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A new model of gross primary productivity for North American ecosystems based solely on the enhanced vegetation index and land surface temperature from MODIS

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Abstract

Many current models of ecosystem carbon exchange based on remote sensing, such as the MODIS product termed MOD17, still require considerable input from ground based meteorological measurements and look up tables based on vegetation type. Since these data are often not available at the same spatial scale as the remote sensing imagery, they can introduce substantial errors into the carbon exchange estimates. Here we present further development of a gross primary production (GPP) model based entirely on remote sensing data. In contrast to an earlier model

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based only on the enhanced vegetation index (EVI), this model, termed the *T*emperature and *G*reenness (TG) model, also includes the land surface temperature (LST) product from MODIS. In addition to its obvious relationship to vegetation temperature, LST was correlated with vapor pressure deficit and photosynthetically active radiation. Combination of EVI and LST in the model substantially improved the correlation between predicted and measured GPP at 11 eddy correlation flux towers in a wide range of vegetation types across North America. In many cases, the TG model provided substantially better predictions of GPP than did the MODIS GPP product. However, both models resulted in poor predictions for sparse shrub habitats where solar angle effects on remote sensing indices were large. Although it may be possible to improve the MODIS GPP product through improved parameterization, our results suggest that simpler models based entirely on remote sensing can provide equally good predictions of GPP.

Keywords: Gross photosynthesis; GPP; Carbon modeling; Eddy covariance; Flux tower; Surface temperature

1. Introduction

The MODIS product termed MOD17 (Running et al., 2004) is one of the primary sources of remote sensing based gross primary productivity (GPP) estimates at the global scale. It provides an 8-day mean GPP at 1 km spatial resolution for the entire vegetated land surface. However, several recent studies have highlighted limitations of this model (Heinsch et al., 2006; Turner et al., 2003, 2005; Yuan et al., 2007; Zhao et al., 2006). The most serious limitation arises from the uncertainties of coarse resolution DAO meteorological reanalysis data used in MOD17 (Heinsch et al., 2006; Zhao et al., 2006). MOD17 also depends on estimates of light use efficiency (LUE) obtained from lookup tables based on vegetation type, which may contain errors either in the original estimate of LUE for a particular vegetation type or in the assignment of vegetation type to a pixel.

Although it may be possible to correct problems with the current version of MOD17 by improving the accuracy of the meteorological and other data inputs, it is also worthwhile to explore alternative methods for estimation of global GPP that may not require so many inputs. The simplest possible model would be a direct correlation between GPP and greenness indices such as the normalized difference vegetation index (NDVI) or the enhanced vegetation index (EVI). Sims et al. (2006b) demonstrated that this simpler model, using EVI alone, could provide estimates of GPP that were as good as or better than MOD17 for many sites during the period of active photosynthesis. This result was possible because of correlations between LUE and EVI that made an independent estimate of LUE unnecessary, as well as the elimination of short-term fluctuations in solar radiation and other environmental parameters by the 16-day averaging period. Changes in vegetation greenness would not be expected to be rapid enough to allow this simple relationship to hold over short time periods of hours to days, but EVI did show significant variation from one 16-day period to the next.

However, this simplest model, based entirely on EVI, does have its limitations. It provided no means for estimating the timing of the photosynthetic inactive period for sites with strongly evergreen vegetation. It also resulted in poor active season GPP estimates for sites subject to summer drought or with strongly evergreen vegetation. Since the inactive periods were mostly the result of low temperatures, and summer drought periods are characterized by high temperatures and vapor pressure deficits (VPD), it is clear that incorporating some measure of temperature and drought stress might improve the model. This is consistent with the MOD17 model, where temperature and VPD were chosen as the two scalars directly modifying LUE (Running et al., 2004).

Consequently, our objective in this study was to add temperature and drought stress information to the simple model, while keeping the model based entirely on remotely sensed variables without any ground based meteorological inputs. The land surface temperature (LST, Wan et al., 2004) product from MODIS can potentially be used both as a measure of temperature and VPD (Hashimoto et al., in press). Combined data from the Terra and Aqua satellites provide LST values 4 times a day; in late morning and early afternoon and twice during the night as well. LST is, strictly speaking, a measure of surface or “skin” temperature, rather than air temperature, which is more commonly used in physiological studies. However, since physiological activities of leaves are likely to be more closely related to their actual temperature, rather than air temperature, LST should be a useful measure of physiological activity of the top canopy leaves, provided that leaf cover is great enough that LST is not significantly affected by soil surface temperature. LST has also been shown to be closely related to VPD (Granger, 2000; Hashimoto et al., in press) and thus may provide a measure of drought stress. We explored the relationship between LST and various meteorological variables that are important determinates of carbon flux and developed a simple model (the *T*emperature and *G*reenness model or “TG model”) for estimation of GPP. By including LST in addition to EVI, the TG model avoids many of the limitations present in the simpler model using EVI alone.

2. Methods

2.1. Study sites

The eddy covariance tower flux data came from the same 9 AmeriFlux tower sites used previously (Sims et al., 2006b) plus two additional deciduous forest sites (Michigan and Willow Creek) (Table 1). These sites represent a wide diversity of natural vegetation across North America (see

Table 1
Vegetation type, location (lat/long in decimal degrees), years from which data were used and methods references for the 11-eddy covariance flux tower sites used in this study

Site name	Vegetation type	Latitude	Longitude	Years	Methods references
Blodgett	Evergreen needleleaf forest	38.895	120.633	2000–2005	Goldstein et al. (2000)
Niwot Ridge	Evergreen needleleaf forest	40.033	105.546	2000–2005	Monson et al. (2002)
Northern Old Black Spruce (NOBS)	Evergreen needleleaf forest	55.879	98.481	2000–2005	Dunn et al. (2006)
Howland forest	Evergreen needleleaf forest	45.204	68.740	2000–2005	Hollinger et al. (1999), Hollinger et al. (2004)
Harvard forest main tower	Deciduous broadleaf forest	42.538	72.171	2000–2005	Goulden et al. (1996)
Michigan Biological Station	Deciduous broadleaf forest	45.560	84.714	2000–2002	Schmid et al. (2003)
Morgan Monroe State Forest (MMSF)	Deciduous broadleaf forest	39.323	86.413	2000–2005	Schmid et al. (2000)
Willow Creek	Deciduous broadleaf forest	45.806	90.080	2000–2005	Cook et al. (2004)
Lethbridge	Grassland	49.708	112.940	2000–2005	Flanagan et al. (2002), Wever et al. (2002)
Tonzi	Woody savanna	38.432	120.966	2001–2006	Xu and Baldocchi (2004)
Sky Oaks old stand	Semi-arid shrubland	33.375	116.621	2000–2002	Sims et al. (2006a)

Sims et al. (2006b) for detailed vegetation characteristics) and a wide range of climate types, including summer drought and extreme winter cold, in addition to more moderate mesic climates. 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 USA 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 experiences extreme winters but contains more mixed vegetation than some of the other evergreen sites, including deciduous species (aspen) and 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.

