to make seasonal estimates of the carbon budget in spite of the limitations in micrometeorology, and this approach should be considered in other studies at topographically complex sites.

We found that the ecosystem maintained a remarkably constant rate of water use in summer (~1.6–1.7 mm $\mathrm{day^{-1}}$) despite large changes in evaporative demand. Water flow may have been limited by the hydraulic capacity of the whole plant system (roots, stems, leaves). If this were the case, stomata would adjust to maintain a sustainable water flow and minimize the possibility of cavitation. As a direct consequence of partial stomatal closure, the rate of $\mathrm{CO_2}$ diffusion into the leaves becomes limited and assimilation is reduced.

Comparing carbon exchange in a typical summer (1996) and a relatively wet one (1997), we found that respiration was larger in 1997, presumably because wetter soil supported more microbial activity. Large differences in summer precipitation between years had more effect on respiration than did small differences in temperature.

Although summer growing season conditions are harsh in the ponderosa pine forest, the weather from fall through spring is mild, allowing an annual net carbon gain that is mid-range of that reported for temperate forests. Our estimate of NEE from eddy covariance was higher than an estimate of NEE from NPP and R_h. Some of the discrepancy is probably because of errors in the estimation of belowground carbon components. Improved methods are needed for estimating heterotrophic respiration, such as a stable isotope approach (Lin et al., 1999).

The carbon balance of the ponderosa pine ecosystem is quite sensitive to climatic variability. In the short term, the ecosystem has a very dynamic response to changing weather. In the dry season, as the ecosystem stabilizes its water use, NEE can change from positive (gaining carbon from the atmosphere) to negative over a just few days (Fig. 3). The net seasonal result depends on the frequency of cool air masses (decreasing evaporative demand) and accompanying rainfall (increasing respiration). The implication of these short-term responses is that the annual carbon budget of the ecosystem is very sensitive to weather and climate, but the water balance is not.

Acknowledgements

This study was funded by NASA (grant #NAGW-4436). We are grateful to Richard Vong, Steve Van Tuyl and Will Hutchinson for their field assistance. Steve Acker provided stem biomass equations for the site. We thank Laurel Groves for her editorial comments. Larry Mahrt and Dennis Baldocchi provided helpful comments on the eddy flux measurements and analysis. We thank Richard Waring for his continuing advice and many encouraging discussions. We gratefully acknowledge the assistance of the Sisters Ranger District of the US Forest Service in site selection, and Sarah Greene for aid in establishing the study site. The study site is located in a Research Natural Area – areas selected to represent vegetation types in a natural condition.

Appendix A

Missing carbon exchange data were estimated from an empirical relationship (Eq. (1)), where model parameters were determined seasonally from valid flux data for surrounding days. Carbon assimilation (A_c) was estimated as the difference between measured CO_2 flux and an estimate of ecosystem respiration, R_e, from scaled-up chamber data. From half-hour values of A_c and measured PAR, Michaelis–Menten light-response parameters (P_{max} = maximum ecosystem photosynthetic assimilation in $\mu mol\ m^{-2}\ s^{-1}$, K_m = Michaelis–Menten constant in $\mu mol\ m^{-2}\ s^{-1}$) were determined for low-VPD conditions with a non-linear least-square (NLS) regression model. The low-VPD threshold was adjusted seasonally to have enough data for the regression analysis. Fig. 8 shows the relationship between A_c and PAR for 20 days in late summer 1996 and early spring 1997. The light-response parameters determined for the two periods, with a VPD threshold of VPD < 1 kPa in late summer 1996 and VPD < 0.5 kPa in early spring 1997, are shown in Table 3. Residual values of A_c from the light-response curve fitted for the low-VPD condition were calculated for high-VPD periods. The reduction in A_c due to high VPD was then estimated by linear regres-

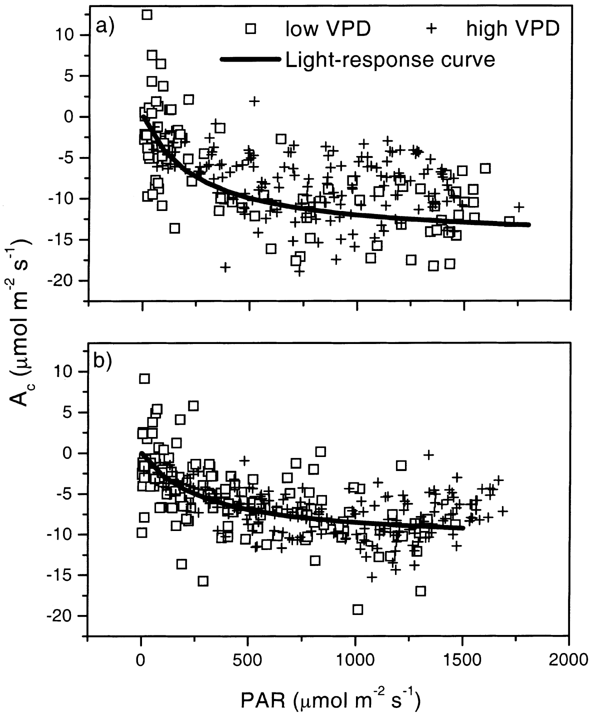

Fig. 8. Ecosystem light-response curve of carbon assimilation for 20 days in (a) late summer 1996 and (b) early spring 1997. A_c is shown with the sign convention that a negative value indicates carbon uptake by the plant. Light-response curve was determined from periods with low VPD; (a) VPD < 1 kPa, (b) VPD < 0.5 kPa.

