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Seasonal differences in carbon and water vapor exchange in young and old-growth ponderosa pine ecosystems

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Abstract

Eddy covariance measurements of carbon dioxide and water vapor exchange were made above a young and an old-growth ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws) ecosystem located in a semiarid environment in central Oregon. The old-growth stand (O site) is a mixture of 250- and 50-year-old ponderosa pine trees with no significant understory (summer maximum leaf area index (LAI) (m^2 half-surface area foliage per m^2 ground) is 2.1). The young stand (Y site; 15 years old in 2000), about 10 km southeast of the old stand, is naturally regenerating following the clear-cut of an old stand in 1978 and has at present about 40% of its LAI in understory shrubs (summer maximum LAI of 1.0).

Even though climatic conditions at both sites were very similar, ecosystem carbon exchange differed substantially between the two ecosystems. The old-growth forest with about two times the LAI of the young site, had higher carbon assimilation rates per unit ground area than the young forest, with trends similar between the two forests in spring and fall. Deviations from the trend occurred during summer when water stress in trees at the young site led to a significant reduction in transpiration, and consequently carbon assimilation due to stomatal limitations. Throughout the year, ecosystem respiration (R_e) and gross ecosystem production (GEP) were generally greater at the O site than Y site, and the net of these two processes resulted in a lower net carbon uptake at the Y site. © 2002 Elsevier Science B.V. All rights reserved.

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

1. Introduction

Micrometeorological measurements of the exchange of carbon dioxide, water vapor, and energy between terrestrial ecosystems and the atmosphere are being made at sites worldwide (e.g. the AmeriFlux, EUROFLUX and AsiaFlux networks) to evaluate responses of exchange rates to biotic and abiotic factors (Baldocchi et al., 2001). Net carbon dioxide exchange (NEE) measured above a canopy is the small difference between two large fluxes, photosynthetic uptake of CO_2 by plants (A_c), and ecosystem release of CO_2 by plant respiration and decomposition (R_e).

Increasingly, research groups are attempting to quantify the influence of forest age and disturbance on A_c and R_e. For example, losses of carbon from decomposing organic matter in recently disturbed ecosystems may exceed the uptake of CO_2 by new vegetation,

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at least until vegetation reaches its maximum potential (Schulze et al., 2000). Conversely, it has been suggested that old-growth forests may be only weak sinks for CO_2 because of reduced photosynthetic potential (Hubbard et al., 1999), and decomposition of accumulated woody detritus (Harmon et al., 1990).

Previously, we compared carbon dioxide, water vapor, and energy exchanges of ponderosa pine in a young forest in California and an old-growth forest in Oregon (Law et al., 2001b). The study suggested that the young forest was a considerably larger annual sink for carbon than the old forest, and could support a much larger leaf area. Model results suggested that this was primarily due to differences in climate (California site wetter and warmer), rather than age. To determine the effect of forest developmental stage on fluxes, we initiated measurements of carbon dioxide and energy exchange in 1999 using the eddy covariance technique in young regenerating and old-growth ponderosa pine forests situated only about 10 km apart in central Oregon. Our aim was to explore the differences between sites in NEE, R_e, gross ecosystem production (GEP), and evapotranspiration (LE). To interpret the underlying processes, and to assess the accuracy of our methods, we draw on chamber-based gas exchange measurements made at the sites (Irvine and Law, 2002; Law et al., 2001b).

The specific aims of this paper are: (1) to report how CO_2 exchange rates differed in their response to environmental factors between the young and old-growth ecosystems; and (2) to compare differences in the seasonal patterns of carbon and energy exchange between the sites. In Appendices A and B, we summarize associated investigations of the accuracy of eddy covariance measurements in these heterogeneous ecosystems with complex topography, and efforts to establish how respiration fluxes determined by eddy covariance varied with wind speed and direction.

2. Methods

2.1. Site description

Our study was conducted in a young ponderosa pine forest (15 years old, Y site) and a relatively undisturbed old-growth forest (O site) in central Oregon. The Y site (44°26′N, 121°34′W, elevation 1188 m) was previously an old-growth forest that was clear-cut in 1978 and allowed to regenerate naturally (in 2000, ~1200 trees/ha, on average 15 years old). The understory is principally manzanita (*Arctostaphylos patula*) and bitterbrush (*Purshia tridentata*). About 40% of the ecosystem leaf area index (LAI) (summer maximum total LAI of 1.0 (m^2 half-surface area foliage per m^2 ground)) is in the understory shrubs (Law et al., 2001d,e).

The O site is about 10 km northwest of the Y site in a Research Natural Area (RNA) in the Metolius River basin (44°30′N, 121°37′W, elevation 915 m). It has never been logged, and the forest extends several kilometers in all directions. A forested northsouth ridge lies about 1 km to the east of the site, with a rise in elevation of ~400 m. The site consists of about 27% (by area) patches of old trees (approximately >250 years), 25% patches of younger trees (~50 years) and 48% stands of mixed-age trees (50-year-old: 874 trees/ha and >250-year-old: 76 trees/ha). The understory is sparse, with patches of bitterbrush, bracken fern (*Pteridium aquilinum*) and strawberry (*Fragaria vesca*). The summer maximum total LAI was about 2.1 (Law et al., 2001d,e). Details about the surrounding topography of the O and Y sites can be found in Law et al. (2001d).

2.2. Eddy covariance measurements

Eddy covariance and microclimate measurements have been made at the O site since 1996 (Anthoni et al., 1999; Law et al., 1999a,b). Instrumentation for similar measurements was installed at the Y site in 1999.

The eddy covariance instruments at the O site were deployed at a height of 47 m, about 14 m above the dominant trees, and at the Y site at a height of 12 m, about 9 m above the mean tree height. Exchange rates of carbon dioxide (F_c), water vapor (LE) and sensible heat (H) were estimated following methods of Baldocchi and Vogel (1996). Wind speed and virtual temperature were measured with three-dimensional sonic anemometers (model 1012 R2, Gill Instruments, Lymington, England; model CSAT-3, CSI, Logan, Utah). Open-path (OP) infrared gas analyzers (IRGAs) from NOAA/ATDD (Auble and Meyers, 1992) and LI-COR (model LI-7500, LI-COR Inc., Lincoln, NE) were used to measure CO_2 and water vapor fluctuations. The 1/2 h eddy covariances and statistics were computed on-line and by post-processing raw data collected at ~10 Hz. When raw data were not available, on-line calculated fluxes were used to estimate exchange rates. Above-canopy fluxes were rotated to allow interpretation of the exchange rates normal to the streamlines following the local terrain (McMillen, 1988). Where necessary, appropriate corrections for cross-wind contamination of virtual temperature (Schotanus et al., 1983) and for air density fluctuations (the WPL term) (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.

The rate of change in CO_2 storage (F_s) in the canopy at the O site was calculated from CO_2 profiles measured at three heights (1, 8, and, 46 m). The system was operated continuously from spring to fall and periodically at other times when power supplied from solar panels was limited. A good correlation between change in above-canopy CO_2 concentration and change in CO_2 storage in the canopy air layer (0–46 m) was used to fill in missing periods ($r^2 = 0.90$, $n = 4160$). At the Y site, CO_2 profile measurements at 1, 3, and 12 m during an intensive summer field study were used to derive a similar relation ($r^2 = 0.79$, $n = 1090$). Hollinger et al. (1994) used this approach above an old-growth temperate forest.

For calculation of daily CO_2 exchange rates from $F_c + F_s$, data gaps were filled using a seasonal empirical relation with PAR and vapor pressure deficit (VPD) (Anthoni et al., 1999). Gaps in measured sensible and latent heat exchange were filled using an empirical relation to measured net radiation.

At the Y site, flux measurements began on 31 March 2000 (DOY 90), using a CSAT-3 sonic anemometer and LI-7500 OP IRGA. At the O site, flux measurements with identical instrumentation began on 17 June 2000 (DOY 168). Prior to this date, a NOAA/ATDD IRGA and Gill Solent R2 flux system was used (Anthoni et al., 1999). To facilitate comparison between the systems, corrections to the NOAA/ATDD IRGA were applied between DOY 90 and DOY 168. The eddy flux data analyzed for this paper extend from 31 March to 31 December 2000.

For about 54 days in summer we also operated a closed-path (CP) eddy flux system at the Y site, using a LI-COR 6262 IRGA. The IRGA sample inlet was co-located with the OP gas analyzer; both systems used the same CSAT-3 sonic anemometer. We derived the correction for tube lag time by determining the maximum cross-correlation between time lagged vertical velocity and concentration, and derived frequency response corrections by determining time constants of the system for CO_2 and water vapor following step changes in concentration during routine calibrations with gases fed into the sampling tube near the sonic anemometer (Massman and Lee, 2001; Munger et al., 1996). The frequency response correction increased fluxes measured with the CP system on average by about 8 and 14% during day and night, respectively.