The four deciduous forest sites are characteristic of the Eastern deciduous forests of North America, and represent a range of annual temperature regimes. Morgan Monroe State Forest (MMSF) in Indiana is the warmest site and Willow Creek in Wisconsin is the coldest site. All of the deciduous forest sites experience high summer rainfall (typically between 225 and 300 mm over the 3 summer months). 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, semi-arid site with a Mediterranean climate, representing US Southwestern shrublands with a mixture of needleleaf and broadleaf evergreen shrubs.

2.2. MODIS products

EVI and LST data were obtained from the 7×7 km subsets of MODIS products available at Oak Ridge National Laboratory'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 the central 3×3 km area within the 7×7 km cutouts. 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). All LST and EVI data come from the Terra satellite which has a morning overpass time between 1000 and 1100 h. The Terra data were used since they start in 2000, as opposed to 2002 for Aqua data. Two large gaps in these data for the NOBS and Tonzi sites during 2004 were filled using Aqua data (afternoon overpass time between 1300 and 1400 h). Differences between the Aqua and Terra data were compensated for based on linear correlations ($r^2 > 0.95$) between the Aqua and Terra data for other years at these sites.

The MODIS EVI is calculated from the following equation (Huete et al., 2002):

$$\mathrm{EVI} = G\frac{\rho_{\mathrm{NIR}} - \rho_{\mathrm{Red}}}{\rho_{\mathrm{NIR}} + C_1\rho_{\mathrm{Red}} - C_2\rho_{\mathrm{Blue}} + L} \tag{1}$$

where ρ_{Red}, ρ_{NIR} and ρ_{Blue} are the spectral reflectances in MODIS bands 1, 2 and 3 respectively. G, L, C_1 and C_2 are constants with values of 2.5, 1, 6.0 and 7.5 respectively.

The MOD17 GPP data (collection 4.8) 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 the mean for the central 3×3 km area surrounding each tower site for comparison with the tower flux data.

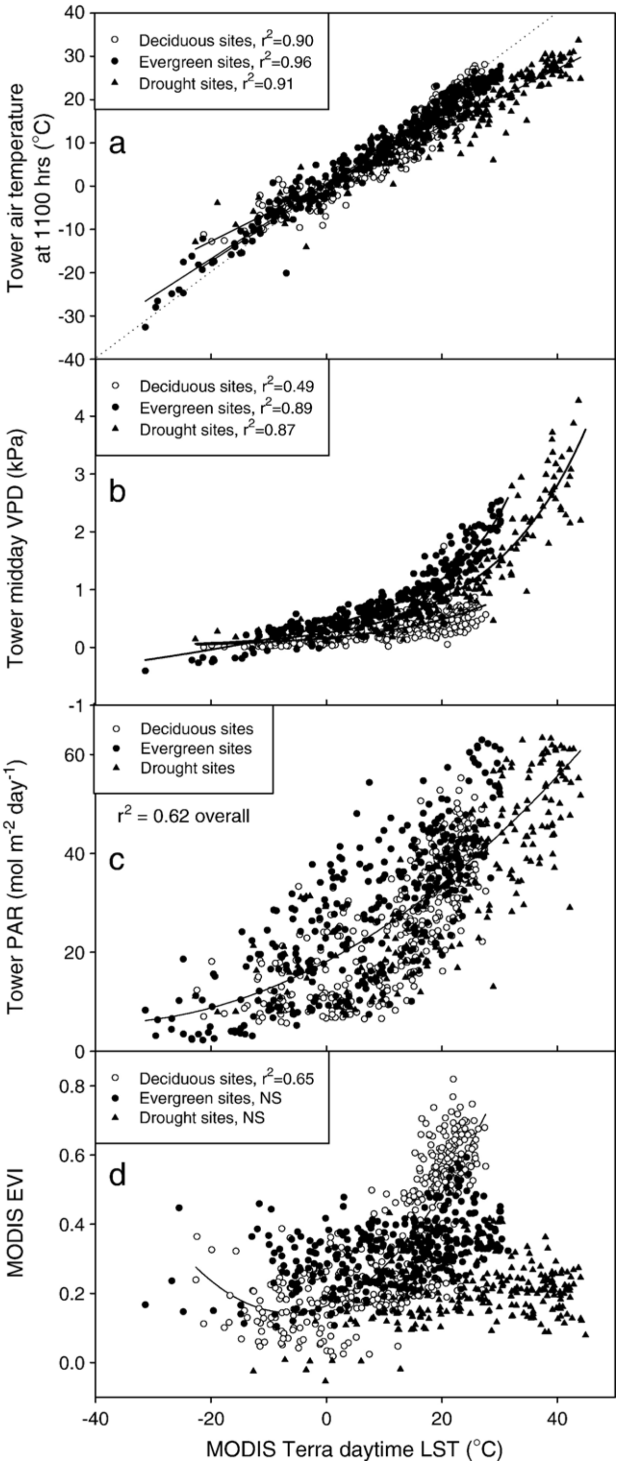

Fig. 1. Relationship between land surface temperature (LST) from MODIS (Terra daytime) and eddy covariance tower measurements of air temperature (above canopy), midday (1000 to 1400 h) vapor pressure deficit (VPD), daily total photosynthetically active radiation (PAR) and MODIS enhanced vegetation index (EVI). All points represent 16-day means.

The MOD17 GPP is calculated using a model based on LUE (Running et al., 2004) as follows:

$$\mathrm{GPP} = \varepsilon_{\max} \times m(T_{\min}) \times m(VPD) \times \mathrm{FPAR} \times \mathrm{SWrad} \times 0.45 \quad (2)$$

where $\varepsilon_{\max}$ is the maximum LUE and the scalers $m(T_{\min})$ and m (VPD) reduce $\varepsilon_{\max}$ 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 short wave solar radiation. $\varepsilon_{\max}$ is obtained from lookup tables based on vegetation type. $T_{\min}$, VPD and SWrad are obtained from large spatial scale meteorological datasets 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 (although it should be noted that a simpler backup algorithm based on NDVI is sometimes used to estimate FPAR for high latitude sites).

2.3. Calculation of tower-based C fluxes

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). Gap-filled GPP estimates were obtained from data posted to Ameriflux and/or directly from the site administrators. Gap-filled GPP for Sky Oaks was calculated as in Sims et al. (2006a). The sign convention for all the data presented in this paper is that carbon flux from the atmosphere into the vegetation is positive.

2.4. Model development

We examined the relationships between LST and several environmental variables (air temperature, VPD and PAR, Fig. 1a–c) that are known to be important determinants of carbon fluxes (Law et al., 2002). Since both LST and the environmental variables were averaged over 16-day periods, short term (hours to days) variability has been removed and this analysis looks only at longer term seasonal variability. Also note that the tower environmental means include all days (both sunny and cloudy), whereas the satellite data include only clear days.

