

Remote sensing of ecosystem light use efficiency with MODIS-based PRI

A. Goerner¹, M. Reichstein¹, E. Tomelleri¹, N. Hanan², S. Rambal³, D. Papale⁴, D. Dragoni⁵, and C. Schmullius⁶

¹Max Planck Institute for Biogeochemistry, 07745 Jena, Germany

²Natural Resources Ecology Lab, Colorado State University, Fort Collins, USA

³CEFE-CNRS, 34293 Montpellier cedex 5, France

⁴Department of Forest Science and Environment, University of Tuscia, 01100 Viterbo, Italy

⁵Department of Geography, Indiana University, Bloomington, Indiana, USA

⁶Friedrich-Schiller-University Jena, 07743 Jena, Germany

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Abstract. Several studies sustained the possibility that a photochemical reflectance index (PRI) directly obtained from satellite data can be used as a proxy for ecosystem light use efficiency (LUE) in diagnostic models of gross primary productivity. This modelling approach would avoid the complications that are involved in using meteorological data as constraints for a fixed maximum LUE. However, no unifying model predicting LUE across climate zones and time based on MODIS PRI has been published to date. In this study, we evaluate the effectiveness with which MODIS-based PRI can be used to estimate ecosystem light use efficiency at study sites of different plant functional types and vegetation densities. Our objective is to examine if known limitations such as dependence on viewing and illumination geometry can be overcome and a single PRI-based model of LUE (i.e. based on the same reference band) can be applied under a wide range of conditions. Furthermore, we were interested in the effect of using different faPAR (fraction of absorbed photosynthetically active radiation) products on the in-situ LUE used as ground truth and thus on the whole evaluation exercise. We found that estimating LUE at site-level based on PRI reduces uncertainty compared to the approaches relying on a maximum LUE reduced by minimum temperature and vapour pressure deficit. Despite the advantages of using PRI to estimate LUE at site-level, we could not establish an universally applicable light use efficiency model based on MODIS PRI. Models that were optimised for a pool of data from several sites did not perform well.

1 Introduction

Sound estimates of gross primary productivity (GPP) are essential for an accurate quantification of the global carbon cycle and an understanding of its variability (Schulze, 2006). Many diagnostic models of primary productivity are based on a light use efficiency approach (Running et al., 2000; Yuan et al., 2007; Beer et al., 2010, e.g.).

All light use efficiency models represent photosynthetic assimilation of vegetation as a function of the amount of photosynthetically active radiation absorbed by plants (aPAR) (Monteith, 1972; Running et al., 2000). In these models, all environmental and biophysical constraints on the conversion of photo energy to plant biomass are aggregated in the term light use efficiency (LUE). GPP is thus calculated as:

$$\text{GPP} = \text{LUE} \times \text{aPAR} \quad (1)$$

$$\text{aPAR} = \text{faPAR} \times \text{PAR} \quad (2)$$

where faPAR is the fraction of absorbed photosynthetically active radiation. The simplicity of this approach, with little need for ancillary data, makes it possible to base these models on remote sensing products and meteorological fields (Hilker et al., 2008c; McCallum et al., 2009). Thus, an important prerequisite for application on the global scale is fulfilled.

It should be noted, although the definition of aPAR is clear, faPAR and incident PAR derived from different sources and can differ substantially (e.g. McCallum et al., 2010).

LUE is influenced by many factors and thus varies in space and time. Factors limiting LUE include plant water availability and atmospheric water demand as well as temperature and



Correspondence to: A. Goerner
(anna.goerner@bgc-jena.mpg.de)

plant nutrition. LUE is usually modelled by constraining a certain maximum LUE according to a set of environmental conditions (e.g. Running et al., 2000; Yuan et al., 2007; Horn and Schulz, 2010). The determinants of LUE and on which time-scales they act are only partially resolved. Among the main difficulties on the daily to annual time-scales are finding a suitable surrogate for ecosystem water limitation (Garbulsky et al., 2010a) and the accuracy of the available meteorological data (Heinsch et al., 2006).

