

Parallel adjustments in vegetation greenness and ecosystem CO₂ exchange in response to drought in a Southern California chaparral ecosystem

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Abstract

Some form of the light use efficiency (LUE) model is used in most models of ecosystem carbon exchange based on remote sensing. The strong relationship between the normalized difference vegetation index (NDVI) and light absorbed by green vegetation make models based on LUE attractive in the remote sensing context. However, estimation of LUE has proven problematic since it varies with vegetation type and environmental conditions. Here we propose that LUE may in fact be correlated with vegetation greenness (measured either as NDVI at constant solar elevation angle, or a red edge chlorophyll index), making separate estimates of LUE unnecessary, at least for some vegetation types. To test this, we installed an automated tram system for measurement of spectral reflectance in the footprint of an eddy covariance flux system in the Southern California chaparral. This allowed us to match the spatial and temporal scales of the reflectance and flux measurements and thus to make direct comparisons over time scales ranging from minutes to years. The 3-year period of this study included both “normal” precipitation years and an extreme drought in 2002. In this sparse chaparral vegetation, diurnal and seasonal changes in solar angle resulted in large variation in NDVI independent of the actual quantity of green vegetation. In fact, one would come to entirely different conclusions about seasonal changes in vegetation greenness depending on whether NDVI at noon or NDVI at constant solar elevation angle were used. Although chaparral vegetation is generally considered “evergreen”, we found that the majority of the shrubs were actually semi-deciduous, leading to large seasonal changes in NDVI at constant solar elevation angle. LUE was correlated with both greenness indices at the seasonal timescale across all years. In contrast, the relationship between LUE and PRI was inconsistent. PRI was well correlated with LUE during the “normal” years but this relationship changed dramatically during the extreme drought. Contrary to expectations, none of the spectral reflectance indices showed consistent relationships with CO₂ flux or LUE over the diurnal time-course, possibly because of confounding effects of sun angle and stand structure on reflectance. These results suggest that greenness indices can be used to directly estimate CO₂ exchange at weekly timescales in this chaparral ecosystem, even in the face of changes in LUE. Greenness indices are unlikely to be as good predictors of CO₂ exchange in dense evergreen vegetation as they were in the sparse, semi-deciduous chaparral. However, since relatively few ecosystems are entirely evergreen at large spatial scales or over long time spans due to disturbance, these relationships need to be examined across a wider range of vegetation types.

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1. Introduction

Most models of ecosystem carbon exchange based on remote sensing use some form of the light use efficiency (LUE) model. The LUE model states that carbon exchange is a function of the amount of light energy absorbed by vegetation and the efficiency with which that light energy is used to fix carbon

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(Monteith, 1972). Although this is an inherently simple concept, there still are a wide range of definitions of LUE. These differ in the units of carbon exchange (net vs. gross, CO₂ vs. biomass) and light (incident vs. absorbed, total absorbed light vs. absorption only by green tissues) as well as the time period over which the values are summed (instantaneous to annual) (see Gower et al., 1999 for discussion of these issues). In this study we used ecosystem carbon exchange data from an eddy covariance system and consequently defined LUE with an instantaneous form (i.e. half hourly instead of yearly or seasonal data) of the equation:

$$A = \varepsilon' f_{\text{apar}} I_0 \quad (1)$$

where A is the half hourly rate of gross carbon dioxide assimilation, ε' is the half hourly efficiency of conversion of light energy into fixed carbohydrate (i.e. LUE), and f_{apar} is the fraction of incident photosynthetically active radiation (I_0) absorbed by green tissues. Note that we will use “LUE” to signify the general light use efficiency concept and “ ε' ” to signify the specific instantaneous definition of LUE in Eq. (1).

The LUE model is attractive because of the close relationship between absorbed photosynthetically active radiation (APAR) of green tissues and a widely available spectral reflectance index, the normalized difference vegetation index (NDVI) (Choudhury, 1987; Gallo et al., 1985; Goward & Huemmrich, 1992; Hatfield et al., 1984; Sellers, 1985). Estimation of LUE has, however, proven more problematic. LUE can be estimated from mechanistic models based on leaf biochemistry and micrometeorological parameters but these models are complex and generally require many parameters that cannot directly be estimated from remote sensing (Running et al., 1999; Sellers et al., 1995). Several attempts have been made to simplify the situation by proposing that LUE can be considered relatively constant (Monteith, 1972; Field, 1991; Goetz & Prince, 1999). However there is now considerable evidence that LUE does in fact vary over a wide range between vegetation types and in response to environmental conditions (Hunt, 1994; Gower et al., 1999; Green et al., 2003).

Although LUE is clearly not constant, there is another simplifying assumption that could be made. If vegetation chlorophyll content or leaf area index varies in synchrony with photosynthetic activity, as is the case for most annual and deciduous vegetation (Gamon et al., 1995), then we would expect a correlation between greenness indices (e.g. NDVI) and LUE. Furthermore, if investment in green photosynthetic tissue and photosynthetic activity scales with resource availability (e.g. water and nutrients), then we might expect a correlation between greenness and LUE. This is not an unreasonable assumption since vegetation in stressed environments, such as desert and tundra, tend to have low LUEs relative to more productive environments (Gower et al., 1999) and these stressed environments also tend to have low green vegetation cover relative to highly productive environments (Defries & Townshend, 1994). In this hypothetical discussion, when we refer to greenness we mean the amount of investment in green tissues by plants. But for practical purposes in our experiments

greenness will be measured as the value either of NDVI corrected for solar elevation angle effects or a red edge index. The hypothetical relationship between LUE and vegetation greenness is not a mechanistic relationship in the sense that increased greenness directly results in higher LUE. Rather, we hypothesize that greenness and LUE both tend to respond to the same environmental factors over ecological and evolutionary timescales. In this sense it is similar to the functional convergence hypothesis proposed by Field (1991) except that that paper hypothesized a constant LUE.

In Fig. 1, we illustrate the consequences of two hypothetical relationships between LUE and vegetation greenness. Note that units in this figure are arbitrary and thus this figure is not intended to represent absolute values of these parameters, only their relative values. The first hypothesis is a direct proportional relationship between LUE and vegetation greenness (labeled “high plasticity”). This might occur where the vegetation is dominated by deciduous or annual species so that greenness drops to zero at times when gross photosynthesis is also zero. This might also apply to data collected from a wide range of vegetation types where the greenness represents the long-term adjustment of the green vegetation cover to the resource availability in the environment (e.g. “functional convergence”, Field, 1991). The alternative hypothesis (“low plasticity”)

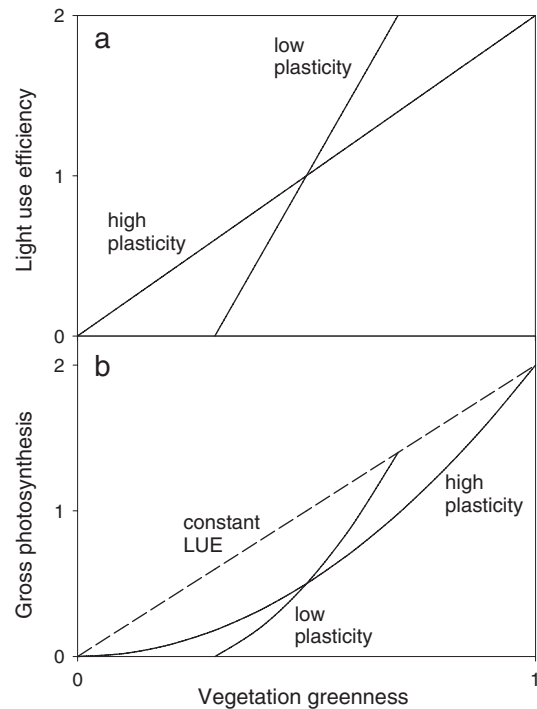


Fig. 1. Hypothetical relationships between light use efficiency (LUE), gross photosynthesis and vegetation greenness. Units are arbitrary. Top panel shows hypothetical relationships between LUE and vegetation greenness for vegetation with a high plasticity in greenness (where LUE and greenness are directly proportional) and for vegetation with low plasticity (where the variation in greenness is less than the variation in LUE). Values of gross photosynthesis in the bottom panel are the mathematical product of LUE and vegetation greenness (making the assumption that vegetation greenness is directly proportional to absorbed photosynthetically active radiation). The dashed line is based on a constant LUE=2.

represents the response of partially evergreen vegetation to seasonal variation in the environment where the range in vegetation greenness is more limited and LUE may drop to zero while vegetation greenness remains significantly above zero. The bottom panel of Fig. 1 shows the effect of these hypotheses on the relationship between gross photosynthesis and vegetation greenness. For this calculation we assumed that APAR was directly proportional to vegetation greenness. This is not true when incident PAR varies but we will ignore this effect for the purposes of the present hypothetical discussion. Both hypotheses result in curvilinear relationships between gross photosynthesis and vegetation greenness with the low plasticity case having a higher slope and a non-zero intercept. The dashed line labeled “constant LUE” represents the upper limit imposed by physiological limits on maximal LUE. Although the relationship between LUE and vegetation greenness is seldom examined explicitly, curvilinear relationships between NDVI and NPP similar in form to our hypotheses in Fig. 1b have in fact been reported (Lo Seen et al., 1993; Paruelo et al., 1997).