We assessed the accuracy of our eddy covariance systems in several ways described in Appendix A. We selected valid nighttime CO_2 flux data by screening the measured CO_2 exchange ($F_c + F_s$) for wind speed and wind direction effects (see Appendix B). In summary:

- When OP flux systems from the O and Y sites were co-located, they gave flux estimates within 3, 4 and 4% for H, LE, and F_c, respectively. Therefore, we are confident that observed differences between sites larger than these values are associated with real effects and not systematic differences between instruments. These real effects may be biological (e.g. differences in sensitivity to water shortage), or physical (e.g. differences in advection in complex terrain, or in low frequency contributions to fluxes; Finnigan et al., 2002).
- A comparison of OP and closed-path (CP) IRGAs at the Y site showed significant differences in nighttime estimates of F_c, with the CP system estimating ~1.0 $\mu mol\,m^{-2}\,s^{-1}$ higher respiration on average. Daytime differences between the OP and CP systems were smaller, with the CP system estimating NEE ~0.4 $\mu mol\,m^{-2}\,s^{-1}$ lower in magnitude than the OP system. Overall differences between OP and CP systems appeared systematic and could lead to differences in estimated annual NEE of the order of 200–300 $g\,C\,m^{-2}$ per year if extrapolated to the whole year.
- Comparisons between OP systems and chamber-based measurements of ecosystem respiration agreed very well at the Y site (Law et al., 2001c). Based on this good agreement, we have used respiration estimates derived from our OP systems for calculating carbon exchange.

- At the Y site, when the wind was from the north, we observed nighttime CO_2 fluxes anomalously larger than respiration measured with chambers in the near vicinity (100 m) of the flux tower. We excluded these nighttime flux data from further analysis. In addition, only data with friction velocity (u^*) in the range $0.1 < u^* < 0.55\,\mathrm{m\,s^{-1}}$ showed a temperature-normalized respiration rate that was independent of wind speed. Consequently, data outside this range were excluded.
- At the O site, no wind direction dependence of nighttime CO_2 exchange nor flux loss at low u^* was evident. Therefore, we accepted all nighttime data at the O site for further analysis.

2.3. Climate measurements

Microclimate was measured at both sites with identical systems, recording data on a Campbell Scientific Inc. (CSI) datalogger (model CR10X, CSI, Logan, UT). Above-canopy net radiation (R_n) was measured with net radiometers (model Q7, REBS, Seattle, WA), deployed from the south side of the towers at the height of the eddy covariance systems. Incident photosynthetically active radiation (PAR) was measured with radiation sensors (LI-190SZ, LI-COR Inc., Lincoln, NE). Air temperature (T_a) and relative humidity (RH) were measured with a thermistor and capacitive RH sensor probe (model HMP45C, Vaisala, Helsinki, Finland). Wind speed and direction were monitored with a Wind Sentry set (model 03001, RM Young, Traverse City, MI). To ensure comparability in microclimate data between sites, we ran a third set of instruments for several weeks at each site and corrected for differences by linear regression analysis.

2.4. Ecosystem respiration

Ecosystem respiration (R_e) was determined by two approaches, micrometeorology and chamber measurements. Nighttime CO_2 exchange measured by the eddy covariance system, and corrected for change in CO_2 storage (F_s) within the canopy airspace, was used to determine the seasonal variation of ecosystem respiration. Respiration rates were modeled with an Arrhenius type equation (Lloyd and Taylor, 1994):

$$R_e = R_{e_{10}}\, e^{(E_a/R)[(1/T_{10})-(1/T_K)]} \tag{1}$$

where $R_{e_{10}}$ is the respiration rate at 10 °C, T_{10} is 283 K (=10 °C), E_a the activation energy in $\mathrm{J\,mol^{-1}}$, T_K the soil temperature (at 2 cm) in K, and R is the universal gas constant ($8.314\,\mathrm{J\,K^{-1}\,mol^{-1}}$). Values of E_a and $R_{e_{10}}$, estimated seasonally from measured nighttime $F_c + F_s$ are given in Table 1. The temperature curves derived from nighttime $F_c + F_s$ were used to fill in missing data and estimate daytime ecosystem respiration ($R_{e,fc}$).

An independent chamber-based estimate of ecosystem respiration ($R_{e,ch}$) was made by adding an estimate of foliage (R_f) and wood (R_w) respiration to soil respiration (R_s) measured with an automated soil respiration system consisting of six normally-open chambers that were closed sequentially. More details of the automated soil respiration system are given in Irvine and Law (2002).

Respiration for ponderosa pine foliage at the O site was calculated from temperature equations developed from chamber measurements on tree foliage in 1996 and 1997 (Law et al., 1999b). Respiration from the sparse understory at the O site was assumed to also follow these equations. At the Y site, where the understory was more substantial, separate temperature

Table 1
Fitted values of the coefficients E_a (activation energy) and $R_{e_{10}}$ (respiration rate at 10 °C) in an Arrhenius type equation (Eq. (1)) relating ecosystem respiration R_e to soil temperature at 2 cm

Day of year	Young site		Old site	
	E_a ($\mathrm{J\,mol^{-1}}$)	$R_{e_{10}}$ ($\mathrm{\mu mol\,m^{-2}\,s^{-1}}$)	E_a ($\mathrm{J\,mol^{-1}}$)	$R_{e_{10}}$ ($\mathrm{\mu mol\,m^{-2}\,s^{-1}}$)
80–120	64760	1.39	53372	1.82
121–244	23915	2.07	28749	2.53
245–365	34582	1.16	31393	2.22

Note: the fitted values should not be assigned biophysical significance, since additional environmental factors also influence R_e (Irvine and Law, 2002; Lloyd and Taylor, 1994).

equations for trees and understory species were developed in 2000, using seasonal chamber measurements of nocturnal foliage respiration (Law et al., 2001b).

Wood respiration for trees and shrubs (a small component of total respiration) was calculated following methods in Law et al. (2001b), using (at both sites) an equation relating R_w to air temperature (Law et al., 1999b). R_w was scaled to site by an estimate of total sapwood volume per ground area at each site.

3. Results and discussion

3.1. Seasonal climate

In general, weather and climate were very similar between the young and old-growth sites. Fig. 1 and Table 2 show daily and annual observations. The 24 h mean air temperature was, on average, about 1 °C lower at the Y site, but the differences were not significant ($P = 0.153$). However, minimum and maximum temperatures were significantly different, with larger diurnal temperature amplitude at the O site.

Early in the day, VPD was lower at the O site than at the Y site, but in the afternoons, VPD was higher at the O site, resulting in similar daylight means.

Table 2
Annual and seasonal climate at the old-growth and young ponderosa pine ecosystems in 2000

	Old-growth	Young
Annual mean T_a (°C)	8.1 (0.4)	7.0 (0.41)
Summer mean T_a (°C)	16.6 (0.45)	15.9 (0.49)
Annual diurnal T_a amplitude (°C)	11.9 (0.34)	10.0 (0.23)
Summer diurnal T_a amplitude (°C)	16.5 (0.62)	12.9 (0.38)
Annual daytime mean VPD (kPa)	0.73 (0.03)	0.73 (0.04)
Summer daytime mean VPD (kPa)	1.46 (0.06)	1.46 (0.07)
Annual rain (mm)	426.1	381.5
Summer rain (mm)	9.8	6
Annual PAR (MJ m^{-2})	2268.4	2428.9
Annual R_n (MJ m^{-2})	3203	3115

Standard errors are in parantheses. The summer period is July to September (day 182–243).

PAR was slightly greater at the Y site than at the O site. The difference could be due to the influence of the ridge to the east of the O site, which blocks direct radiation for about 1 h in the early morning from reaching the above-canopy sensor. The ridge also influences the diffuse radiation field during the whole day.

