



On the use of MODIS EVI to assess gross primary productivity of North American ecosystems

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[1] Carbon flux models based on light use efficiency (LUE), such as the MOD17 algorithm, have proved difficult to parameterize because of uncertainties in the LUE term, which is usually estimated from meteorological variables available only at large spatial scales. In search of simpler models based entirely on remote-sensing data, we examined direct relationships between the enhanced vegetation index (EVI) and gross primary productivity (GPP) measured at nine eddy covariance flux tower sites across North America. When data from the winter period of inactive photosynthesis were excluded, the overall relationship between EVI and tower GPP was better than that between MOD17 GPP and tower GPP. However, the EVI/GPP relationships vary between sites. Correlations between EVI and GPP were generally greater for deciduous than for evergreen sites. However, this correlation declined substantially only for sites with the smallest seasonal variation in EVI, suggesting that this relationship can be used for all but the most evergreen sites. Within sites dominated by either evergreen or deciduous species, seasonal variation in EVI was best explained by the severity of summer drought. Our results demonstrate that EVI alone can provide estimates of GPP that are as good as, if not better than, current versions of the MOD17 algorithm for many sites during the active period of photosynthesis. Preliminary data suggest that inclusion of other remote-sensing products in addition to EVI, such as the MODIS land surface temperature (LST), may result in more robust models of carbon balance based entirely on remote-sensing data.

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1. Introduction

[2] Many current models for estimation of carbon fluxes between vegetation and the atmosphere use some variant of

the light use efficiency (LUE) model proposed by *Monteith* [1972]. In this model, carbon flux is a function of the photosynthetically active radiation absorbed by green vegetation (APAR) and the efficiency with which this absorbed light is utilized for carbon fixation (LUE). APAR is relatively easy to estimate from remote sensing since the fraction of incident PAR (f_{apar}) that is absorbed by green tissues is a strong function of the normalized difference vegetation index (NDVI) [*Goward and Huemmrich*, 1992]. LUE, on the other hand, has proved more difficult to estimate. Early models such as those of *Monteith* [1972] assumed that LUE was relatively constant. However, more recent studies have shown that LUE does in fact vary over a considerable range between vegetation types and in response to environmental variation such as drought and diffuse radiation [*Hunt*, 1994; *Ruimy et al.*, 1995; *Gower et al.*, 1999; *Green et al.*, 2003]. Many carbon exchange models estimate LUE using look-up tables of maximum LUEs for a given vegetation type and then adjust those values downward on the basis of environmental stress factors [*Ruimy et al.*, 1994; *Anderson et al.*, 2000; *Running et al.*, 2004; *Xiao et al.*, 2004b, 2005]. This can lead to considerable errors, however, because of the coarse resolu-

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tion of the data inputs. Some meteorological parameters are only available at 1° latitude \times 1.25° longitude resolution and the resolution of vegetation maps varies widely. Use of look-up table LUE inputs and coarse resolution meteorological data may result in significant errors in estimates of carbon fluxes between the vegetation and the atmosphere [Turner et al., 2003, 2005; Zhao et al., 2005; Heinsch et al., 2006].

[3] It would be simpler and more direct if we could base carbon exchange models entirely on remote-sensing data and thus have truly continuous output at the spatial resolution of the satellite data. The photochemical reflectance index (PRI) [Gamon et al., 1992] has been shown to correlate with light use efficiency (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, the relationship between LUE and PRI has been found to vary considerably between vegetation types at the stand scale [Nichol et al., 2002; Sims et al., 2006a] and between years at the same site [Sims et al., 2006b]. Another limitation of PRI is that the spectral bands of many current satellites are insufficient for calculation of this index. Consequently, we were interested in the extent to which carbon fluxes could be estimated directly from greenness indices such as the NDVI and the enhanced vegetation index (EVI) without direct estimation of LUE. This does not necessarily require an assumption of a constant LUE. Good relationships between carbon fluxes and greenness indices would also occur if LUE tends to be correlated with greenness indices, thus making an independent estimate of LUE unnecessary [Sims et al., 2006b].

[4] Earlier studies have shown good relationships between NDVI and net primary productivity when the data were integrated over an entire growing season [Goward et al., 1985; Box et al., 1989]. However, it remains unclear to what extent shorter-term fluctuations in carbon exchange can be estimated from greenness indices alone. Clearly, over very short time periods (minutes to hours), carbon flux can be extremely variable because of changes in PAR, temperature, humidity etc, while greenness remains basically constant. However, much of this short-term variability in fluxes should be damped out as averaging times are lengthened to periods longer than a week. Strong relationships between NDVI and carbon flux have in fact been observed for some ecosystems (sagebrush steppe; Wylie et al. [2003], chaparral; Sims et al. [2006b]) when the flux data are averaged over one or two weeks. However, these relationships have not been measured across enough different vegetation types to be able to determine whether a general relationship exists.

[5] A limitation to the use of NDVI is that it tends to saturate at high vegetation densities and is highly sensitive to differences in background reflectance [Huete et al., 2002]. The enhanced vegetation index (EVI), which is one of the MODIS satellite products, is more sensitive to variation in dense vegetation than is NDVI [Huete et al., 2002]. EVI was better correlated with gross primary production (GPP) than was NDVI, both for evergreen [Xiao et al., 2004a] and deciduous [Xiao et al., 2004b] forest sites.

Rahman et al. [2005] found a strong overall relationship between the MODIS 16 day EVI product and GPP across 10 AmeriFlux tower sites representing a wide range of vegetation types. This suggests that EVI alone can be used to estimate GPP with relatively high accuracy. However, examination of the relationships presented by Rahman et al. [2005] shows that there was variation between the sites in terms of the strength of the relationship between EVI and GPP. In this study, we explore the causes of this variation, and the implications for our ability to estimate GPP in different regions of the country.

2. Methods

2.1. Study Sites

[6] We used carbon flux data from nine AmeriFlux tower sites (Table 1). These sites represent a wide diversity of natural vegetation across North America (see Table 2 for detailed vegetation characteristics). The four evergreen needleleaf forest sites represent considerable variation in regions, climate and species composition. Blodgett is a young ponderosa pine forest in the Sierra Nevada mountains of the western United States with moderate winters and relatively dry summers. Niwot Ridge is a subalpine temperate coniferous forest in the Rocky Mountains, with more extreme winters and somewhat wetter summers than Blodgett. The Northern Old Black Spruce site in Canada also experiences extreme winters and the vegetation is more mixed than some of the other evergreen vegetation types, including deciduous species (aspens) as well as a more open canopy that allows a greater development of understory species. The Howland Forest in Maine is a dense evergreen forest with a closed canopy and little understory. Winters are relatively cold but not as extreme as the Niwot and Old Black Spruce sites.

[7] The two deciduous forest sites are characteristic of the eastern deciduous forests of the United States, with diverse species composition. Morgan Monroe State Forest (MMSF) in Indiana is a warmer site than the Harvard Forest in Massachusetts. Both deciduous forest sites experience high summer rainfall. The Lethbridge site in Canada is representative of the short grass prairies east of the Rocky Mountains whereas Tonzi is representative of the Oak savannas in the foothills of the Sierra Nevada Mountains of California. The oak trees at Tonzi are winter deciduous but the grass between the trees is green from winter into spring and then becomes inactive during the summer drought. Finally, Sky Oaks in southern California is a sparse, semiarid site with a Mediterranean climate, representing U.S. southwestern shrublands with a mixture of needleleaf and broadleaf evergreen shrubs.

2.2. Site Climate Variables

[8] Mean climate variables were calculated for each site, since we wished to examine the relationship between climate variables and the strength of the relationships between EVI or MOD17 GPP and tower GPP. Annual means (over the years included in this study) and summer and winter means (three month summer or winter period) of air temperature and rainfall were calculated either from the flux tower meteorological data or from weather stations close to the flux tower. We also calculated the thermal

Table 1. Vegetation Type, Location, Years From Which Data Were Used, and Methods References for the Nine-Eddy Covariance Flux Tower Sites Used in This Study^a

Site Name	Vegetation Type	Latitude	Longitude	Years	Methods References
Blodgett	Evergreen needleleaf forest	38.895	120.633	2000–2002	Goldstein et al. [2000]
Niwot Ridge	Evergreen needleleaf forest	40.033	105.546	2000–2003	Monson et al. [2002]
Northern Old Black Spruce (NOBS)	Evergreen needleleaf forest	55.879	98.481	2000–2004	Jarvis et al. [1997]
Howland Forest	Evergreen needleleaf forest	45.204	68.740	2000–2003	Hollinger et al. [1999], Hollinger et al. [2004]
Harvard Forest main tower	Deciduous broadleaf forest	42.538	72.171	2000–2003	Goulden et al. [1996]
Morgan Monroe State Forest (MMSF)	Deciduous broadleaf forest	39.323	86.413	2000–2003	Schmid et al. [2000]
Lethbridge	Grassland	49.708	112.940	2000–2004	Flanagan et al. [2002], Wever et al. [2002]
Tonzi	Woody savanna	38.432	120.966	2001–2004	Xu and Baldocchi [2004]
Sky Oaks old stand	Semiarid shrubland	33.375	116.621	2000–2002	Sims et al. [2006b]

^aLatitude/Longitude given in decimal degrees.

amplitude (difference between annual maximum and minimum temperature) and the summer mean midday VPD (midday defined as 1000 to 1400 hours).