Since the hypothesized relationship between LUE and vegetation greenness is ecologically based and dependent on changes in vegetation structure, it is unlikely to apply over short physiological timescales. Over timescales of minutes and hours, changes in spectral reflectance resulting from pigment inter-conversions in the xanthophyll cycle have been found to correlate with LUE (Gamon et al., 1992). The photochemical reflectance index (PRI, which was developed to measure the reflectance changes from these xanthophyll cycle inter-conversions) has shown promise as a measure of LUE at the leaf level (Gamon et al., 1992, 1997; Peñuelas et al., 1995, 1998). Good relationships have also been found between measurements of canopy PRI and LUE for closed canopies or stands of the same species (Gamon et al., 1992; Filella et al., 1996; Gamon et al., 2001; Stylinski et al., 2002; Trotter et al., 2002). However, since canopy structure is predicted to have large effects on the relationship between LUE and PRI (Barton & North, 2001), it is unclear whether these same relationships would apply to structurally complex, patchy, natural vegetation composed of a wide range of species. In fact, a recent study of a sparse, structurally complex Mediterranean shrubland found no relationship between PRI and photosynthesis or LUE (Filella et al., 2004).

We are aware of only a few papers that have compared PRI and LUE at the stand scale for structurally complex, patchy stands (Nichol et al., 2000, 2002; Rahman et al., 2001; Strachan et al., 2002). Although all of these studies found significant relationships between LUE and PRI, they defined LUE in ways that make it difficult to assess the mechanistic basis of the relationships. Nichol et al. (2000, 2002) and Strachan et al. (2002) defined LUE based on incident photosynthetically active radiation (PAR) rather than PAR absorbed by green vegetation (APAR). In contrast, Rahman et al. (2001) considered variation in the fraction of PAR absorbed by green vegetation (F_{apar}) but implicitly assumed a constant PAR between sites and measurement dates. Consequently, it remains unclear how well PRI predicts ecosystem LUE calculated on an APAR basis.

Our objective in this study was to examine correlations between photosynthesis, LUE and various spectral reflectance indices over a range of timescales in a Southern California chaparral ecosystem as a basis for evaluating the LUE model. Although the chaparral is generally considered an evergreen ecosystem with many species retaining some green leaves year round, there is substantial intra-annual variation in greenness resulting from cycles of leaf growth, senescence, and seasonal leaf movement. Consequently, we were able to use this dataset to compare greenness indices (NDVI corrected for solar elevation angle effects, and a new red edge index) with physiological indices (PRI) as predictors of ecosystem LUE and carbon exchange. The period of this study included not only variation resulting from normal seasonal drought cycles but also an extreme drought in 2002 that pushed the system far beyond its normal range of variation and altered the seasonal phenology. Because this extreme drought perturbed the system in unusual ways, it provided a way to determine which relationships between carbon flux and reflectance indices were most robust across a wider range of environmental conditions than are typically encountered in shorter field studies.

2. Methods

2.1. Study site

This study was conducted at Sky Oaks Field station (33.37N, – 116.62W, San Diego County, CA, USA). This region is characterized by a Mediterranean climate with most precipitation falling between the months of October and April. The mean annual temperature and precipitation are 14 °C and 50 cm, respectively (Marion & Black, 1988). Elevations range from approximately 1260–1500 m. Soil types include Sheephead (Ultic Haploxeroll), and Tollhouse (Entic Haploxeroll), both of which are considered loamy, mixed, mesic, and shallow (Marion & Black, 1988). In general, the landscape is rough and broken with soils of low fertility overlying a substrate consisting of granite and micaceous schist.

Reflectance and eddy covariance measurements were made in a hard chaparral stand that last burned in 1901 (Krausemann, 1981; Zammit & Zedler, 1992). This stand was dominated by *Adenostoma fasciculatum*, and *Adenostoma sparsifolium*, with a smaller component of *Arctostaphylos pungens* (roughly 60%, 30% and 10% of vegetation cover, respectively). Overall, roughly 50% of the ground surface was covered by vegetation.

2.2. Eddy covariance instrumentation

Net ecosystem CO₂ exchange (NEE) was measured with the eddy covariance technique (Baldocchi et al., 1988; Verma, 1990). Eddy covariance measurements have been made continuously at this site since the spring of 1997, but in this paper we use a subset of flux data only from 2000–2002, coinciding with the dates when whole-ecosystem optical measurements were also available. The flux tower is located at 33.37386N, – 116.62204W (UTM, decimal degrees). The terrain is fairly level and uniform for approximately 200 m in

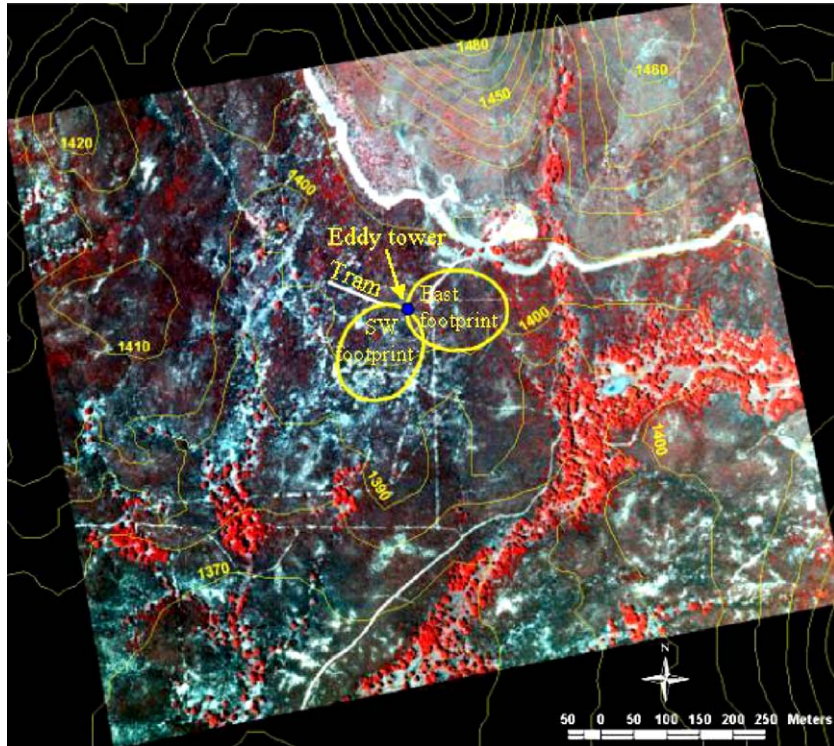


Fig. 2. False color image of the study region obtained from the ADAR imager in June 1998 (see text for details). Labeled on the image are the locations of the eddy covariance tower, the two predominant footprint regions, the tram and 10 m elevation contour lines.