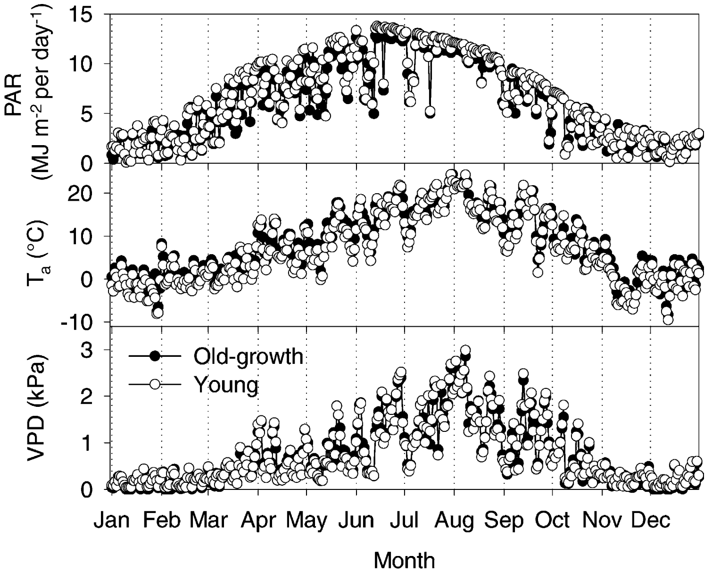

Fig. 1. Young and old-growth daily climate in year 2000, showing day total photosynthetically active radiation (PAR), 24 h mean air temperature (T_a), and daylight mean vapor pressure deficit (VPD).

Table 3
Ecosystem respiration (in $\mathrm{g\,C\,m^{-2}}$) from eddy flux ($R_{\mathrm{e,fc}}$) and chamber ($R_{\mathrm{e,ch}}$) data, summed over all operational 1/2 h periods of the automatic soil respiration system at each site

	Chamber method ($R_{\mathrm{e,ch}}$)	Eddy flux method ($R_{\mathrm{e,fc}}$)	Difference (%)	n
Old-growth				
24 h	254	285	11	4179
Nighttime	92	95	3	1658
Daytime	162	190	15	2521
Young-growth				
24 h	213	223	4	4691
Nighttime	72	76	5	2013
Daytime	141	146	3	2678

The eddy flux daytime respiration was calculated from daytime soil temperature and the respiration temperature curve derived from nighttime data. n = number of 1/2 h periods used for comparison.

3.2. Nighttime ecosystem respiration from eddy flux and chamber data

Using data from the acceptable turbulence regimes at each site (see Appendix B), ecosystem respiration ($R_{\mathrm{e,fc}}$), estimated from $F_{\mathrm{c}} + F_{\mathrm{s}}$, with missing data estimated using respiration–temperature curves, compared well with independent estimates of ecosystem respiration from chamber data ($R_{\mathrm{e,ch}} = R_{\mathrm{s}} + R_{\mathrm{f}} + R_{\mathrm{w}}$) most of the time (Table 3 and Fig. 2a and b). The differences seen during some periods of the year were small (generally $<1\ \mu\mathrm{mol\,m^{-2}\,s^{-1}}$), but seasonal patterns of difference were evident. Such differences could be due to systematic errors in either measurement system or to seasonally-dependent spatial variation in respiration rates between the respective source areas of each system. For example, Irvine and Law (2002) and Law et al. (2001c) suggest that the automated chambers underestimate soil CO_2 effluxes by about 14 and 8% at the O and Y site, respectively, due to a reduction in the natural diffusion gradient when CO_2 is allowed to increase above ambient in the chambers. Thus, the chamber data likely result in slight underestimates of $R_{\mathrm{e,ch}}$.

Agreement between the two methods of estimating ecosystem respiration was good at night, but less so during the day (Table 3), especially at the O site. Table 3 shows that estimating daytime respiration from temperature curves derived from nighttime $F_{\mathrm{c}} + F_{\mathrm{s}}$ can lead to an overestimation of daytime R_{e} (compared to chamber measurements at the O site). This problem arises when temperatures during daytime are outside the nighttime temperature range and because the temperature coefficient (E_{a}) is large. The daytime overestimation was less at the Y site, probably because the temperature coefficient was smaller for most of the summer.

Overall, the comparisons with chamber estimates give confidence that our screened eddy flux data provide good estimates of the seasonal course of nighttime respiration at both sites, and also indicate the magnitude of uncertainties introduced in estimating seasonal respiration totals from eddy covariance measurements.

3.3. Response of daytime carbon exchange to environmental factors

To determine the response of the ecosystem CO_2 uptake to environmental factors, ecosystem carbon assimilation (A_{c}) was calculated from measured daytime NEE ($F_{\mathrm{c}} + F_{\mathrm{s}}$) and an estimate of daytime ecosystem respiration ($R_{\mathrm{e,fc}}$) developed from nighttime respiration temperature curves, i.e. $A_{\mathrm{c}} = -\mathrm{NEE} + R_{\mathrm{e,fc}}$. Fig. 3 shows light response curves, plotting the bin-averaged A_{c} during low VPD conditions (<50% quantile for each period: ∼0.6 kPa in April/May; ∼1.6 kPa in June/July; ∼1.4 kPa in August/September; and ∼0.4 kPa in October/November) against PAR for consecutive 2-month periods at the Y and O sites from April until November 2000. Carbon assimilation was larger at the O site than at the Y site in all periods. At high light ($\mathrm{PAR} > 1000\ \mu\mathrm{mol\,m^{-2}\,s^{-1}}$), the O site had about 40% higher carbon assimilation than the Y site in spring and about twice the Y site A_{c} in summer and fall, when drought stress was more severe in the young trees compared with trees at the O site (Fig. 3). At the O site (Fig. 3b), A_{c} at large irradiance was smaller before bud-break (which occurred in mid-June) than later in the summer, and A_{c} declined slightly in October/November. Tree foliage at this site showed little seasonal variability in maximum carboxylation efficiency ($V_{\mathrm{c,max}}$, data not shown), and showed insignificant declines in canopy conductance due to soil moisture reductions over summer. Thus, the significantly greater LAI at the O site, and lack of significant soil moisture limitation on carbon assimilation in comparison to the Y site, led to the significantly higher rates of carbon uptake

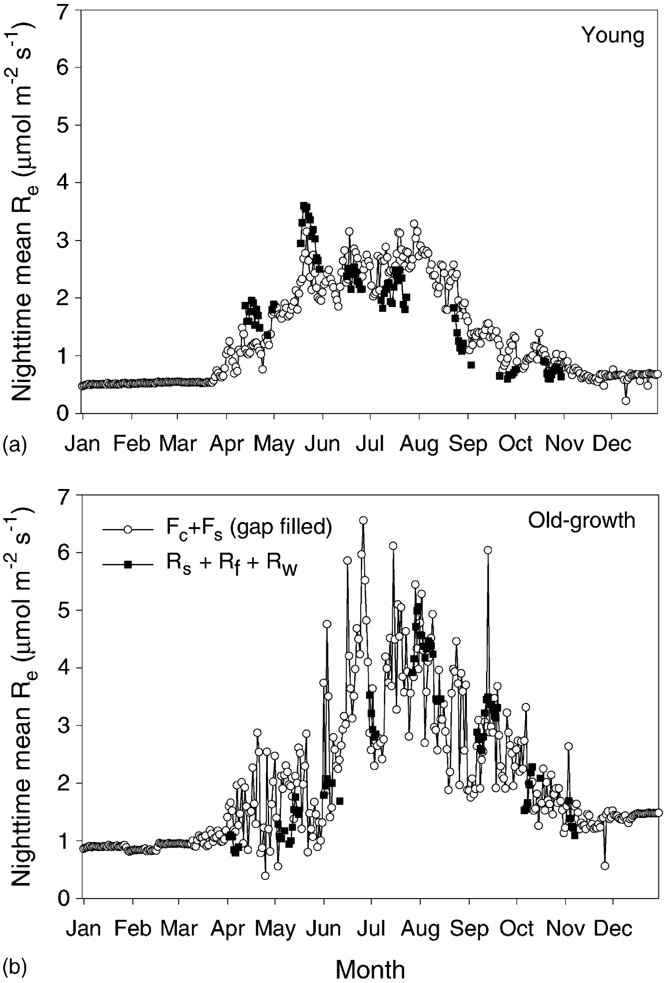

Fig. 2. Estimates of nighttime ecosystem respiration at the young (a) and old-growth (b) sits, derived from measured $F_c + F_s$ (with data gaps filled by temperature curves derived from $F_c + F_s$). Also shown are chamber estimates of ecosystem respiration ($R_s + R_f + R_w$), estimated from soil respiration (R_s) measured with an automated soil chamber system and estimates of foliage (R_f) and wood (R_w) respiration from temperature curves.

per unit ground area in the old-growth ecosystem. At the Y site (Fig. 3a), a stronger seasonal pattern in A_c was observed, with high rates from April until July, decreased rates in August/September, and the lowest rates in October/November. These changes are probably caused by drought stress, as indicated in the strong seasonal decline in canopy conductance (see later) and a small decline in $V_{c,\max}$ between June and August.