It is thus attractive to derive LUE directly from just one kind of satellite data, without relying on estimates of different meteorological variables. Two types of remotely sensed data are candidates for this: fluorescence and the photochemical reflectance index (PRI).

While studies using airborne fluorescence measurements had promising results, the signal-to-noise ratio needs to be improved to be useful for satellite-based observations; efforts are ongoing (Meroni et al., 2009). The PRI combines reflectance at 531 nm (ρ_{531}) with a reference wavelength insensitive to short-term changes in light energy conversion efficiency (ρ_{ref}) and normalises it (Gamon et al., 1992; Peñuelas et al., 1995):

$$\text{PRI} = (\rho_{531} - \rho_{\text{ref}}) / (\rho_{531} + \rho_{\text{ref}}) \quad (3)$$

The original PRI formulation by Gamon et al. (1992) used 550 nm as the primary reference band since, according to a study on sunflowers, it seemed least affected by changes in green canopy structure. It also had 531 nm and reference wavelength swapped compared to recent use (c.f. Eq. 3). Later studies noted that for leaf-level reflectance, 570 nm appears to normalise best for confounding effects like pigment content and chloroplast movement (Gamon et al., 1993, 1995). Thus, 570 nm became the most widely used PRI reference band. Recently, Middleton et al. (2009) showed for a douglas fir forest that reference bands in the ranges 540–574 nm, 480–515 nm and 670–680 nm have a high correlation with foliage LUE. An overview on protocols used for PRI studies can be found in a review by Garbulsky et al. (2010b).

PRI can be a useful proxy for LUE because changes in reflectance at 531 nm are a side effect of mechanisms that protect the photosynthetic system in the leaves from excess light by down-regulating carbon assimilation (for an extensive summary, see Middleton et al., 2009; Coops et al., 2010). PRI also correlates with the total content of carotenoid pigments (Stylinski et al., 2002), this needs to be considered when looking at seasonal changes in PRI.

At site level, PRI has been shown to give good estimates of LUE when derived from field spectrometers (Gamon et al., 1992), but also from airborne sensors (Nichol et al., 2000, 2002; Rahman et al., 2001). Recently, the MODIS sensor on TERRA and AQUA has also been used successfully at ecosystem scale (Rahman et al., 2004; Drolet et al., 2005, 2008; Garbulsky et al., 2008; Goerner et al., 2009; Xie et al., 2009). MODIS provides a useful temporal resolution, a band

around 531 nm, but not the reference band at 570 nm. Thus, the MODIS PRI has been based on several alternative reference bands. However, the PRI has some well known limitations (Grace et al., 2007). Multiple studies showed that the PRI signal is affected by the viewing and illumination geometry, including the fraction of sunlit and shaded leaves seen by the sensor, canopy structure, and background reflectance (Barton and North, 2001; Nichol et al., 2002; Suárez et al., 2008; Sims and Gamon, 2002; Louis et al., 2005; Drolet et al., 2008; Hilker et al., 2009; Middleton et al., 2009). These difficulties, along with data access problems, might have hindered the evaluation of an LUE model based on MODIS PRI across space and time. So far it is unclear if one model can be applied at multiple sites. Also, the question remains whether one MODIS PRI reference band can be recommended for all sites, or if different reference bands have to be used depending on for example plant functional type and vegetation density.

Despite the fluctuations in illumination geometry, dimension of the surface area sensed by each instantaneous field-of-view and background reflectance at every site, the site level models based on MODIS PRI published so far yielded good agreement with observed LUE. That considerable potential exists for mapping LUE with a common model has also been shown by Drolet et al. (2008), who found a unifying model for eight sites in central Saskatchewan. These boreal sites are close to each other (within the confines of one satellite scene), hence they can be simultaneously monitored instead of by comparing data from different image acquisitions. The viewing geometry and atmospheric disturbance of the satellite signal is therefore similar. Consequentially, the next step is to evaluate PRI based models across sites and satellite scenes.