the east, south and west directions from the tower (encompassing a measurement field of view of 60–300°, Fig. 2) that includes the predominant footprint areas. A small hill is located 50 m to the north of the tower and thus data from this wind direction were not used. Because of this asymmetry in the terrain and the prevailing southwest wind direction, the instruments were mounted on the south side of the tower, 4.25 m above the ground surface and 2.5 m above the mean height of the vegetation. Fluctuations in vertical, streamwise and lateral wind speed and temperature were measured at 10 Hz using a three-dimensional sonic anemometer–thermometer (prior to Oct 25, 2001, Model SWS-211/3K, Applied Technologies Inc, Boulder, CO, USA, then switched to a Windmaster Pro, Gill Instruments Ltd., Lymington, Hampshire, UK). CO₂ and H₂O vapor fluctuations were measured using a fast response, 10 Hz, closed-path infra-red gas analyzer with a pressure transducer (Model LI-6262, Li-COR Inc., Lincoln, NE, USA) on dates prior to Oct 25, 2001. After this date, CO₂ and H₂O vapor fluctuations were measured using a 10 Hz open path analyzer (Model LI-7500, Li-COR Inc., Lincoln, NE, USA). For the closed path analyzer a 10 LPM flow rate was maintained using a rotameter and a diaphragm pump through a clear plastic inlet tube (3 mm ID by 3 m long). The inlet for the gas sample tube was located 13 cm behind the vertical path of the sonic anemometer and was affixed with a downward pointing plastic cover to minimize the influx of precipitation in the sample tube. The open-path analyzer was mounted approximately 25 cm behind the sonic anemometer. Calibration was carried out every 2–4 weeks using a gas standard for CO₂ and a dew point generator (Model LI-6110, Li-COR Inc. Lincoln, NE, USA).

At 6 m, wind direction and speed data were collected using an anemometer (RM Young Wind Monitor, R.M. Young Company, Traverse City, MI, USA). At 5.8 and 2.5 m, relative humidity and temperature were measured by a temperature and relative humidity probe (HMP45C, Vaisala, Inc. Woburn, MA, USA) enclosed within a radiation shield (RM Young 12-Plate radiation shield, R.M. Young Company, Traverse City, MI, USA). Photosynthetically active radiation (PAR) between 400 and 700 nm (LI-190SB, Li-COR Inc. Lincoln, NE, USA) was measured at 2.3 m on the tower. All data from the meteorological sensors were averaged over 30 min intervals from observations made every 10 s and stored using a solid-state datalogger (model CR23X, Campbell Scientific Inc., Logan, UT, USA) as well as being transmitted and stored for public viewing at <http://www.sci.sdsu.edu/GCRG/>, “On Line Data Pages”.

2.3. Eddy covariance flux calculations

Raw CO₂ and H₂O vapor fluctuations were output as mean voltages and converted to densities by multiplying by the requisite calibration constant (Vourlitis & Oechel, 1997). Mass (CO₂, and H₂O vapor), energy and momentum fluxes (10 Hz) were computed following a coordinate rotation of the vertical, horizontal, and lateral axes, and stored on a laptop computer as 30-min averages using a 200 s running mean and digital recursive filtering technique (McMillen, 1986, 1988). Carbon and water flux estimates were corrected for the simultaneous flux of heat and H₂O vapor (Suyker & Verma, 1993; Webb et al., 1980).

2.4. Eddy covariance data analysis

Only data with friction velocities (u^*) greater than 0.2 were used. Low u^* is associated with calm air conditions which tend to result in underestimation of CO₂ exchange rates (Goulden et al., 1996). To fill gaps and reduce noise in the data, CO₂ exchange data for each 1/2 h interval over the 24 h cycle were averaged over the week prior to the reflectance measurement. For example, if there were 5 good data points for the 1000–1030 time interval over the 7 days prior to the reflectance measurement, these 5 values were averaged to arrive at a mean value for the 1000–1030 time interval. However, the 1/2 h means were not used (and the data for that 1/2 h interval were considered missing) when there were less than 3 good data points during this week. Using this procedure we were able to fill all gaps during daylight hours.

For calculation of gross photosynthesis we needed an estimate of daytime respiration rates. These are typically estimated from an exponential relationship between dark respiration (R) and temperature (e.g. Reichstein et al., 2002b) such as the following:

$$R = R_n * e^{(k*(T_a - T_n))} \quad (2)$$

where R_n is a baseline dark respiration rate, T_n is the mean nighttime air temperature corresponding to the data points used to calculate the baseline respiration rate, T_a is the air temperature for the time of estimation of R , and k is a coefficient relating respiration to air temperature. However, because of the limited number of good data points during the dark period and changes in respiration in response to seasonal changes in ecosystem water status, it was not possible to determine the value of k from the nighttime data. Instead, we estimated k from both day and nighttime data during August and September of 2002 when severe drought resulted in leaf photosynthetic rates close to zero so that we could assume that net flux equaled respiration. All good net ecosystem flux (F) values during this period were fit to the following equation (which is a simplified version of Eq. (2) with F substituted for R):

$$F = F_0 * e^{(k*T_a)} \quad (3)$$

where F_0 and k were fitted constants and T_a was the air temperature. The value of k was found to be 0.10, which translates into a $Q_{10}=2.72$. This value is on the high side of the range of values reported for whole ecosystem respiration Q_{10} (Goulden et al., 1996; Reichstein et al., 2002a; Tjoelker et al., 2001) although much higher values of Q_{10} have been reported for soil respiration (Janssens & Pilegaard, 2003). We cannot rule out a small residual photosynthetic rate during this period (i.e. F not equal to R). However, if this were the case it would have resulted in a higher, not lower Q_{10} . Thus the measured value of apparent Q_{10} likely represents the minimum apparent Q_{10} during this period. This apparent Q_{10} may be elevated because of differences between air temperature and the temperature of the soil and vegetation. Measurements of soil and canopy temperatures with an infrared thermometer showed that soil surface and canopy temperatures were substantially (10–20 °C)

greater than air temperature during periods of high solar radiation input.

We cannot be sure if this apparent Q_{10} also applies to periods of more adequate moisture supply. However, since other studies have shown decreases in Q_{10} with increasing drought (Reichstein et al., 2002a, 2002b), we again feel that it is safe to assume that the value of Q_{10} measured during the extreme drought represents a minimum value. Lacking any further information about possible changes in Q_{10} , we used this value of Q_{10} for all calculations of day respiration in this study. If there were an increase in Q_{10} corresponding with more favorable growing conditions, this would increase day respiration and gross photosynthesis estimates. However, the effect on gross photosynthesis should be relatively small and since the increases would tend to be positively correlated with the overall value of gross photosynthesis (given the correlation between photosynthesis and respiration), this would not change the qualitative pattern of our results.

2.5. Eddy covariance footprint analysis

Midday wind direction measured at the eddy covariance tower had a bimodal distribution with wind coming from the east about 1/3 of the time and from the southwest about 2/3 of the time. This resulted in two distinct footprints for the eddy covariance tower. The footprints were calculated using a Flux Source Area Model (FSAM-2.0; available through the web site: http://www.indiana.edu/~climate/SAM/SAM_FSAM.html). The FSAM is a probabilistic model based on an estimate of what area of the surface is most effectively influencing the flux value at the measurement point (Schmid, 1994; Schmid & Lloyd, 1999).

2.6. Tram system and spectral reflectance measurements

To obtain reflectance data that matched the spatial and temporal scales of the eddy covariance measurements as closely as possible, an automated tram system (based on the NOAA ATDD tram design, Baldocchi & Vogl, 1996) was installed near the eddy tower. In contrast to satellite based remote sensing, this system allowed us to measure spectral reflectance repeatedly over the diurnal cycle and thus characterize diurnal changes in vegetation reflectance and the effects of changing solar elevation angle. Since we wished to avoid affecting the eddy covariance measurements through our presence while making measurements, the tram was positioned near but not actually within the predominant eddy covariance footprints (Fig. 2). Spectral reflectance images collected from aircraft imaging spectrometers (ADAR System 5500, Positive Systems Inc., Whitefish, MT, USA, and AVIRIS, NASA-JPL, Pasadena, CA, USA) during both wet and dry periods were used to compare the vegetation in the footprint areas to that along the tram-line. NDVI along the tram-line was within 5% of that in the footprint regions for both dry and wet periods, and this variation was much smaller than the seasonal and year-to-year variability, demonstrating a good match between the flux tower footprint and the tram footprint.