Table 3
Light – (P_{max} in μmol m^{-2} s^{-1}, K_m in μmol m^{-2} s^{-1}) and VPD – (a_0 in μmol m^{-2} s^{-1}, a_1 in μmol m^{-2} s^{-1} kPa^{-1}) response parameters for empirically filling in missing data during two 20 days periods (i.e., late summer 1996 and early spring 1997)[a]

JD	Year	P_{max}	K_m	n_{MM}	a_0	a_1	n_{VPD}	B	r^2	n
261–280	1996	−15.2	263	109	−2.24	2.40	172	0.96	0.70	281
74–93	1997	−11.1	299	155	−0.79	1.19	188	0.97	0.74	343

[a] n_{MM} = number of observation for light response curve; n_{VPD} = number of observations for residual A_c to VPD regression; b = slope of predicted F_{cp} to measured CO$_2$ flux with forced zero intercept; r^2 = squared correlation coefficient of predicted F_{cp} to measured CO$_2$ flux; n = total number of observation in the period.

sion of the residual A_c versus VPD (a_0 = intercept in μmol m^{-2} s^{-1}, a_1 = slope in μmol m^{-2} s^{-1} kPa^{-1}; Fig. 9, Table 3). Carbon assimilation (A_{cp}) was then predicted for each half hour using the determined light – (P_{max}, K_m) and VPD – (a_0, a_1) response parameters with measured PAR and VPD. Predicted net carbon exchange (F_{cp}) was calculated from predicted A_{cp} and R_e. Fig. 10 shows the predicted F_{cp} versus measured CO$_2$ flux for 20 days in late summer 1996 and early spring 1997.

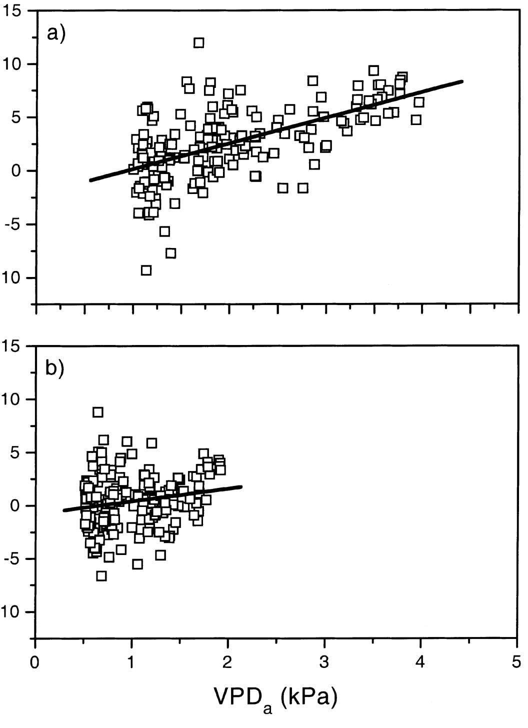

Fig. 9. Residual A_c (= A_c minus predicted carbon assimilation obtained from light-response curve; see Fig. 8) versus VPD for 20 days in (a) late summer 1996 and (b) early spring 1997. A positive residual A_c indicates a reduction in carbon assimilation.

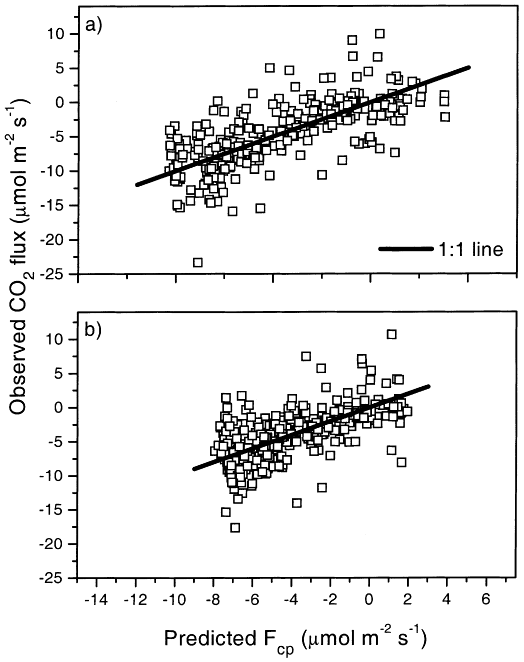

Fig. 10. Predicted (F_{cp}) versus observed CO$_2$ flux for 20 days in (a) late summer 1996 and (b) early spring 1997. F_{cp} was modeled based on Eq. (1), with the light- and VPD-response parameters determined for each period (see Table 3).

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