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A cross-biome comparison of daily light use efficiency for gross primary production

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Abstract

Vegetation light use efficiency is a key physiological parameter at the canopy scale, and at the daily time step is a component of remote sensing algorithms for scaling gross primary production (GPP) and net primary production (NPP) over regional to global domains. For the purposes of calibrating and validating the light use efficiency (ε_g) algorithms, the components of ε_g – absorbed photosynthetically active radiation (APAR) and ecosystem GPP – must be measured in a variety of environments. Micrometeorological and mass flux measurements at eddy covariance flux towers can be used to estimate APAR and GPP, and the emerging network of flux tower sites offers the opportunity to investigate spatial and temporal patterns in ε_g at the daily time step. In this study, we examined the relationship of daily GPP to APAR, and relationships of ε_g to climatic variables, at four micrometeorological flux tower sites – an agricultural field, a tallgrass prairie, a deciduous forest, and a boreal forest. The relationship of GPP to APAR was close to linear at the tallgrass prairie site but more nearly hyperbolic at the other sites. The sites differed in the mean and range of daily ε_g, with higher values associated with the agricultural field than the boreal forest. ε_g decreased with increasing APAR at all sites, a function of mid-day saturation of GPP and higher ε_g under overcast conditions. ε_g was generally not well correlated with vapor pressure deficit or maximum daily temperature. At the agricultural site, a ε_g decline towards the end of the growing season was associated with a decrease in foliar nitrogen concentration. At the tallgrass prairie site, a decline in ε_g in August was associated with soil drought. These results support inclusion of parameters for cloudiness and the phenological status of the vegetation, as well as use of biome-specific parameterization, in operational ε_g algorithms.

Keywords: absorbed photosynthetic radiation, carbon cycle, eddy covariance, gross primary production, light use efficiency, remote sensing

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Introduction

Understanding vegetation light use efficiency for gross primary production (ε_g) is of interest in relation to application of satellite data for monitoring gross primary production (GPP) and net primary production (NPP) at regional to global scales (Field *et al*., 1995; Oechel *et al*., 2000; Running *et al*., 2000; Behrenfeld *et al*., 2001). In light use efficiency (LUE) algorithms (e.g. Goetz *et al*., 1999), daily absorbed photosynthetically active radiation (APAR) is derived from satellite-based estimates of incident PAR (↓PAR) and the fraction of ↓PAR absorbed by the vegetation canopy (f_{APAR}). APAR is then multiplied by ε_g at the daily time step to estimate GPP. ε_g is usually varied depending on biome type and/or environmental stressors (Landsberg & Waring, 1997). The Land Science Team for the Moderate Imaging Spectroradiometer (MODIS) is currently producing an 8-day GPP and an

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annual NPP at the 1 km spatial resolution for the global terrestrial surface using this general scheme (Running *et al*., 2000). A key uncertainty in these applications is the spatial and temporal variation in daily ε_g (Goetz & Prince, 1999; Turner *et al*., 2002).

Eddy covariance (EC) flux towers offer the opportunity for estimating APAR and GPP, hence ε_g, at spatial and temporal scales relevant to the satellite-based scaling algorithms (Ruimy *et al*., 1996). The spatial scale of an EC tower is the tower footprint ($\sim$1 km^2) and the temporal scale is integration at half hourly intervals with subsequent summation to the daily time step. APAR is measured with above and below canopy PAR sensors and GPP is estimated by subtracting an estimate of ecosystem respiration from the measurement of net ecosystem exchange during the daylight hours (Goulden *et al*., 1996a). The concurrent measurement of meteorological variables such as temperature and vapor pressure, as well as water balance variables including evapotranspiration and soil water status, can be used to understand controls on daily ε_g. A network of EC towers now includes a wide range of biomes (Baldocchi *et al*., 1996) and, more recently, successional stages within biomes (Law *et al*., 2001).

The objective of this study was to examine the relationship of daily GPP to daily APAR over the growing season at four flux tower sites representing different biomes. Relationships of ε_g to ↓PAR, APAR, vapor pressure deficit, and daily maximum temperature were studied to assess their relative importance in different biomes. Results were considered in relation to design of algorithms for satellite-based monitoring global NPP.

Methods

Sites

Four sites were included in the study (Table 1). The AGRO site is a cornfield in an agricultural setting in the American Midwest. The KONZ site is at the Konza Long Term Ecological Research (LTER) station in the Great Plains region of the central US and is dominated by tallgrass prairie. The Harvard Forest LTER site in the northeastern US (HARV) represents the northern hardwoods biome. The NOBS site is in the boreal forest biome in northern Manitoba, Canada. Detailed information on the vegetation, climate, and soils at these sites is available at the AmeriFlux Internet site (AmeriFlux, 2001). These sites are participating in a project specifically designed to develop GPP and NPP data layers for comparison with the MODIS, GPP and NPP products (Reich *et al*., 1999b).

Gross primary production

Calculation of daily GPP efficiency requires estimates of GPP and of APAR.

$$\varepsilon_g(\text{gC MJ}^{-1}) = \text{GPP}/\text{APAR} \quad (1)$$

where GPP is gross primary production (gC m^{-2} d^{-1}) and APAR = absorbed PAR (MJ m^{-2} d^{-1}). Gross primary production (GPP) estimates were derived from micrometeorological flux measurements of net ecosystem exchange (NEE) at each site. The micrometeorological methods are described for AGRO at the AmeriFlux Internet site (AmeriFlux, 2001), for KONZ in Ham & Knapp (1998), for HARV in Wofsy *et al*. (1993), and for NOBS in Goulden *et al*. (1997). Eddy covariance analysis was used at all sites except KONZ where the eddy accumulation technique was used. GPP was calculated as:

$$\text{GPP} = \text{NEE} - R_e \text{ during daylight periods} \quad (2)$$

where NEE = net ecosystem exchange (μmol m^{-2} s^{-1}), R_e = ecosystem respiration (μmol m^{-2} s^{-1}).

In this sign convention, the flux from the surface to the atmosphere is negative.