In this study, we evaluate the effectiveness with which MODIS-based PRI can be used to estimate ecosystem light use efficiency (LUE) at study sites of four distinct plant functional types and different vegetation densities. Our objective is to find out if the limitations can be overcome and a single PRI-based model of LUE (i.e. based on the same reference band) can be applied under a wide range of conditions. Furthermore, we were interested in how different fAPAR products affect the in-situ LUE estimates which are used as ground truth.

2 Data and methods

2.1 Selection of study sites

To be able to properly evaluate the PRI-based LUE estimates, we conducted this study at a selection of sites from the FLUXNET LaThuile data set that provides the necessary gross primary productivity and site meteorology data (www.fluxdata.org).

Table 1. Overview of the sites used in this study.

Site code	Site name	Lat, Lon (flux tower)	Data used	PFT (dominant species)	LAI	References
ZA-Kru	Skukuza, Kruger National Park (South Africa)	−25.0197, 31.4969	2001– 2003	Savanna (Combretum apiculatum, Sclerocarya birrea, Acacia nigrescens)	1 (area average trees, max.) 3 (within tree canopy, max.) 1 (herbaceous layer, avg.)	Scholes et al. (2001); Kutsch et al. (2008)
FR-Pue	Puechabon (France)	43.7414, 3.59583	2000– 2006	evergreen broad-leaved forest (Quercus ilex L.)	2.8 ± 0.4	Allard et al. (2008)
IT-Cpz	Castelporziano (Italy)	41.7052, 12.3761	2000– 2006	evergreen broad-leaved forest (Quercus ilex L.)	3.2–3.8	Tirone et al. (2003)
US-MMS	Morgan Monroe State Forest (US)	39.3231, −86.4131	2000– 2005	deciduous broad-leaved forest (sugar maple, tulip poplar, sassafras, white and red oak)	4.8	Schmid et al. (2000)
US-Me2	Metolius – intermediate aged ponderosa pine (US)	44.4523, −121.557	2003– 2005	evergreen needle-leaved forest (Pinus ponderosa)	2.8 (overstorey), 0.2 (understorey)	Thomas et al. (2009)

Here, we focus on non-boreal forest/savanna sites with water stress during part of the year. Some sites have to be excluded because of too few valid PRI data. Such data scarcity can be caused by frequent cloud cover or saturation of the satellite signal at sparsely vegetated sites. The largest limitation on the number of relevant sites is the size of the targeted ecosystem surrounding the flux tower. It must be large enough to contain the footprint of a $\geq 1 \times 1$ km MODIS pixel so that the flux tower footprint is representative of the remotely sensed footprint.

We thus conducted our analysis on 5 sites: two dry-summer subtropical evergreen broad-leaved forests, a site with vegetation typical for tropical savanna, a humid-subtropical deciduous forest and a dry-summer subtropical evergreen needle-leaved forest. All years for which eddy covariance and MODIS data are available simultaneously were analysed (Table 1). Castelporziano is a borderline case regarding the extension of the target ecosystem. For this site, we discarded satellite scenes in which the pixel containing the flux tower is partially made of non-forest.

2.2 In-situ LUE

We define LUE as the effectiveness with which an ecosystem uses absorbed photosynthetically active radiation (aPAR) to produce photosynthates (recorded as gross primary productivity, GPP):

$$\text{LUE} = \frac{\text{GPP}}{\text{faPAR} \times \text{PAR}} \quad (4)$$

We used daily and half-hourly GPP data derived from eddy covariance measurements, in-situ PAR measurements from the Fluxnet LaThuile data base, and different satellite based faPAR data sets. The eddy covariance data were processed using the standardised methodology described in Papale et al. (2006); Reichstein et al. (2005). We calculated aPAR as the product of available photosynthetically active radiation (PAR, here in the form of average daylight photosynthetic photon flux density – $\mu\text{mol m}^{-2} \text{s}^{-1}$) and the fraction of PAR that is actually absorbed by the vegetation (faPAR).