2.3. MODIS Products

[9] EVI data were obtained from the 7×7 km subsets of MODIS products available at Oak Ridge National Labora-

tory's Distributed Active Archive Center (DAAC) web site (<http://www.modis.ornl.gov/modis/index.cfm>). Although the flux tower footprint is generally less than 1 km [Schmid, 2002], it can be difficult to precisely locate which pixel the footprint falls within. Consequently, we extracted both the central pixel and the central 3×3 km area within the 7×7 km cutouts to determine which provided the best correlation

Table 2. Vegetation Characteristics for the 3×3 km Region Around the Flux Towers Used in This Study^a

Site Name	Deciduous Species	Evergreen Species	Understory
Blodgett	<i>Quercus kelloggii</i> (5%)	<i>Pinus ponderosa</i> (28%) <i>Abies concolor</i> (28%) <i>Pseudotsuga menziesii</i> (28%) <i>Pinus lambertiana</i> (5%) <i>Calocedrus decurrens</i> (5%)	Evergreen: <i>Arctostaphylos manzanita</i> <i>Ceanothus cordulatus</i> <i>Lithocarpus densiflora</i>
Niwot Ridge	<i>Populus tremuloides</i> (5%)	<i>Abies lasiocarpa</i> <i>Picea engelmannii</i> <i>Pinus contorta</i>	Evergreen
Northern Old Black Spruce (NOBS)	<i>Populus tremuloides</i> <i>Betula spp.</i>	<i>Picea mariana</i> <i>Pinus banksiana</i>	Mixed
Howland Forest	<i>Acer rubrum</i> (8%) <i>Betula papyrifera</i> (8%)	<i>Picea rubens</i> (27%) <i>Tsuga Canadensis</i> (33%) <i>Abies balsamea</i> (17%)	Evergreen
Harvard Forest main tower	<i>Quercus rubra</i> <i>Acer rubrum</i> <i>Betula lenta</i>	<i>Pinus strobes</i> <i>Tsuga Canadensis</i>	Deciduous
Morgan Monroe State Forest (MMSF)	<i>Acer saccharum</i> <i>liriodendron tulipifera</i> <i>Sassafras albidium</i> <i>Quercus alba</i> <i>Quercus nigra</i>	None	Deciduous
Lethbridge	<i>Agropyron smithii</i> (50%) <i>Stipa comata</i> <i>Koeleria cristata</i> <i>Vicia americana</i> <i>Artemisia frigida</i> <i>Carex filifolia</i>	None	None
Tonzi	<i>Quercus douglasii</i> (30%)	<i>Pinus sabiniana</i> (<2%)	Deciduous: <i>Brachypodium distachyon</i> <i>Hypochaeris glabra</i> <i>Trifolium dubium</i> <i>Trifolium hirtum</i> <i>Dichelostemma volubile</i> <i>Erodium botrys</i>
Sky Oaks old stand	None	<i>Adenostoma fasciculatum</i> (50%) <i>Adenostoma sparsifolium</i> (20%) <i>Ceanothus greggii</i> (10%) <i>Arctostaphylos pungens</i> (10%) <i>Quercus agrifolia</i> (10%)	None

^aOnly the most common evergreen and deciduous species are listed, and their approximate percent cover (percentage of total vegetation cover on area basis) is given when that information was available.

with GPP. We used only EVI data that had aerosol values listed as “low” and the “usefulness” value listed as greater than 8 (on a scale of 0–10).

[10] The MOD15 FPAR and MOD17 GPP data (collection 4.5) from the University of Montana’s NTSG ftp site (<ftp.ntsg.umt.edu/pub/MODIS>) were available as 8 day composites. We averaged two consecutive periods of these data in order to conform to the 16 day period of the MODIS EVI data. Similar to the EVI, we used both the central pixel and the mean for the central 3×3 km area surrounding each tower site for comparison with the tower flux data.

[11] The MOD17 GPP is calculated using a LUE type model with the following equation:

$$GPP = \varepsilon_{\max} \times m(T_{\min}) \times m(VPD) \times FPAR \times SWrad \times 0.45 \quad (1)$$

where ε_{\max} is the maximum LUE and the scalers $m(T_{\min})$ and $m(VPD)$ reduce ε_{\max} under unfavorable conditions of low temperature and high VPD. FPAR is the Fraction of Photosynthetically Active Radiation absorbed by the vegetation (both green and brown components) and SWrad is shortwave solar radiation. The ε_{\max} is obtained from lookup tables on the basis of vegetation type. T_{\min} , VPD and SWrad are obtained from large spatial-scale meteorological data sets available from the NASA Data Assimilation Office (DAO; <http://gmao.gsfc.nasa.gov/>). MOD15 FPAR is a complex function of reflectance in up to seven MODIS spectral bands, vegetation and soil characteristics, and solar and look angles.

[12] The MODIS researchers at the University of Montana also provided us with the scaled LUE values from equation (1) so that we could examine the extent to which lack of correlation between tower GPP and MOD17 GPP resulted from errors in estimation of LUE. The MODIS-scaled LUE values were converted from MJ to mol(photon) units using a conversion factor of 0.218 MJ/mol photons. As for the other variables, we calculated 16 day means for the 3×3 km region around the flux towers.

2.4. Definition of Photosynthetic Active Period

[13] For all of the comparisons between EVI and GPP or LUE in this paper, we used data only from the period when active photosynthesis was occurring. This period was defined by examination of the tower GPP data to determine the 16 day periods in which there was positive GPP. For three of the sites (Blodgett, Sky Oaks, Tonzi), photosynthesis continued year around. Another four sites (Harvard, Lethbridge, MMSF and Niwot) had active periods running from day of year 96 to 304 (the beginning and ending days for the range of 16 day periods used). Howland had an active period from day of year 80 to 320 and NOBS had an active period from day of year 96 to 288.

2.5. Calculation of Tower-Based C Fluxes

[14] Measurements of CO_2 exchange between the vegetation and the atmosphere for each site were made with the eddy covariance technique (for methods references see Table 1). When gap filled GPP estimates were available from the site databases, we used these values. For three sites (Lethbridge, Niwot and Sky Oaks) where GPP estimates

were not available, we estimated daytime respiration (R) using the following relationship [Sims *et al.*, 2005]:

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

where R_n is the nighttime respiration rate, T_n is the mean nighttime air temperature corresponding to the data points used to calculate R_n , T_a is the air temperature at the time of estimation of R , and k is a coefficient relating respiration to air temperature (0.07), which results in a Q_{10} of 2 [Goulden *et al.*, 1996; Reichstein *et al.*, 2002]. R_n and T_n were calculated individually for each 16 day period so that the base respiration changed seasonally. GPP was then estimated from the following equation:

$$GPP = NEE - R \quad (3)$$

where NEE is the net ecosystem(vegetation and soil) exchange of CO_2 measured by the flux tower. The sign convention for all the terms in equation (3) is that carbon flux from the atmosphere into the vegetation is positive.

[15] To calculate 16 day averages for non-gap-filled data, all tower GPP data for each half hour (or hour, as available) interval over the 24 hour cycle were averaged over each 16 day period. Then these half hourly (or hourly) averages were summed to give a daily total flux. Data were not used when there were fewer than six good data points for each half (or hourly) average period over the 16 day period.

2.6. Calculation of Light Use Efficiency

[16] Calculation of light use efficiency (LUE) from the flux tower data requires an estimate of the absorbed photosynthetically active radiation (APAR). APAR can be calculated from the incident PAR recorded at the eddy covariance tower and an estimate of the fraction of incident PAR absorbed by green vegetation (f_{apar}). Since NDVI is often found to be well correlated with f_{apar} [Goward and Huemmrich, 1992], we used a linear relationship between NDVI and f_{apar} of green tissues [Sims *et al.*, 2006b]. This relationship was determined empirically using a linear PAR ceptometer (AccuPar, Decagon Devices Inc. Pullman, WA, United States) for direct measurements of f_{apar} . A total of 16 species were measured, including annuals, vines, deciduous and evergreen shrubs and trees. Canopy green f_{apar} for the woody species was calculated as total f_{apar} times the 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 nongreen tissues and measuring their projected areas with an area meter (model 3100, Li-COR Inc., Lincoln, Nebraska, United States). NDVI and green f_{apar} were highly correlated ($r^2 = 0.95$) with the following linear equation:

$$f_{APAR} = 1.24 * NDVI - .168 \quad (4)$$

APAR was then calculated as:

$$APAR = f_{APAR} * PAR \quad (5)$$

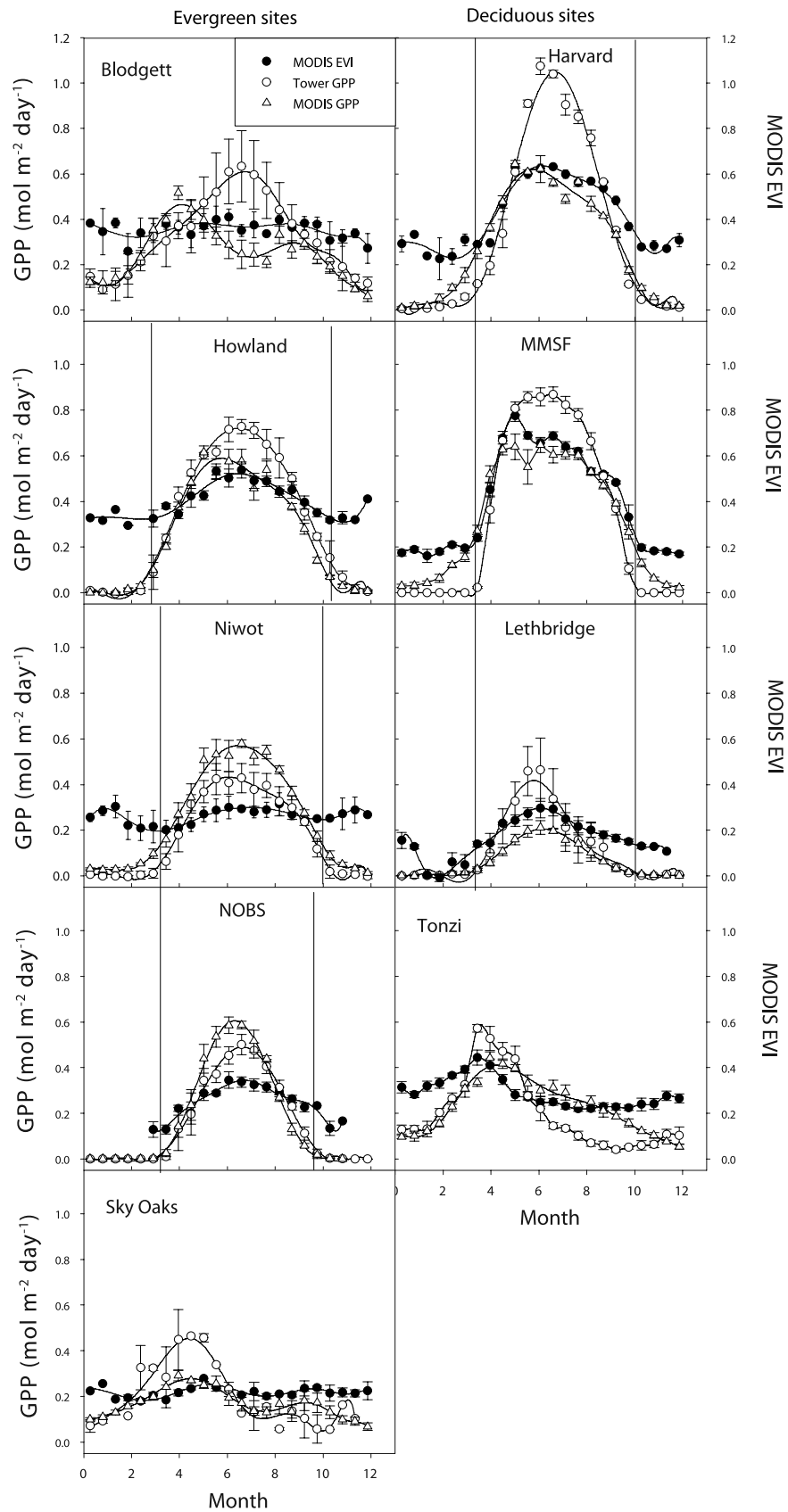


Figure 1. Annual timecourses of the MODIS-enhanced vegetation index (EVI, 3×3 km mean), gross primary production measured at the flux tower (Tower GPP) and MOD17 GPP (3×3 km mean) for each site. Data are means (\pm standard error) across all years used in this study. Vertical lines mark the start and end of the active period for those sites with inactive periods.

Table 3. Coefficients of Determination (r^2 , Linear Model) Between the Enhanced Vegetation Index (EVI) and Eddy Covariance Tower Measurements of Either Gross Primary Productivity (GPP) or Gross Light Use Efficiency (LUE)^a

	EVI 1 pix Versus Tower GPP	EVI 3 × 3 Versus Tower GPP	EVI Versus Tower LUE	MODIS GPP 1 pix Versus Tower GPP	MODIS GPP 3 × 3 Versus Tower GPP
	<i>Site</i>				
Blodgett	0.004	0.086*	0.000	0.150**	0.155**
Harvard	0.754**	0.793**	0.739**	0.609**	0.617**
Howland	0.543**	0.736**	0.204**	0.803**	0.819**
Lethbridge	0.850**	0.764**	0.346**	0.753**	0.653**
MMSF	0.810**	0.826**	0.641**	0.644**	0.625**
Niwot	0.441**	0.286**	-0.105	0.781**	0.799**
NOBS	0.628**	0.845**	0.434**	0.843**	0.861**
Sky Oaks	0.024	0.013	0.004	0.023	0.146**
Tonzi	0.497**	0.477**	0.633**	0.245**	0.480**
	<i>Vegetation Type</i>				
Cold climate evergreen	0.563**	0.671**	0.344**	0.656**	0.661**
West Coast evergreen	0.140**	0.249**	0.153**	0.135**	0.204**
Deciduous forest	0.717**	0.743**	0.606**	0.584**	0.589**
Grassland	0.514**	0.465**	0.159**	0.306**	0.329**
All sites	0.632**	0.684**	0.441**	0.552**	0.575**

^aEVI in the first column is based on the central 1 km pixel most closely overlapping the eddy covariance tower footprint. EVI in the rest of the columns is the mean for the 3 × 3 km area centered on the tower. Correlations between the MODIS GPP product (for either the 1 km central pixel or a 3 × 3 km mean) and tower measured GPP are also shown. All relationships were based on data from the period of active photosynthesis (i.e., excluding the winter period). Significance levels: * $p < 0.05$, ** $p < 0.01$.

Where the PAR was that measured at the eddy covariance tower. LUE was calculated from the following formula:

$$LUE = \frac{GPP}{APAR} \quad (6)$$

Where GPP and APAR have the same molar units.

3. Results

[17] Examination of the seasonal time courses of EVI (3 × 3 km mean) and tower GPP for each site (Figure 1) shows that there was a good general correspondence between EVI and tower GPP for most of the sites, at least during the period of active photosynthesis. The deciduous sites showed the largest changes in EVI and thus the clearest relationships between EVI and GPP. Although smaller than the EVI variation of the deciduous sites, several of the evergreen sites also showed summer increases in EVI that corresponded to increases in GPP. Use of EVI from the central 1 km pixel rather than the 3 × 3 km mean had little effect on the correlation with tower GPP for the deciduous vegetation sites but resulted in substantially poorer correlations for many of the evergreen sites (Table 3). Since the overall correlation between EVI and tower GPP was better for the 3 × 3 km mean EVI, we used this EVI for the rest of our analyses. The correlation between MOD17 GPP and tower GPP was also slightly better for the 3 × 3 km mean than for the central pixel (Table 3) so we also used the 3 × 3 km mean MOD17 GPP in our analyses. While capturing the seasonal trend of tower GPP for most of the sites, MOD17 GPP significantly underestimated peak GPP values in several cases (Figure 1). MOD17 GPP also failed to capture the seasonal trend of tower GPP for the Blodgett data.

[18] The correlation between EVI and tower GPP was strongest for eastern deciduous forests and weakest for

western evergreen sites (Figures 2 and 3 and Table 3). It is notable that there was considerable variation in the strength of this correlation within the sites dominated by evergreen species. For example, there was a strong correlation between EVI and gross flux for the Northern Old Black Spruce (NOBS) site in central Canada but a very weak correlation for Blodgett in California, even though both sites are dominated by needle leaved evergreens. MOD17 also failed to adequately estimate GPP for a couple of the evergreen sites (Sky Oaks and Blodgett). However, MOD17 provided better estimates of GPP for the rest of the evergreen sites than did EVI. For the deciduous vegetation sites, the relationships between tower GPP and EVI were generally stronger than those between tower GPP and MOD17 GPP. In many cases the MOD17 GPP also consistently underestimated tower GPP (points falling above the 1:1 line in Figures 2 and 3).

[19] We examined a number of vegetation and climate variables that might explain the variation in the strength of the correlations between tower GPP and either EVI or MOD17 GPP (Table 4). The difference between the annual maximum and minimum EVI (a measure of the degree of seasonality in the vegetation) was the best predictor of variation in the strength of the correlation between EVI and tower GPP. However, this relationship was not linear (Figure 4). The relationship between EVI and tower GPP broke down only when the seasonal EVI variation became quite small. Seasonal variation in EVI explained little of the variation in the correlation between tower GPP and MOD17 GPP, since correlations were quite high for some of the evergreen sites (Figure 4). Mean winter temperature, as well as the ratio of winter temperature to summer rainfall, were the best predictors of variation in the correlation between tower GPP and MOD17 GPP (Table 4).

[20] In order to further explore why some sites dominated by evergreen species showed more variation in EVI than

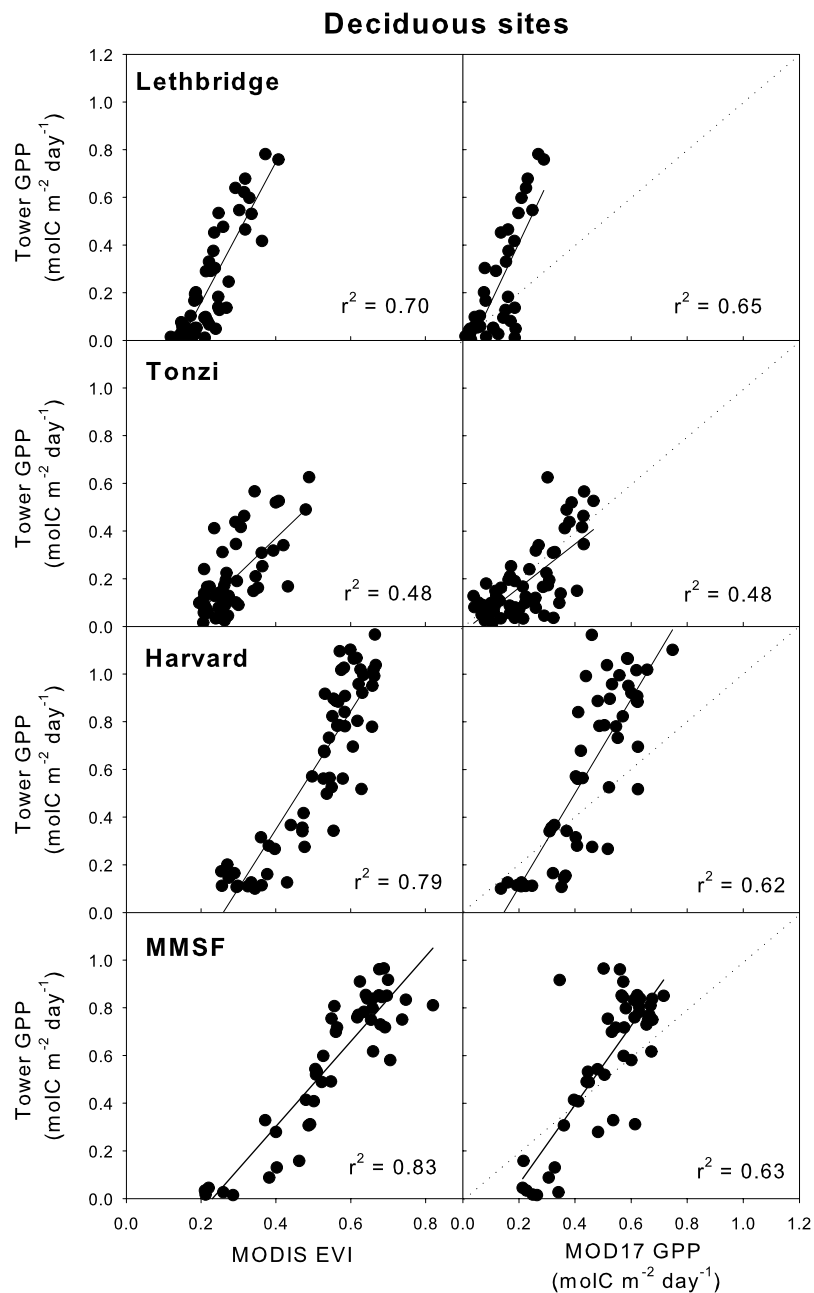


Figure 2. Gross primary production measured at the flux towers (Tower GPP) as a function of the MODIS-enhanced vegetation index (EVI) and the MOD17 GPP for each of the sites with predominantly deciduous vegetation. Data are means for the 3×3 km area centered on the tower and include only the active period. All relationships are statistically significant at $p < 0.01$.

others, we also examined the relationship between the annual variation in EVI and the climate variables. In this case, mean summer rainfall and mean midday summer VPD resulted in the strongest correlations (Table 4). EVI variation increased with increasing summer rainfall and decreased with increasing summer VPD. Interestingly, the data fell into two groups (corresponding to deciduous and evergreen sites) when the annual variation in EVI was plotted as a function of mean summer rainfall or mean midday summer VPD (Figure 5). Although the evergreen and deciduous relationships were not statistically significant by themselves, they follow the same trends. This suggests

that annual variability in EVI was a function both of vegetation type and climate.