R_e was estimated at the AGRO, HARV, and NOBS sites from the relationships of half hourly NEE at night to air

Table 1 Name, location, dominant vegetation, year of micrometeorological observations, GPP measurement interval (day of year), and measurement days in interval for the study sites

Site	Lat./Long.	Dominant vegetation	Year	Measurement interval	Measurement days
AGRO	40.0066°N 88.2910°W	Corn	1999	154–250	96
KONZ	39.0823°N 96.5602°W	Tallgrass prairie	1997	122–279	152
HARV	42.5382°N 72.1714°W	Mixed conifer/deciduous forest	2000	120–300	180
NOBS	55.8795°N 98.4808°W	Boreal conifer forest	1997	101–290	146

temperature during periods above a threshold friction velocity (Goulden *et al*., 1996a, b; 1997). At KONZ, R_e was estimated by scaling soil respiration and aboveground autotrophic respiration based on chamber measurements and temperature data (Ham & Knapp, 1998). Thus, daytime air temperatures strongly influenced R_e estimates. Gross primary production (GPP) was calculated for each day of the growing season for which flux data were available and estimated APAR (see below) was greater than $0.5\,MJ\,m^{-2}\,d^{-1}$. Short gaps in NEE were filled in where possible following Falge *et al*. (2001), however, some multiple day gaps remained because of equipment failures.

The reliance of the GPP estimates on effective modeling of daytime R_e introduces significant uncertainties. Variations in the threshold friction velocity used for screening out periods of low turbulence at night results in variations in R_e estimates (e.g. Barford *et al*., 2001). Underestimation of R_e is associated with possible nighttime advective flow that is not detected by the EC approach (Massman & Lee, 2002). There is also an issue with the assumption of similar temperature adjusted foliar respiration (R_f) rates at night and during the day. R_f rates indicated by photosynthetic light response curves can be lower than foliar dark respiration (Villar *et al*., 1995). On the other hand, temperature adjusted nighttime R_f rates may be lower than daytime rates (Hubbard *et al*., 1995), perhaps because of depletion of labile substrates. The contribution of the R_e term to daily GPP was small at the AGRO site, intermediate at the HARV and NOBS sites, and relatively large at the KONZ site (Fig. 1). The importance of the uncertainties in R_e estimation thus varies widely and continued progress in assessing these issues will be based on intensive site-level studies as well as cross-site synthesis.

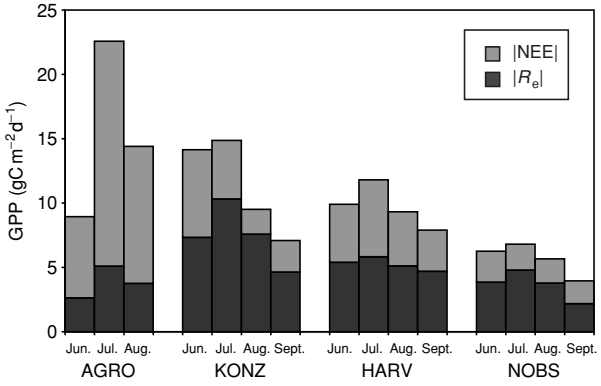

Fig. 1 The contribution of net ecosystem exchange (NEE) and ecosystem respiration (R_e) to mean daily gross primary production (GPP) by month at each site.

APAR

APAR was derived from measurements of solar short wave radiation or PAR, which were summed over a day (↓PAR) and multiplied by estimates of f_{APAR}. At NOBS and HARV, ↓PAR was measured with a quantum sensor at the top of the EC tower and half hourly means were recorded. The data are available at the AmeriFlux Internet site (AmeriFlux, 2001). At AGRO, ↓PAR was measured with a quantum sensor at a station in the SURFRAD network, which was within 5 km of the EC tower (SURFRAD, 2001). At KONZ, short wave radiation was measured at the Konza Long-term Ecological Research (LTER) station within 5 km of the tower (Konza, 2001). In cases of missing ↓PAR data, daily minimum and maximum temperature were used to estimate daily ↓PAR following Thornton & Running (1999).

Estimates of f_{APAR} were derived from seasonal trajectories of leaf area index (LAI) using a simple relationship between LAI and f_{APAR} based on the Beer–Lambert Law (Jarvis & Leverenz, 1983):

$$\mathrm{LAI} = (-1/K)\ \ln(I_z/I_0), \tag{3}$$

where I_z = below canopy PAR, I_0 = incoming PAR (↓PAR) and K = radiation extinction coefficient.

Ignoring canopy reflection, which is relatively low (Gower *et al*., 1999), f_{APAR} is then derived as:

$$f_{APAR} = 1 - (I_z/I_0),$$

where $I_z/I_0 = e^{(\mathrm{LAI}(-K))}$.

At NOBS, evergreen conifers dominate the vegetation and the LAI from Gower *et al*. (1997) was assumed constant year round. This approach probably produces an overestimate of canopy f_{APAR} at NOBS because of the columnar arrangement of the foliage on the black spruce trees. However, much of the transmitted PAR is absorbed in any case by the bryophyte layer on the ground and the bryophytes contributed significantly to GPP (Goulden & Crill, 1997). At HARV, above and below canopy measurements of PAR were used with (Eqn 3) to derive a weekly LAI. At AGRO, monthly measurements of LAI were made in 1999 (Campbell *et al*., 1999) and daily estimates were available based on reflectance measurements at the EC tower (AmeriFlux, 2001; Turner *et al*., 2002). The seasonal LAI trajectory for KONZ was from periodic measurements made in 1997 (Bremer & Ham, 1999). Values of K were approximated as 0.4 for KONZ (Massman, 1992), 0.46 for AGRO (Daughtry *et al*., 1992), and 0.5 at the other sites (Jarvis & Leverenz, 1983). PAR absorbed by below canopy vegetation such early spring herbs at HARV was not included in the analysis.