The tram was 100 m long (a dimension similar to that of the eddy covariance footprints), was oriented roughly east–west, and began approximately 30 m west of the eddy tower (Fig. 2). The tram track was mounted just above the top of the vegetation which varied from approximately 1.5 m above the ground at the east end to 4 m at the west end. A spectrometer (Unispec or Unispec DC, PP Systems, Haverhill, MA, USA) mounted in a motorized cart ran along the track and measured downwelling and upwelling radiance at approximately 1 m intervals. The cart took 10 min to run from one end of the track to the other. A fiber optic cable (Part# 400010-0200, Romack Inc, Williamsburg, VA, USA) used as a foreoptic for the spectrometer was mounted on a boom at the side of the cart. With a field of view restrictor, this fiber provided an approximately 20° angle of view from a point 1 m above the track and offset 1 m to the south. This provided a view footprint of approximately 0.3 m at the top of the canopy and 1–2 m at the ground surface (depending on the tram height, which varied with topography).

The spectrometers have a nominal spectral range from approximately 305 nm to 1135 nm with approximately 3 nm nominal bandwidth (10 nm full width, half max). Thus, for each measurement, the spectrometer program automatically collected 256 data points covering the entire spectral range. For most of the measurements, we were able to use a version of the spectrometer that has dual detector arrays (Unispec DC, PP systems, Haverhill, MA, USA). This instrument allowed measurements to be conducted under any weather conditions since one of the sensors looked up to measure incoming solar irradiance while the other measured reflected radiance. Spectral reflectances were calculated using a horizontal, lambertian 99% reflectance panel (Spectralon, Labsphere Inc., North Sutton, NH, USA).

2.7. Calculation of reflectance indices

A linear interpolation routine was used to estimate values at 1 nm intervals prior to calculation of indices. The normalized difference vegetation index (NDVI) was calculated from the following formula:

$$\text{NDVI} = \frac{(R_{800} - R_{680})}{(R_{800} + R_{680})} \quad (4)$$

where R_{xxx} is the reflectance at wavelength xxx in nm. Note that all the transect reflectance indices reported in this paper are means of index values calculated for each point measured along the tram line (approximately 100 points). This is in contrast to the alternative method of averaging where the mean reflectance in the index wavebands is calculated across all the spatial points prior to calculation of the indices. Although the method of averaging did in some cases result in small changes in the absolute values of the indices, the overall relationships were not affected, and we decided to use only the first method of averaging in this paper.

In order to more closely measure the greenness of individual leaves, we also developed an index based on the relative height of the two peaks often observed in the first derivative of canopy

reflectance spectra in the red edge region (Horler et al., 1983; Lamb et al., 2002; Shaw et al., 1998; Smith et al., 2004; Zarco-Tejada et al., 2003). Examination of preliminary data suggested that the wavelength position of these peaks was relatively constant at around 700 and 720 nm. Thus we defined the canopy chlorophyll index (CCI) as:

$$\text{CCI} = \frac{D_{720}}{D_{700}} \quad (5)$$

where D_{xxx} is the first derivative of reflectance at wavelength xxx . Similar indices have been developed by Shaw et al. (1998) and Smith et al. (2004) using slightly different wavelengths (719/703 nm and 725/702 nm, respectively). Preliminary data suggested that CCI was closely correlated with the wavelength position of the peak in a Gaussian curve fitted to the first derivative of the red edge region.

PRI was calculated from the following equation (Gamon et al., 1997):

$$\text{PRI} = \frac{(R_{531} - R_{570})}{(R_{531} + R_{570})} \quad (6)$$

2.8. Calculation of solar elevation angle

In order to determine the relationship between solar elevation angle and NDVI, the solar elevation angle at the time of the midpoint of each tram run was calculated with an online program provided by the United States National Oceanic and Atmospheric Administration Surface Radiation Research Branch at <http://www.srrb.noaa.gov/highlights/sunrise/azel.html>.

2.9. Estimation of f_{apar}

We used NDVI to estimate f_{apar} , rather than direct measurements of f_{apar} (i.e. using PAR sensors above and below the canopy), for several reasons. NDVI is more closely related to green f_{apar} than total f_{apar} for systems with a large component of non-green tissues (Daughtry et al., 1992; Gallo et al., 1985, 1993; Gamon et al., 1995; Hatfield et al., 1984; Serrano et al., 2000; Wiegand & Richardson, 1984). The relationship between NDVI and f_{apar} is also fairly insensitive to solar elevation angle (Goward & Huemmrich, 1992; Pinter et al., 1983) meaning that NDVI can be used to estimate changes in f_{apar} over the diurnal cycle. In addition, use of NDVI allows a direct link to satellite measurements.

The relationship between NDVI and canopy green f_{apar} was determined empirically in preliminary measurements using a linear PAR ceptometer (AccuPar, Decagon Devices Inc. Pullman, WA, USA) for direct measurements of f_{apar} . The plants used to develop this relationship included species common at Sky Oaks as well as a wide range of other plant species and functional types (including annuals, vines, deciduous and evergreen shrubs and trees, 16 species in all) common throughout the Southwestern US. Canopy green f_{apar} for the woody species was calculated as total f_{apar} times the

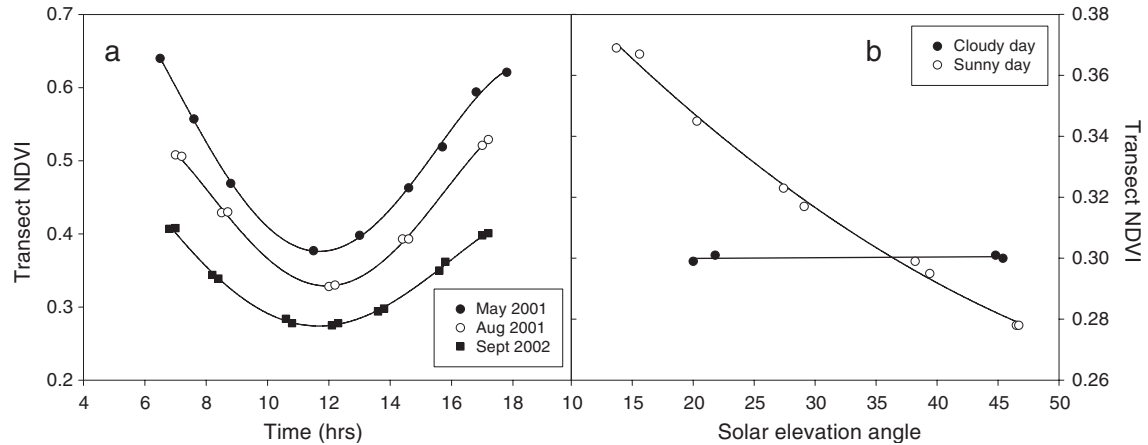


Fig. 3. Representative diurnal timecourses of transect normalized difference vegetation index (NDVI) for three dates ranging from wet conditions (May 2001) to severe drought (Sept 2002) and the effect of sunny (open symbols) vs. cloudy (closed symbols) conditions on the relationship between NDVI and solar elevation angle for two consecutive days in October 2002.

fraction of total tissue projected area that was composed of green tissues. The green fraction was calculated after harvesting the measured portion of canopy, separating green and non-green tissues and measuring their projected areas with an area meter (model 3100, Li-COR Inc., Lincoln, NE, USA). NDVI and green f_{apar} were highly correlated ($r^2=0.95$) with the following linear equation:

$$f_{\text{apar}} = 1.24 \cdot \text{NDVI} - .168. \quad (7)$$

2.10. Calculation of light use efficiency

Hourly and daily light use efficiencies were calculated by solving Eq. (1) for ϵ' and inputting gross CO_2 flux and APAR integrated over the corresponding time periods. Since NDVI and f_{apar} varied with solar elevation angle in this sparse chaparral vegetation, both incident PAR and f_{apar} varied diurnally. Hourly sums of incident PAR were obtained from the eddy covariance tower data. Hourly estimates of f_{apar} were derived from hourly values of NDVI (which in turn were based on measured relationships between NDVI and solar elevation angle) using Eq. (7). Hourly ϵ' was calculated as the ratio of the hourly CO_2 flux and APAR, where APAR was the product of the hourly values of f_{apar} and incident PAR. The incident PAR and CO_2 flux values were the hourly means for the week prior to the reflectance measurements. Daily ϵ' values were calculated as the daily sum of gross CO_2 flux divided by the daily sum of APAR.