[21] Even though there was variation in the strength of the correlation between EVI and tower GPP within sites, the correlation across sites was quite strong when the data were plotted as site means for the whole photosynthetically active period (Figure 6a). This correlation was better than the correlation between MOD17 GPP and tower GPP for the same active period means at each site (Figure 6b). The strong correlation between EVI and tower GPP was possible, at least in part, because EVI was also strongly correlated to tower LUE (Figure 6c). However, the correlation

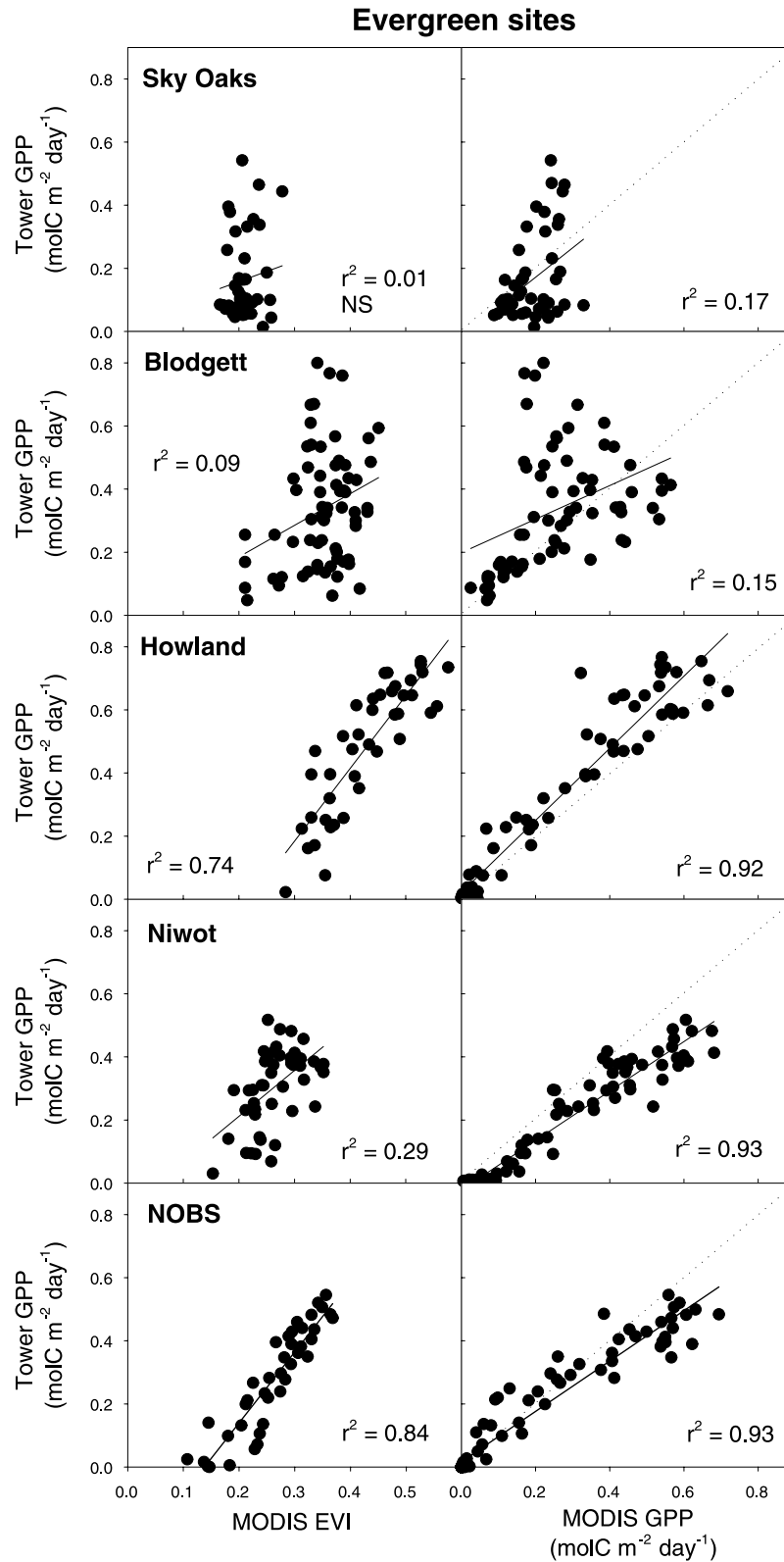


Figure 3. Gross primary production measured at the flux towers (Tower GPP) as a function of the MODIS-enhanced vegetation index (EVI) and the MOD17 GPP for each of the sites with predominantly evergreen vegetation. Data are means for the 3×3 km area centered on the tower and include only the active period. All relationships are statistically significant at $p < 0.01$ except Sky Oaks EVI versus GPP.

Table 4. An Examination of the Extent to Which Seasonal Variation in EVI ($EVI_{max} - EVI_{min}$) and Several Measures of Climate Explain the Variation in the Coefficients of Determination (r^2 , Linear Model) Between Either the Enhanced Vegetation Index (EVI) and Eddy Covariance Tower Measurements of Gross Primary Productivity (Tower GPP) or the MOD17 GPP and Tower GPP^a

	$EVI_{max} - EVI_{min}$	Relationship Between EVI and Tower GPP	Relationship Between MOD17 GPP and Tower GPP
$EVI_{max} - EVI_{min}$	—	0.611*	0.134
Annual mean air temperature	0.093	-0.019	-0.404
Summer mean air temperature	0.341	-0.100	-0.136
Winter mean air temperature	-0.005	-0.267	-0.601*
Annual thermal amplitude	0.033	0.457*	0.530*
Annual mean rainfall	0.183	0	0.036
Summer mean rainfall	0.652*	0.484*	0.408
Summer midday mean VPD	-0.440*	-0.309	-0.310
Ratio of summer rain to winter temp.	0.365	0.555*	0.634*

^aThis table is a correlation matrix where values are coefficients of determination (r^2 , linear model) between the variables in the rows and columns. Coefficients of determination marked with a star are statistically significant ($p < 0.05$).

between EVI and tower LUE was often weak for 16 day data within sites (Table 3). Within individual sites, the correlation between EVI and tower LUE was strongest for the deciduous forests and weakest for the evergreen dominated sites (Table 3).

[22] The primary weakness of MOD17 GPP appears to be in the estimation of LUE. For active period means across sites, the correlation between MOD17 LUE and

tower LUE was weaker than that between EVI and tower LUE (Figure 6d). Comparison of the seasonal timecourse of MOD17 LUE and tower LUE show large discrepancies, particularly for the deciduous sites (Figures 7 and 8). In contrast, seasonal trends in the f_{apar} that we calculated from NDVI were quite similar to the MOD15 FPAR, although the MOD15 FPAR was larger in many cases (Figures 7 and 8). MODIS FPAR would be expected to be

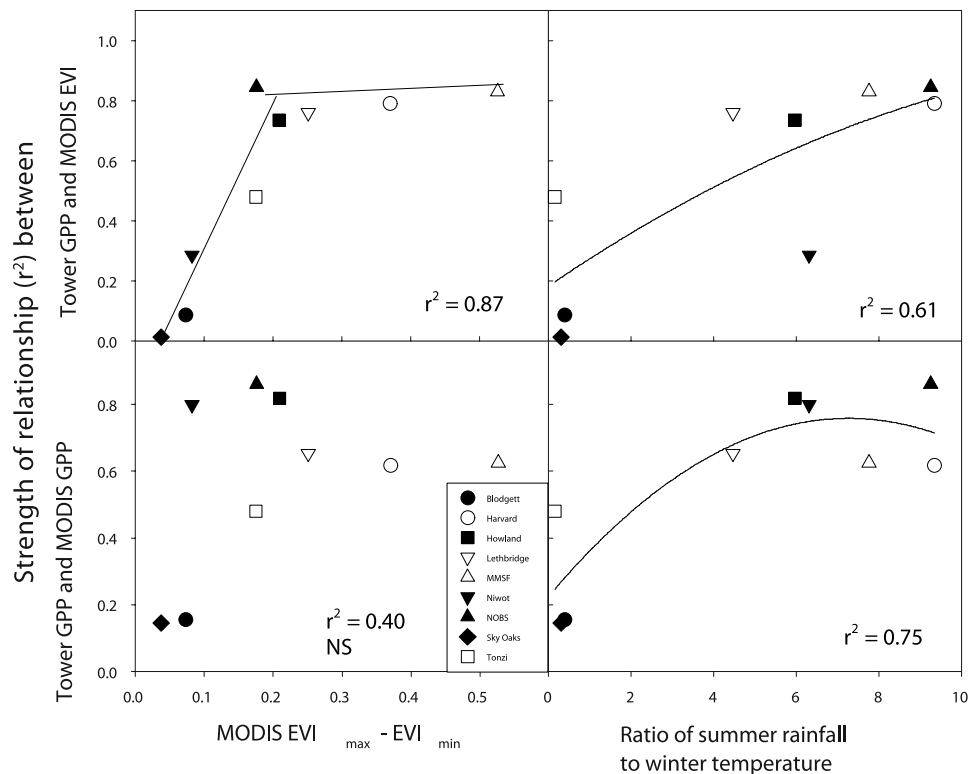


Figure 4. Coefficients of determination (r^2) between gross primary production measured at the flux towers (Tower GPP) and either the MODIS-enhanced vegetation index (EVI, 3×3 km mean) or the MOD17 GPP (3×3 km mean) for each of the nine sites as a function either of the seasonality in the vegetation ($EVI_{max} - EVI_{min}$, the difference between the mean EVI for the two month period with the highest EVI and the two month period with the lowest EVI) or the ratio of summer rainfall to winter mean temperature. Coefficients of determination for the relationships in this figure result from second-order polynomial fits and are statistically significant at $p < 0.01$, except as noted by “NS”.