LST would be expected to most closely correlate with measures of vegetation or soil surface temperatures. However, these measurements were not available for all the sites and thus we could not adequately check this correlation. Instead, we examined the correlation between LST and air temperature directly above the canopy. Although this correlation was quite strong (Fig. 1a), there was a tendency for LST to be higher than air temperature at the upper end of the temperature range and lower than air temperature at the low end of the range. This effect was most pronounced for the sites subject to summer drought (Lethbridge, Tonzi and Sky Oaks).

LST also showed strong relationships to midday vapor pressure deficit (VPD, Fig. 1b), but again the relationship differed with vegetation type. Evergreen sites had the highest VPDs at a given LST and deciduous sites had the lowest VPDs. Sites subject to drought had intermediate VPDs. The correlation between LST and VPD was substantially weaker for the deciduous sites than for the other two vegetation types. This

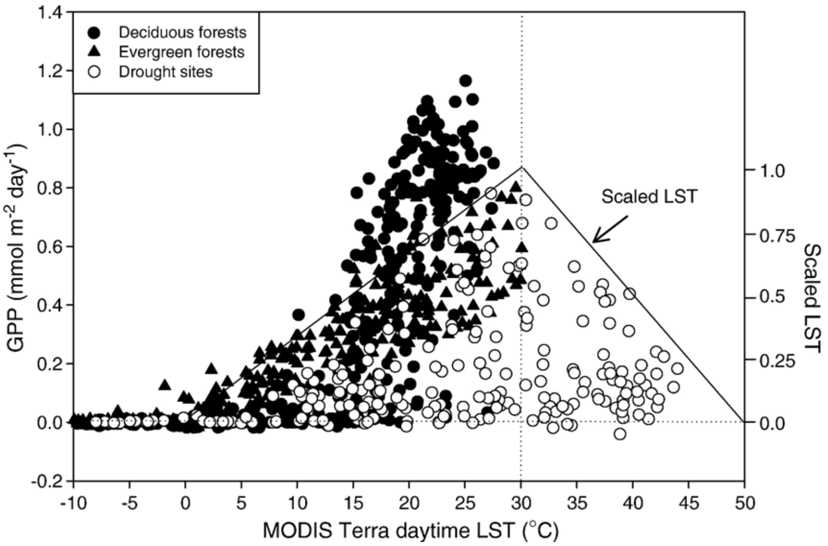

Fig. 2. Gross ecosystem exchange (GPP) measured at the eddy covariance flux towers as a function of daytime land surface temperature (LST) measured by the MODIS Terra satellite. All points represent 16-day means. Solid line represents scaled LST from TG model.

may be at least partially explained by the smaller overall range of LST and VPD for the deciduous sites. LST was also significantly correlated with daily mean PAR (Fig. 1c), although this relationship was weaker than that for air temperature and VPD. These relationships demonstrate that LST has the potential to serve as a proxy for several important environmental variables.

When considering the addition of a variable to a model, it is also important to determine the degree of independence of that variable from other variables in the model. Thus we also examined the correlation between LST and EVI (Fig. 1d). Although there was a reasonably good correlation between LST and EVI for the deciduous sites, there was no significant correlation for the evergreen and drought sites. Since these latter sites also had the weakest correlations between EVI and GPP in the simple model, it is clear that LST has the potential to provide additional independent information for at least those sites.

Examination of the data shows that GPP increased fairly linearly with LSTs above zero for the non-drought sites (Fig. 2). However, the relationship between LST and GPP for the drought sites was less clear. This is not surprising given that the drought sites tend to have low and variable EVIs (i.e. vegetation cover is often sparse). Consequently, GPP will be a combined function of EVI and LST for these sites and the relationship with either one alone may be weak. The relationship between LST and GPP for the drought sites is further complicated by the direct relationship between LST and drought stress. LST is related to VPD (Fig. 1) and high LSTs are also probably related to low soil water contents.

Based on leaf level temperature responses, we expected to see a bell shaped relationship between LST and GPP since leaf photosynthetic responses tend to have temperature optimums in the 20–30 °C range (Berry & Björkman, 1980). However, canopy GPP often does not show the same saturation responses that are observed at the leaf level (Baldocchi & Harley, 1995). The relationship between GPP and LST for the non-drought sites does not show any sign of reaching an optimum, but for the drought sites there does appear to be an optimum around 30 °C, with GPP declining to zero as LST declines to 0 °C or increases to 50 °C. Although it is unclear to what extent this results from direct temperature effects on photosynthetic rates as opposed to relationships between LST and drought stress, the relationship was consistent enough to allow us to define a scaled LST with the following equation:

$$\text{scaledLST} = \min\left[\left(\frac{\text{LST}}{30}\right); (2.5 - (0.05 \times LST))\right] \tag{3}$$

Where the scaledLST is defined as the minimum of two linear equations. This results in a maximum value of scaledLST = 1.0 when LST = 30 and minimum values of scaledLST = 0 when LST declines to 0 or increases to 50 °C (see Fig. 2). ScaledLST is also defined as zero when LST is greater than 50 or less than 0. When used in the model, this scaledLST serves several functions. First it sets GPP to zero when LST is less than zero and thus defines the inactive winter period. Second, it accounts for low temperature limitations to photosynthesis when LST is between 0 and 30 °C. Third, it accounts for high temperature and high VPD stress in sites that exceed LST values of 30 °C. Note that only the sites designated as "drought" sites experienced 16-day mean LST values greater than 30 °C.

Since earlier studies (Sims et al., 2006b) have reported that GPP drops to zero around an EVI value of 0.1, we also defined a scaled EVI according to the following equation:

$$\text{scaledEVI} = \text{EVI} - 0.1 \tag{4}$$

And the new "TG" model for GPP was thus defined as:

$$\text{GPP} = (\text{scaledEVI} \times \text{scaledLST}) \times m \tag{5}$$

Where m is a scalar with units of mol C m^{-2} day^{-1}.