To separate the influence of VPD on ecosystem CO_2 exchange from that of irradiance, we followed the method of Anthoni et al. (1999). Light response curves were fitted to 2-month data sets of A_c, using only data when VPD was low (data shown in Fig. 3). Residual A_c was calculated for periods with high VPD (>50% quantile for each period) by subtracting from the measured A_c a modeled A_c derived from the low VPD light response curve. Fig. 4a and b shows the variation of residual A_c with VPD at Y and O sites. For each 2-month period, the negative influence of VPD on residual A_c was smaller at the Y site than at the O site. At both sites, the dependence on VPD was

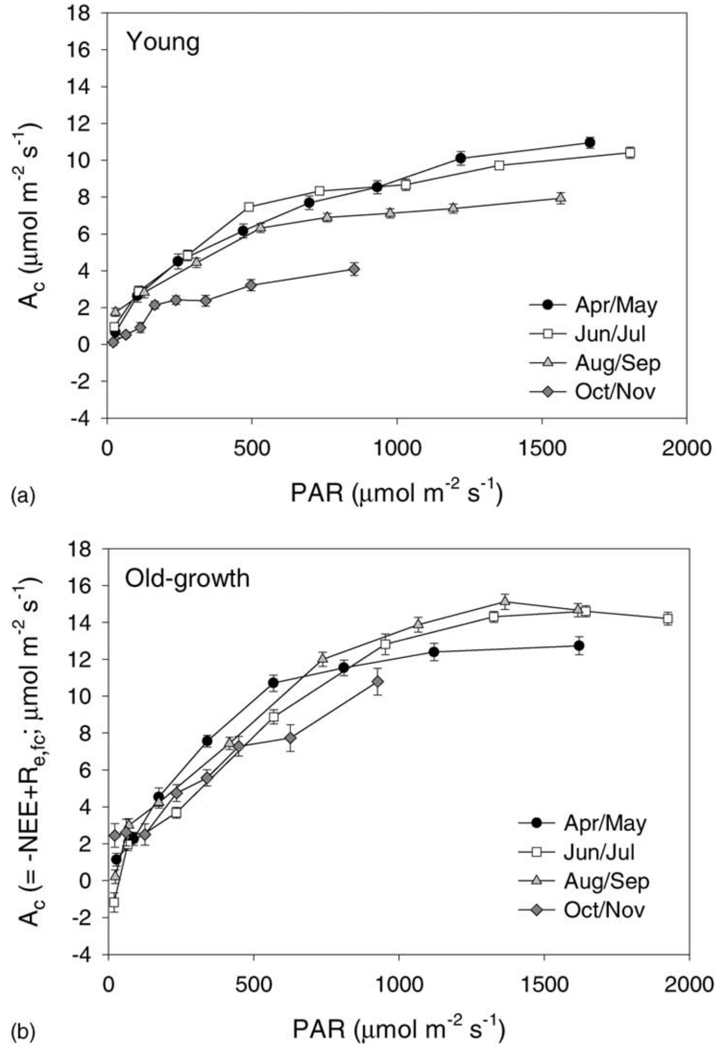

Fig. 3. Variation of carbon assimilation A_c (=daytime $F_c + R_{e,fc}$) with photosynthetically active radiation (PAR) for 2-month period at the young (a) and old-growth (b) sites. A_c during low VPD periods (VPD < 50% quantile for the 2-month period) are averaged into PAR bins with equal number of data points per bin. Error bars are standard errors.

largest in April/May. The smaller residual response to VPD in summer at the Y site is because A_c at that site was already reduced by the seasonal effects of soil water deficit on canopy conductance. This interpretation is also consistent with the large responses to VPD in April/May when soil water was not a limiting factor at either site.

Fig. 5 shows the variation of ecosystem conductance (g_e) with VPD at the Y and O sites, calculated using the same methods as in Law et al. (2001b). The sites had similar g_e throughout spring and early summer, then there was a substantial (∼30%) decline in g_e in August/September at the Y site, but not at the O site. These results suggest that the carbon exchange of young ponderosa pine stands is potentially more sensitive to water stress than that of old-growth ponderosa pine stands, which can access water from greater depth (Williams et al., 2001).

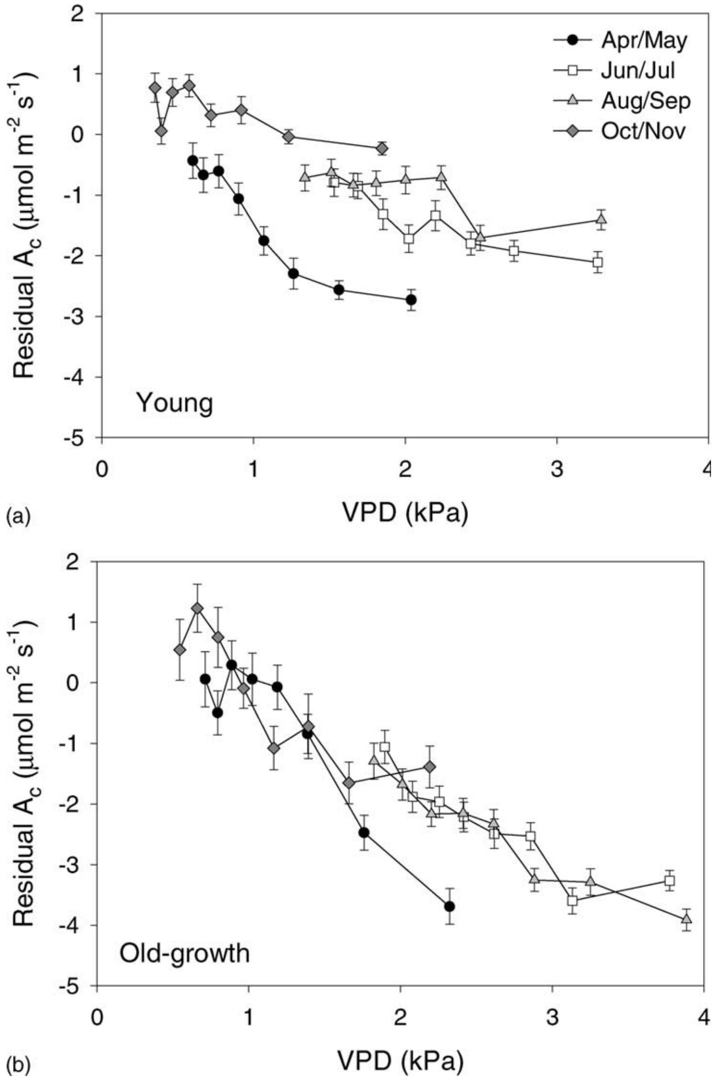

Fig. 4. Variation of residual A_c ($=A_c$ − model A_c) with VPD for 2-month period at the young (a) and old-growth (b) site. Model A_c is calculated from light response curves for low VPD conditions. Residual A_c values during high VPD (VPD $>$ 50% quantile for the 2-month period) are averaged into VPD bins with equal number of data points per bin. Error bars are standard errors.

3.4. Seasonal carbon and water vapor exchange

Fig. 6a shows the weekly exchange of water vapor (LE) and CO_2 (NEE, R_e and GEP (calculated as $-\text{NEE} + R_e$)) at the Y and O sites. Up to July, while soil water deficits were low, the ecosystems lost similar amounts of water per week. Foliage conductances derived from sap flow measurements by Irvine et al. (2001) provide some explanation for this result. Their data show that in spring, the combination of larger leaf area, but lower foliage conductance at the O site, and smaller leaf area, but larger conductance at the Y site resulted in similar rates of tree transpiration between sites. Soil surface evaporation and understory transpiration also contributed to ecosystem water loss, so our explanation implies either that these