Since representative in-situ faPAR measurements are scarce, and considering potential application of the PRI model to a larger area, we used satellite based faPAR data to calculate aPAR. Readymade faPAR products are known to differ from each other (McCallum et al., 2010). To test the impact of product choice on the evaluation of the PRI-models we used three different faPAR sets: the MODIS collection 5 MOD15A2 and MYD15A2 products (https://lpdaac.usgs.gov/lpdaac/products/modis/products_table/leaf_area_index_fraction_of_photosynthetically_active_radiation/8_day_14_global_1km/mod15a2) (2000–2006, 8-days-composite), the SeaWiFS-based faPAR of the Joint Research Centre (<http://fapar.jrc.ec.europa.eu>) (2000–2006, although much of the 2006 data were discarded because of poor quality flags, 10-days-composite) and the SPOT-Vegetation based Cyclopes faPAR product (Baret et al., 2007) (only available for 2000–2003, 10-days-composite). The faPAR data were quality checked and linearly interpolated to daily time steps, except for periods where no good data were recorded for longer than 19 days (equal to 1 missing value in the aggregated SeaWiFS and Cyclopes

Table 2. Bandwidth of the MODIS spectral bands used in this study. The narrow red bands 13 and 14 were excluded right from the beginning because they tend to saturate over land (Goerner et al., 2009).

Band	Bandwidth (nm)	Use in this study
1	620–670	PRI, NDVI
2	841–876	NDVI
4	545–565	PRI
10	482–493	PRI
11	526–536	PRI
12	546–556	PRI

products) or 23 days (equal to 2 missing values in the aggregates MODIS product). The light use efficiency calculated with these faPAR data is denoted as LUE_{MODIS} , $LUE_{SeaWiFS}$ and $LUE_{Cyclopes}$. For the US-Me2 site, no valid aPAR is contained in the Cyclopes data set throughout the study period.

2.3 Modelling LUE from MODIS based PRI

2.3.1 Acquisition and processing of MODIS reflectance data

To process the MODIS data for this study, we modified the procedure described by Drolet et al. (2005) as follows. Three MODIS products were downloaded from the Level 1 and Atmosphere Archive and Distribution System (<http://ladsweb.nascom.nasa.gov>). Of those products, from both the Terra and Aqua satellite, we selected all scenes containing the tower locations. The MOD/MYD021KM product contains calibrated digital signals measured by the MODIS sensor, from which at-sensor reflectances and radiances can be calculated from two pairs of scale and offset terms included in the product (Toller et al., 2005). We calculated top-of-atmosphere reflectances for the spectral bands listed in Table 2. The MOD/MYD03 product has the same spatial extent and resolution and provides the geographic coordinates as well as the solar and sensor zenith and azimuth angles of each pixel. These geolocation data were used to extract the spectral information of the pixel closest to each tower location. The MOD/MYD04 were used for an initial cloud cover screening.

Those acquisition dates were discarded where the quality flags attached to the MODIS products indicated saturation of a detector, where cloud cover is likely or where the sensor viewing angle at the tower site is more than 40° (otherwise the MODIS pixel footprint would get too large, the result being a mixed signal from different land cover classes, c.f. Wolfe et al., 1998).

Light reaching a satellite sensor after traveling through the atmosphere is inevitably affected by scattering and absorption. In addition, natural surfaces reflect light differently subject to the viewing geometry. Ideally, data recorded by

a satellite sensor should be corrected for these wavelength-dependent effects to make the reflectances computed from these records comparable. Albeit, from a previous study (Goerner et al., 2009) and preliminary experiments we know that correcting MODIS reflectances with bidirectional reflectance distribution function (BRDF) parameters from existing data bases either has no effect on the PRI signal (when using POLDER/PARASOL based parameters (Bacour and Bréon, 2005), see Fig. 2 in the Supplement) or only seems to increase noise in the PRI signal (when using the MODIS MOD43 product, see Fig. 3 in the Supplement). Additional doubt about the usefulness of correcting reflectance data for this study using ready made products is caused by the unavailability of a BRDF model and atmospheric parameters at the exact acquisition time and spatial resolution of the radiance data and some of the spectral bands listed in Table 2. Because the need for synchronous estimates of atmospheric parameters flagged as high quality also reduces the number of available observations, we chose not to correct specifically for atmospheric or surface anisotropy effects. To some degree, a correction is inherent in a ratio made of reflectances that are not too far apart in the visible part of the solar spectrum.