Analysis of ε_g

To make comparisons across sites, GPP and APAR data for the period June 1 to September 30 were used. The temporal constraint criteria served to eliminate days early and late in the growing season when uncertainties in APAR and GPP were greatest. Linear and rectangular hyperbola response curves (Ruimy *et al*., 1995) were fit to the plots of GPP against APAR. Mean daily ε_g was compared across months within a site, and for all months across sites. The month of September at AGRO was omitted from the ε_g comparisons because the foliage was rapidly changing from green to brown (Gallo *et al*., 1993). Relationships of ε_g to ↓PAR, APAR, daytime average vapor pressure deficit (VPD), and maximum daily temperature (T_{max}) were assessed within each site across the growing season. The VPD and T_{max} data were from the same sources as the ↓PAR data.

Results and Discussion

Daily ↓PAR, LAI, and GPP

The plots of ↓PAR against DOY showed expected patterns across the year associated with solar-surface geometry, and strong day-to-day variation associated with weather events (Fig. 2). Maximum daily ↓PAR over the growing season reached approximately $14\,MJ\,d^{-1}$ for all sites. At HARV, the summertime values tended to be lower than the maximum value because of recurrent cloudiness and/or a greater optical depth of the atmosphere.

The maximum values and the seasonal LAI trajectories (Fig. 3) differed widely among the biomes. The highest LAIs were measured in the agricultural field and the lowest at the tallgrass prairie. The forested sites had intermediate LAIs of about 4. These values are generally consistent with earlier measurements of LAI in these biomes (Gallo *et al*., 1985; Schimel *et al*., 1991; Amthor *et al*., 1994; Chen & Cihlar, 1996).

The maximum daily GPP was relatively low at NOBS, reaching only $8\,gC\,m^{-2}\,d^{-1}$, compared with values of 14 for HARV, 18 for KONZ, and 27 for AGRO (Fig. 4). All sites showed a symmetrical seasonal pattern in GPP that tracked the seasonal trend in ↓PAR. Day to day variation in GPP was not as great as the variation in ↓PAR. The beginning of the measured GPP was significantly delayed at AGRO compared to the other sites, reflecting crop-planting dates in May.

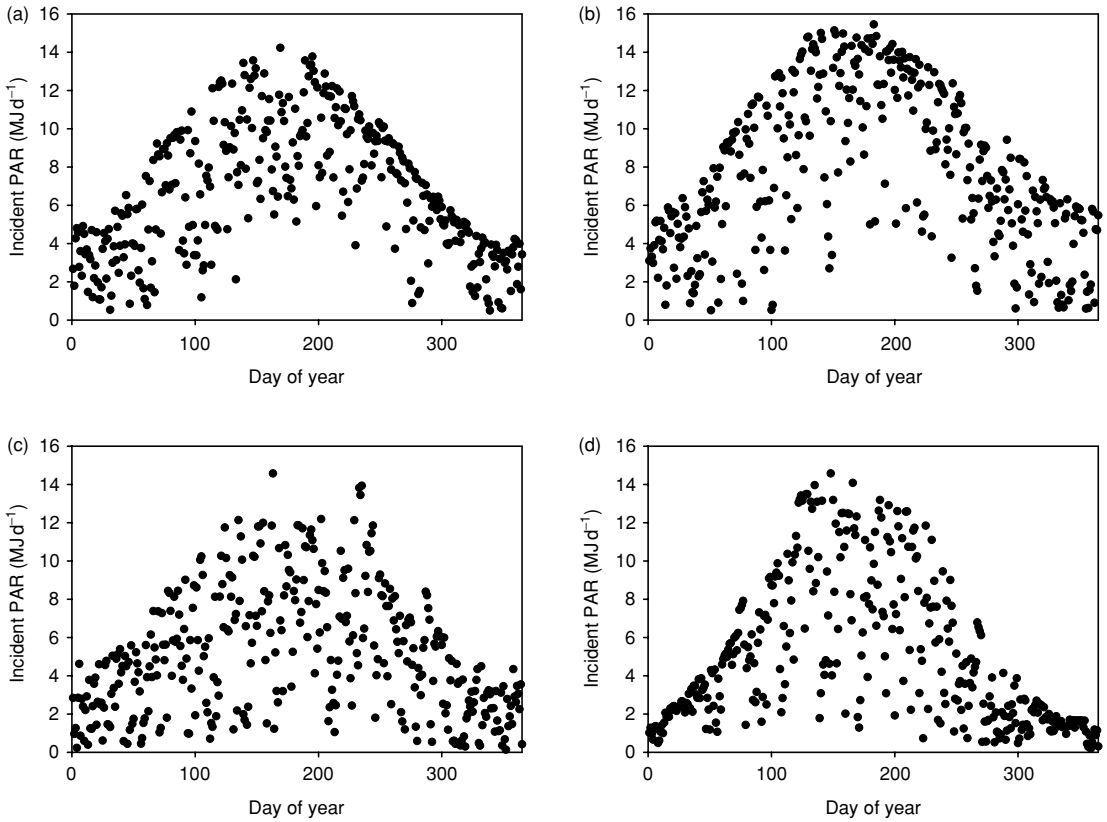

Fig. 2 Daily incident photosynthetically active radiation (↓PAR) at each site (a = AGRO, b = KONZ, c = HARV, d = NOBS).

Daily GPP

The relationship of GPP to APAR varied widely between the sites (Fig. 5). At the AGRO, HARV and NOBS sites, a rectangular hyperbola fit gave the highest r^2, whereas at KONZ the linear fit was as good as the rectangular hyperbola. The nonlinear relationships suggest the possibility of overestimating GPP using an LUE algorithm if the ε_g were based on data with low APAR.

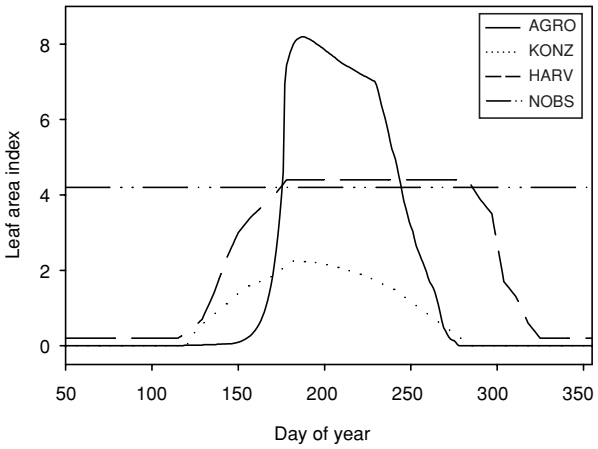

Fig. 3 The seasonal trajectory for canopy leaf area index at each site.