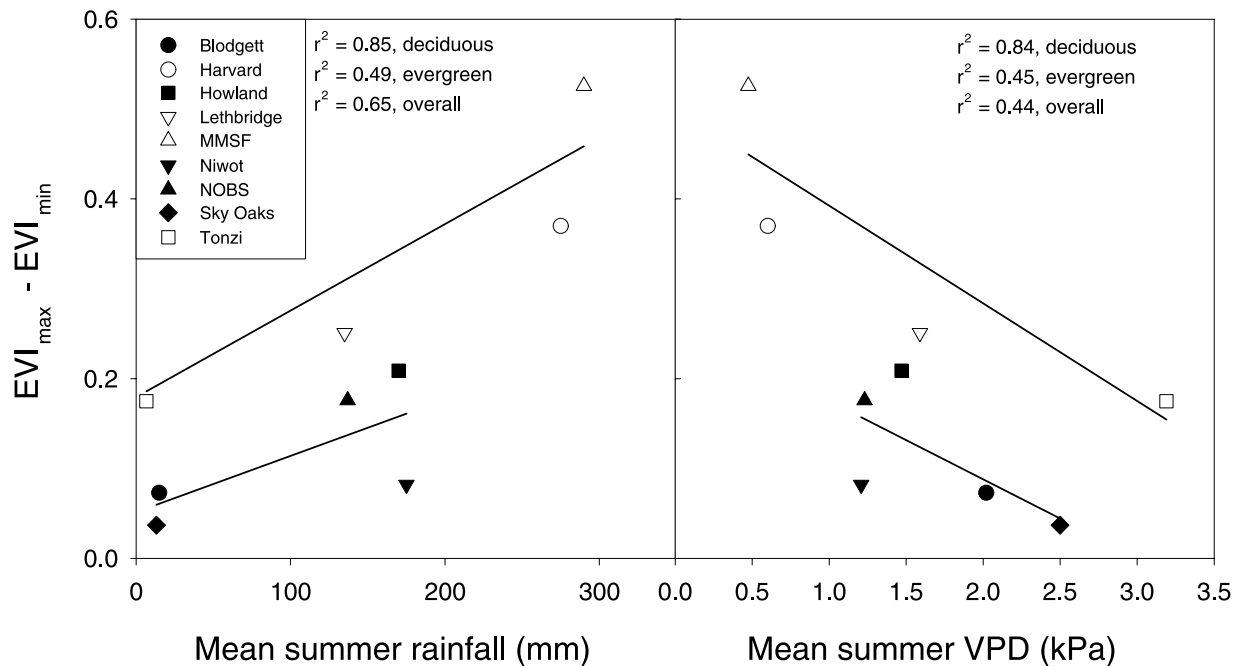


Figure 5. Relationship between two measures of summer water stress (mean rainfall during the summer months and mean summer midday (1000 to 1400 hours) vapor pressure deficit (VPD)) and the difference between the mean EVI (3×3 km mean) for the two month period with the highest EVI and the two month period with the lowest EVI ($EVI_{\max} - EVI_{\min}$) for the nine sites in this study. Regression lines were calculated separately for sites dominated by deciduous (open symbols) or evergreen (solid symbols) species. The overall relationships were statistically significant ($p < 0.05$) but not the relationships split by vegetation type.

somewhat higher, since it represents total PAR absorbed by green and nongreen vegetation components, whereas our $f_{\text{apar}}/\text{NDVI}$ relationship was based only on PAR absorbed by green tissues.

4. Discussion

[23] Our results suggest that simple models based entirely on remote-sensing data can provide at least as good, if not better, estimates of GPP for many sites than do more complex LUE based models, such as MOD17 GPP. This does not necessarily imply that there is anything wrong with the more complex LUE models in principle. Detailed LUE models such as Biome BGC can provide excellent fits to flux tower data when properly parameterized [Turner *et al.*, 2003, 2005]. The limitation of LUE models, however, is that they require meteorological inputs that are often not available at sufficiently detailed temporal and spatial scales, resulting in substantial errors in the outputs [Zhao *et al.*, 2005; Heinsch *et al.*, 2006]. Consequently, we feel that it is worthwhile to consider ways in which models might be simplified by basing them entirely on remote-sensing data.

[24] We previously reported [Rahman *et al.*, 2005] that a simple linear model based solely on EVI was at least as good as, if not better than, MOD17 GPP for estimation of tower GPP across a wide range of vegetation types in North America. However, this EVI/GPP relationship was not

equally strong at all the sites. Here we have shown that correlations between EVI and tower GPP were best for those sites with the largest seasonal variation in vegetation greenness (as measured by EVI). However, not all sites dominated by evergreen species had poor correlations between EVI and tower GPP. This most likely resulted from the presence of deciduous species components in some of these sites. Although vegetation type (evergreen versus deciduous) explained much of the difference in seasonal variation in EVI between sites, the summer climate was also significantly correlated with seasonal variation in EVI. Among the sites included in this study, summer drought, measured as low summer rainfall and high summer VPD, resulted in less seasonal variation in EVI compared to sites with wetter summers.

[25] Whereas there has been considerable interest in the climatic factors determining the geographic distribution of evergreen and deciduous species and variation in leaf life span (for reviews see Woodward [1987] and Chabot and Hicks [1982]), we are aware of only one group [Parelo and Lauenroth, 1995, 1998] that has looked at the relationship between seasonal variation in greenness of the ecosystem as a whole and climate. Parelo and Lauenroth [1995] found a larger seasonal variation in NDVI for sites with high mean annual precipitation, low mean annual temperature or large annual thermal variation. This contrasts with our results, since we did not find significant relationships between any

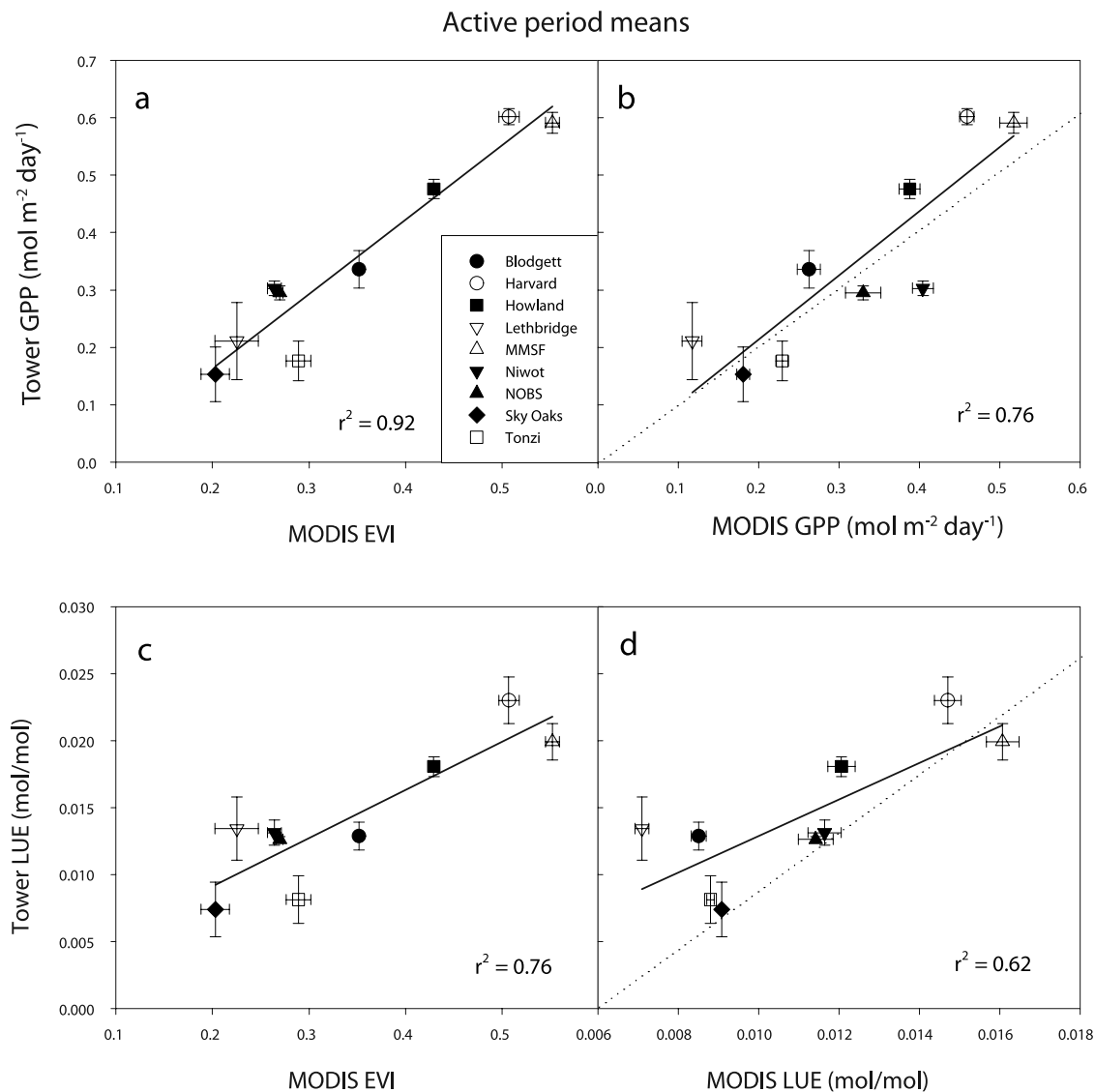


Figure 6. Flux tower measurements of gross primary productivity (GPP) and light use efficiency (LUE) as a function of either the MODIS-enhanced vegetation index (EVI) or the MOD17 calculation of GPP or LUE, respectively. Data points represent mean (\pm standard error) for each site during the period of active photosynthesis across all years used in this study. Dashed lines mark the 1:1 line. All relationships were statistically significant ($p < 0.01$).

of these factors and the seasonal variation in EVI (Table 4). However, *Paruelo and Lauenroth* [1995] only examined grassland and shrubland sites in the western United States. Thus the range of vegetation types and environmental conditions was considerably more limited in their study than in ours. These relationships between EVI variation and climatic variables may be useful in defining regions where EVI is likely to be more useful as a predictor of GPP.