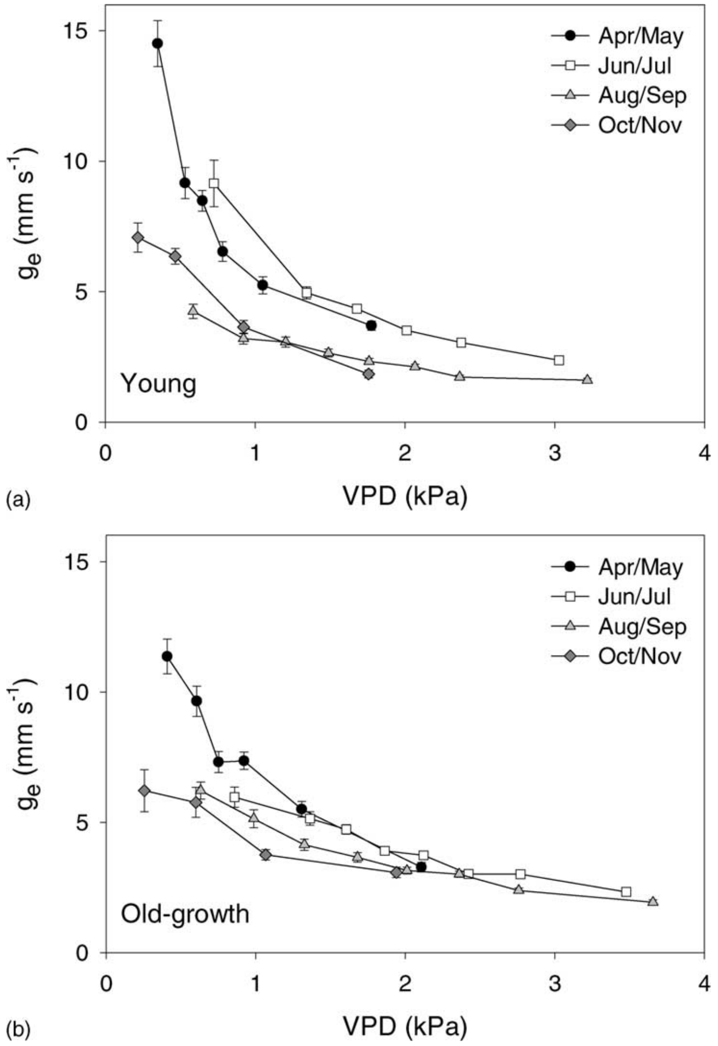

Fig. 5. Estimate of midday imposed ecosystem conductance ($g_e = (p_a/\rho_a 0.622)(E/D)$, where D is the vapor pressure deficit (VPD) and E is ecosystem water vapor exchange in $\mathrm{kg\,m^{-2}\,s^{-1}}$) vs. VPD for 2-month period at the young (a) and old-growth (b) site. Values of g_e are averaged into VPD bins with an equal number of data points per bin. Days with rain were excluded from the analysis. Error bars are standard errors.

terms were small or that their sum was similar at each site.

Measurements of rooting zone soil water potential indicated that trees at the Y site became more drought stressed after July, and soil moisture was being utilized from greater depths at the O site (Irvine et al., 2001). Brooks et al. (2002) found that approximately 35% of the daily water utilized from the upper 2 m of soil during July and August was attributable to hydraulic redistribution of water by deeply rooted trees at the O site, and the magnitude of hydraulic redistribution appeared to be much larger at the O site than the Y site.

The drought stress at the Y site is detectable in LE after July (Fig. 6). A similar pattern was observed at a young ponderosa pine plantation in California during a dry year (Goldstein et al., 2000). The pattern at our sites appears to be driven principally by differences in access to soil moisture and not by large VPD constraining leaf conductance, as the Y and O sites

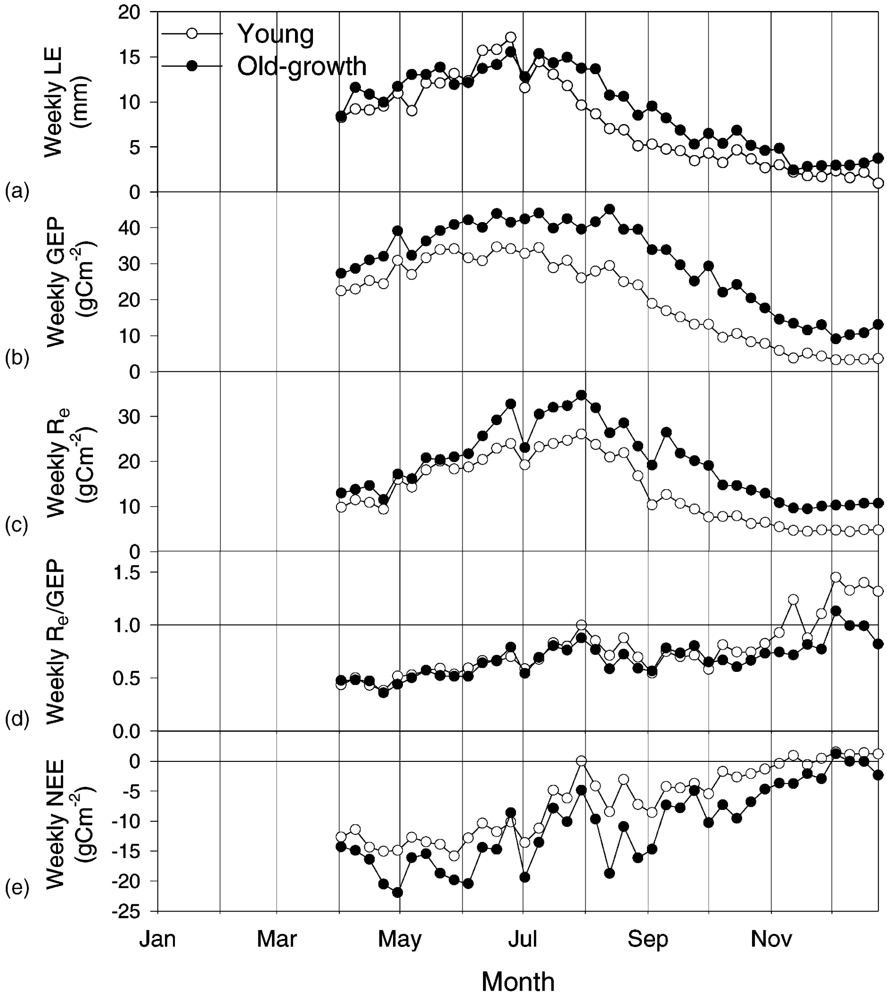

Fig. 6. Weekly water vapor (LE: a) and carbon (GEP, R_e, R_e/GEP, and NEE: b–e) exchange at young and old-growth ponderosa pine site. Month labels are plotted at the beginning of each month.

experienced similar VPDs during this period. It is also possible that compensating effects could be important in these low LAI ecosystems at high vapor pressure deficit, so that the vegetation response to high VPD might be compensated by increased evaporation from soil (Law et al., 2001a; Schulze et al., 1999).

At both sites, NEE was negative (i.e. the ecosystems were a sink for CO_2 from the atmosphere) from about April to November (Fig. 6e). The NEE at the O site was more negative in almost every week than at the Y site. Seasonal trends in NEE were similar between sites, indicating the similarity of ecosystem level responses to factors such as PAR, VPD and temperature, but the variability of NEE was larger at the O site. When our estimates of ecosystem respiration were included in the carbon budget to estimate GEP, GEP was considerably larger at the O site than at the Y site (Fig. 6b). At the O site, GEP remained approximately constant from May to August, then declined; at the Y site, the decline started about a month earlier. Interestingly, NEE was much more variable than GEP, particularly at the O site. This may be a consequence of the dependences of assimilation and respiration on environmental factors having different sensitivities.

The ratio R_e/GEP varied seasonally, and ranged from 0.4 to 1.45 and 0.35 to 1.15 at the Y and O site, respectively. R_e/GEP was similar at both sites until mid-July, with increasing values from spring to summer as ecosystem respiration increased faster than GEP. In mid-July, GEP at the Y site decreased due to water stress, but R_e decreased less, resulting in an increase of R_e/GEP compared to the O site. In November–December, R_e/GEP at the Y site became larger than at the O site and even exceeded unity, probably because soil CO_2 efflux increased in the wet season, while GEP changed proportionately less.

3.5. Estimating annual exchange of carbon: uncertainties and unresolved issues

Fig. 6 demonstrates that the O site, with a mix of 50- and 250-year-old trees, was more productive than our Y site ecosystem throughout the measurement period. Based on biomass data, the O site was also more productive than two pure old-growth ponderosa pine stands in the near vicinity, but less productive than some mid age (50–100 years) stands within a ponderosa pine chronosequence (Law et al., 2001d). In principle, we could calculate totals for NEE at the O and Y sites over the measurement period or over future years by summing 1/2 h eddy flux observations, corrected for storage terms, and filling data gaps by the methods described earlier. However, there are cumulative errors and unresolved issues that are compounded when integrating to make annual flux estimates, even at the most ideal sites for micrometeorology (Baldocchi et al., 2000; Goulden et al., 1996; Moncrieff et al., 1996; Wilson and Baldocchi, 2001). At our sites, there are particular uncertainties and issues that we believe are also likely to apply at other sites where the canopy is heterogeneous and aerodynamically rough, and the topography is complex.

