



Midday values of gross CO₂ flux and light use efficiency during satellite overpasses can be used to directly estimate eight-day mean flux

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Abstract

Most satellites provide, at best, a single daily snapshot of vegetation and, at worst, these snapshots may be separated by periods of many days when the ground was obscured by cloud cover. Since vegetation carbon exchange can be very dynamic on diurnal and day-to-day timescales, the limited temporal resolution of satellite data is a potential limitation in the use of these data

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to estimate integrated CO₂ exchange between vegetation and the atmosphere. Our objective in this study was to determine whether consistent relationships exist between midday carbon flux on clear days and daily or 8-day mean values. CO₂ flux data were obtained from eight sites, covering a wide range of vegetation types, which are part of the AmeriFlux system. Midday gross CO₂ exchange was highly correlated with both daily and 8-day mean gross CO₂ exchange and these relationships were consistent across all the vegetation types. In addition, it did not make any difference whether the midday data were derived from the AM or PM satellite overpass times, indicating that midday depression of photosynthesis was not a significant factor in these relationships. Inclusion of cloudy days in the 8-day means also did not affect the relationships relative to single clear days. Although there was a relationship between photosynthetic rates and photosynthetically active radiation (PAR) for half hour data, this relationship tended to saturate at PAR values less than half of full sun and for many of the sites the relationship between daily total photosynthesis and PAR was very weak. Consequently, cloudy conditions had less effect on daily gross CO₂ exchange than would have been expected. Conversely, the saturation of photosynthesis at moderate PAR values resulted in considerable variation in light use efficiency (LUE). LUE was higher for daily and 8-day means than it was at midday on clear days and the correlation between midday and 8-day mean LUE was relatively weak. Although these results suggest that it may not be possible to estimate 8-day mean LUE reliably from satellite data, LUE models may still be useful for estimation of midday values of gross CO₂ exchange which could then be related to longer term means of CO₂ exchange.

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1. Introduction

Satellite data are increasingly being used to estimate carbon exchange between the vegetation and the atmosphere at regional and global scales (Sellers et al., 1995; Ruimy et al., 1996a; Running et al., 2004). A limitation of satellite data, however, is that they provide only a snapshot in time, generally once a day around midday. In addition, cloud cover results in many missing days of data. Consequently, it is necessary to develop models that predict integrated carbon exchange from these infrequent snapshots. Most such models use satellite data to estimate leaf area index (LAI) and/or the fraction of incident photosynthetically active radiation absorbed by green plants (f_{par} ; Myneni et al., 2002) and then estimate carbon exchange from physiological or light use efficiency (LUE, Monteith, 1972) models.

Although LUE is generally estimated either from lookup tables based on vegetation type or from physiological models, recent studies have suggested that it can also be estimated directly from spectral reflectance indices. Of primary interest has been the photochemical reflectance index (PRI, Gamon et al., 1992) that has been shown to correlate with LUE at leaf (Gamon et al., 1992, 1997; Peñuelas et al., 1995, 1998), canopy (Gamon et al., 1992, 2001; Filella et al., 1996; Styliniski et al., 2002; Trotter et al., 2002), stand (Nichol et al., 2000, 2002; Rahman et al., 2001;

Strachan et al., 2002) and landscape (Rahman et al., 2004) levels. However, since both LUE and PRI are dynamic (PRI can change rapidly, on the order of 10–30 min, in response to changing environmental conditions, Gamon et al. (1992), estimates of LUE based on a single midday snapshot on clear days may not be representative of the diurnal variation in LUE or of its value on cloudy days. Because of the tendency of photosynthetic processes to saturate at high light intensities, LUE is generally higher at low light intensities. Consequently, LUE is higher early and late in the day, as well as on cloudy days, relative to midday on clear days. LUE may also decline as a result of midday depression of photosynthesis resulting from water limitation or other stresses (Larson et al., 1981; Roessler and Monson, 1985; Hirasawa and Hsiao, 1999; Franco and Lüttge, 2002).

Our objective in this study was to examine the extent to which midday values (corresponding to satellite overpass times) of net and gross carbon uptake, as well as midday LUE, are correlated with daily-integrated values of the same variables. To the extent that such correlations exist, and are consistent across vegetation types, midday values estimated from satellite spectral reflectance data could be used to estimate integrated daily totals without the need of more complex models. We also examined the correlations between midday values and 8-day means that included both clear and cloudy days. The 8-day time-period was chosen since

the MODIS satellite data products, such as photosynthesis (MOD17), are often produced as 8-day composites (Running et al., 2004).