2.11. Leaf reflectance measurements

In order to examine the effects of changes in leaf reflectance on transect reflectance, measurements of leaf spectral reflectance were made with a field portable spectrometer (Unispec, PP Systems, Haverhill, MA, USA) similar to the detectors used for the tram measurements. Leaf reflectance was measured with a bifurcated fiber optic cable and a leaf clip (models UNI410

and UNI501, PP Systems, Haverhill, MA, USA). The leaf clip held the fiber at a 60° angle to the leaf surface (30° from normal). Leaf illumination was provided through one side of the bifurcated fiber from a halogen lamp in the spectrometer, allowing rapid, repeatable measurements under field conditions.

To quantify the maximal diurnal change in reflectance resulting from light induced changes in leaf pigments (Gamon et al., 1992), measurements were made both on leaves exposed to full sun at midday and on similar leaves that had been enclosed in black bags since before dawn so that they had not been exposed to any light on the day of measurement. Preliminary measurements demonstrated that dark reflectance measurements were similar for leaves measured before dawn and for leaves enclosed in black bags and measured at mid morning.

Three plants each of the three dominant species (*A. fasciculatum*, *A. sparsifolium* and *A. pungens*) were selected for leaf measurements along the transect. On each plant, measurements were made on three different attached leaves and the results averaged. For *A. pungens* and *A. fasciculatum* measurements were made on individual leaves. However, since the individual leaves of *A. sparsifolium* were too small to cover the end of the fiber optic it was necessary to measure clumps of leaves and thin green stems for this species. A leaf chlorophyll index (CI, Gitelson & Merzlyak, 1994; Sims & Gamon, 2002) was calculated from the following equation:

$$\text{CI} = \frac{R_{750} - R_{705}}{R_{750} + R_{705}} \quad (8)$$

Leaf PRI was also calculated from leaf reflectance using Eq. (6).

3. Results

3.1. Diurnal and seasonal variation in reflectance indices

Transect NDVI varied almost 2 fold over the diurnal cycle and this variation was larger than the seasonal variation

(Fig. 3a). NDVI was strongly related to solar elevation angle on sunny, but not on cloudy days (Fig. 3b), indicating that the angle of incidence of direct light was the controlling factor in the diurnal variation in NDVI in this sparse stand. The sunny and cloudy lines intersect around a solar elevation angle of 36–37°, suggesting that NDVI measured around this solar elevation angle on a sunny day might be useful for estimation of NDVI on cloudy days.

Each of the three indices (NDVI, CCI and PRI) showed a different pattern of response to solar elevation angle (Fig. 4). NDVI had the strongest sensitivity to solar elevation angle, whereas CCI had the smallest. All three indices tended to converge on the soil value as solar elevation angle increased,

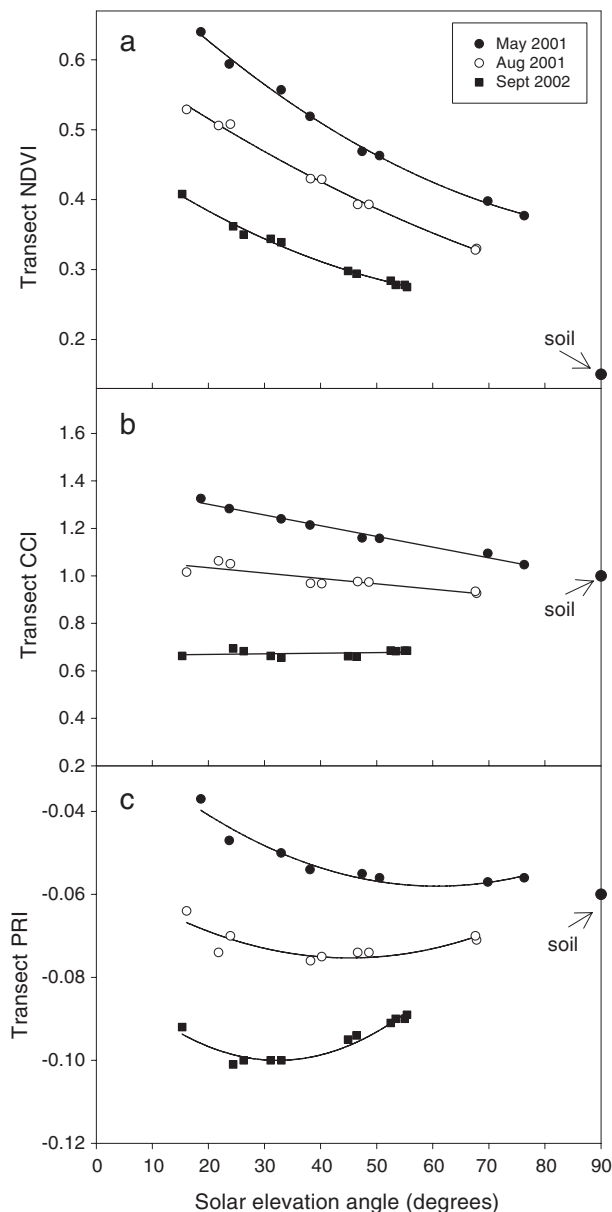


Fig. 4. The effect of solar elevation angle on transect means of normalized difference vegetation index (NDVI), canopy chlorophyll index (CCI) and the photochemical reflectance index (PRI) for three representative days ranging from wet conditions (May 2001) to severe drought (Sept 2002). Representative pure soil values for these indices are also shown.

but note that the extrapolation of these non-linear relationships would still be somewhat offset from the soil point even at a solar elevation angle of 90°. The response of transect PRI to solar elevation angle was more non-linear and complex than the other indices. Since PRI is a dynamic index, this may in part have resulted from diurnal variation in leaf PRI, in addition to solar elevation angle/canopy structure interactions. Although the diurnal change in leaf PRI was small relative to the seasonal changes (Fig. 5a), it was large enough to account for much of the non-linearity in the PRI vs. solar elevation angle relationships (Fig. 4). Across seasons, temperature appeared to account for much of the variation in leaf PRI (Fig. 5b), confounding a simple relationship between PRI and LUE for this vegetation. At a given temperature, leaf PRI was substantially higher for high LUE leaves than for low LUE leaves, but leaf PRI also increased strongly with increasing temperature for leaves with similar LUE.

In this southern California location, solar elevation angle at noon varies from a minimum of 33° in the winter to a maximum of 79° in the summer. Based on the diurnal solar elevation angle relationships (Fig. 4), this change in solar elevation angle would result in as much as a 40% decline in midday NDVI from winter to summer even if there were no change in the greenness of the vegetation. In fact, one would come to entirely different conclusions about seasonal changes in vegetation greenness depending on whether NDVI at noon or NDVI at constant solar elevation angle were used (Fig. 6). In 2001, NDVI at noon was lowest in summer and highest in the winter. In contrast, NDVI at a constant solar elevation angle of 40° showed nearly the opposite trend, with the highest values occurring in the late spring and lowest in the fall and winter. PRI and CCI exhibited seasonal patterns qualitatively similar to those of NDVI corrected to constant solar elevation angle (Fig. 6). Unlike NDVI, correction of PRI and CCI for solar elevation angle effects did not change their seasonal patterns. Consequently, CCI and PRI were more robust measures of seasonal changes in canopy reflectance than was NDVI.