First, we (like many others) report a lack of energy closure (Appendix A). One interpretation is that sonic anemometers systematically underestimate sensible heat flux at our sites, even though similar instruments compared well with other sonic anemometers in a wind tunnel and over grassland (Foken et al., 1997; Vogt et al., 1997). If sensible heat flux was underestimated by 10%, Appendix A shows that this could lead to an overestimate of up to 100 g C m^{-2} per year in C uptake at our sites. Improvements in assessing advection and in resolving low frequency contributions to fluxes may eventually reduce this pervasive energy closure problem.

Alternatively, there is some evidence that if energy balance is not achieved with eddy covariance measurements, then measured CO_2 fluxes are underestimated as well (Twine et al., 2000). If failure to account for all vertical velocity fluctuations at our sites (e.g. because of unidentified mesoscale motion) was the cause of inadequate energy closure, all fluxes may have been underestimated. If that was the case, the raw CO_2 flux from our OP systems (uncorrected for WPL terms) would be underestimated, but the WPL term, which is positively correlated to the sensible heat flux, and often large on summer days at our sites, would be underestimated as well. As a result, the relative uncertainty in the corrected CO_2 flux would be less than the uncertainties in the raw fluxes, but could still be substantial for annual sums. Massman and Lee (2001) reviewed several other ways by which the ‘true’ net exchange may fail to be measured at sites where three-dimensional effects occur and when strongly stable and unstable conditions apply.

Second, a major source of uncertainty lies in the discrepancies, we observed between nighttime measurements of ecosystem respiration with OP and CP eddy flux systems (see Appendix A). If the analysis method we adopted after the careful comparisons was not appropriate, and the CP measurements were to be used, then Appendix A shows that annual NEE would be reduced by up to 200–300 g C m^{-2}. Since CP systems are used by many groups worldwide, it is important to resolve this uncertainty by conducting comparisons of instrumentation over different surface types and in a wide range of atmospheric stabilities.

Given uncertainties of the magnitude we have estimated earlier, we do not think it useful to estimate absolute values of micrometeorologically-determined annual NEE at the Y and O sites. However, it is clear from Fig. 6 that ecosystem respiration (R_e) and GEP were generally greater at the O site than Y site, and the net of these two processes resulted in a lower net carbon uptake at the Y site. Although we are not confident of the absolute values of fluxes summed over long periods, we are much more confident in weekly and seasonal comparisons between the sites, and the analysis of environmental controls on fluxes.

4. Conclusions

Application of eddy covariance methods to measure carbon and water exchange at our sites is challenging because of the semi-arid climate, heterogeneous vegetation and non-ideal topography for micrometeorology. It is clear from our results and from other critical analysis (Baldocchi et al., 2000; Goulden et al., 1996; Moncrieff et al., 1996; Wilson and Baldocchi, 2001) that eddy covariance can be problematic for determination of absolute values of annual net carbon exchange, particularly at sites with complex topography. To improve the capabilities of eddy covariance at non-ideal sites, further research is needed on the causes of differences between OP and CP measurement systems, reasons for lack of energy closure, assessment of advective fluxes, and source area definition in stable conditions.

Using eddy covariance studies of carbon and water exchange with associated work at chamber and plot scales, we have shown how the carbon and water cycles interact in this semi-arid environment, and how the interaction varied between the different aged stands. In particular, we found a strong contrast between the young and old-growth ecosystems in their water and carbon exchange after July, as the ecosystem at the Y site experienced more water stress. The influence of age on responses to seasonal water shortage that we have observed may be typical of trees in semi-arid environments. During early growth, trees partition more assimilate into foliage than into stems (Law et al., 2001d; Smith and Paul, 1988). This creates a hydraulic system that is vulnerable to water stress. As the trees reach maturity, roots extend deeper and access more water, the water storage capacity in stems increases to provide a buffer against short-term water stress, and stomatal conductance decreases. These changes with age all reduce the probability of older trees experiencing the extreme water stresses of their youth. To establish the relationships between carbon uptake and age, and the interactions between water stress and age, we need to extend measurements to other age classes, and to use the information presented here to help improve physiological process models applied to water-limited forest ecosystems.

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Appendix A. Accuracy of eddy covariance

A.1. Energy closure

Evaluation of energy closure is helpful in diagnosing the quality of the flux data. Energy closure, expressed as $((H + \mathrm{LE})/(R_\mathrm{n} - G - S))$, where G is the soil heat flux, S is the heat storage beneath the flux system, and other terms have been defined earlier, was similar at both sites, about 75–80% on a daily basis and about 75% on a 1/2 h basis (the y-intercepts ($\mathrm{MJ\,m^{-2}}$) and slopes of linear regressions between $(H + \mathrm{LE})$ and $(R_\mathrm{n} - G - S)$ using daily data were -0.63 and 0.79 (O site, $r^2 = 0.93$) and -0.48 and 0.78 (Y site, $r^2 = 0.98$)). The failure to achieve closure may be because the eddy covariance instruments systematically underestimated fluxes, or because we have not accounted for advection or mesoscale transport, which may be important in the frequently strong convective conditions that occurred on summer days. In addition, significant low-frequency contributions to fluxes may not be detected because of time series de-trending and calculation of fluxes on 1/2 h basis. Overestimation of net radiation in these open-canopy ecosystems is unlikely to be the main cause for the lack of closure (Anthoni et al., 2000). A review by Wilson et al. (2002) demonstrated that energy closure at several FLUXNET sites worldwide was ∼80%, indicating that the problem is widespread and needs explanation.

The lack of energy closure has implications for the determination of CO_2 flux using an OP IRGA design. The CO_2 flux associated with density fluctuations (the WPL term, $\delta F_{c,d}$) was calculated following Webb et al. (1980). At our sites, the main contribution to $\delta F_{c,d}$ was generally from sensible heat exchange (i.e. $\delta F_{c,d} = 0.044H$, $r^2 = 0.99$, at the Y site, where $\delta F_{c,d}$ is in μmol m^{-2} s^{-1} and H is in W m^{-2}). If H was underestimated due to systematic sensor characteristics, this would result in a selective systematic overestimate of daytime CO_2 exchange rates, since daytime H is generally many times larger than nighttime H in semi-arid ecosystems. For example, consistent underestimation of ~10% in H would lead to an overestimate of annual net carbon gain of ~100 gC m^{-2} at our sites. Seasonal differences in sensible heat exchange between sites could lead to a bias in the WPL term between sites, but for a 10% error in H these would result in $<0.3\ \mu$mol m^{-2} s^{-1} bias in F_c between the Y and O site. Although there is uncertainty in the absolute magnitude of CO_2 fluxes at the sites, we are confident that our flux comparisons between sites are valid because the energy imbalance was about the same at the Y and O sites.

A.2. Eddy covariance system intercomparison

We assessed the accuracy of our eddy covariance measurements in several ways: by operating OP (LI-COR model 7500) and CP (LI-COR model 6262) systems at the same height for relatively long periods; by operating the O site eddy covariance system next to the eddy covariance system at the young site; and by comparing nighttime eddy covariance fluxes with those estimated independently from chamber measurements. Additionally, for about a month in summer 2000, we operated two additional OP systems at the Y site (Law et al., 2001c). Instruments were calibrated using molar concentration units.

We co-located the O and Y eddy covariance systems at the Y site for 3 days in spring of 2001. Exchange rates (F_c, LE, and H) measured by the two systems were within 3, 4 and 4% for H, LE, and F_c, respectively. Consequently, flux differences between our sites exceeding 4% are likely to be real. Eugster et al. (1997) reported similar accuracy from intercomparisons.

In summer of 2000, we operated several flux systems at various heights at the Y site. There was good agreement between OP flux systems and the scaled ecosystem respiration from chamber data at night. Specifically, on the night of DOY 206/207, we found no significant difference between the scaled-up chamber estimates of ecosystem respiration (2.41 μmol m^{-2} s^{-1}, S.E. 0.83) and eddy fluxes measured at 3.6 m height ($P > 0.05$), and there was no significant difference at night between eddy fluxes measured at 3.6 m (2.64 μmol m^{-2} s^{-1}, S.E. 0.14), and 12 m (2.85 μmol m^{-2} s^{-1}, S.E. 0.15; $P > 0.05$) (Law et al., 2001c). But the nighttime CO_2 flux measured with a CP system was significantly higher (4.2 μmol m^{-2} s^{-1}, S.E. 0.15; $P = 0$) than both OP systems and the chamber estimate of R_e. Fig. 7a compares CO_2 flux measured with the OP ($F_{c,OP}$) and CP IRGAs ($F_{c,CP}$) at the Y site over 54 days in summer 2000. There was generally good agreement between the measured CO_2 fluxes ($F_{c,CP} = 1.033F_{c,OP} + 0.706\ \mu$mol m^{-2} s^{-1}, $n = 2475$, $r^2 = 0.95$), but consistent small differences were evident at night. Fig. 7b shows that the nighttime difference ($F_{c,CP} - F_{c,OP}$) appears to be related to the friction velocity u^*, with the OP system tending to estimate lower respiration than the CP system with increasing turbulence. Over a deciduous forest, Baldocchi and Evans (personal communication) also measured higher nighttime CO_2 flux with a CP system than with an OP system. Interestingly, the difference between OP and CP is less if no frequency response corrections are applied to the CP data (Fig. 7b). Frequency response corrections to closed-path IRGAs (to account for high frequency losses caused by sampling through tubing), and to sonic anemometers, depend on atmospheric turbulence spectra, and it is not certain that currently used methods, which were derived from measurements over less aerodynamically rough surfaces, often in neutral stability, are valid in the ranges of stability that we observed (Massman and Lee, 2001).