A potential complicating factor in the LUE relationships is the effect of diurnal changes in f_{par} resulting from changes in solar elevation angle. In sparse vegetation, diurnal variation in f_{par} can be dramatic (Pinter et al., 1983, 1985; Sims et al., in press) and this could substantially affect the calculation of daily APAR and LUE. Here we use data for diurnal variation in f_{par} for a sparse chaparral vegetation from Sims et al. (in press) to explore the effect of this variation on the relationship between midday and daily LUE. In summary, the two main objectives addressed in this article are: (1) to determine if any relationship exists between the mid-day instantaneous and daily or 8-day composite values of net and gross CO₂ flux and LUE of different ecosystems and (2) to determine the effect of diurnal variation in f_{par} on the relationship between midday and daily LUE.

2. Methods

2.1. Flux data

Carbon flux data were downloaded from the AmeriFlux site (<http://public.ornl.gov/ameriflux/>). Eight sites were chosen that included a wide range of vegetation types (see Table 1). Methods references for each site are also listed in Table 1. One year's data were processed for each site. The year chosen varies somewhat based on availability of both flux data and MODIS satellite data.

Data covering the period from 1000 to 1100 h were averaged to represent the morning (MODIS Terra) satellite overpass time and data from 1300 to 1400 h were averaged to represent the afternoon (MODIS Aqua) satellite overpass. Gap filled data were not used for these midday means. For calculation of daily-integrated values, gap filled data were used whenever they were available for a site. For those sites where gap filled data were not available, daily means were calculated after filling small gaps (less than 2 h) by linear interpolation. Daily means were not calculated for these sites on days with larger gaps.

Eight day means of flux values were calculated using the same 8-day periods as the MODIS 8-day composite products. For sites where gap filled data were not available, we first calculated the 8-day mean for each 1/2 or 1 h interval using all good data points. Then the 8-day mean daily-integrated fluxes were calculated by summing the 1/2 or 1 h means over 24 h. Any 8-day periods where there were fewer than three good data points for any of the 1/2 or 1 h intervals were not used.

2.2. Estimation of gross flux

Since LUE is directly relevant only to photosynthesis, as opposed to respiration by non-photosynthetic tissues, we estimated gross photosynthesis rates from the net carbon flux rates measured by the eddy covariance towers. Where gross flux estimates were available from the eddy tower investigators, we used those values. When gross flux estimates were not available, we estimated daytime respiration based on an exponential relationship between dark

Table 1
Listing of the sites used in this study

Site name	Vegetation type	Latitude	Longitude	Year	Methods references
Blodgett	Evergreen needleleaf forest	38.895	120.633	2001	Goldstein et al. (2000)
Niwot Ridge	Evergreen needleleaf forest	40.033	105.546	2000	Monson et al. (2002)
Howland forest	Evergreen needleleaf forest	45.204	68.740	2001	Hollinger et al. (1999), Hollinger et al. (2004)
Harvard forest	Deciduous broadleaf forest	42.538	72.171	2002	Goulden et al. (1996)
Morgan Monroe	Deciduous broadleaf forest	39.323	86.413	2001	Schmid et al. (2000)
Lethbridge	Grassland	49.708	112.940	2000	Flanagan et al. (2002), Wever et al. (2002)
Vaira	Grassland	38.407	120.951	2002	Xu and Baldocchi (2004)
Tonzi	Woody savanna	38.432	120.966	2002	

No methods reference is yet available for the Tonzi site but methods are similar to those for Vaira

respiration (R) and temperature (Sims et al., in press):

$$R = R_n \times e^{(k(T_a - T_n))} \quad (1)$$

where R_n is the nighttime respiration rate, T_n the mean nighttime air temperature corresponding to the data points used to calculate R_n , T_a the air temperature at the time of estimation of R , and k is a coefficient relating respiration to air temperature (defined here as 0.07, which results in a Q_{10} of 2). Although there is some variability in the reported values of Q_{10} for ecosystem respiration between sites, a value of 2 is in the middle of the range (Goulden et al., 1996; Tjoelker et al., 2001; Reichstein et al., 2002). Since our primary objective was to compare midday to daily values of flux and LUE, rather than assessing the absolute values of these parameters, small errors in estimation of respiration should tend to cancel out.

Gross CO_2 flux (F_{CO_2}) was then estimated from the following equation:

$$F_{\text{CO}_2} = \text{NEE} - R \quad (2)$$

where NEE is the net ecosystem exchange of CO_2 measured by the flux tower.

2.3. Estimation of LUE

We calculated light use efficiency (LUE) from the following equation:

$$\text{LUE} = \frac{F_{\text{CO}_2}}{\text{PAR} \times f_{\text{par}}} \quad (3)$$

where both gross CO_2 flux (F_{CO_2}) and photosynthetically active radiation (PAR) have the same molar units and f_{par} is the fraction of PAR absorbed by green vegetation. For LUE over the longer time periods, daily and 8-day sums of gross CO_2 flux and ($\text{PAR} \times f_{\text{par}}$) were calculated first and then LUE was calculated from the ratio of these sums.