Saturation of net photosynthesis with increasing photosynthetic photon flux density (PPFD), hence nonlinearity in the relationship, is commonly observed at the leaf-level with cuvette measurements (e.g. Teskey *et al*., 1994). At the canopy scale, short-term estimates of gross canopy photosynthesis from eddy covariance measurements over a range of solar radiation regimes have also found saturation to some degree (Ruimy *et al*., 1995), as indicated by a hyperbolic fit of canopy CO_2 uptake to PPFD under conditions of high f_{APAR}. Theoretically, the hyperbolic relationship would be most expected under conditions of low LAI or low photosynthetic capacity (Baldocchi & Amthor, 2001). A trend towards linearity would be expected at high LAIs because mutual shading results in more of the foliage operating in the linear part of the leaf-level light response curve (Teskey *et al*., 1995).

GPP at the daily time step integrates periods of high and low PPFD, and thus nonlinearity in the daily APAR–GPP relationship is likely to be moderated relative to short-term leaf-level and canopy-level light response curves. Leuning *et al*. (1995) found a nearly linear relationship of daily-simulated canopy photosynthesis to daily incident PPFD using a short time step, multilayer

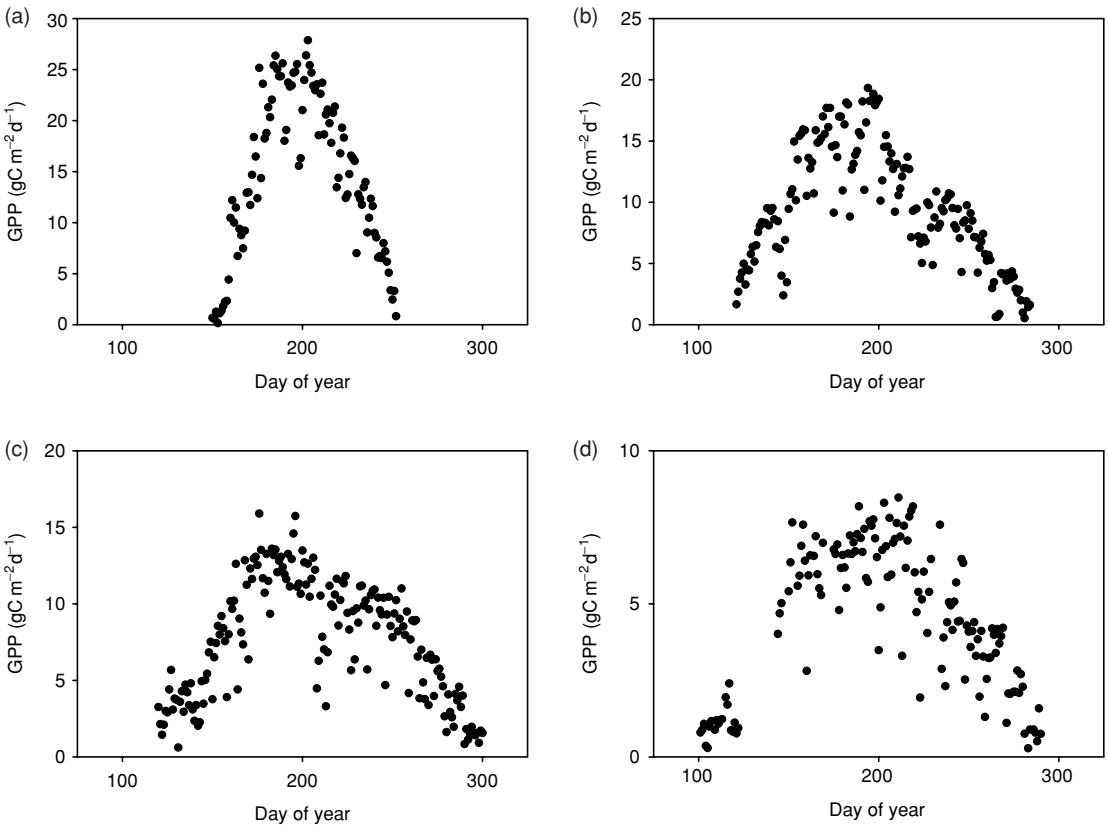

Fig. 4 Daily gross primary production (GPP) for one year at each site (a = AGRO, b = KONZ, c = HARV, d = NOBS).