3.2. Relationships between reflectance indices and CO₂ exchange

We did not find consistent relationships between CO₂ exchange or ϵ' and any of the reflectance indices over the diurnal timescale (data not shown), presumably due to the confounding effects of sun angle and stand structure on these indices (Fig. 4). However, there were strong relationships between gross CO₂ exchange and spectral reflectance indices over the seasonal timescale (Fig. 7). Since the relationships with net CO₂ exchange were substantially weaker than those with gross CO₂ exchange, we will present only the gross CO₂ exchange relationships. The best correlation across all years was between CCI and gross CO₂ exchange (Fig. 7a). The correlation of gross CO₂ exchange with NDVI at 40° solar elevation angle (Fig. 7b) was somewhat weaker because of a large decline in NDVI during the extreme drought of 2002 that was not accompanied by any further decline in photosynthesis (Fig. 8). Gross photosynthesis was already zero at the start of the stand

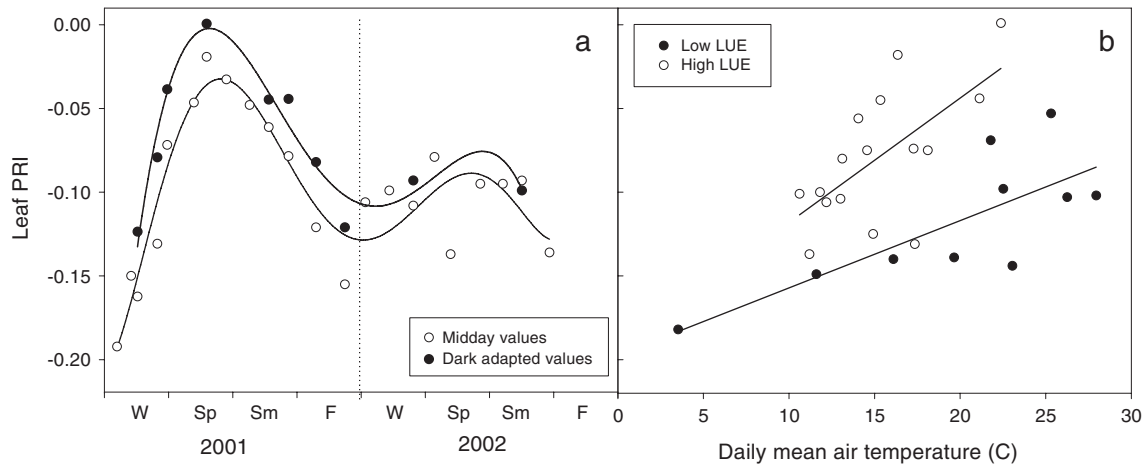


Fig. 5. The left panel shows dark adapted (closed symbols) and midday (open symbols) values of the leaf photochemical reflectance index (PRI) over 2 years (Sp=spring, Sm=summer, F=fall, W=winter). Values represent weighted (by relative cover) means for the three species along the transect. The right panel shows leaf PRI as a function of mean air temperature for the week prior to the reflectance measurement. The data are split between low (0–0.005) and high (>0.005) leaf light use efficiency (LUE) to show the interacting effects of LUE and temperature on leaf PRI.

senescence induced by the extreme drought. Since transect CCI is more closely related to greenness of individual leaves (correlation between transect CCI and leaf CI had $r^2=0.85$, data not shown), whereas NDVI is more a function of canopy structure, the greater decline in NDVI than in CCI during the extreme drought of 2002 suggests that canopy structure was affected more than individual leaf greenness, i.e. the total loss of leaves was greater than the loss of chlorophyll from the remaining leaves.

In contrast to the relationships between gross CO_2 exchange and vegetation greenness, the relationship between PRI and gross CO_2 exchange was not consistent across years (Fig. 7c). The relationship in the “normal” years of 2000–2001 was markedly different from that during the extreme drought in 2002. This was also the case for the relationship between PRI and ϵ' (Fig. 7f). The seasonal pattern of transect PRI was similar in the years before and during the extreme drought (Fig. 8), although maximum values of PRI were lower during the extreme drought. In contrast, the seasonal pattern of ϵ' changed dramatically during the extreme drought year (Fig. 8), causing asynchrony between PRI and ϵ' under these conditions (Fig. 7f). Since canopy structure might have confused the relationship between PRI and ϵ' , we also examined the relationships between ecosystem carbon fluxes and mean leaf PRI. The relationships between gross carbon exchange and leaf PRI were similar to those in Fig. 7c but there were no significant relationships between gross ecosystem ϵ' and leaf PRI (data not shown). Consequently, it does not appear that canopy structure effects were responsible for the lack of good correlations between transect PRI and carbon flux or ϵ' at the seasonal timescale.

Since PRI is expected to be most closely correlated with short-term changes in ϵ' , calculation of ϵ' from weekly means of carbon exchange (as was done for the data in Fig. 7), rather than a single day only, might also have resulted in poor correlations between PRI and ϵ' . However, we did not find any significant change in the relationships when we used ϵ'

calculated for the measurement day only (data not shown). We also failed to find any consistent correlations between ϵ' and PRI over the diurnal cycle (data not shown).

The relationships between ϵ' and both measures of canopy greenness (NDVI at constant solar angle and CCI, Fig. 7d,e) were more consistent across all years than was the relationship with PRI. This confirms our hypothesis (Fig. 1a) that LUE and vegetation greenness would be correlated under conditions where pigment content and leaf area index varies seasonally. Also note that the curvilinear relationship, with non-zero intercept, between NDVI and gross CO_2 exchange in Fig. 7b is what was predicted for partially evergreen vegetation where greenness and LUE are correlated (Fig. 1b). It is also interesting that these relationships were strongest for the transect as a whole. When we divided the transect into sections dominated by different species, gross carbon exchange was significantly correlated with the greenness of sections dominated by semi-deciduous species such as *A. fasciculatum* but not with sections dominated by the fully evergreen species (*A. pungens*, Fig. 9). However, none of the correlation coefficients for the sections dominated by the individual species were greater than that for the transect as a whole, suggesting that these relationships were not simply a function of the semi-deciduous vegetation components.

4. Discussion

Our results show a high degree of inter-correlation between ecosystem CO_2 exchange, ϵ' and vegetation greenness for this chaparral ecosystem. Filella et al. (2004) found similar relationships for a Mediterranean shrubland in Spain and suggested that this unexpected result could be accounted for by the unusual characteristics (brevi-deciduous leaves and sparse canopy structure) of this vegetation type and would not necessarily apply to other vegetation types. Based on studies of single leaves, individual plants or dense stands of single species, it would be logical to conclude that there are no general

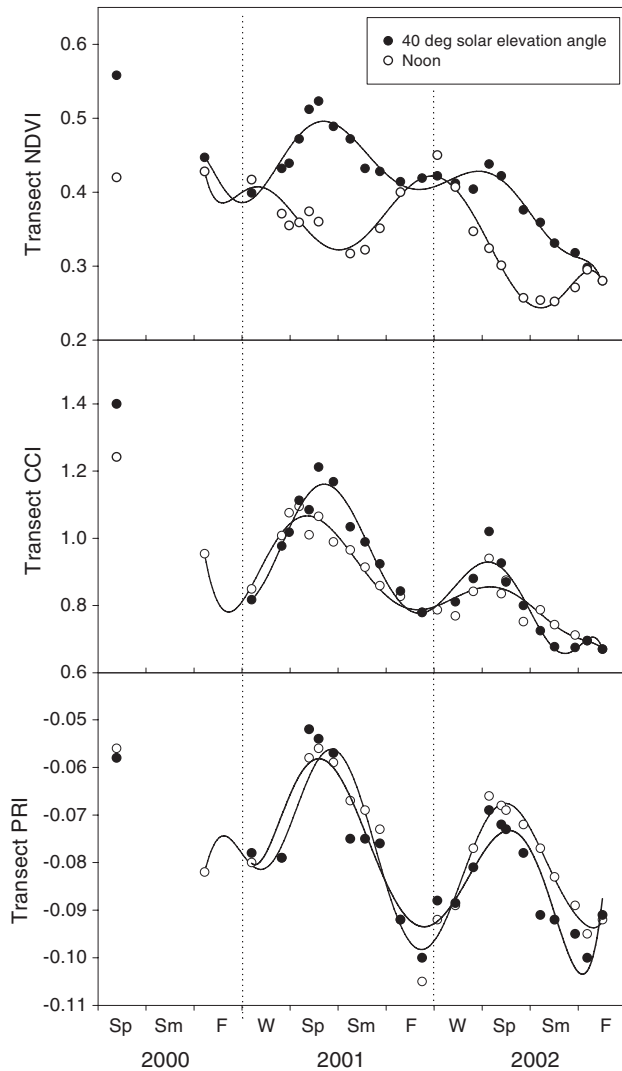


Fig. 6. Transect means of the normalized difference vegetation index (NDVI), the canopy chlorophyll index (CCI) and the photochemical reflectance index (PRI) calculated for noon solar elevation angle (open symbols) or at a constant solar elevation angle of 40° (closed symbols) over the 3 year course of the study (Sp=spring, Sm=summer, F=fall, W=winter).

relationships between greenness and CO_2 exchange or LUE. In fact, this was the conclusion of an earlier study on this same chaparral stand (Stylinski et al., 2002). They found NDVI to be relatively constant seasonally and found no correlation between NDVI and CO_2 exchange. Partly, this conclusion resulted from making reflectance measurements only of leaves and individual plant canopies, which are likely to vary less than the stand average. However, it also resulted from the unusually wet conditions during the experimental period (a result of the large El Niño event in 1998–1999) that eliminated the normal summer drought and resulted in unusually small seasonal changes in vegetation greenness.