PAR data were those collected at the eddy covariance towers. We decided not to use the MODIS FPAR product (MOD15, <http://modis.gsfc.nasa.gov/data/dataproducts.html>) for estimation of f_{par} because some studies have shown a substantial overestimation of f_{par} by the MOD15 product (Fensholt et al., 2004). Instead, we calculated f_{par} directly from MODIS NDVI (the mean NDVI for nine pixels (3 km \times 3 km)

centered on the eddy covariance tower site) using the relationship reported by (Sims et al., in press):

$$f_{\text{par}} = 1.24 \times \text{NDVI} - 0.168 \quad (4)$$

This relationship was developed from ground measurements of canopies from a wide range of plant functional types (including annuals, vines, deciduous and evergreen shrubs and trees, 16 species in all) where f_{par} was measured with a linear PAR ceptometer (AccuPar, Decagon Devices Inc., Pullman, WA, USA). Since NDVI is sensitive only to green tissues (and light absorbed by non-green tissues does not contribute to photosynthesis) the f_{par} of the woody species was adjusted to represent green f_{par} by multiplying the measured f_{par} by the fraction of total tissue projected area that was composed of green tissues.

In most of these calculations, we were forced to assume that f_{par} was constant over the diurnal cycle since we did not have diurnal data for NDVI. However, some studies have shown that diurnal changes in solar elevation angle can dramatically affect f_{par} , causing it to vary as much as two-fold in a sparse chaparral ecosystem (Sims et al., in press). To test the effect of this variation on the relationship between midday and daily LUE, we used data from the study of Sims et al. (in press) to calculate diurnal LUE either with a constant midday value of f_{par} or with the actual f_{par} that varied diurnally. Sims et al. (in press) calculated diurnal variation in f_{par} based on measurements of diurnal variation in NDVI, which was found to be linearly correlated with f_{par} .

3. Results

3.1. Seasonal patterns of flux and LUE

The selected sites provided a wide range of flux rates and LUEs. Deciduous forests had the highest gross flux rates and one of the grasslands had the lowest (Fig. 1). Seasonal patterns also varied widely. Maximum gross flux rates generally occurred in mid summer for the forest sites, whereas peak rates for the grassland and savanna sites occurred in spring.

Overall, the gross fluxes on clear days (open symbols in Fig. 1) were very similar to the mean