Parameterization of the TG model primarily involves estimation of this slope "m". In order to be able to do a rigorous

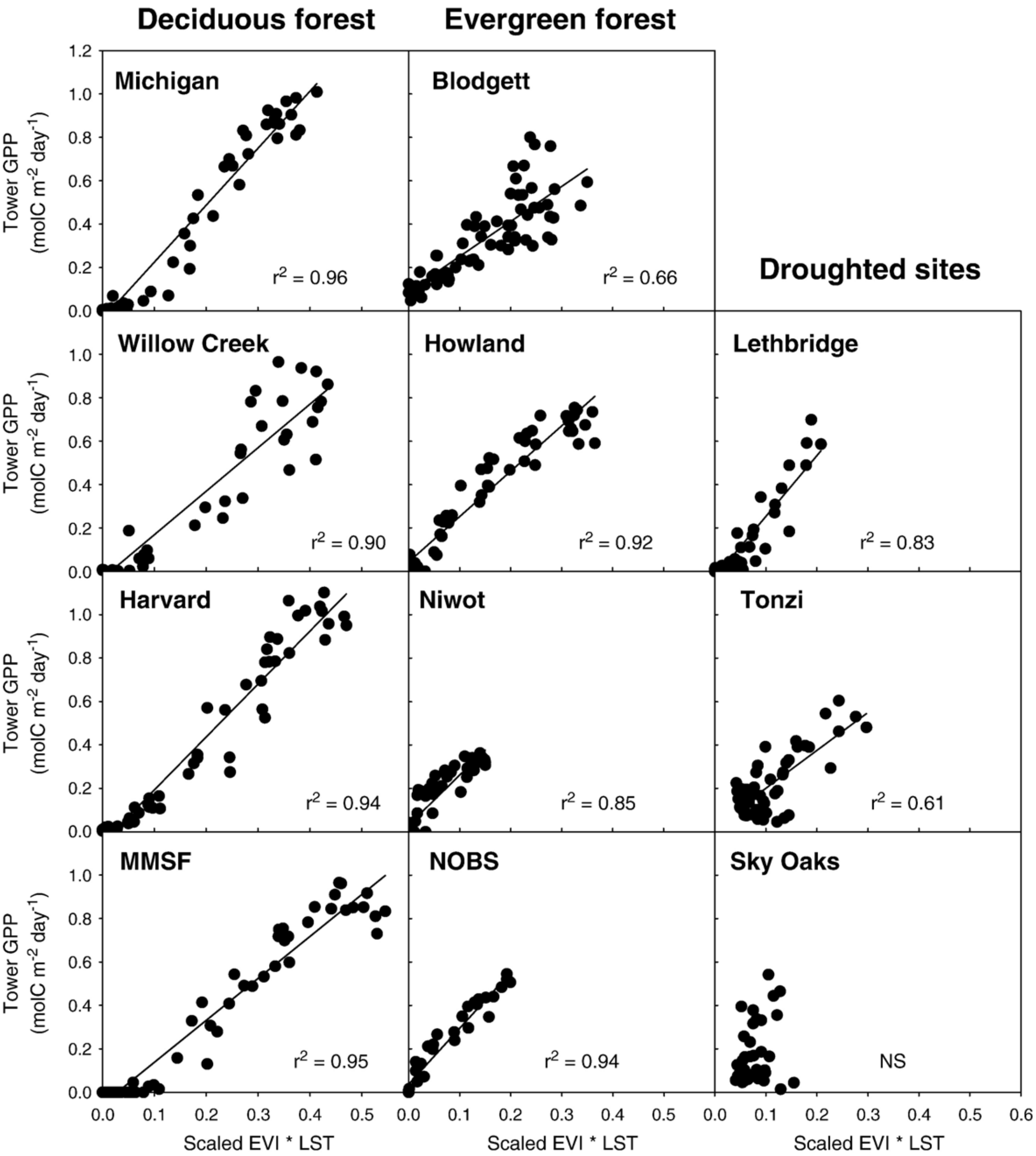

Fig. 3. Daily gross primary production (GPP) measured at the eddy covariance flux towers as a function of scaledEVI * scaledLST (see text for details on this parameter). All points represent 16-day means from years 2000–2002 (except Tonzi data from 2001–2003).

test of the model, we parameterized it using only the first 3 years of tower flux data (2000–2002 for all sites except Tonzi where we used 2001–2003). The remaining 3 years of data were then used to test the model. Strong correlations were found between GPP and (scaledEVI * scaledLST) for all of the sites except Sky Oaks (Fig. 3). However, the slope (m) of this relationship varied between sites. This slope was found to be correlated with the annual mean nighttime LST for each site and to be higher for deciduous than for evergreen sites at a given nighttime LST (Fig. 4). Mean nighttime LST was used as opposed to daytime LST simply because it produced a better correlation. It may be that nighttime values represent a better estimate of the baseline temperature that regulates plant phenology. This annual mean nighttime LST ($\mathrm{LST}_{\mathrm{an}}$) was based on Terra data (overpass time between 2200 and 2300 h) and gaps were filled by first calculating a mean nighttime LST across years for each 16-day period during the year and then averaging these 16-day values across the annual cycle. Based in the relationships shown in Fig. 4, the slope (m) in Eq. (5) was defined as follows:

$$m = 2.49 - 0.074 \times \mathrm{LST}_{\mathrm{an}} \qquad \text{for deciduous sites} \tag{6}$$

$$m = 2.10 - 0.0625 \times \mathrm{LST}_{\mathrm{an}} \qquad \text{for evergreen sites.} \tag{7}$$

3. Results

To test the TG model, we generated model predictions of GPP for the 3 years of tower flux data which were not used to

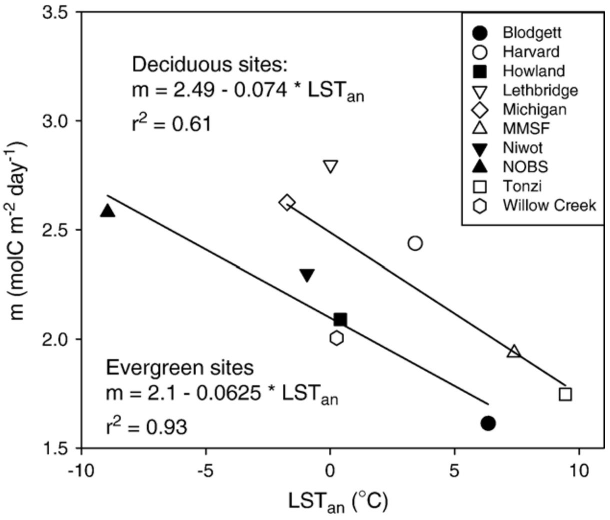

Fig. 4. The slope (m) of the relationship between scaled EVI * scaled LST and tower GPP (these relationships shown in Fig. 3), and the annual mean nighttime land surface temperature (LST$_{an}$, measured by MODIS Terra) for each site.

parameterize the model. Since only the data from 2000 to 2002 were available for the Michigan and Sky Oaks sites, we were not able to properly test the model for these sites. As a comparison to our model, we also compared the MODIS GPP product to tower GPP for these 3 years. To get an overall impression of how well the models predicted seasonal time-courses of GPP for each site, we calculated mean 16-day GPPs across the 3 years of data. In addition, as a more rigorous test of the models, we also calculated correlation coefficients between model and tower GPPs for all the 16-day mean values across the three test years (Table 2). These correlations are unaffected by simple scaling errors, i.e. if the model results are consistently too high or low by a certain percentage, and measure only how well the models predicted the relative changes in GPP across these 3 years.