The MODIS cloud mask does not allow the detection of cloud cover or cloud shadows with absolute certainty. To rule out cloudiness, we visually checked for each day if the daily course of incident PAR (measured in-situ as Photosynthetic Photon Flux Density on half-hourly basis) follows an ideal curve. Acquisition dates at which the measured PAR at the flux towers notably differs from the PAR pattern during cloud free days at the same time of year were excluded from further analysis (see Fig. 1 in the Supplement for example).

2.3.2 Preparation of vegetation indices

The standard configuration of the PRI (Eq. 3) has to be adapted to the spectral bands available on MODIS (Drolet et al., 2005). The MODIS band 11 is centred at 531 nm (cf. Table 2). As the MODIS-sensor is not equipped with a spectral band centred at 570 nm, we tested bands 1 (620–670 nm), 4 (545–565 nm), and 12 (546–556 nm) as potential reference bands, in accordance with the proposition of Drolet et al. (2005, 2008). A modification of PRI has been computed from top-of-atmosphere reflectances for each of the 4 reference bands, denoted by PRI_1 , PRI_4 , PRI_{10} , and PRI_{12} . We compared the performance of the PRI as a proxy of LUE against what can be achieved with a well known broadband vegetation index. The NDVI is known to respond to changes in biomass, but also chlorophyll content as well as leaf water stress (Myneni et al., 1995; Treitz and Howarth, 1999). The index is hence useful to see which part of the variation in LUE can be explained already by factors other than changes in the composition of xanthophyll pigments. We calculated the Normalised Difference Vegetation Index

Table 3. Overview of abbreviations used for “in-situ” light use efficiency and for LUE modelled from vegetation indices (The models denoted with * were established for each site (for all MODIS viewing angles and also specifically for viewing angles $<10^\circ$) as well as for all evergreen sites combined and the two evergreen oak sites combined.)

abbreviation	explanation
<i>LUE used for evaluation</i>	
LUE _{MODIS}	light use efficiency calculated from site GPP, site PAR, and MODIS faPAR
LUE _{SeaWiFS}	light use efficiency calculated from site GPP, site PAR, and JRC SeaWiFS faPAR
LUE _{Cyclopes}	light use efficiency calculated from site GPP, site PAR, and Cyclopes faPAR
<i>LUE modelled from vegetation indices, general scheme*</i>	
LUE _{PRI_X, Y}	LUE modelled from regression between PRI _X (i.e. with reference band X) and LUE _Y
<i>LUE modelled from vegetation indices, example</i>	
LUE _{PRI₁, SeaWiFS}	LUE modelled from regression between PRI ₁ and LUE _{SeaWiFS}
LUE _{PRI}	LUE modelled from regression between PRI and observed LUE (summary term for multiple models)
LUE _{NDVI, MODIS}	LUE modelled from regression between NDVI and LUE _{MODIS}
<i>LUE calculated using look-up table and site meteorology</i>	
LUE _{MOD17}	LUE calculated from biome specific MOD17 parameters and site T_{\min} , VPD
LUE _{MOD17, opt}	LUE calculated from optimised biome specific MOD17 parameters and site T_{\min} , VPD

(NDVI) (Tucker, 1979) from reflectance data:

$$\text{NDVI} = \frac{\rho_{\text{NIR}} - \rho_{\text{red}}}{\rho_{\text{NIR}} + \rho_{\text{red}}} = \frac{\rho_{\text{bd2}} - \rho_{\text{bd1}}}{\rho_{\text{bd2}} + \rho_{\text{bd1}}} \quad (5)$$