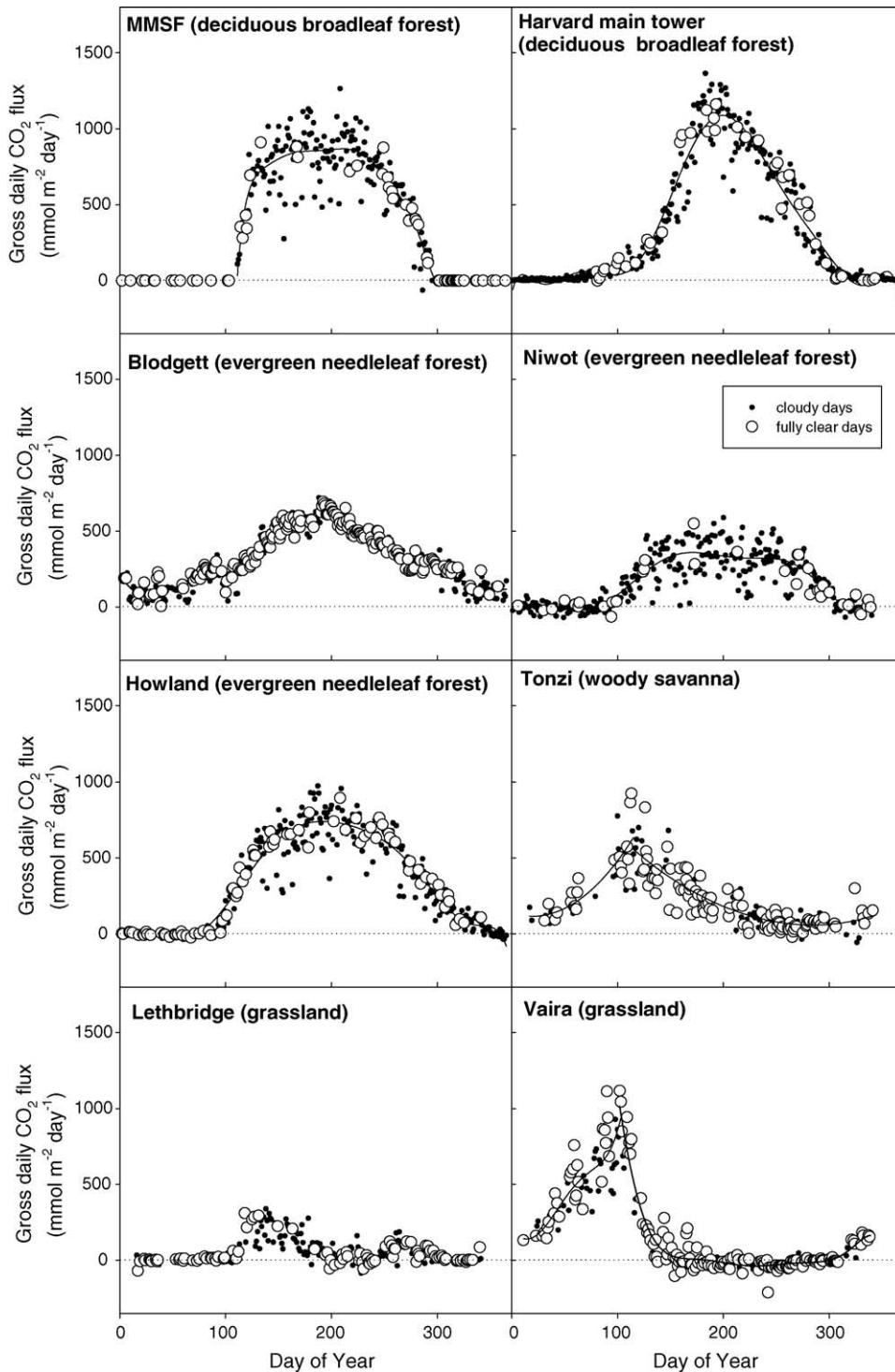


Fig. 1. Gross daily CO₂ flux (24 h totals) as a function of day of year for the eight sites in this study. Large open symbols represent clear days and small closed symbols represent cloudy and partly cloudy days.