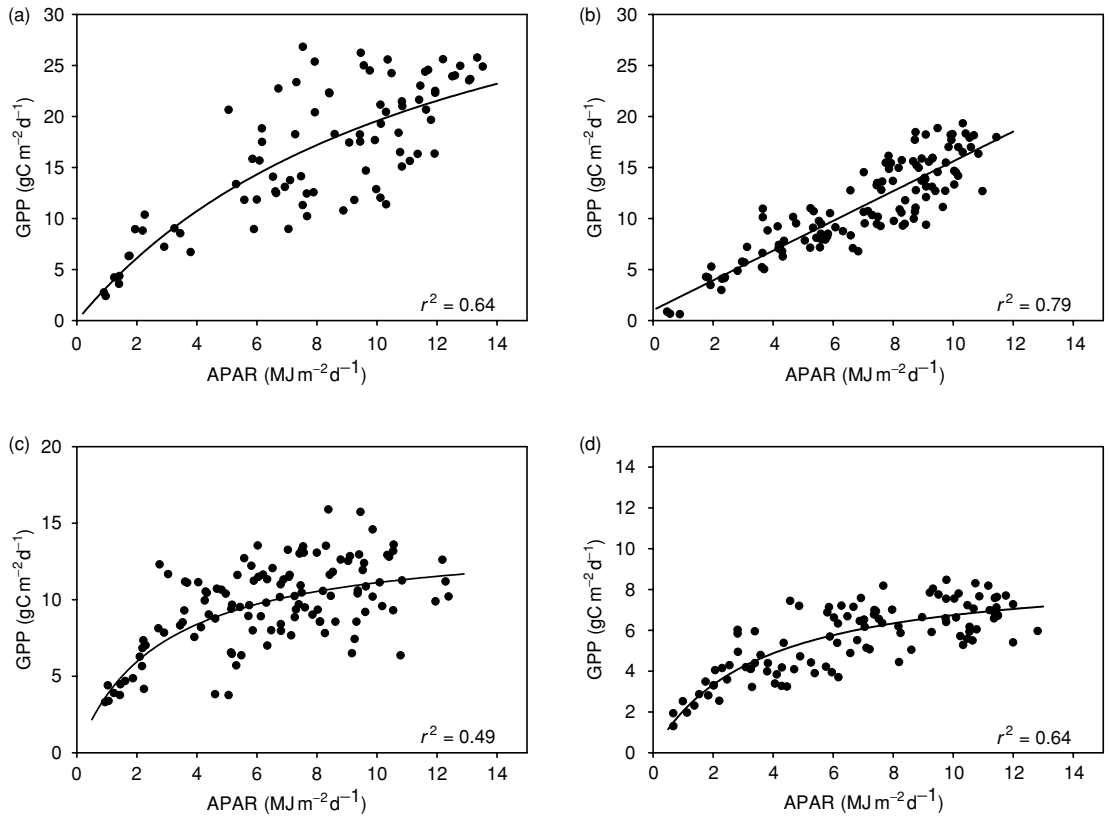

Fig. 5 The relationship of gross primary production (GPP) to absorbed photosynthetically active radiation (APAR) at each site. The KONZ plot is linear and the others are rectangular hyperbolas (a = AGRO, b = KONZ, c = HARV, d = NOBS).

canopy photosynthesis model. The strong linear relationship of GPP to APAR at the grassland site in this study is consistent with this interpretation.

Nevertheless, as is evident from this study and others (Williams *et al*., 1998; Oechel *et al*., 2000), there may remain a hyperbolic relationship of GPP to ↓PAR, and more specifically APAR, at the daily time step. The two forested sites showed the strongest nonlinearity in their relationships of GPP to APAR. At a boreal forest site, photosynthetic capacity of the conifers (Woodward & Smith, 1994) and mosses (Green & Lange, 1994) is relatively low, which would lead to saturation and the observed nonlinear relationship. In a branch chamber study with black spruce (*Picea mariana* (Mill.) BSP), the dominant conifer species at the NOBS site, the upper bound of carbon uptake per unit leaf area per day was also hyperbolically related to the daily sum of ↓PAR (Rayment & Jarvis, 1999). At the deciduous forest site, the photosynthetic capacity of the tree species is higher than in the boreal forests (Woodward & Smith, 1994). In addition, the LAI is relatively high and the leaves in the dominant deciduous species tend towards random distribution in space and spherical distribution of leaf inclination angles (Norman & Campbell, 1989). These features would favor penetration of sunlight deep into the canopy and in principle promote a linear relationship. However, shade leaves have relatively low photosynthetic capacity (Ellsworth & Reich, 1993) and high APAR days may be associated with feedback inhibition of photosynthesis in the afternoon (Amthor *et al*., 1994), both of which would reduce GPP relative to APAR.

Annual and monthly ε_g

Mean daily ε_g over the June to September period was lowest at the boreal forest site, highest at the agricultural site, and intermediate at the grassland and hardwood forest sites (Table 2). This pattern is generally consistent with differences among the biomes in net primary production (Saugier *et al*., 2001) and in light use efficiency for net primary production (Gower *et al*., 1999). The season average ε_g at AGRO is low relative to what would be expected based on light use efficiency for net primary production in corn (Sinclair & Horie, 1989; Major *et al*., 1991), which suggests a possible underestimation of night-time fluxes (hence ecosystem respiration and daytime GPP) with the EC approach. At Konza, the mean daily ε_g value is close to the daily values derived from

chamber studies near the EC tower site (Norman *et al*., 1991). At NOBS, the annual GPP from Ryan *et al*. (1997) divided by the annual APAR from this study gives an ε_g of 0.8 gC MJ^{-1}, close to the 1.0 gC MJ^{-1} for June to September in this study. The relatively low value at NOBS is also consistent with the inverse relationship of ε_g to mean annual temperature among 9 forest sites reported by Lafont *et al*. (2002). The low nitrogen availability in boreal forests and relatively high nitrogen availability in agricultural fields have a strong influence on the relative ε_g values among biomes.

Besides, differences in mean daily ε_g, the sites differed in how ε_g varied over the growing season. The strongest seasonal pattern was at AGRO where the decline in ε_g after day 200 was closely related to a decline in foliar nitrogen concentration (Fig. 6). Other studies of light use efficiency in corn have reported similar trends (Tollenaar & Bruulsema, 1988). At KONZ, ε_g decreased significantly in the month of August, but recovered late in the growing season. The tallgrass prairie is sensitive to soil drought (Knapp *et al*., 2001) and the volumetric soil water content at the KONZ site in 1997 hit a seasonal low around DOY 220 (Bremer & Ham, 1999) which corresponds to the period of relatively low ε_g. Drought related decline in ε_g is also evident in short grass prairie (Nouvellon *et al*., 2000).

The effect of seasonality on ε_g was also evident at the NOBS site, which showed an increase in ε_g between June and August (Table 2). That observation is consistent with the EC flux measurements at another boreal forest flux tower site where a seasonal cycle in the initial slope of the rectangular hyperbola fit of PPFD and canopy flux was evident (Hollinger *et al*., 1999). The changing solar zenith angle, hence improved penetration of sunlight into the canopy, may in part account for this trend (Gu *et al*., 1999) but seasonality in light saturated photosynthesis in boreal conifer species has also been observed (Middleton *et al*., 1997; Rayment & Jarvis, 1999). Leaf-level measurements at HARV show a consistent light saturated photosynthesis in July and August but a decline in that parameter between August and September (Bassow & Bazzaz, 1998). The decrease in ε_g from August to September in this study was relatively small but the change was in the expected direction. Some species at Harvard Forest show a significant early season lag in achieving maximum photosynthetic capacity (Morecroft & Roberts, 1999) but that effect may not have been resolved in this analysis because it did not include May.