2.3.3 Empirical PRI-based LUE models

Exponential relationships between observed LUE (LUE_{MODIS}, LUE_{SeaWiFS}, LUE_{Cyclopes}) and PRI were explored with Bayesian hierarchical models. Models were established separately for each version of PRI with data binned as follows:

- observations from all evergreen sites combined (i.e. FR-Pue, IT-Cpz, US-Me2; separate models for NDVI, PRI₁, PRI₂, PRI₁₀ and PRI₁₂),
- observations from the two evergreen broad-leaved sites combined (i.e. FR-Pue, IT-Cpz; also separate models for each vegetation index),
- one site specific model (for sensor viewing zenith angles $\leq 40^\circ$), this results in five models per vegetation index,
- separate bins for each range of viewing zenith angles (0–10°, 10–20°, 20–30°, 30–40°) for each site, this results in 20 models per vegetation index.

Results for all those viewing angle bins are listed in the Supplement. In the following we will only show outcomes for the complete range of viewing angles and near-nadir observations (0–10°). The variance explained with models fitted to the other bins lies in between those two. Table 3 gives an overview of how observed and modelled light use efficiencies are denoted in this study.

2.4 LUE modelled from T_{\min} , VPD and plant functional type

For benchmarking the performance of vegetation index-based LUE proxies, we also calculated the LUE in the way it is operationally used in the MODIS GPP algorithm (Heinsch et al., 2003). In this approach, a biome-specific maximum light use efficiency is reduced by a vapour pressure deficit scalar and a minimum temperature scalar. These attenuation scalars are calculated from daily daylight VPD and T_{\min} based on linear ramp functions, the parameters of which are contained in the biome property look-up table (BPLUT).

$$\text{LUE}_{\text{MOD17}} = \text{LUE}_{\text{max, BLUT}} \times f(\text{VPD}) \times f(T_{\min}) \quad (6)$$

We computed LUE_{MOD17} using the standard MOD17 parameters and LUE_{MOD17, opt} using parameters that have been optimised per site and year by Enrico Tomelleri (see section on LUE models in the Supplement of Beer et al., 2010).

As this study is concerned with the site level, we use for both LUE_{MOD17} and LUE_{MOD17, opt} site measurements of VPD and T_{\min} from the Fluxnet LaThuile data set instead of the 1° by 1.25° NASA Data Assimilation Office (DAO) data routinely fed into the MODIS GPP algorithm. This way we also exclude uncertainties in the DAO meteorology as an additional source of error.

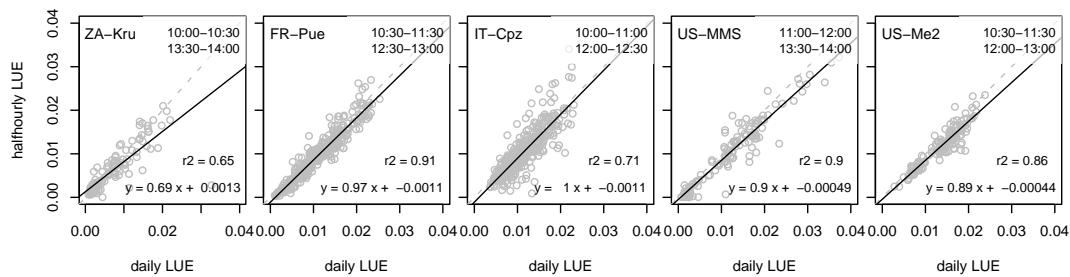


Fig. 1. Comparing daily and half-hourly light use efficiency (based on MODIS faPAR) for all the cloud free times where MODIS PRI is available. The times of MODIS overpass are given in the upper right corner of each panel.