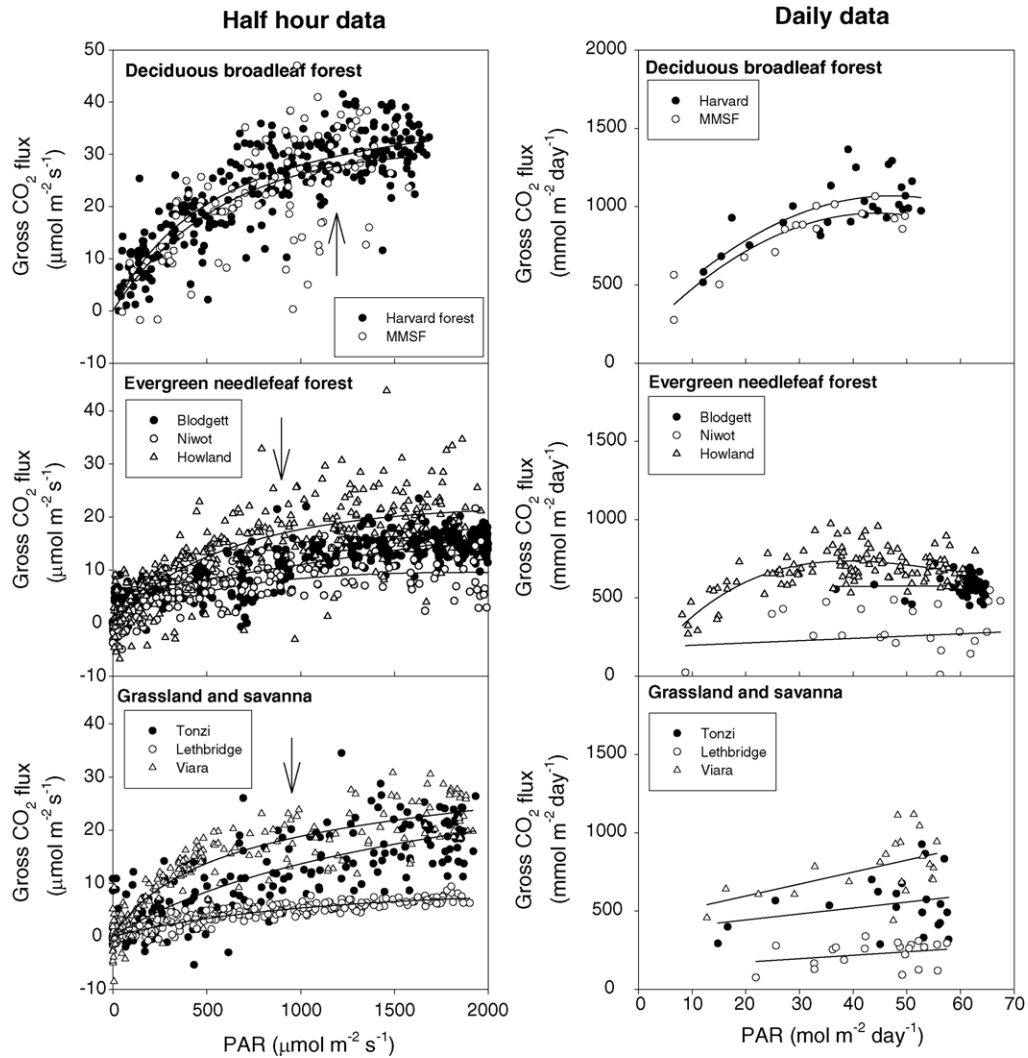


Fig. 2. Gross CO_2 flux as a function of incident photosynthetically active radiation (PAR) for the eight sites in this study. Sites are grouped by vegetation types. Panels on the left side show all the 1/2 or 1 h means of CO_2 flux and PAR during daylight hours over a period of several weeks when photosynthetic rates were highest. Arrows indicate the approximate point of light saturation. The right hand panels show all the daily totals of CO_2 flux and PAR during the same period.

fluxes for all days (indicated by the fitted lines in Fig. 1). One factor contributing to the similarity of CO_2 flux rates on clear and partly cloudy days was the saturation of photosynthesis at PAR values around half of full sun for many of the sites (Fig. 2, left side). In this figure, we used data from only a few weeks during the peak photosynthesis period. This should reduce the effects of factors other than PAR, such as seasonal variation in temperature, leaf area

and leaf physiology. Saturation at high PAR was more pronounced for the evergreen forest and grassland sites than for the deciduous forests. Consequently, although there was a fairly strong relationship between daily PAR and gross CO_2 flux for the deciduous forest sites, this relationship was relatively weak for the other sites (Fig. 2, right side).

In contrast to the gross fluxes (Fig. 1), gross LUE on clear days tended to be lower than the overall mean