We found that ecosystem gross CO_2 flux was better correlated with the greenness of sections of the transect dominated by the semi-deciduous species (*A. fasciculatum*) than it was with sections dominated by the evergreen species (*A. pungens*, Fig. 9). However, the strength of the correlation between mean transect greenness and gross flux cannot be

entirely attributed to a single species since the individual species correlations were all weaker than that for the transect mean. These results suggest that measurements of vegetation greenness at larger spatial scales may actually be more useful for prediction of CO_2 exchange than would measurements at smaller spatial scales (i.e. the correlation between carbon exchange and vegetation greenness is an “emergent property” of the ecosystem). Averaging across large pixels tends to average the relationships for different species and may result in more general relationships than would be suggested by examination of the species in isolation. This is the basic concept of functional convergence, that although there may be some variation between species there is a tendency for functional traits of organisms to converge on general relationships determined by environmental limitations (Field, 1991; Meinzer, 2003).

One of the assumptions we made in our hypothesis in Fig. 1 was that vegetation types that only partially adjusted their allocation to green tissues would reach the same upper limit of LUE as the fully adjusting types but would reach it at a lower greenness. Comparison of the maximal ϵ' for the chaparral with those of crop systems confirms this assumption. In order to make this comparison across multiple datasets, we calculated ϵ' as gross photosynthesis (midday maximum net photosynthesis minus apparent dark respiration rate) divided by midday maximum APAR. The highest midday gross ϵ' that we observed for the chaparral was around $0.02 \text{ mol mol}^{-1}$ in the spring of 2000 and 2001. Comparable values for crops range from 0.013 to $0.021 \text{ mol mol}^{-1}$ for wheat (Baldochi, 1994; Soegaard & Thorgeirsson, 1998; Wall & Kanemasu, 1990), 0.018 to $0.030 \text{ mol mol}^{-1}$ for corn (Baldochi, 1994; Rochette et al., 1996), 0.018 for soybean (Rochette et al., 1995) and $0.032 \text{ mol mol}^{-1}$ for rice (Campbell et al., 2001). However, the high LUE in the chaparral does not necessarily mean that the chaparral will be as productive as crops since chaparral often has lower vegetation cover, which results in lower APAR. The similarity in maximal ϵ' between the chaparral and crop plants supports the view that LUE under optimal conditions may be relatively constant between species and ecosystems (Landsberg et al., 1996). However, the wide seasonal and inter-annual variation in ϵ' for the chaparral ecosystem emphasizes the importance of environmental factors in determining the actual ϵ' .

Over short timescales, ϵ' was expected to be better correlated with PRI than with the greenness indices. However, we did not find significant relationships between PRI and ϵ' over diurnal timescales. Diurnal changes in PRI were most likely a complex function of shifting illumination in this sparse stand (shifting from leaves to soil or from shade leaves to sun leaves as solar elevation angle increased, see Barton and North (2001) for discussion of these issues), in addition to actual changes in leaf PRI (Fig. 5). Studies that have reported good diurnal relationships between PRI and ϵ' have either focused on individual leaves or canopies (e.g. Peñuelas et al., 1995) or have reported these results only for dense canopies (Gamon et al., 1992) or low measurement look angles that minimized background and canopy structure effects (e.g. Nichol et al., 2002). Since we did observe some diurnal variation in leaf PRI for the chaparral species in this study, it remains possible that PRI could be used

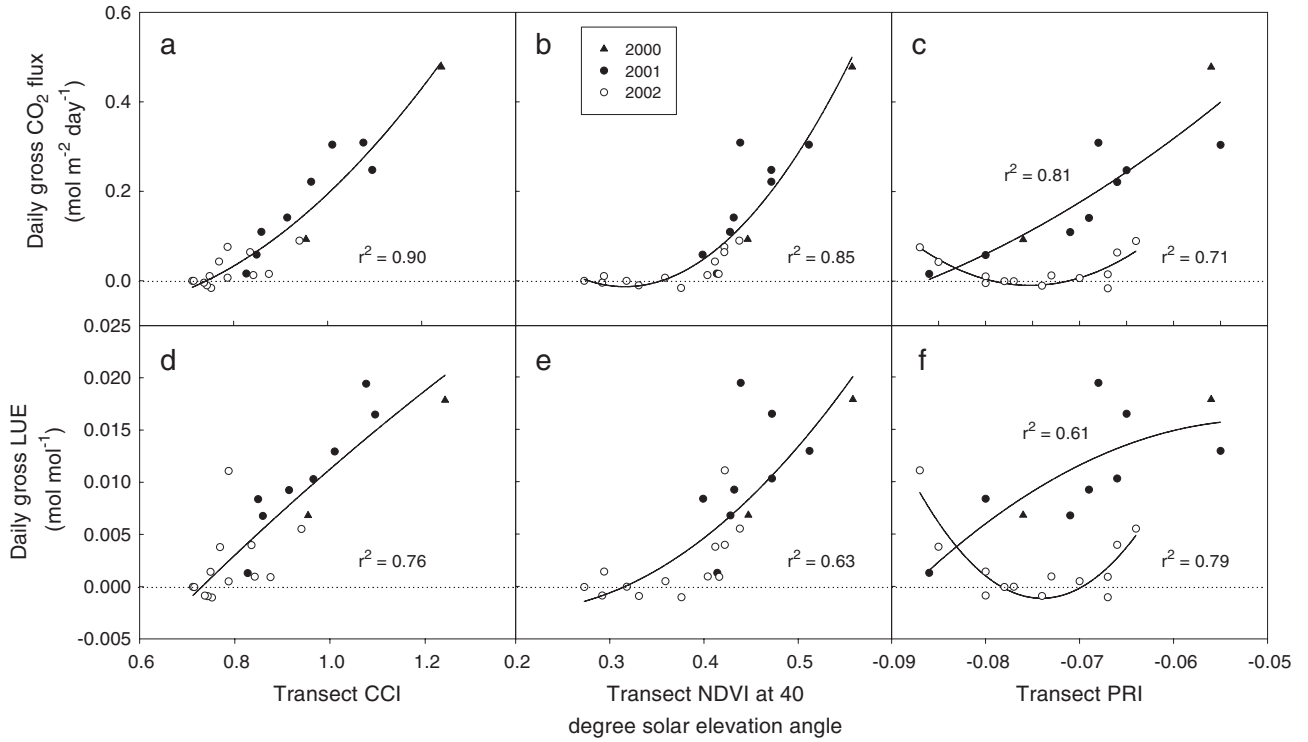


Fig. 7. Gross CO₂ exchange and gross light use efficiency (ϵ') as a function of the transect means of canopy chlorophyll index (CCI), normalized difference vegetation index (NDVI) at a solar elevation angle of 40° and photochemical reflectance index (PRI). All CO₂ exchange and ϵ' values are daily sum means for the week prior to transect spectral reflectance measurements. Data are split between years; 2000 closed triangles, 2001 closed circles and 2002 open circles.