For the deciduous forest sites, the TG model results were much closer to the tower GPP values than were the MODIS GPP product results (Fig. 5). Note that for comparison purposes we have included the Michigan site in this figure even though we did not have independent test data for this site. The comparison between the MODIS and tower GPP is valid for the Michigan site since the MODIS GPP was parameterized independently of any of these tower data. However, the comparison between the TG model and tower GPP is not a valid test since the model was parameterized on these data. For the deciduous forest sites, the correlation coefficients between the TG model results and tower GPP were all higher than the correlation coefficients between the MODIS and tower GPP (Table 2). The MODIS GPP product consistently overestimated GPP early in the year and underestimated GPP during the peak summer season (Fig. 5). The TG model also showed a slight overestimation of GPP early in the year but this error was much reduced compared to the MODIS product. Further examination of the data suggest that this overestimation of GPP early in the year was related to a non-linearity in the relationship between GPP and (scaledEVI * scaledLST) for the deciduous sites (Fig. 6). This non-linearity was not seen in the other vegetation types. Use of a sigmoid function in place of the linear function used in the TG model might improve the estimation of GPP for the deciduous sites. However, when we tested a model based on a sigmoid function for the deciduous sites, it actually reduced the correlation between the model results and the measured GPP (results not shown). This apparently resulted from the increased complexity of the model and consequently poor estimation of the model parameters. Consequently, we decided to keep the linear form of the TG model for all vegetation types.

For the evergreen forest sites, the TG model results closely followed the seasonal trend of tower GPP (Fig. 7). The overestimation of GPP early in the year that was seen for the deciduous sites was not observed for the evergreen sites. For all of the evergreen forest sites except Niwot, the TG model provided a better fit to the tower data than did the MODIS GPP product (Table 2). The discrepancy between the MODIS GPP product results and tower GPP was most pronounced for Blodgett during the summer. The MODIS GPP product predicted a large mid-summer depression in photosynthesis that was not observed in the tower data and was not predicted by the TG model (Fig. 7).

For the droughted sites, the MODIS GPP product substantially underestimated tower GPP for Lethbridge, whereas the TG model came much closer (Fig. 8). However, the two models were similar in terms of their ability to predict the relative changes in GPP at Lethbridge (Table 2). Both models resulted in reasonably good predictions of the seasonal pattern of GPP at Tonzi (Fig. 8) although the MODIS GPP model was slightly better correlated with measured GPP overall (Table 2). Both models correctly predicted the timing of the spring peak in GPP but incorrectly predicted a small peak in GPP as temperatures cooled in the fall (Fig. 8). Neither the MODIS GPP product nor the TG model was able to accurately predict the seasonal pattern of GPP at Sky Oaks (Fig. 8, Table 2). Although we were unable to properly test the TG model on Sky Oaks data due to having only 3 years of tower flux data, the lack of correlation between tower GPP and scaled EVI-LST even at the parameterization

Table 2
Correlation coefficients (r^2) between 16-day means of tower GPP and either MODIS GPP or the TG model output for years 2003–2005 (except Tonzi 2004–2006)

Site	MODIS GPP vs tower GPP	TG model GPP vs tower GPP
Blodgett	0.15	0.79
Harvard	0.81	0.89
Howland	0.88	0.92
Lethbridge	0.87	0.88
Michigan	0.90	–
MMSF	0.81	0.92
Niwot	0.85	0.69
NOBS	0.92	0.94
Sky Oaks	0.09	–
Tonzi	0.55	0.48
Willow Creek	0.85	0.91

Coefficients are missing for the TG model for Michigan and Sky Oaks since we did not have sufficient years of flux data to test the model for these sites. Correlations with MODIS GPP for these two sites are based on data from 2000–2002.

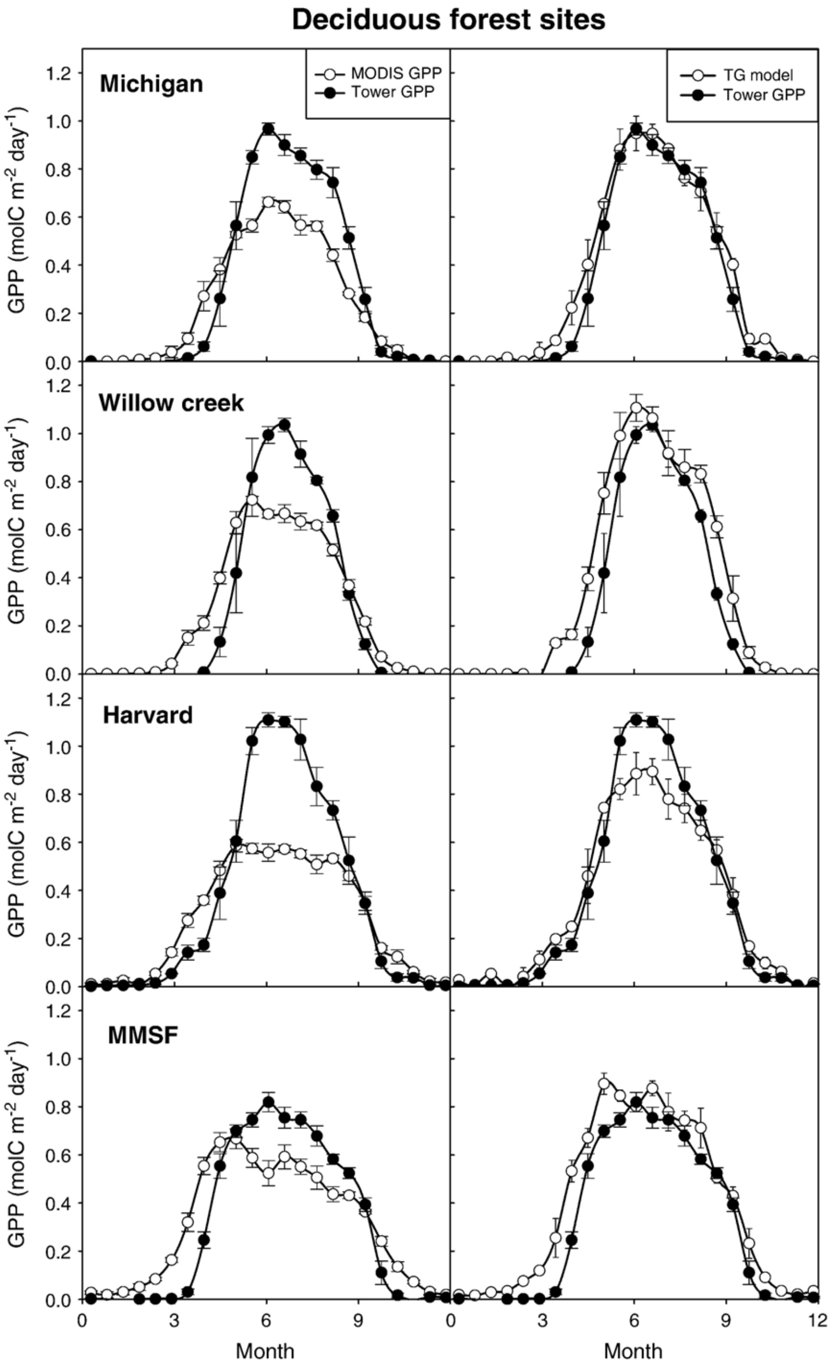

Fig. 5. Seasonal timecourses of daily mean gross primary production for the deciduous forest sites measured either at the eddy covariance flux towers (Tower GPP) or predicted by the MODIS GPP product or the TG model. Points represent means (±std error) across years 2003–2005 (except Michigan 2000–2002).

step in Fig. 3 makes this somewhat of a moot point. However, both models got the overall magnitude of GPP at Sky Oaks approximately correct.