Table 2 Light use efficiency for gross primary production (ε_g gC MJ^{-1}) during the growing season. Values are means of daily ε_g with standard deviations in parentheses

Site	June	July	August	September	June–September
AGRO	2.3 (0.6)	2.4 (0.6)	1.7 (0.4)	–	2.2 (0.7)
KONZ	1.7 (0.2)	1.8 (0.4)	1.4 (0.3)	1.9 (0.5)	1.7 (0.4)
HARV	1.9 (1.0)	1.8 (0.6)	1.8 (0.8)	1.6 (0.7)	1.8 (0.8)
NOBS	0.8 (0.3)	1.0 (0.4)	1.2 (0.6)	1.2 (0.5)	1.0 (0.5)

Daily ε_g

Within months, ε_g decreased with increasing ↓PAR and APAR at all sites (APAR relationships are shown in Fig. 7). The ↓PAR and APAR relationships were similar because f_{APAR} was generally high during the June–September period. The slopes of the monthly linear relationships of ε_g to APAR were most negative at the hardwood forest site. For all sites the decline of ε_g with increasing APAR was strongest in mid summer: for the month of July, an r^2 between 0.65 and 0.89 for the least squares regression linear fit was observed at each site, with ε_g generally varying by nearly a factor of 3 during the month (Fig. 7). At the agricultural site, the slope was appreciably less negative in August than in July.

The relationships of ε_g to APAR reflect in part, the nonlinear relationships of GPP to APAR (Fig. 5). If the

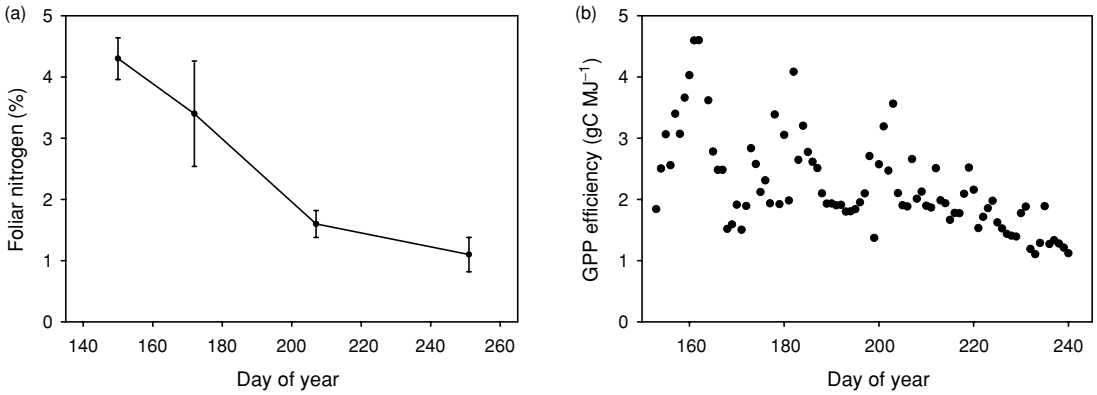

Fig. 6 Foliar nitrogen concentration and GPP efficiency at the AGRO site 1999. Foliar nitrogen data are from ORNL (2001).

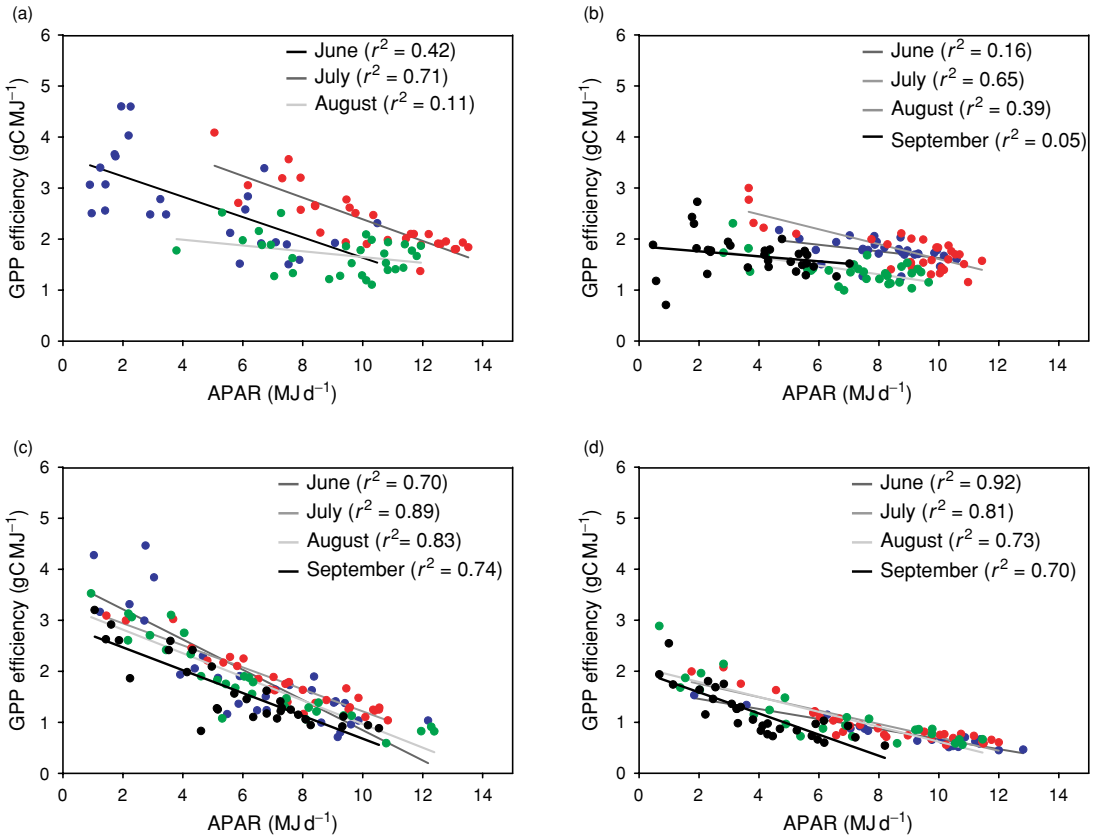

Fig. 7 The relationship of light use efficiency for gross primary production (ε_g) to absorbed photosynthetically active radiation (APAR) at each site (a = AGRO, b = KONZ, c = HARV, d = NOBS). The plots are linear fits for each month.

canopy is light saturated for a significant proportion of the day on high APAR days, the daily ε_g will come down. These relationships are also related to canopy-level observations that photosynthesis per unit PPFD is higher under overcast skies, when PPFD is relatively low, than under clear skies (Rochette *et al.*, 1996). This mechanism would tend to raise ε_g at low to mid APAR values.