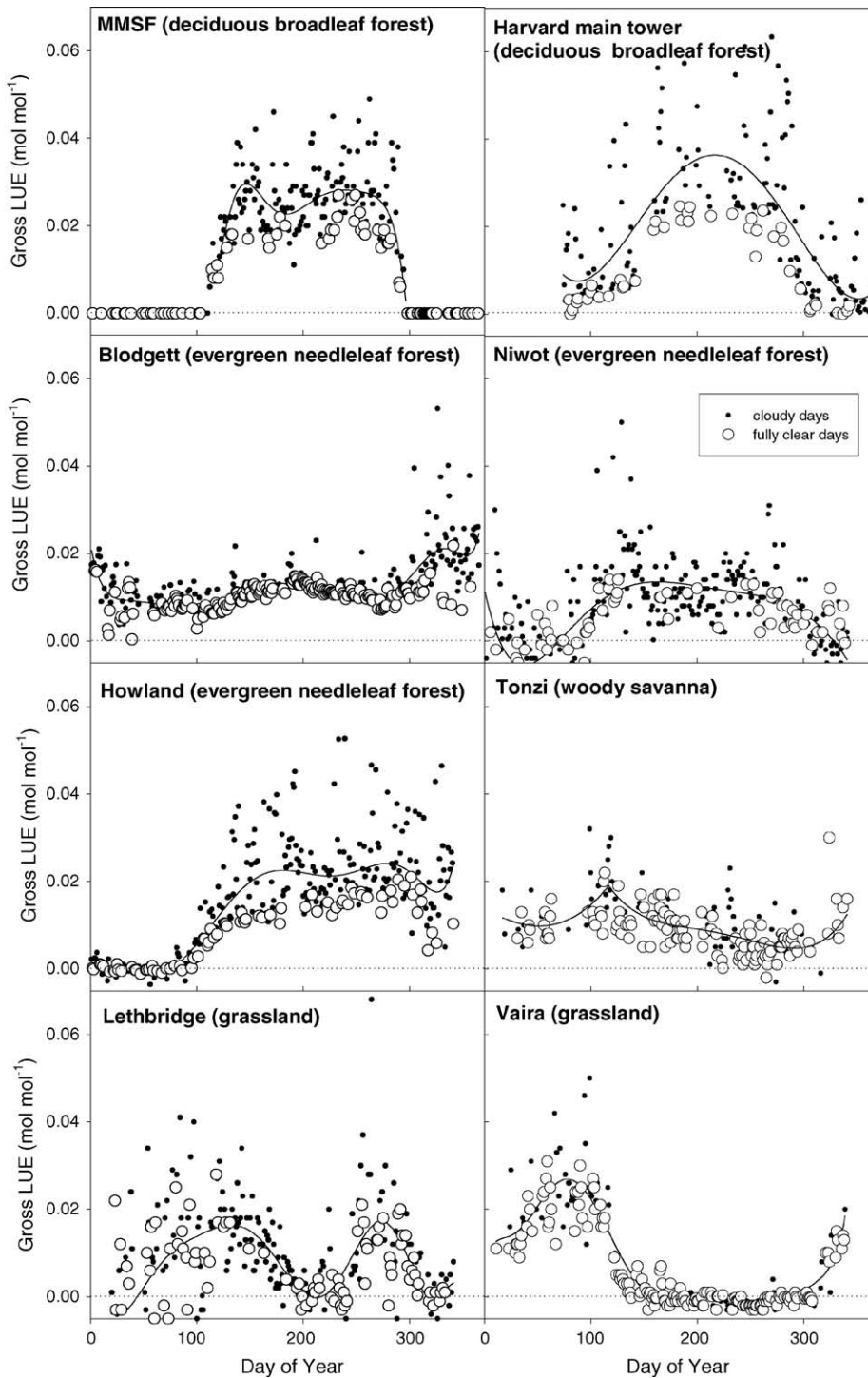


Fig. 3. Gross daily LUE (calculated from 24 h totals of gross CO₂ flux and absorbed photosynthetically active radiation) as a function of day of year for the eight sites in this study. Large open symbols represent clear days and small closed symbols represent cloudy and partly cloudy days.

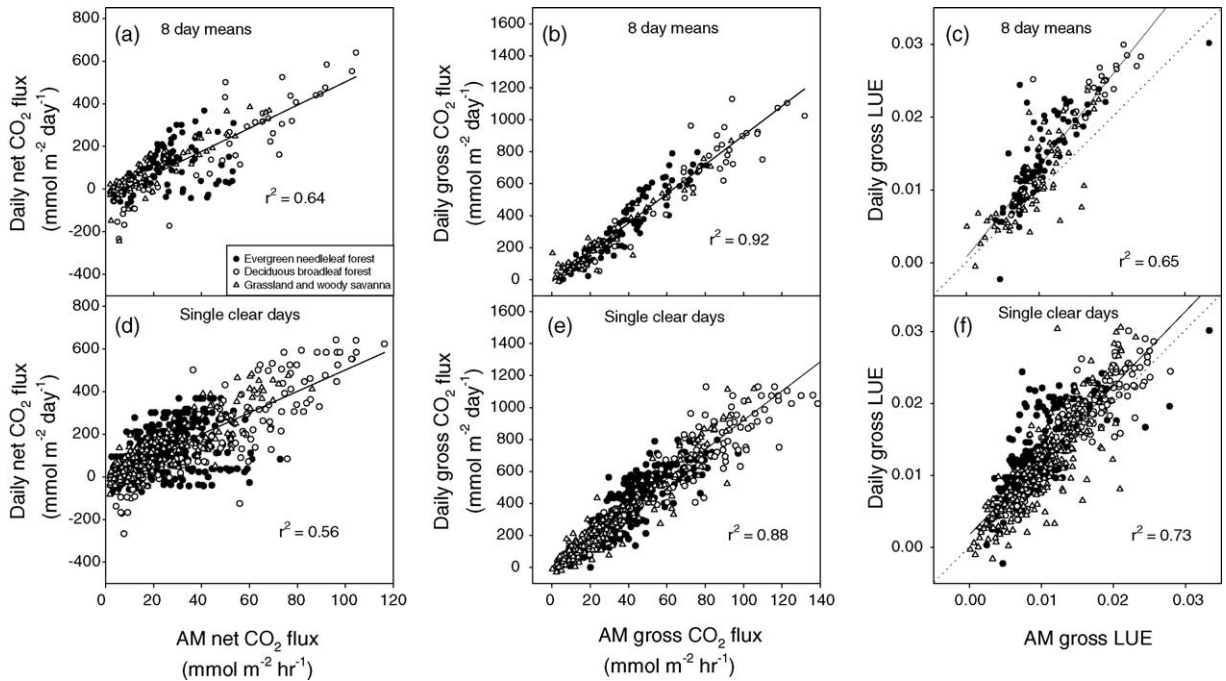


Fig. 4. Relationships between daily (24 h totals) and midday values. Midday values represent the flux or LUE during the morning overpass time of the MODIS satellite on clear days. Data are included both for days that were entirely clear and for days that were partly cloudy but the morning overpass time was clear. For the panels marked single clear days, the morning overpass value and daily values represent the same day. For the panels marked 8-day means, the morning overpass values are the means of all clear overpass periods during those 8 days, and the daily values are the means for all 8 days. Since we wished to examine these relationships only for periods when significant photosynthesis was occurring, data from days with morning net flux rates less than $0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ were excluded from this analysis. Data are split by vegetation type. See Table 2 for slope and intercept of fitted lines.