Recognizing the differences between OP and CP systems in measuring nighttime fluxes at large friction velocities (Fig. 7b), we estimated the potential bias that would be introduced by these differences in estimating NEE. We estimated parameters of the soil respiration model (Eq. (1)) with data from each (CP and OP) system, using only valid data (Appendix B), and also calculated the light response relationship between NEE and PAR as determined from each system. During the 54 days with the CP system operational,

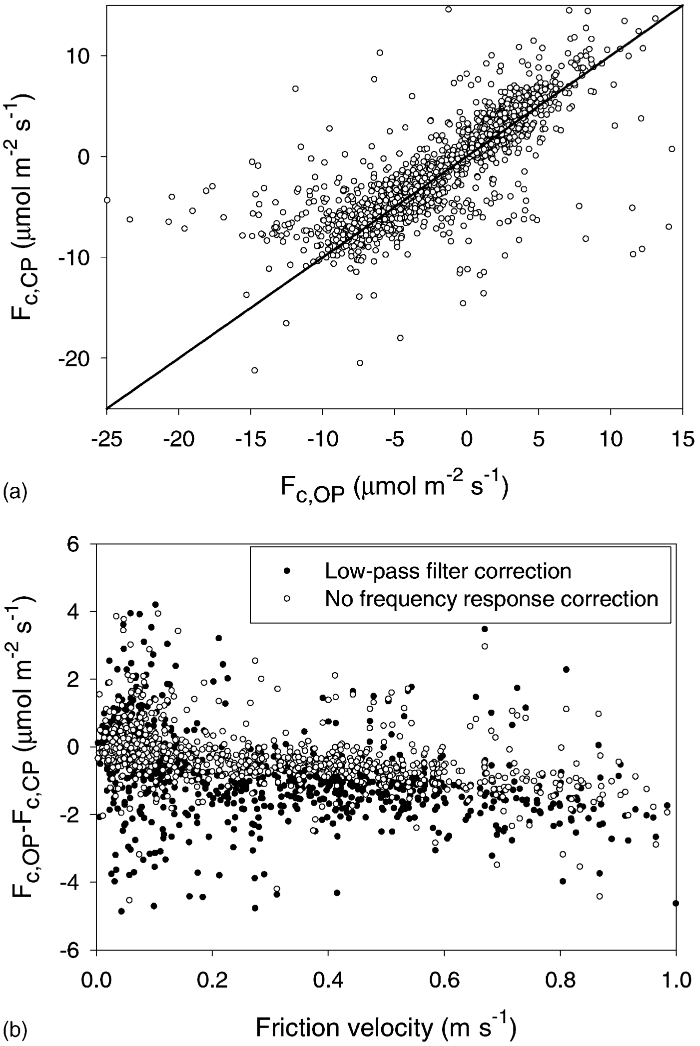

Fig. 7. (a) Open-path ($F_{c,OP}$) vs. closed-path ($F_{c,CP}$) CO_2 flux during 54 days in summer at the young site. (b) Nighttime difference between open- and closed-path estimate of CO_2 flux with respect to nighttime turbulence. The difference is shown for the cases of the closed-path sensor corrected (solid symbols) and not corrected (open symbols) for high frequency attenuation; in both cases, a correction for tube lag was applied.

the estimated nighttime respiration was 79 g C m^{-2} (CP) and 57 g C m^{-2} (OP). Using the light response curves, the estimated daytime net carbon gain was −111 g C m^{-2} (CP) and −129 g C m^{-2} (OP). Thus, the model estimate of NEE summed over the 54 days was −33 g C m^{-2} (CP) and −72 g C m^{-2} (OP), i.e. the CP estimate was 54% smaller than the OP estimate. If this bias was maintained, and applicable on an annual basis, annual NEE measured with a CP system could have been ~200–300 g C m^{-2} per year less than NEE measured with an OP system. The weight of evidence reported earlier supports the OP system, but clearly, it is desirable to make OP/CP intercomparisons on a year-round basis to assess possible errors (power limitations at our sites do not allow this to be done at present).

Appendix B. Variation of measured nighttime flux with wind speed and direction

To determine turbulence conditions that would lead to acceptable nighttime flux data, ecosystem respiration rates $R_{\mathrm{e,fc}}$ ($F_{\mathrm{c}} + F_{\mathrm{s}}$) measured by eddy covariance (OP system) were first normalized to 10 °C using Eq. (1). Fig. 8, showing the variation in normalized values ($R_{\mathrm{e}_{10}}$) with friction velocity (u^*), demonstrates that at both sites $R_{\mathrm{e}_{10}}$ was not constant over the range of turbulence conditions, and that wind direction had a large influence on $R_{\mathrm{e}_{10}}$ at the Y site.

For calm conditions ($u^* < 0.15\,\mathrm{m\,s^{-1}}$), and winds from the north, we believe that the micrometeorological estimates of respiration at the Y site are very likely underestimates (as is evident in the drop of the normalized respiration rate). This underestimating of respired CO_2 at low u^* is commonly observed at other

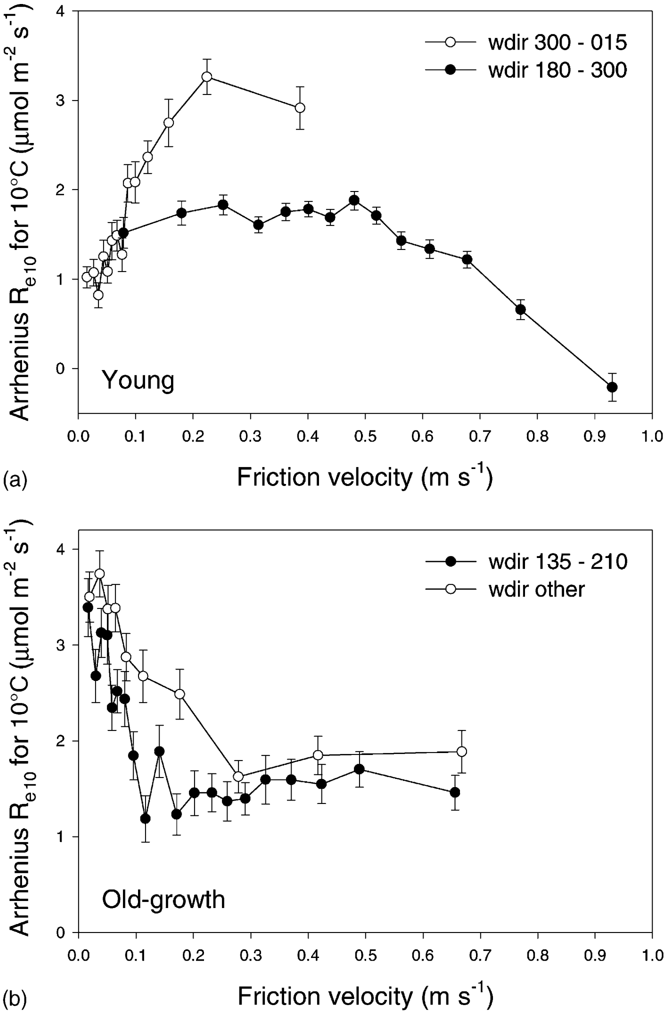

Fig. 8. Normalized respiration rate for 10 °C ($R_{\mathrm{e}_{10}}$) vs. measure of turbulence (u^*, friction velocity): (a) young site; data were separated into two main wind direction sectors (180–300° with 51% and 300–15 with 34%). The third sector (15–180) is not shown since insufficient data points are available for analysis. (b) Old-growth site; data were separated into two wind sectors, 135–210° (46%), and all other wind directions (excluding directions with winds blowing through the flux tower). Data are binned in both panels (a and b) with an equal number of data points per bin. Error bars are estimated standard errors.

research sites and may lead to significant overestimation of NEE (Goulden et al., 1996; Massman and Lee, 2001). The region to the north of the tower at the Y site is slightly elevated, and observations by Mahrt (personal communication) indicate that a shallow gully to the northeast could generate drainage flow of CO_2 in calm conditions away from and around the tower. The decline in $R_{e_{10}}$ for calm conditions was not apparent for winds from the southwest.