4. Discussion

The TG model demonstrates that GPP can be estimated with a high degree of accuracy using only satellite remote sensing data. In most cases, the TG model actually resulted in better estimates of the mean seasonal timecourse of tower GPP than did the MODIS GPP product, which is a more complex model using inputs from meteorological and vegetation databases in addition to remote sensing data. Inclusion of LST in the TG model resulted in considerable improvement over the simplest model based solely on EVI (Sims et al., 2006b). The TG model appears to be applicable across a very wide range of vegetation types, with the notable exception of those with very sparse vegetation such as Sky Oaks, for estimation of seasonal time courses of GPP.

The lack of good model predictions for the Sky Oaks site may be the result of solar elevation angle effects on spectral reflectance. Both NDVI and EVI are strongly affected by

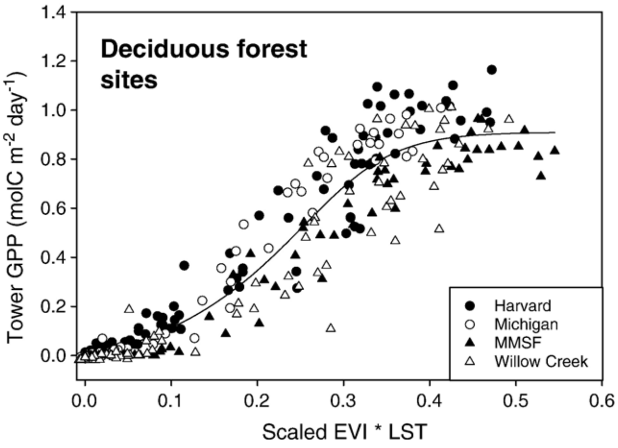

Fig. 6. Daily gross primary production (GPP) measured at the eddy covariance flux towers as a function of scaled EVI * scaled LST (see text for details on this parameter). Data are combined for all the deciduous forest sites to show the sigmoid nature of this relationship. All points represent 16-day means.

diurnal and seasonal changes in solar elevation angle when vegetation is sparse (Goward & Huemmrich, 1992; Pinter et al., 1983, 1985; Sims et al., 2006a). Increasing solar elevation angles in the spring tend to reduce the values of NDVI and EVI, counteracting the increase in leaf area index usually seen at that time of year. Sims et al. (2006a) found that GPP was well correlated with NDVI at Sky Oaks only when NDVI was corrected to a constant solar elevation angle. Sims et al. (2006b) demonstrated a similar result for relationships between EVI and GPP. Solar angle effects on reflectance indices are expected to be much smaller when vegetation is dense (Goward & Huemmrich, 1992), however, relatively few data are available to directly test this. Further development of the Specnet system (Gamon et al., 2006) for measuring reflectance diurnally in the footprints of flux towers would help address these issues. Further work is also needed to develop techniques to compensate for solar angle effects when diurnal reflectance measurements are not available.

The generality of the TG model across a wide range of vegetation types and environmental conditions suggests that it captures some basic ecological relationships. It is likely that the observed relationships are combined functions of multiple ecological and physiological processes occurring at smaller temporal and spatial scales. For example, it is likely that the observed LST optimum at 30 °C results from both direct and indirect effects of temperature on photosynthetic processes. At leaf and stand scales, the temperature optima for photosynthesis vary widely between species and growth conditions (Baldocchi et al., 2001; Berry & Björkman, 1980; Medlyn et al., 2002). In fact, Baldocchi et al. (2001) found that the temperature optimum for canopy flux closely matched the maximum monthly mean temperature at the site and this relationship held over a large range of maximum site temperatures. Consequently, a single temperature optimum would not be expected to apply to all sites and conditions and the observed optimum in the LST/GPP relationship for the drought sites is probably more a function of drought effects than temperature per se. The long 16-day averaging time in the TG model eliminates short term (minutes, hours, days) fluctuations in temperature and allows time for plants to acclimate to seasonal changes in temperature between time-steps in the model. This may explain why no LST optimum was observed for the sites not subject to drought.

LST is intimately related not only to temperature but also to drought stress because of its relationship to VPD (Granger, 2000; Hashimoto et al., in press) and the extent of evaporative cooling by the vegetation. Thus surface temperatures over 30 °C are associated with high VPDs and low soil moisture. Under these conditions, vegetation water stress significantly reduces transpiration and evaporative cooling. This can be seen in the relationship between LST and air temperature (Fig. 1). For the forest sites there is little difference between LST and air temperature, but for the drought sites, LST is substantially greater than air temperature when temperatures are above zero and this difference increases at higher temperatures. These elevated LSTs are most likely a result both of reduced stomatal conductance of the vegetation and reduced vegetation cover. Sites subject to drought are characterized by either sparse shrubby vegetation or ephemeral vegetation that dies back during periods of drought.

It is not entirely clear why the slope of the relationship between scaled LST-EVI and GPP is a function of the annual mean nighttime LST. When the slopes of the relationships between either GPP and LST or GPP and EVI are considered separately, only the slope of the GPP/EVI relationship is correlated with annual mean nighttime LST. Since annual mean nighttime LST is strongly correlated with the length of the growing season (data not shown), this may suggest that plants in areas with short growing seasons attain higher photosynthetic rates per unit leaf area (and thus higher GPP per unit EVI). It has been known for some time that there is an inverse relationship between leaf lifespan and the maximum leaf photosynthetic rate (Chabot & Hicks, 1982). However, we are not aware of studies of the relationship between maximum GPP at the ecosystem scale and growing season length. The higher slope of the relationship between scaled LST-EVI and GPP for the deciduous as opposed to the evergreen sites may also be related to the shorter productive season for the deciduous species. Evergreens can begin photosynthesis immediately when conditions become favorable but deciduous species require some time for leaf development.