(Fig. 3). Again, this results from the saturation of photosynthesis at moderate PARs. Since photosynthesis no longer increases with PAR at the higher PAR values, LUE tends to decrease. In general, gross LUE values were more similar between sites than were the gross fluxes since sites with low gross flux also tended to have low f_{par} . Note, in particular, the values of gross LUE for Lethbridge, which are similar to the deciduous forest sites, even though Lethbridge is a grassland in the Canadian prairie with gross fluxes much lower than the other sites. However, there does appear to be a tendency for the evergreen forest sites to have lower LUE.

3.2. Relationship between midday and daily values

The graphs in Fig. 4 examine our ability to predict daily and 8-day means of flux and LUE from values

measured during the MODIS satellite overpass times on clear days. Since the relationships were very similar using either the morning or afternoon overpass times, only the relationships using the morning overpass times (10:00–11:00 AM) are shown. Data from days with morning net flux rates less than $0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ were excluded from this analysis, since we wished to examine these relationships only for periods when significant photosynthesis was occurring. For the panels marked 8-day means, the morning overpass values are the means of all clear overpass periods during those 8 days, whereas the daily values are the means for all 8 days. The strongest relationships between midday and daily values were for gross flux (Fig. 4) and this relationship actually became stronger for data averaged over 8 days than it was for single days. Also note that the slopes of the daily and 8-day gross flux relationships were virtually the same (9.15 and 9.14 for the daily and 8-day

Table 2

Linear regression coefficients for the relationships between midday and daily or 8 day values of net and gross flux and LUE shown in Figs. 4 and 5

	Slope	Intercept	r^2
Midday vs. daily			
Net flux	5.02	−0.93	0.56
Gross flux	9.15	−5.58	0.88
Gross LUE	1.03	−0.0018	0.73
Sky Oaks constant LUE	1.17	0.0022	0.94
Sky Oaks variable LUE	0.89	0.0018	0.91
Midday vs. 8 days			
Net flux	5.44	−41.2	0.64
Gross flux	9.14	−12.2	0.92
Gross LUE	1.25	−0.00075	0.65

relationships, respectively, Table 2). The relationship between midday and daily net flux was considerably weaker. The relationships between midday and daily or 8-day values of LUE were also weaker than those for gross flux. The majority of the data points for the relationships between midday and daily or 8-day LUE fell above the 1:1 line, reflecting increased LUE at low PAR early and late in the day (data not shown), as well as the increased values of LUE under partly cloudy relative to clear conditions (Fig. 3). This effect was most pronounced for the 8-day periods since the 8-day periods included both cloudy conditions and low PFD during early and late day periods, whereas the single day data included only clear days.

3.3. Effect of constant versus variable f_{par}

For a site with a large diurnal variation in f_{par} , making the assumption that f_{par} is constant rather than variable does significantly affect the slope of the relationship between midday and daily LUE (Fig. 5). Most of the points fall above the 1:1 line whether or not a variable f_{par} was used. This results from higher LUE during morning and afternoon periods when light levels were low (below light saturation for photosynthesis) than during midday when photosynthetic processes were light saturated. However, when the observed variable f_{par} was used, as opposed to a constant f_{par} , the daily LUE was lower and the data were closer to the 1:1 line. f_{par} was much higher early and late in the day than it was at midday (data not shown) resulting in lower LUE during those periods when a variable f_{par} was used.

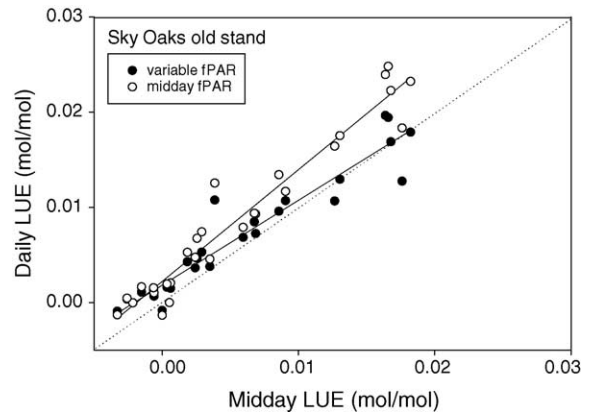


Fig. 5. Comparison of the effect of two assumptions about diurnal variation in f_{par} (constant at the midday value vs. the measured diurnal variation) on the relationship between daily and midday (noon) LUE for the old stand chaparral at Sky Oaks field station in Southern California. See Table 2 for slope and intercept of fitted lines.