An increased efficiency at low ↓PAR is believed to be an effect of lower leaf temperature, lower leaf to air VPD, and a more uniform distribution of irradiance under overcast conditions (Lloyd *et al.*, 1995). Goulden *et al.* (1997) observed higher photosynthesis per unit PPFD under cloudy compared to sunny conditions, and similar observations of GPP or net ecosystem exchange have been made at other tower sites (Hollinger *et al.*, 1994; Fan *et al.*, 1995; Freedman *et al.*, 2001; Law *et al.*, 2002). There was a positive relationship of ε_g to cloudiness in July in the four datasets used in this study (Fig. 8), with relatively shallow slopes at KONZ and NOBS compared to HARV and AGRO. At the grassland vegetation site, erectophile leaves that promote an even distribution of radiation throughout the canopy may reduce the difference between ε_g on clear and overcast days. At NOBS, the photosynthetic rates are quite low to begin with (Middleton *et al.*, 1997) and responses to variation in the light environment may be modest relative to more productive ecosystems.

VPD tends to be positively correlated with ↓PAR and APAR (e.g., Fig. 9) because clear days with high ↓PAR are also likely to have high temperatures and VPD. There was a weak inverse relationship of ε_g to VPD at all sites (i.e. r^2 always < 0.30, plots not shown) but VPD was probably not the critical factor. The strength of the decline in ε_g with increasing APAR was not diminished when data were screened for days with average VPD < 750 Pa. Leaf-level studies at Harvard Forest and canopy studies at other deciduous forest sites have indicted relatively weak effects of VPD on photosynthesis in most cases (Baldocchi *et al.*, 1987; Bassow & Bazzaz, 1998), which is consistent with the lack of a relationship at the canopy scale seen in this study. Eddy flux evaluations of canopy photosynthesis in relation to VPD in boreal forests have also not indicated much sensitivity (Goulden *et al.*, 1997; Jarvis *et al.*, 1997). Generally, crop and grasslands are short and dense, thus tending to be decoupled from the atmosphere and also relatively unresponsive to VPD (Jarvis & McNaughton, 1986).

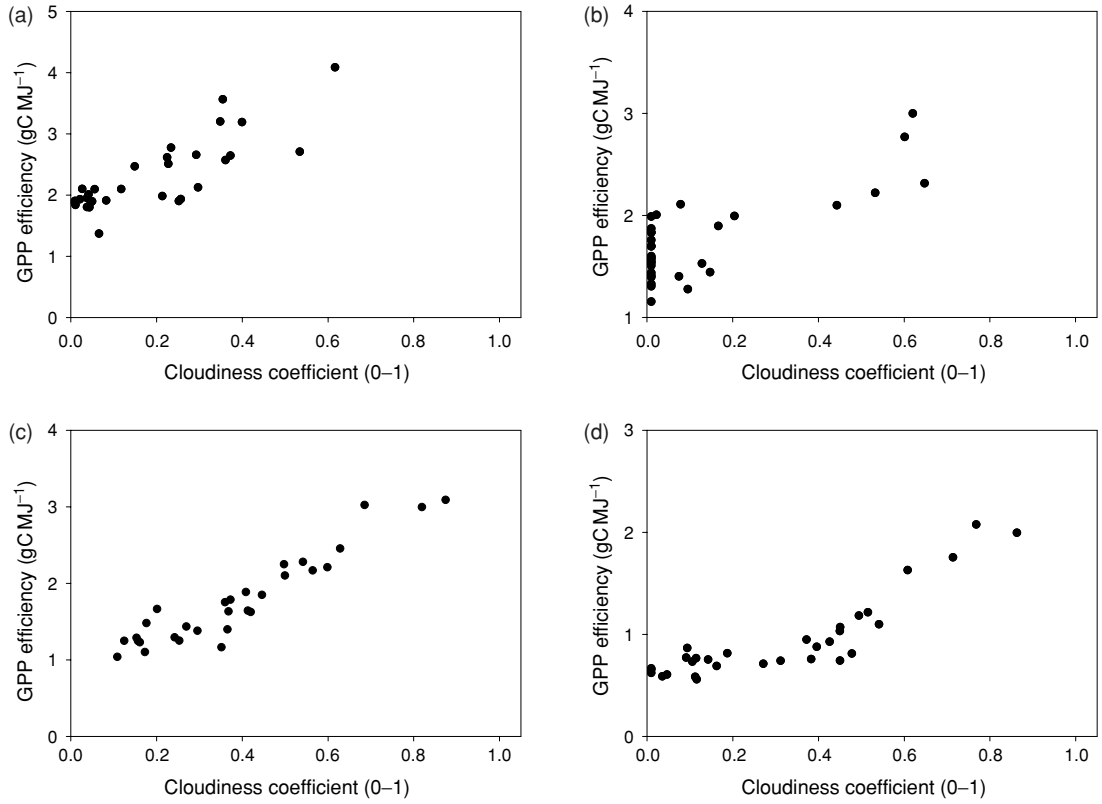

Fig. 8 Site-specific relationships of light use efficiency for gross primary production (ε_g) to cloudiness in July (a = AGRO, b = KONZ, c = HARV, d = NOBS). The cloudiness coefficient is equal to 1 minus the ratio of observed photosynthetically active radiation (PAR) to clear sky PAR. The clear sky condition was modeled following Thornton & Running (1999).