[26] Another factor contributing to the poor correlation between EVI and tower GPP for sites in arid regions may be the sparseness of the vegetation. When vegetation cover is sparse, high solar elevation angles during summer result in more illumination of the background soil and thus reduce the vegetation index signal [Pinter *et al.*, 1983, 1985; Goward and Huemmrich, 1992; Sims *et al.*, 2006b]. Con-

versely, lower solar elevation angles in winter primarily illuminate the vegetation and tend to increase vegetation indices. This can have substantial effects on our ability to estimate GPP from vegetation indices. Sims *et al.* [2006b] found no correlation between seasonal trends in tower GPP and NDVI at Sky Oaks when reflectance measurements were made at noon, but found a strong correlation when NDVI values were corrected to a constant solar elevation angle. When we similarly calculated a solar angle corrected EVI for Sky Oaks (from the data of Sims *et al.* [2006b]), the correlation with tower GPP increased to $r^2 = 0.50$ (data not shown). Since sparse vegetation cover is most often associated with semiarid conditions, this may be a further reason why sites with low summer rainfall tend to have little seasonal variation in measured EVI and weak correlations

Deciduous sites

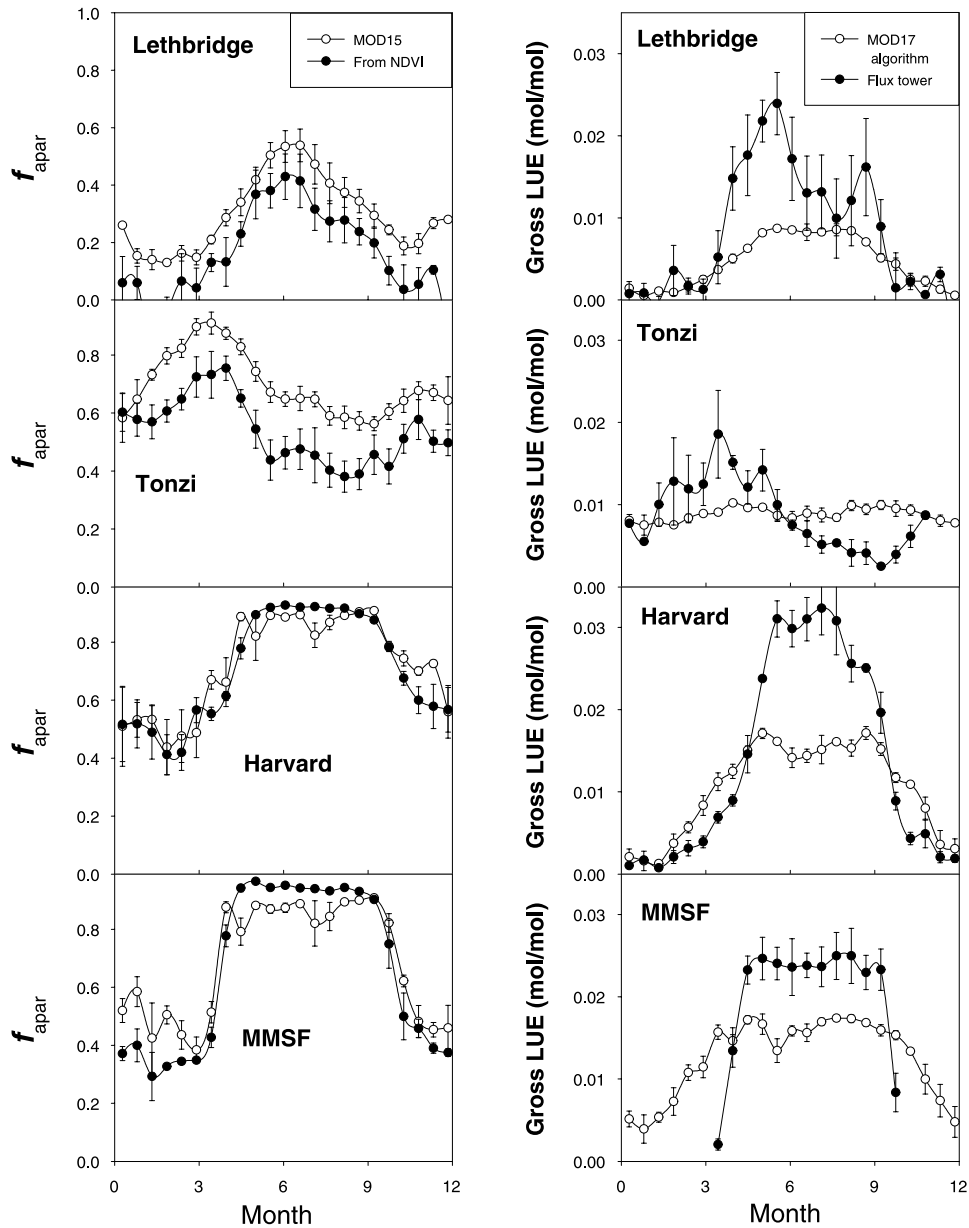


Figure 7. Comparison of the annual timecourses of the fraction of absorbed photosynthetically active radiation (f_{apar}) calculated either as a linear function of the normalized difference vegetation index (NDVI) or from the MOD15 product, and the gross light use efficiency (LUE) calculated from the flux tower data or using the MOD17 algorithm. Data are means (\pm standard error) across all years used in this study.

between EVI and tower GPP. Further work is needed to develop ways to compensate for the effects of solar elevation angle on vegetation indices in sparse vegetation types.

[27] Correlations between EVI and LUE, when data are averaged over 16 day or annual periods, are also important in explaining the strong simple correlations between EVI and tower GPP. Since LUE was calculated from tower GPP, these variables are not truly independent and a correlation between one of them and EVI may lead to a correlation of the other with EVI. However, for the relationship between EVI and LUE in Figure 6 to be entirely the product of

autocorrelation would require more than 30% errors in both tower GPP and APAR, and these errors would have to be in opposite directions for the sites with the highest and lowest LUEs. Thus it appears likely that there is some true relationship between EVI and LUE. *Sims et al.* [2006b] reported a similar relationship between NDVI and LUE for the Sky Oaks site on the basis of ground measurements of spectral reflectance, but we are not aware of other studies that have reported a correlation between EVI and LUE across sites. Studies of variation in LUE between vegetation types have, however, reported lower LUE for vegetation

Evergreen sites

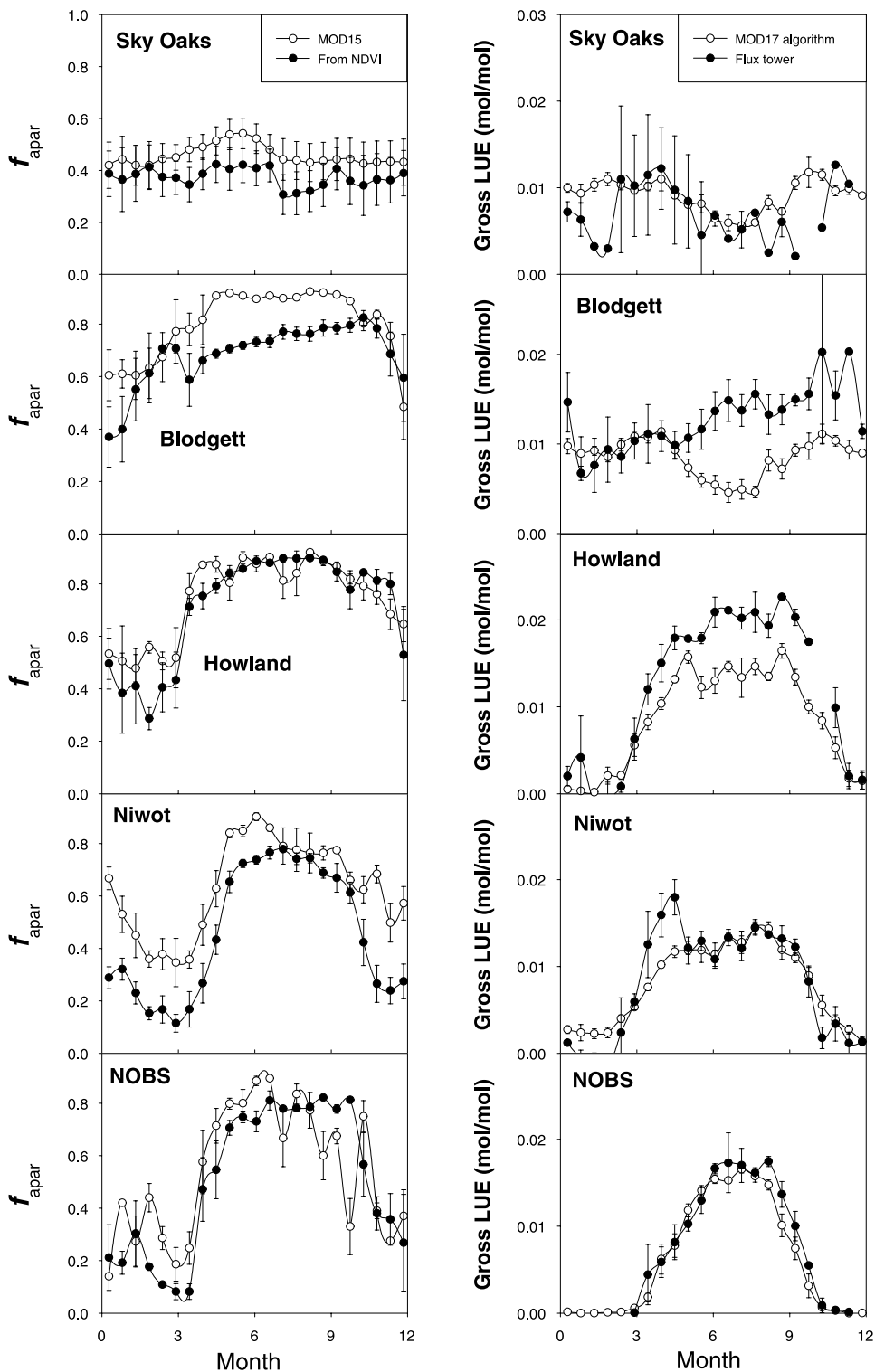


Figure 8. As in Figure 7 except for sites dominated by evergreen vegetation.

types that would also be expected to have low NDVI or EVI (i.e., desert, dry grasslands, arctic tundra [Gower et al., 1999]).