If the fitted lines in Fig. 3 are forced through the origin, the slopes of the relationships for the deciduous sites become much more similar to those for the evergreen sites. This results from a difference in the shape of the relationship between scaled LST-EVI and GPP for the deciduous and evergreen sites. Whereas the relationship for the evergreen sites was linear, with intercepts very close to zero, the relationship for the deciduous sites had a distinct sigmoid character (Fig. 6). The lag in response of GPP at low LST-EVI values is most likely related to the lag in leaf development of deciduous tree leaves in the spring relative to air temperature increases. The early development of understory species and spring ephemerals prior to canopy closure clearly shows that air temperatures are sufficient for growth and photosynthesis prior to the full development of the deciduous forest canopy. The onset of photosynthesis in deciduous forest trees has been shown to be related more to soil temperature than to air temperature (Baldocchi et al., 2005). Low soil temperatures likely limit water and nutrient uptake early in the spring. In addition, the lag in leaf out of deciduous tree species has been shown to correlate with the extent of winter damage to the tree's hydraulic system and the time required to repair that damage (Wang et al., 1992). Deciduous trees with larger diameter conducting vessels in their xylem are much more susceptible to winter embolism than are evergreens which depend on narrower diameter tracheids and become active earlier in the spring.

The importance of the apparent saturation of GPP in Fig. 6 at high values of scaled LST-EVI is unclear. When the data for each site are considered alone, only the MMSF site shows a clear saturation response. Consequently, the true relationship between GPP and scaled LST-EVI for deciduous sites may be better characterized as an initial lag followed by a linear rise. We found that lack of compensation for this lag produced only very small errors for the deciduous sites in terms of overall GPP

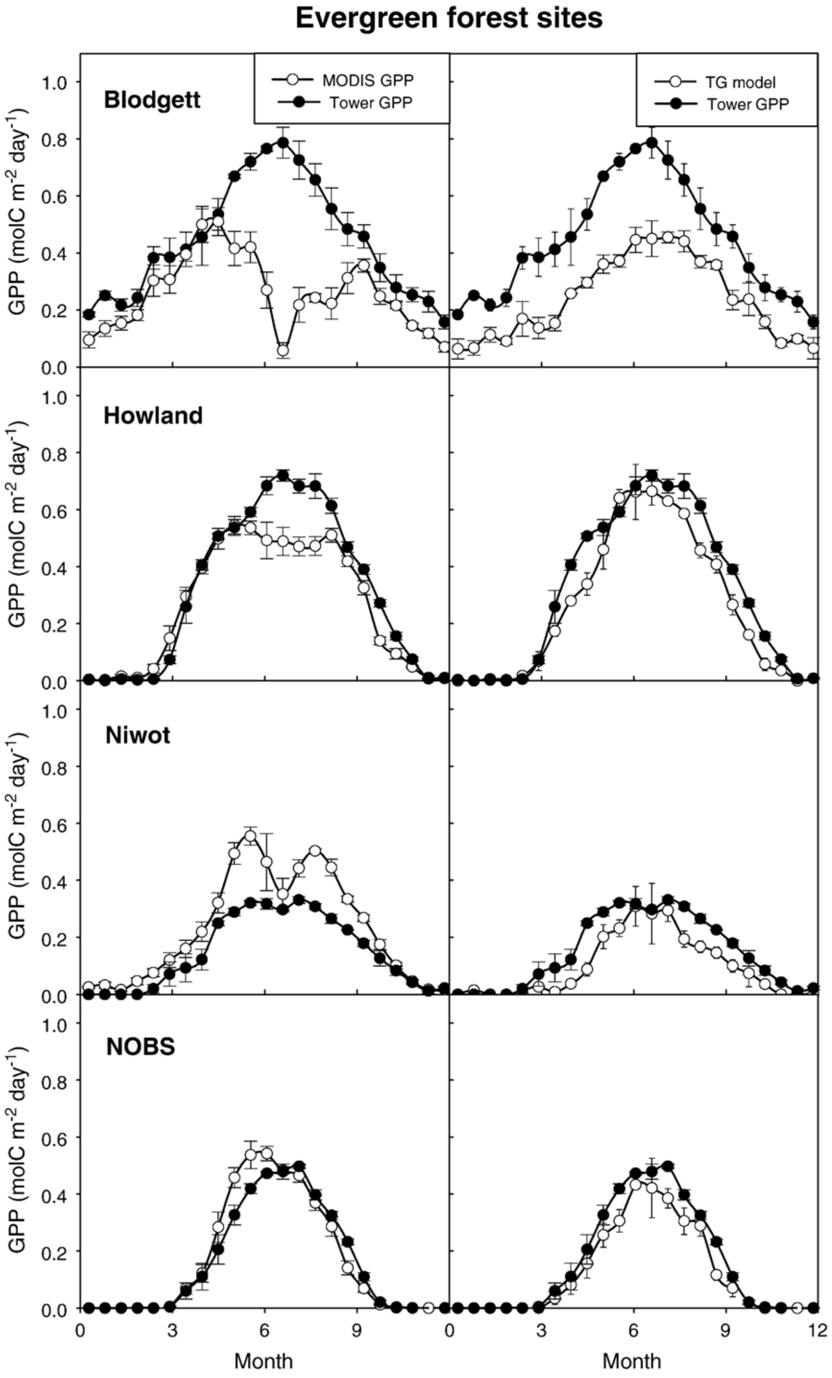

Fig. 7. Seasonal timecourses of daily mean gross primary production for the evergreen forest sites measured either at the eddy covariance flux towers (Tower GPP) or predicted by the MODIS GPP product or the TG model. Data are means (±std error) across years 2003–2005.