4. Discussion

These results demonstrate that midday values of gross CO_2 exchange on clear days can be used to estimate, with fairly high accuracy, both the daily and 8-day means of gross CO_2 exchange, and that these relationships were consistent across diverse vegetation types and sites. Such relationships are of great value for remote sensing of vegetation carbon exchange since satellite measurements of spectral reflectance are generally only available for midday on clear days.

This strong relationship between midday values on clear days and 8-day means is somewhat surprising given the variability in PAR that is likely to occur over an 8-day time-period. Although averaging over 8 days reduces the magnitude of this variation, mean PAR still varied over a range as large as 50% of the mean from one 8-day period to another. This suggests that PAR is not as important in determining gross CO_2 flux as might be expected. In fact, for many of the sites, daily gross CO_2 flux was only a weak function of PAR. This lack of effect of PAR on daily stand photosynthesis results at least in part from light saturation during midday, since the hourly data show saturation around half of full sun. This would result on about three quarters of the photosynthesis on a clear day occurring under light saturated conditions. Light saturation is often more pronounced for sparse natural canopies

with low photosynthetic rates than it is for highly productive closed canopies such as crops (Ruimy et al., 1996b; Baldocchi and Amthor, 2001). This may explain why the deciduous broadleaf forest sites in our study, which had higher photosynthetic rates and more dense canopies, showed less light saturation than the other sites. Another potential explanation for the weak PAR effect on gross CO₂ flux is that light is used more efficiently by plants under cloudy than clear conditions. In fact, some studies have noted higher photosynthetic rates under cloudy as opposed to clear conditions when PAR was the same (Hollinger et al., 1994; Baldocchi and Amthor, 2001).

The relationship between PAR and gross CO₂ flux was stronger for most of the sites when full annual data were used (data not shown), as opposed to just a few weeks during the period of highest photosynthetic rates, as is the case in Fig. 2. However, it appears likely that at least some of this relationship resulted from changes in photosynthetic capacity of the vegetation (through changes in leaf area or leaf physiology), and or effects of temperature, rather than direct effects of PAR. Since light saturation is least pronounced when photosynthetic capacities are highest, the relationships in Fig. 2 should represent the strongest direct effect of PAR at these sites.

It is also interesting that we found the relationships between midday and daily flux to be the same regardless of whether we used the AM or PM satellite overpass times as the midday value. Although midday depression of photosynthesis (Larson et al., 1981; Roessler and Monson, 1985; Hirasawa and Hsiao, 1999; Franco and Lüttge, 2002) might be expected to result in lower values of CO₂ flux in the afternoon than in the morning, we did not observe that in the data for this study. This does not necessarily mean that midday depression of photosynthesis was entirely absent in our data. It may simply be that when it occurred, the photosynthetic rates were relatively low both in the morning and afternoon and thus these points had relatively little effect on the overall relationships.

Unfortunately, midday and daily net carbon flux were not as well correlated, as were midday and daily gross carbon flux. This indicates that respiration rates were not well correlated with midday photosynthetic rates. This is not surprising, given that respiration rates may be controlled by different environmental

variables than are photosynthetic rates (Reichstein et al., 2003). Over longer time periods, gross photosynthesis and respiration tend to be correlated since current photosynthates provide much of the fuel for respiration (Högberg et al., 2001; Janssens et al., 2001) but these relationships would not be expected to be as strong over diurnal time-periods. In addition, some studies have suggested that respiration as a percentage of gross photosynthesis increases with increasing latitude (Valentini et al., 2000). Since estimation of net primary production is often the goal in carbon balance studies, more consideration of the respiratory component is needed.

The same factor (i.e. light saturation of photosynthesis) that tends to result in good relationships between midday and 8-day values of gross flux also leads to poor relationships between midday and 8-day values of gross LUE. The more saturation there is in the photosynthetic light response, the more variability there will be in LUE, since LUE is equivalent to the slope of the relationship between photosynthesis and PAR. Diurnal variation in f_{par} may also contribute to a poor correlation between midday and daily LUE across diverse vegetation types since this would be more of a factor for sparse than for closed canopies. The poor relationships between midday and daily or 8-day mean LUE relative to those for gross flux, suggest that it will be more difficult to use satellite data to estimate LUE over longer time periods. Although the midday value of LUE on a clear day may be a fairly good predictor of the daily LUE (Fig. 4f), it cannot be reliably used to estimate LUE over longer periods that include cloudy conditions. Our results suggest that the better strategy would be to use a satellite based LUE model to predict midday gross flux on clear days and then use the relationship between midday and 8-day mean gross flux to extrapolate these values over longer time periods. Using this strategy would also mean that it would not be necessary to consider the effect of diurnally varying f_{par} on the relationship between midday and daily LUE.

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