[28] These results do not suggest that variation in LUE is unimportant across these sites. In fact, LUE was quite

variable both between sites and across seasons within a site (Figures 7 and 8). Similar variability in LUE has been reported in other studies [Hunt, 1994; Ruimy et al., 1995; Gower et al., 1999; Green et al., 2003]. However, the correlation between EVI and LUE means that it may not

be necessary to develop independent estimates of LUE in order to estimate GPP from EVI, at least for some vegetation types.

[29] LUE has been predicted to be a more important factor for estimation of carbon flux in evergreen than in deciduous vegetation [Gamon *et al.*, 1995]. Our results generally confirm that prediction, since correlations between 16 day means of EVI and LUE were weaker for the evergreen sites than the deciduous forest sites (Table 3). In addition, MOD17 GPP (which is based on an LUE model) was better correlated than was EVI with tower GPP for some of the evergreen sites. Consequently, an independent estimate of LUE would improve the estimation of GPP more in the evergreen forest sites than it would in the deciduous sites. It is interesting, however, that the deciduous forest sites showed just as large a variation in LUE as did the evergreen sites. Consequently, the greater importance of LUE in evergreen sites results from its lack of correlation with vegetation greenness, rather than a greater variation in LUE.

[30] Although LUE is not well correlated with EVI across seasons for evergreen sites, the active season means of LUE and EVI for these sites are consistent with the overall relationship across sites (Figure 6c). This suggests that EVI may be useful as an estimate of baseline LUE, even for evergreen sites. This could be quite useful, since the intercept of the PRI and LUE relationship (i.e., the baseline LUE) has been found to vary between sites [Nichol *et al.*, 2002; Sims *et al.*, 2006a]. It may be that EVI could be used in calibration of the PRI/LUE relationship at a given site. PRI can be estimated from the ocean bands of MODIS [Rahman *et al.*, 2004] and we are in the process of assessing the relationship between MODIS derived PRI and LUE at a wide range of flux tower sites.

[31] The relationship between the active season means of EVI and LUE might also be useful for parameterizing the ε_{\max} term in the MOD17 model, since this relationship was stronger than the relationship between active period means of tower LUE and MODIS LUE. Poor correlations between MOD17 GPP and tower GPP appeared to result primarily from errors in estimation of LUE. Other studies have suggested that one of the primary sources of error in the MODIS LUE calculation is parameterization of the VPD scaler, and/or lack of a direct measure of soil water deficit [Turner *et al.*, 2003, 2005; Zhao *et al.*, 2006; Heinsch *et al.*, 2006]. It is suggestive that the sites with the lowest correlation between MOD17 GPP and tower GPP were those that were most subject to summer drought.

[32] The use of EVI alone to estimate tower GPP clearly still has some limitations. This paper represents only one step in an ongoing process of developing a new model for GPP based entirely on remote-sensing data. We need a model that does a better job of estimating GPP for sites in arid regions, as well as a definition of the “inactive” period that does not require a priori knowledge of GPP. A means to predict the small variations in the slope of the relationship between EVI and GPP between sites would also improve the model. Somewhat surprisingly, inclusion of PAR in the model resulted in improved estimation of tower GPP for only two of the sites (Blodgett and Niwot, data not shown) and actually reduced the correlation for some of the decid-

uous sites. Consequently, PAR does not appear to be a particularly useful model component. It would also have the limitation of not being directly estimated from satellite data.

[33] Preliminary results suggest that inclusion of the MODIS land surface temperature (LST) in the model can address all of the above limitations. LST can be used to estimate low-temperature limitations to photosynthesis, and thus the inactive period. It also provides a measure of drought stress through its correlation with vapor pressure deficit (H. Hashimoto *et al.*, personal communication, 2006), and the annual mean LST appears to be related to the slope of the relationship between the model parameters and tower GPP.

[34] Another area that needs further attention is the effect of variable pixel size on the relationship between EVI and GPP. We found that EVI measured over a larger area (the 3×3 km cutouts) produced better correlations with tower GPP than did EVI for the central 1 km pixel for the evergreen sites. It is possible that some of the 1 km pixels were not properly centered on the eddy covariance tower footprint. However, it is also possible that inclusion of vegetation outside the footprint, which may have included deciduous as well as evergreen components, improved the predictive ability of the model when the vegetation within the footprint was primarily evergreen. These deciduous components could have provided some measure of the seasonal variation in environmental parameters without significantly affecting the overall EVI of the site. On the basis of detailed ground measurements at the Sky Oaks site, Sims *et al.* [2006b] came to a similar conclusion, that is, that use of larger pixels and inclusion of a range of vegetation types improves prediction of GPP from greenness indices. A more systematic study of the change in the strength of these correlations as pixel sizes are varied is needed.

5. Conclusions

[35] Current LUE based models of GPP, such as the MOD17 GPP product, are limited by the spatial resolution and accuracy of their necessary meteorological inputs. We are exploring the potential of models based entirely on remote-sensing indices. Here we have shown that a model based solely on EVI provided as good or better estimates of GPP for most of the sites than did the much more complex MOD17 model. This simple modeling approach worked best for sites with wet summers and cold winters where availability of resources (light, water and warm temperature) tends to be correlated in time, i.e., concentrated in the summer months. Thus further modeling efforts should be concentrated primarily on sites that experience summer drought. These sites showed the least seasonal variation in EVI, probably a result both of a very limited deciduous component to the vegetation and effects of seasonal variation in solar elevation angle on EVI in sparse vegetation types. Methods to estimate the solar elevation angle effect on EVI in these sites, such as satellites in geostationary orbits, would aid in this modeling effort. We are also exploring the potential for use of the MODIS LST product to produce a more robust model still based entirely on remote-sensing products.