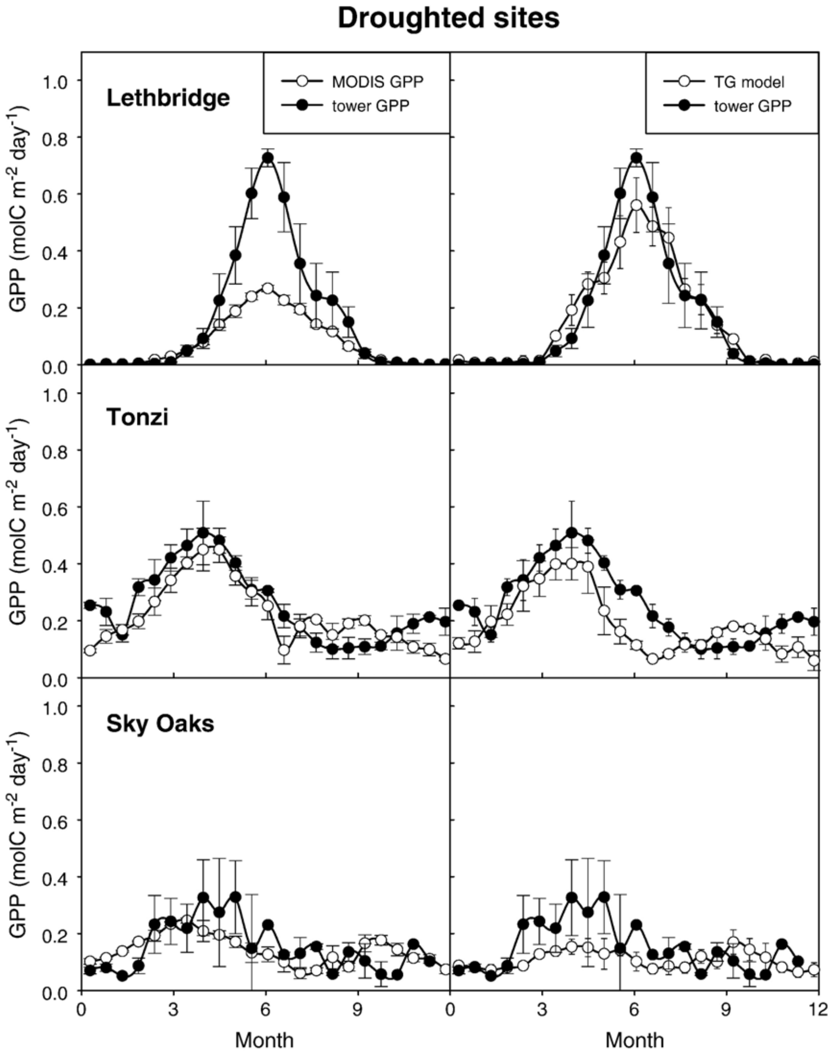

Fig. 8. Seasonal timecourses of daily mean gross primary production for the sites subject to drought measured either at the eddy covariance flux towers (Tower GPP) or predicted by the MODIS GPP product or the TG model. Data are means (±std error) across years 2003–2005 for Lethbridge, 2004–2006 for Tonzi and 2000–2002 for Sky Oaks.

across the annual cycle. However, preliminary results suggest that this error is much more significant when attempting to estimate NEE from modeled GPP and respiration. Consequently, it may be necessary to account for this lag when the final objective is the estimation of net carbon flux.

Although we have found clear differences between evergreen and deciduous vegetation in terms of the TG model parameters, these differences are not large enough to result in huge errors if vegetation is improperly classified. Based on the relationships in Fig. 4, misclassification of deciduous vegetation as evergreen, or vise versa, would result in an average error in GPP of 17%. Alternatively, if a single relationship between *m* and annual mean nighttime LST, based on all the sites, were used, the error would be ±9%. These errors are considerably smaller than the error that would result if the slope *m* were held constant and not varied at all between sites. This would result in potential errors as large as ±25%. Consequently, if the vegetation type is uncertain, it is best to use a single relationship ($m=2.4–0.53*\mathrm{LST}_{an}$) between *m* and annual mean nighttime LST based on all the sites.

It may appear that the TG model has similarities to LUE models often used to estimate vegetation-atmosphere carbon exchange (e.g. Anderson et al., 2000; Coops et al., 2005; Landsberg & Waring, 1997; Potter et al., 1993; Xiao et al., 2004, 2005; Yuan et al., 2007). The scaled EVI*LST on the *x* axis in the plots in Fig. 3 is in fact correlated with APAR across sites ($r^2=0.64$, where APAR is calculated from tower PAR and FPAR estimated from MODIS NDVI, see Sims et al., 2006a for details) and thus it would seem that the slope *m* should be related to LUE. However, the slope *m* is not correlated with LUE calculated as the slope of the relationship between tower GPP and APAR (data not shown). Further examination of the data suggests that although the correlation between scaled EVI*LST and APAR is quite strong for most sites ($r^2=0.70$–0.93 for all sites except Sky Oaks and Tonzi) the slope of this relationship varies by as much as 3 fold. Thus one would not expect a correlation between *m* and LUE. Consequently, the TG model appears to function in a manner distinct from LUE models. In addition, the strength of the correlations between GPP and scaled EVI*LST in Fig. 3 are generally greater than the strength of the correlations between GPP and APAR (data not shown), suggesting that the TG model has the potential to perform better than a simple LUE model even if we were able to accurately estimate LUE and APAR.

Weakness in the correlation between GPP and APAR suggests variation in LUE across time. LUE is known to change dramatically across seasons and between vegetation types (Gower et al., 1999; Green et al., 2003; Hunt, 1994; Ruimy et al., 1995). If we were able to accurately estimate these variations in LUE, then LUE models could be quite accurate. Thus our results do not necessarily imply that there is anything wrong with more complex LUE models in principle. Detailed physiologically based models, such as Biome BGC, can also provide excellent fits to flux tower data when properly parameterized (Turner et al., 2003, 2005). The limitation of many of these 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 (Heinsch et al., 2006; Zhao et al., 2005). This is not to say that LUE models could not be parameterized solely from remote sensing data (see Prince (1991) for an example), only that many of the more commonly used LUE models do require meteorological inputs. Sims et al. (2006b) concluded that poor correlations between MOD17 GPP and tower GPP resulted 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 (Heinsch et al., 2006; Mu et al., 2007; Turner et al., 2003, 2005; Zhao et al., 2006). Given the strong relationship between MODIS LST and tower VPD, it may be that LST could be used to improve the MODIS GPP algorithm as well. It can also be argued that EVI is a measure of water stress, at least for averaging times of 16 days or more, since plants experiencing extended periods of drought will tend to either senesce or lose part of their leaf area to conserve water. This occurs even in vegetation that would typically be considered “evergreen”. The chaparral vegetation at Sky Oaks maintains some leaves year-round but the quantity of leaves, and thus NDVI, changes dramatically in response to variation in water availability (Sims et al., 2006a).

Although the TG model works well for 16-day averaging periods, light use efficiency and/or leaf physiology based models are likely to remain better for estimation of diurnal and day to day variation in GPP. Variation in PAR is a more important determinant of GPP over these shorter timescales. Use of the TG model over short timescales is also limited by the availability of satellite remote sensing at these timescales. Diurnal satellite data are not currently available and daily data are limited by cloud cover. Since many good LUE based models are available (e.g. Anderson et al., 2000; Landsberg & Waring, 1997; Xiao et al., 2004; Yuan et al., 2007) that can be parameterized for estimates of short term fluxes at smaller spatial scales, our objective has been to develop models applicable to satellite data that have potentially global application.

So far, our TG model only predicts GPP, not NPP. Further work is needed to determine whether respiration and thus net primary production (NPP), can be estimated from satellite remote sensing data alone. For densely forested sites, respiration is strongly related to LST, with relatively little variation in this relationship between sites (Rahman et al., 2005). Preliminary data suggest that what variation there is between sites is related to variation in standing live biomass, which can be estimated remotely using techniques such as LIDAR (Drake et al., 2002; Dubayah et al., 2000; Lefsky et al., 1999) For more sparsely vegetated sites, respiration appears to be more closely related to EVI (Sims and Rahman, unpublished data).

We have shown in this study that 16-day means of GPP can be estimated using remote sensing data alone on a per pixel basis. The results from the TG model are as good as, and in many cases better than, the more complex MODIS GPP model that requires meteorological and vegetation type data inputs in addition to remote sensing indices. Work is ongoing to test the TG model across a global range of sites and to extend the model to include the estimation of respiration and thus net fluxes.

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