3 Results

3.1 Are LUEs at times of MODIS overpass representative for the whole day?

The MODIS sensors operate sun-synchronous, i.e. images are only acquired within a certain window of local time (morning through midday on the Terra platform, midday through afternoon on the Aqua satellite). As a first step in our analysis, we checked if the LUE at time of satellite overpass is representative for the whole day. For the five sites in this study, half-hourly LUE_{MODIS} during the time of MODIS overpass can explain 65% (ZA-Kru) through 92% (FR-Pue) of the variability in daily LUE_{MODIS} (c.f. Fig. 1). The slope of the regression line between half-hourly and daily LUE for ZA-Kru has the strongest deviation from the 1:1 line. Mid-day LUE at ZA-Kru is lower compared to other sites, while LUE in the late afternoon and evening is on average higher than at the other sites. This might be due to differences in moisture limitation. The atmospheric moisture demand increases during middays stronger than at the other study sites (see Figs. 5 and 6 in Supplement).

The relationship between half-hourly and daily LUE remains the same when using other faPAR products. This justifies the use of PRI “snapshots” to estimate daily LUE.

3.2 Which MODIS-PRI version suits which setting?

In the next step of our analysis, we only use LUE_{MODIS} to evaluate the different modelled LUEs and to figure out which PRI configuration is most useful for which site. Afterwards, the effect of using different faPAR products is scrutinised using only the best suited PRI reference bands.

As an example for the relationship between PRI and LUE, Fig. 2 shows PRI_1 and LUE_{MODIS} for all five studies sites as well as for the combined evergreen and oak models (c.f. Sect. 2.3.3). We chose exponential functions to avoid negative modelled LUEs. The divergences between the fitted models become already apparent in this example.

For all LUE modelled site-specific based on PRI and NDVI, the correspondence with LUE_{MODIS} is better for near-

nadir observations than for all observations together (c.f. R^2 s in Fig. 3).

LUE_{MODIS} can be modelled properly based on PRI for the savanna site ZA-Kru (R^2 for near nadir observations [R^2_{nadir}]=0.78, R^2 for all observations [R^2_{all}]=0.49) and for the deciduous broad-leaved forest site US-MMS (R^2_{nadir} =0.71, R^2_{all} =0.46). LUE_{MODIS} can be reasonably well modelled for the two evergreen oak forest sites (FR-Pue: R^2_{nadir} =0.57, R^2_{all} =0.45; IT-Cpz: R^2_{nadir} =0.43, R^2_{all} =0.44). The modelling of LUE_{MODIS} for the evergreen needle-leaved forest US-Me2 is less successful using PRI (R^2_{nadir} =0.37, R^2_{all} =0.2, see also the table in the Supplement).

The optimal reference band for the PRI differs between sites. For three sites with completely different characteristics, LUE_{PRI_1} , MODIS with a site-specific model explains most of the variability in daily LUE_{MODIS} (ZA-Kru, FR-Pue, US-MMS). PRI_4 is most suitable for modelling LUE at IT-Cpz. $LUE_{PRI_{12}}$, MODIS works best at the US-Me2 site.

3.3 Can LUE estimation from MODIS-PRI be generalised?

Ideally, a model of light use efficiency would be parameterised once for all possible cases, or for well defined categories, and could then be applied to other location in the same range of environmental conditions. When applying the model that has been established for the pooled evergreen-site observations at site level, the correspondence with observed LUE values is low (c.f. Figs. 2b, 3, 4) as it can be expected for sites of different plant functional type and location. Even when parameterising a model for the two evergreen broad-leaved forest sites with the same dominant species, the explained variability is low.

3.4 How does LUE modelled from MODIS-PRI compare to other LUE models?

Of course, estimating LUE from PRI would not be justified if the same or a better accuracy can be achieved with models/data that are already operational.