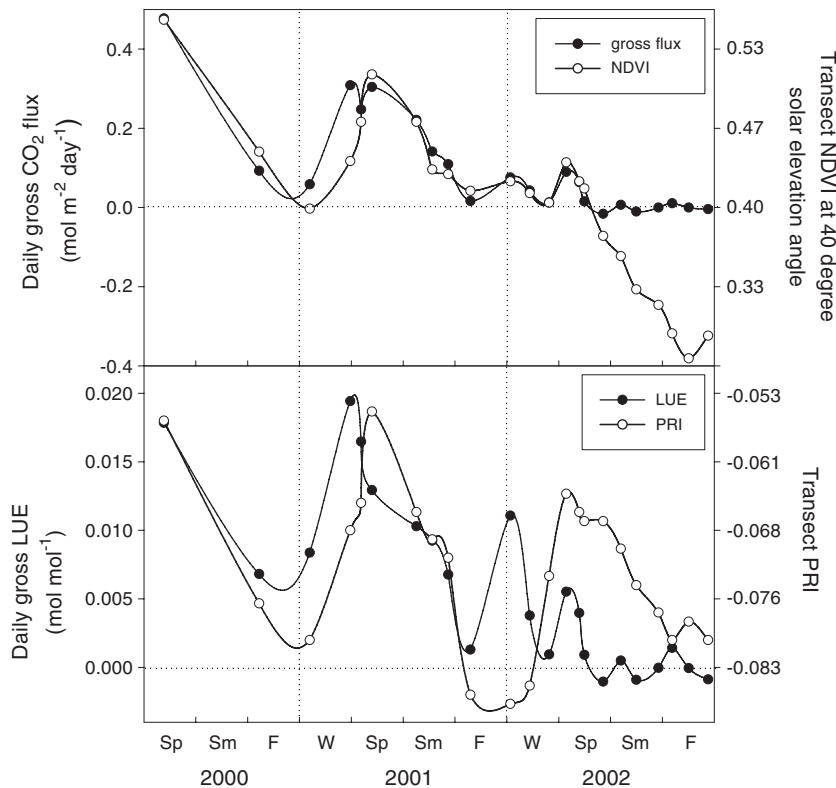


Fig. 8. Comparison of the seasonal cycles of daily gross ecosystem CO₂ flux with transect normalized difference vegetation index (NDVI) at 40° solar elevation angle and daily gross ecosystem light use efficiency (ϵ') with transect photochemical reflectance index (PRI).

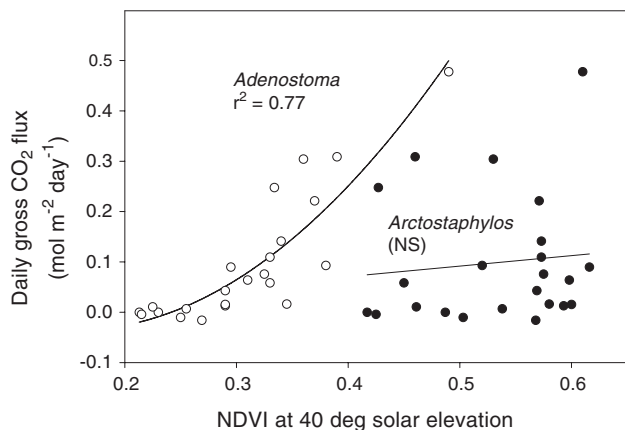


Fig. 9. Gross ecosystem CO_2 flux as a function of normalized difference vegetation index (NDVI) at a solar elevation angle of 40° for transect sections dominated by *Adenostoma fasciculatum* or *Arctostaphylos pungens*. Gross CO_2 exchange values are daily sum means for the week prior to spectral reflectance measurements.

for diurnal estimates of ϵ' in this ecosystem, but it would require a much greater consideration of the canopy structure and background effects on stand PRI. This could be achieved by linking the kind of physiological measurements conducted here with radiative transfer models that explicitly consider canopy structure and sun angle effects. Such linked studies have rarely been done, but the few examples (e.g. Barton & North, 2001) have yielded useful insights into the strong confounding effects of sparse stands on “physiological” reflectance signals.

The relationship between PRI and ϵ' was also inconsistent at longer timescales. This may have been a result of seasonal responses of PRI that were not a direct function of photosynthetic rates. In both 2001 and 2002, the lowest PRI values were observed in the winter and the highest values in the summer, even though the highest ϵ' values were observed at very different times during these 2 years. The observed correlations between temperature and PRI for leaves with similar LUE suggests a temperature effect on PRI, although PRI might also be affected by other seasonal factors such as day length, which are in turn correlated with temperature. Few studies have measured PRI changes in response to cold temperatures, but several studies have shown increases in xanthophyll cycle pool sizes and sustained engagement of pigments in the de-epoxidised state in response to cold treatment (Adams et al., 1994; Krause et al., 1999) and these changes appear to be greater for evergreen than for deciduous and annual species (Kyparissis et al., 2000; Savitch et al., 2002; Verhoeven et al., 1999).

In this study, the seasonal change in PRI appeared to result primarily from changes in the pool sizes of chlorophyll and carotenoid pigments rather than from xanthophyll cycle pigment inter-conversions per se. Carotenoid/chlorophyll ratios of the chaparral species along the tram in our study increased as much as 2 fold from summer to winter (Sims and Gamon, unpublished data). PRI decreases with increasing leaf carotenoid/chlorophyll ratio (Sims & Gamon, 2002; Stylinski et al., 2002) and the observed change in carotenoid/chlorophyll ratio was large enough to account for the seasonal changes in PRI.

Consequently, it appears that xanthophyll cycle pigment inter-conversions may account for only a small part of the observed seasonal variation in PRI in this ecosystem with the larger percentage of this variation in PRI due to changes in relative pool sizes of carotenoid and chlorophyll pigments.

Although other studies have found correlations between PRI and LUE at the ecosystem scale (Nichol et al., 2000, 2002; Rahman et al., 2001; Strachan et al., 2002), these studies did not calculate LUE in the same way as in our study. Nichol et al. (2000, 2002) found correlations between PRI and LUE based on incident PAR at the ecosystem level for data collected in the SSA of BOREAS and in Siberia. However, these relationships differed between the two study locations (Nichol et al., 2002). In addition, when we recalculated the data of Nichol et al. (2000, 2002) to estimate ϵ' based on APAR (using Eq. (7) to estimate APAR from NDVI and PAR), we found no correlation between ϵ' and PRI for either dataset. The inconsistency of these results, combined with the differences we observed in the PRI/ ϵ' relationships between normal and extreme drought years in the chaparral, suggest that it may be difficult to find general relationships between PRI and LUE at the ecosystem level. Empirical relationships clearly exist for a given site and set of environmental conditions, but the mechanistic basis for generalization of these relationships across vegetation types and changing environmental conditions remains unclear and confounded by multiple physiological and structural factors affecting this index.

Our results suggest the need for more studies of the relationships between carbon exchange, LUE and spectral reflectance indices at large spatial scales. The relationships observed in this study could not have been predicted simply by extrapolation from measurements at smaller spatial scales. In particular, the extent to which overall vegetation greenness can be used not only to estimate the fraction of incident PAR absorbed by plants but also the efficiency of utilization of that light needs further examination. Although it is likely that this relationship will be weaker in dense evergreen vegetation, we are not aware of any studies that have adequately addressed this issue at sufficiently large spatial scale for a variety of ecosystems. Installation of tram systems similar to the one used in our study in a wide range of ecosystems would provide valuable baseline data. A network of automated tram systems (“SpecNet”), to be deployed in eddy covariance tower footprints (in conjunction with “Fluxnet”), is currently under development. The advantages of trams for reflectance measurements in eddy covariance footprints include close correspondence between the spatial and temporal scales of the reflectance and CO_2 exchange measurements, the ability to collect data even when skies are cloudy, and the ability to develop relationships between reflectance and solar elevation angle. Our results also emphasize the need for satellites in geo-stationary orbit that can measure reflectance of the same location over diurnal time-courses. The effect of solar elevation angle on NDVI has been known for some time (Goward & Huemmrich, 1992; Pinter et al., 1983, 1985), but we are not aware of any other studies that have shown an actual reversal in the seasonal pattern of NDVI depending on

whether it was measured at noon or at a constant solar elevation angle, which is sure to confound any simple interpretation of this index. Although the solar elevation angle effect on NDVI may be small enough to be ignored for dense vegetation types, as much as 70% of the terrestrial surface consists of open canopies (Graetz, 1990). Clearly, a much broader evaluation of vegetation indices that includes both physiological and structural factors across a wide range of ecosystems, and spatio-temporal scales is now warranted.

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