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References

- Anderson, M. C., J. M. Norman, T. P. Meyers, and G. R. Diak (2000), An analytical model for estimating canopy assimilation fluxes based on canopy light-use efficiency, *Agric. For. Meteorol.*, *101*, 265–289.
- Box, E. O., B. N. Holben, and V. Kalb (1989), Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO₂ flux, *Vegetatio*, *80*, 71–89.
- Chabot, B. F., and D. J. Hicks (1982), The ecology of leaf life spans, *Ann. Rev. Ecol. Syst.*, *13*, 229–259.
- Filella, I., T. Amaro, J. L. Araus, and J. Peñuelas (1996), Relationship between photosynthetic radiation use efficiency of barley canopies and the photochemical reflectance index (PRI), *Physiol. Plant.*, *96*, 211–216.
- Flanagan, L. B., L. A. Wever, and P. J. Carlson (2002), Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland, *Global Change Biol.*, *8*, 599–615.
- Gamon, J. A., J. Peñuelas, and C. B. Field (1992), A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency, *Remote Sens. Environ.*, *41*, 35–44.
- Gamon, J. A., C. B. Field, M. L. Goulden, K. L. Griffin, A. E. Hartley, G. Joel, J. Peñuelas, and R. Valentini (1995), Relationships between NDVI, canopy structure and photosynthesis in three Californian vegetation types, *Ecol. Appl.*, *5*, 28–41.
- Gamon, J. A., L. Serrano, and J. S. Surfus (1997), The photochemical reflectance index: An optical indicator of photosynthetic radiation use efficiency across species, functional types and nutrient levels, *Oecologia*, *112*, 492–501.
- Gamon, J. A., C. B. Field, A. L. Fredeen, and S. Thayer (2001), Assessing photosynthetic downregulation in sunflower stands with an optically-based model, *Photosyn. Res.*, *67*, 113–125.
- Goldstein, A. H., N. E. Hultman, J. M. Fracheboud, M. R. Bauer, J. A. Panek, M. Xu, Y. Qi, A. B. Guenther, and W. Baugh (2000), Effects of climate variability on the carbon dioxide, water, and sensible heat fluxes above a ponderosa pine plantation in the Sierra Nevada (CA), *Agric. For. Meteorol.*, *101*, 113–129.
- Goulden, M. L., J. W. Munger, S. M. Fan, B. C. Daube, and S. C. Wofsy (1996), Measurements of carbon sequestration by long term eddy covariance: Methods and a critical evaluation of accuracy, *Global Change Biol.*, *2*, 169–182.
- Goward, S. N., and K. F. Huemmrich (1992), Vegetation canopy PAR absorptance and the normalized difference vegetation index: An assessment using the SAIL model, *Remote Sens. Environ.*, *39*, 119–140.
- Goward, S. N., C. J. Tucker, and D. G. Dye (1985), North American vegetation patterns observed with the NOAA-7 advanced very high resolution radiometer, *Vegetatio*, *64*, 3–14.
- Gower, S. T., C. J. Kucharik, and J. M. Norman (1999), Direct and indirect estimation of leaf area index, fapar, and net primary production of terrestrial ecosystems, *Remote Sens. Environ.*, *70*, 29–51.
- Green, D. S., J. E. Erickson, and E. L. Kruger (2003), Foliar morphology and canopy nitrogen as predictors of light-use efficiency in terrestrial vegetation, *Agric. For. Meteorol.*, *115*, 163–171.
- Heinsch, F. A., et al. (2006), Evaluation of remote sensing based terrestrial productivity from MODIS using regional tower eddy flux network observations, *IEEE Trans. Geosci. Remote Sens.*, *44*, 1908–1925.
- Hollinger, D. Y., S. M. Goltz, E. A. Davidson, J. T. Lee, K. Tu, and H. T. Valentine (1999), Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest, *Global Change Biol.*, *5*, 891–902.
- Hollinger, D. Y., et al. (2004), Spatial and temporal variability in forest-atmosphere CO₂ exchange, *Global Change Biol.*, *10*, 1689–1706.
- Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira (2002), Overview of the radiometric and biophysical performance of the MODIS vegetation indices, *Remote Sens. Environ.*, *83*, 195–213.
- Hunt, E. R., Jr. (1994), Relationship between woody biomass and PAR conversion efficiency for estimating net primary production from NDVI, *Int. J. Remote Sens.*, *15*, 1725–1730.
- Jarvis, P. G., J. M. Massheder, S. E. Hale, J. B. Moncrieff, M. Rayment, and S. L. Scott (1997), Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest, *J. Geophys. Res.*, *102*, 28,953–28,966.
- Monson, R. K., A. A. Turnipseed, J. P. Sparks, P. C. Harley, L. E. Scott-Denton, K. Sparks, and T. E. Huxman (2002), Carbon sequestration in a high-elevation, subalpine forest, *Global Change Biol.*, *8*, 459–478.
- Monteith, J. L. (1972), Solar radiation and productivity in tropical ecosystems, *J. Appl. Ecol.*, *9*, 747–766.
- Nichol, C. J., K. F. Huemmrich, T. A. Black, P. G. Jarvis, C. L. Walthall, J. Grace, and F. G. Hall (2000), Remote sensing of photosynthetic-light-use efficiency of boreal forest, *Agric. For. Meteorol.*, *101*, 131–142.
- Nichol, C. J., J. Lloyd, O. Shibistova, A. Arneeth, C. Röser, A. Knohl, S. Matsubara, and J. Grace (2002), Remote sensing of photosynthetic-light-use efficiency of a Siberian boreal forest, *Tellus, Ser. B*, *54*, 677–687.
- Paruelo, J. M., and W. K. Lauenroth (1995), Regional patterns of normalized difference vegetation index in North American shrublands and grasslands, *Ecology*, *76*, 1888–1898.
- Paruelo, J. M., and W. K. Lauenroth (1998), Interannual variability of NDVI and its relationship to climate for North American shrublands and grasslands, *J. Biogeogr.*, *25*, 721–733.
- Peñuelas, J., I. Filella, and J. A. Gamon (1995), Assessment of photosynthetic radiation-use efficiency with spectral reflectance, *New Phytol.*, *131*, 291–296.
- Peñuelas, J., I. Filella, J. Llusà, D. Siscart, and J. Piñol (1998), Comparative field study of spring and summer leaf gas exchange and photobiology of the Mediterranean trees *Quercus ilex* and *Phillyrea latifolia*, *J. Exp. Bot.*, *49*, 229–238.
- Pinter, P. J., Jr., R. D. Jackson, S. B. Idso, and R. J. Reginato (1983), Diurnal patterns of wheat spectral reflectance, *IEEE Trans. Geosci. Remote Sens.*, *21*, 156–163.
- Pinter, P. J., Jr., R. D. Jackson, C. E. Ezra, and H. W. Gausman (1985), Sun angle and canopy architecture effects on the reflectance of six wheat cultivars, *Int. J. Remote Sens.*, *6*, 1813–1825.
- Rahman, A. F., J. A. Gamon, and D. A. Fuentes (2001), Modeling spatially distributed ecosystem flux of boreal forest using hyperspectral indices from AVIRIS imagery, *J. Geophys. Res.*, *106*, 33,579–33,591.
- Rahman, A. F., V. D. Cordova, J. A. Gamon, H. P. Schmid, and D. A. Sims (2004), Potential of MODIS ocean bands for estimating CO₂ flux from terrestrial vegetation: A novel approach, *Geophys. Res. Lett.*, *31*, L10503, doi:10.1029/2004GL019778.
- Rahman, A. F., D. A. Sims, V. D. Cordova, and B. Z. El-Masri (2005), Potential of MODIS EVI and surface temperature for directly estimating per-pixel ecosystem C fluxes, *Geophys. Res. Lett.*, *32*, L19404, doi:10.1029/2005GL024127.
- Reichstein, M., J. D. Tenhunen, O. Rouspard, J. M. Ourcival, S. Rambal, S. Dore, and R. Valentini (2002), Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: Drought effects and decomposition dynamics, *Funct. Ecol.*, *16*, 27–39.
- Ruimy, A., B. Saugier, and G. Dedieu (1994), Methodology for the estimation of terrestrial net primary production from remotely sensed data, *J. Geophys. Res.*, *99*, 5263–5284.
- Ruimy, A., P. G. Jarvis, D. D. Baldocchi, and B. Saugier (1995), CO₂ fluxes over plant canopies and solar radiation: A review, *Adv. Ecol. Res.*, *26*, 1–68.
- Running, S. W., R. R. Nemani, F. A. Heinsch, M. Zhao, M. Reeves, and H. Hashimoto (2004), A continuous satellite-derived measure of global terrestrial primary production, *BioScience*, *54*, 547–560.
- Schmid, H. P. (2002), Footprint modeling for vegetation atmosphere exchange studies: a review and perspective, *Agric. For. Meteorol.*, *113*, 159–183.
- Schmid, H. P., C. S. B. Grimmond, F. Cropley, B. Offerle, and H. Su (2000), Measurements of CO₂ and energy fluxes over a mixed hardwood forest in the mid-western United States, *Agric. For. Meteorol.*, *103*, 357–374.
- Sims, D. A., et al. (2005), Midday values of gross CO₂ flux and light use efficiency during satellite overpasses can be used to directly estimate eight-day mean flux, *Agric. For. Meteorol.*, *131*, 1–12.
- Sims, D. A., A. F. Rahman, D. A. Roberts, V. D. Cordova, S. Ogunjemiyo, and D. E. Prentiss (2006a), Use of hyperspectral reflectance indices for estimation of gross carbon flux and light use efficiency across diverse vegetation types, *Int. J. Geoinf.*, *2*, 15–30.
- Sims, D. A., H. Luo, S. Hastings, W. C. Oechel, A. F. Rahman, and J. A. Gamon (2006b), Parallel adjustments in vegetation greenness and ecosystem CO₂ exchange in response to drought in a southern California chaparral ecosystem, *Remote Sens. Environ.*, *103*, 289–303.
- Strachan, I. B., E. Pattey, and J. B. Boisvert (2002), Impact of nitrogen and environmental conditions on corn as detected by hyperspectral reflectance, *Remote Sens. Environ.*, *80*, 213–224.

- Stylinski, C. D., J. A. Gamon, and W. C. Oechel (2002), Seasonal patterns of reflectance indices, carotenoid pigments and photosynthesis of evergreen chaparral species, *Oecologia*, *131*, 366–374.
- Trotter, G. M., D. Whitehead, and E. J. Pinkney (2002), The photochemical reflectance index as a measure of photosynthetic light use efficiency for plants with varying foliar nitrogen contents, *Int. J. Remote Sens.*, *23*, 1207–1212.
- Turner, D. P., W. D. Ritts, W. B. Cohen, S. T. Gower, M. Zhao, S. W. Running, S. C. Wofsy, S. Urbansky, A. L. Dunn, and J. W. Munger (2003), Scaling gross primary production (GPP) over boreal and deciduous forest landscapes in support of MODIS GPP product validation, *Remote Sens. Environ.*, *88*, 256–270.
- Turner, D. P., et al. (2005), Site-level evaluation of satellite-based global terrestrial GPP and NPP monitoring, *Global Change Biol.*, *11*(4), 666–684, doi:10.1111/j.1365-2486.2005.00936.x.
- Wever, L. A., L. B. Flanagan, and P. J. Carlson (2002), Seasonal and interannual variation in evapotranspiration, energy balance and surface conductance in a northern temperature grassland, *Agric. For. Meteorol.*, *112*, 31–49.
- Woodward, F. I. (1987), *Climate and Plant Distribution*, Cambridge Univ. Press, New York.
- Wylie, B. K., D. A. Johnson, E. Laca, N. Z. Saliendra, T. G. Gilmanov, B. C. Reed, L. L. Tieszen, and B. B. Worstell (2003), Calibration of remotely sensed, coarse resolution NDVI to CO₂ fluxes in a sagebrush-steppe ecosystem, *Remote Sens. Environ.*, *85*, 243–255.
- Xiao, X., D. Hollinger, J. Aber, M. Gholz, E. A. Davidson, Q. Zhang, and B. Moore III (2004a), Satellite-based modeling of gross primary production in an evergreen needleleaf forest, *Remote Sens. Environ.*, *89*, 519–534.
- Xiao, X., Q. Zhang, B. Braswell, S. Urbanski, S. Boles, S. Wofsy, B. Moore III, and D. Ojima (2004b), Modeling gross primary production of temperate deciduous broadleaf forest using satellite images and climate data, *Remote Sens. Environ.*, *91*, 256–270.
- Xiao, X., Q. Zhang, S. Saleska, L. Hutyrá, P. De Camargo, S. Wofsy, S. Frolking, S. Boles, M. Keller, and B. Moore III (2005), Satellite-based modeling of gross primary production in a seasonally moist tropical evergreen forest, *Remote Sens. Environ.*, *94*, 105–122.
- Xu, L., and D. D. Baldocchi (2004), Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California, *Agric. For. Meteorol.*, *123*, 79–96.
- Zhao, M., F. A. Heinsch, R. R. Nemani, and S. W. Running (2005), Improvement of the MODIS terrestrial gross and net primary production global data set, *Remote Sens. Environ.*, *95*, 164–176.
- Zhao, M., S. W. Running, and R. R. Nemani (2006), Sensitivity of Moderate Resolution Imaging Spectroradiometer (MODIS) terrestrial primary production to the accuracy of meteorological reanalyses, *J. Geophys. Res.*, *111*, G01002, doi:10.1029/2004JG000004.

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