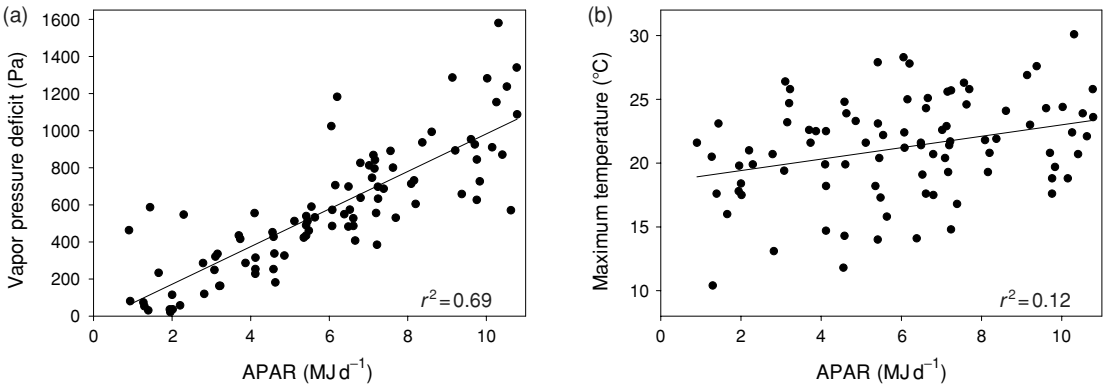

Fig. 9 The relationship of (a) vapor pressure deficit (VPD) to absorbed photosynthetically active radiation (APAR), and (b) daily maximum temperature to APAR for the June to September period at Harvard Forest.

Daily maximum temperature also covaries with APAR (e.g. Fig. 9), so again there was a weak inverse relationship of ε_g to T_{max} ($r^2 < 0.10$ at all sites, data not shown). At the temperate zone sites, temperatures during June through September did not often extend to the high or low values where strong negative effects would be expected (Mebrahtu *et al.*, 1991; Teskey *et al.*, 1995). The results were consistent with earlier leaf-level measurements at the KONZ and HARV sites that did not find strong temperature effects on photosynthesis during this part of the growing season (Polley *et al.*, 1992; Bassow & Bazzaz, 1998). EC measurements of half hourly GPP at NOBS found a positive relationship to air temperature over the May 1 to October 31 period (Goulden *et al.*, 1997)

suggesting significant temperature effects in the colder months of May and October. Low temperatures in April clearly inhibit photosynthesis in boreal forests because of frozen soils and physiological constraints (Larcher, 1995; Goulden *et al.*, 1997).

Implications for development of LUE algorithms

Regular global monitoring of terrestrial GPP and NPP based on LUE approaches has now begun and results will be of continuing interest with regard to mapping spatial patterns in carbon flux and understanding interannual variation in the global carbon cycle. ε_g is a critical component of the LUE algorithms and a variety of approaches to estimating ε_g at a daily time step over gridded areas ranging from the regional to the global scale have been implemented (Goetz *et al.*, 1999; Oechel *et al.*, 2000; Running *et al.*, 2000; Williams *et al.*, 2001). Until recently, opportunities for calibration and validation of ε_g have been limited.

Results of this and other studies suggest that biomes differ significantly with respect to the maximum daily ε_g. Remote sensing has proved effective in mapping vegetation cover, both in terms of biome types (Loveland *et al.*, 1991) and stages of succession (Cohen *et al.*, 1995), which may also differ in ε_g (Chen *et al.*, 2002). Thus the simultaneous classification of land cover and estimation of f_{APAR} by remote sensing provides a strong basis for an LUE algorithm. Recent synthesis efforts have revealed that fundamental vegetation properties such as photosynthetic capacity covary with leaf traits such as leaf thickness (Enriquez *et al.*, 1996; Reich *et al.*, 1999a). These observations suggest that to the degree remote sensing is able to detect these traits (e.g. Pierce *et al.*, 1994) spatially continuous mapping of photosynthetic capacity with remote sensing without recourse to classification may ultimately be possible.

Effects of daily weather on ε_g are also clearly important. Most commonly, LUE algorithms employ temperature and VPD scalars that are adjusted downward as stress increases (Goetz *et al.*, 1999; Running *et al.*, 2000). In this study these variables were not strong correlates of daily ε_g however, they may play a stronger role in regulating ε_g elsewhere. An observation from this study that is generally not used in LUE algorithms is the decline in daily ε_g with increasing $\downarrow$PAR or APAR. The relationship appears to be quite general, although the magnitude of the effect is related to the structural properties of the canopy and the productive capacity of the vegetation. A simple function for the effect could potentially be formulated from maximum ε_g, $\downarrow$PAR, and f_{APAR}. If used in an LUE algorithm (e.g. Lafont *et al.*, 2002), it would in theory prevent overestimation of GPP under clear sky conditions or – depending on how maximum ε_g was parameterized – underestimation on cloudy days.

Flux tower studies also suggest that ε_g changes with time in the growing season. The day of year is readily tracked for use in an LUE algorithm but an important research issue is an improved understanding of the climatic triggers influencing phenology and photosynthetic capacity (Dougherty *et al.*, 1994; White *et al.*, 1997; Botta *et al.*, 2000). Data assimilation approaches that use satellite-based observations to update a general circulation model are beginning to generate relevant weather data fields (DAO, 2002), and these data could be employed to drive phenology algorithms (e.g. Kaduk & Heimann, 1996).

Conclusions

Improving operational LUE algorithms for monitoring global GPP and NPP is desirable in the context of efforts to understand trends in the global carbon budget and to monitor global NPP. Observations at eddy covariance flux towers are made at a spatial and temporal scale relevant to characterizing daily ε_g and its response to environmental and seasonal variation. Results here suggest differences among biomes in maximum and growing season average ε_g, in temporal patterns in the variation of ε_g, and in the degree to which ε_g declines at high APAR. More comprehensive surveys of flux tower observations could provide near real time and long-term information for calibration and validation of globally applied ε_g algorithms.

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