With southwest winds at the Y site, independent estimates of respiration from chamber data ($R_{e,ch}$) which were dominated by soil respiration, compared very well with $R_{e,fc}$ (Law et al., 2001c), but when wind speeds from the southwest were large ($u^* > 0.6\,m\,s^{-1}$), it appears that the eddy flux system underestimated $R_{e_{10}}$ (Fig. 8a). An increasing number of negative CO_2 fluxes (i.e. towards the canopy) were observed as friction velocity increased above about $0.6\,m\,s^{-1}$. These observations at large u^* may be caused by pressure pumping of CO_2 into and out of soil at high turbulent intensities and/or by the wind flow over rough topography. Alternatively, bluff body effects associated with terrain obstacles could produce spatial variation of scalar fluxes, and hence, horizontal advection (Massman and Lee, 2001). As we are unable at present to establish the causes of the apparent decline in respiration flux, we exclude these high wind speed periods from further analysis.

For wind directions at the Y site from the north sector, at $u^* > 0.15\,m\,s^{-1}$, $R_{e_{10}}$ was about $1\,\mu mol\,m^{-2}\,s^{-1}$ larger than for similar wind speeds from the southwest sector (Fig. 8a). Because the 'footprint' from which respired CO_2 reaches the eddy covariance instrumentation is large at night, it is difficult to determine the cause for the wind direction dependence in $R_{e_{10}}$. Since soil respiration R_s, is the major component (∼70%) of ecosystem respiration at our sites (Law et al., 2001d), we examined several independent chamber studies of R_s. Average soil respiration rates were relatively constant within about 100 m of the tower, but microscale variation of R_s associated with vegetation heterogeneity was large (coefficient of variation ∼40%) (Law et al., 2001d).

Given the good agreement between chamber and eddy covariance estimates of respiration with southwest winds, we conclude that the larger respiration rates determined by eddy covariance when winds were from the north are not representative of respiration sources near the Y site flux tower. There is an older stand about 1 km to the north of the tower, and at night the footprint of the above-canopy system may be large enough to include respiration from that stand.

In summary, we conclude that nighttime flux data at the Y site are acceptable only with winds from the southwesterly sector and when $0.1 < u^* < 0.55\,m\,s^{-1}$. Applying these restrictions, about 20% of the available nighttime data are classified as representative of respiration sources near the flux tower. Using these data, we derived relationships between respiration and temperature, which we used for filling in missing or unacceptable nighttime data and for estimating respiration during daytime.

At the O site, there was no clear dependence of $R_{e,fc}$ on wind direction. However, values were quite variable (Figs. 8b and 9b), perhaps partly because of shear-generated gravity wave events that are common in and above vegetation canopies at night (Massman and Lee, 2001). Additionally, soil CO_2 fluxes are significantly higher at the O site in patches of young trees than in patches dominated by old trees (Law et al., 1999a). Young, mixed, and old patches are probably also included in the footprint under stable nocturnal conditions. Thus, variability in nighttime eddy fluxes at the O site may be caused by biological and physical factors. We did not see clear evidence for loss of CO_2 at low u^*, as commonly observed at other research sites (Goulden et al., 1996; Massman and Lee, 2001; Sun et al., 1997).

The increase in $R_{e_{10}}$ at low u^* at the O site (Fig. 8b) is probably an artifact of our simple normalization method. Measured respiration ($F_c + F_s$) was relatively constant with u^* (Fig. 9b). But soil temperature at 2 cm was typically several degrees lower at low u^* than at high u^*, so the Arrhenius normalization generates unrealistic values at this site. On the basis of Fig. 9b and the preceding discussion, we chose to accept data for all u^* conditions at the O site.

Fig. 9 shows the partitioning of nighttime CO_2 exchange between turbulent flux (F_c) and change in CO_2 storage (F_s). At the Y site, F_s was only a minor contribution to nighttime CO_2 exchange for all turbulent conditions. At the O site, F_s was the dominant term for calm conditions and made a significant contribution at medium to high u^*. The counter gradient flux (negative F_c) measured at $u^* < 0.1\,m\,s^{-1}$ accounts for some of the change in CO_2 storage, and may indicate effects of

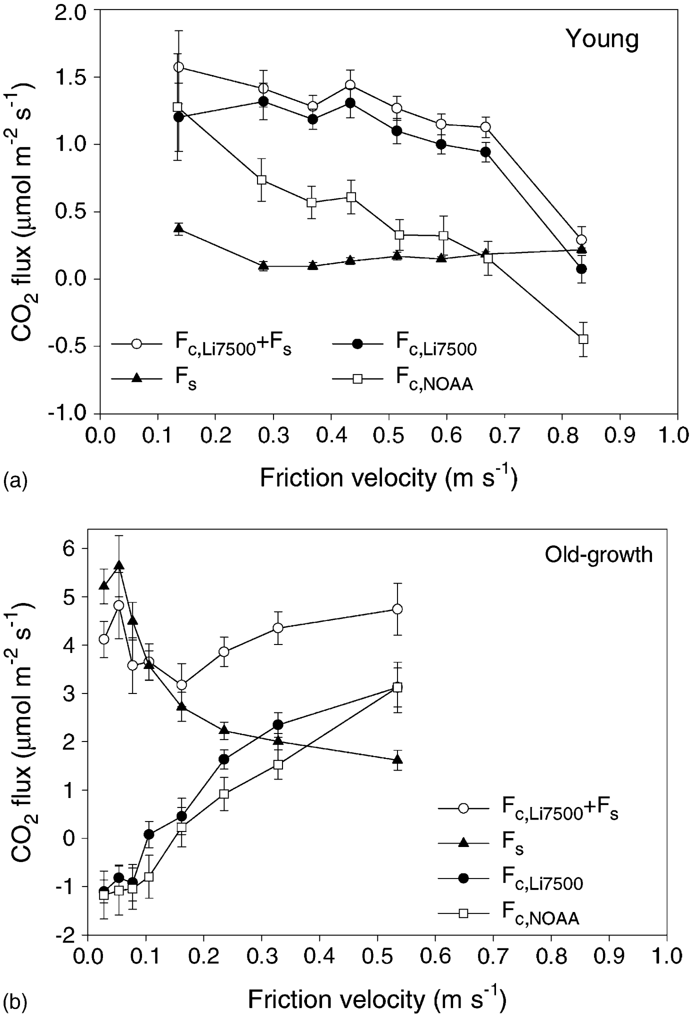

Fig. 9. CO_2 flux components vs. measure of turbulence. F_c is eddy flux, F_s is change in storage. (a) Young site: data are from an intercomparison of Li-7500 ($F_{c,Li\text{-}7500}$) and NOAA/ATDD ($F_{c,NOAA}$) open-path flux systems during 27 days in August and early September. Data are limited to winds from the west. (b) Old-growth site: data are from an intercomparison of Li-7500 and NOAA/ATDD flux systems during 42 days in July–August. Data are bin averaged in both panels (a and b) with an equal number of data points per bin. Error bars are estimated standard errors.

gravity waves, and other sporadic three-dimensional air motion.

We interpret these results as follows. At the O site, the tall vegetation and location in a valley allow CO_2 to accumulate at night, which leads to the large contribution of F_s to nighttime CO_2 exchange over a large range of turbulence. At the Y site, on a slightly sloping plateau, with shorter vegetation and a more open-canopy architecture, respired CO_2 does not accumulate and is easily flushed out and transported upward, even during low wind conditions. In earlier published work at the O site (Anthoni et al., 1999; Law et al., 1999a,b), we reported that $F_c + F_s$ did not compare well with chamber data under higher u^* conditions. We now believe that the discrepancy may be due to a significant underestimation (~1 $\mu mol\,m^{-2}\,s^{-1}$) of nighttime F_c measured by the NOAA/ATDD OP IRGA that we used. However, eddy flux estimates of ecosystem respiration were also reported lower than chamber estimates by 6–42% for six Boreal sites and by 25% for a deciduous hardwood forest (Goulden et al., 1996; Lavigne et al., 1997).

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