LUE_{NDVI} , MODIS resulted only for the two sites with high deciduousness in a slightly better agreement with observed

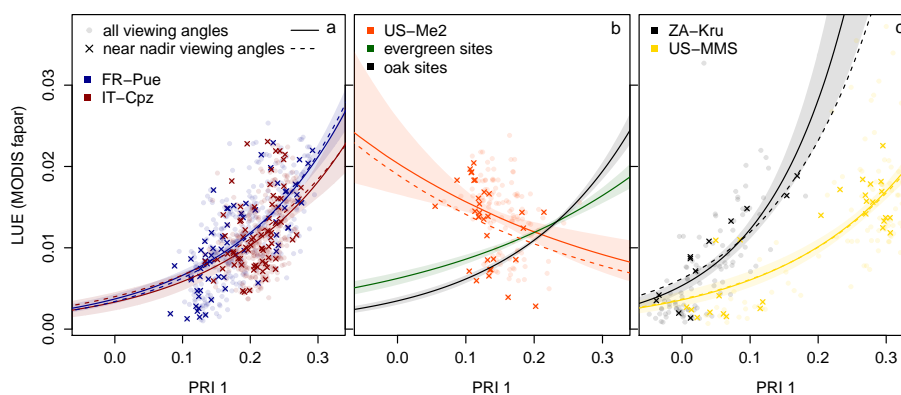


Fig. 2. Light use efficiency (based on MODIS faPAR) versus PRI based on reference band 1 with exponential models fitted to the observations. The shaded areas represent the 95% Bayesian confidence interval. For each site, two different models were calculated. One is using all available observations (solid lines) and the other only observations with near nadir sensor viewing angles (0–10°, dashed lines). In addition, the combined models for evergreen sites (FR-Pue, IT-Cpz, US-Me2) and oak sites (FR-Pue, IT-Cpz) are shown (panel c).

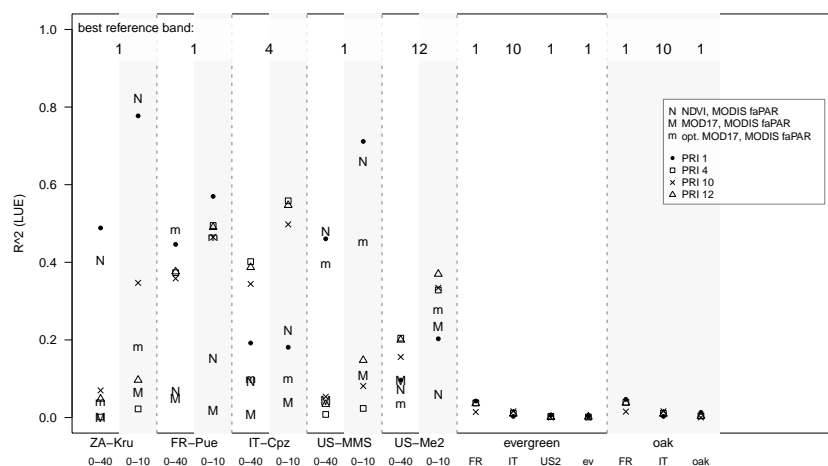


Fig. 3. R^2 of modelled LUE vs. LUE_{MODIS} for two ranges of sensor viewing zenith angle: 0–40° and 0–10°. The most suitable reference band for each site is displayed at the top. The same pattern appears when using the root mean square error (not shown).

LUE: for near-nadir observations in ZA-Kru, and when using all observations in US-MMS. The differences in R^2 to the best LUE_{PRI} are only 0.03% and 0.2% (c.f. Fig. 3, Table in the Supplement).

For the sites we have studied, LUE_{MOD17} has in every setting much less agreement with observations than LUE_{PRI} . $LUE_{MOD17, opt.}$ performs much better, though not superior to LUE_{PRI} except at FR-Pue with MODIS viewing angles ranging from 0–40°. The agreement between $LUE_{MOD17, opt.}$ and the reference LUE increases slightly (without changing any of the statements above) when using faPAR from MODIS collection 4 instead of 5 to calculate LUE_{MOD17} because the MOD17 parameters have been optimised based on collection 4 data (not shown). Note that, while benchmarking with LUE_{MOD17} and $LUE_{MOD17, opt.}$ provides an additional point of reference, the main evaluation is performed with in-situ LUE.

3.5 Which influence does the choice of an faPAR product have on PRI evaluation?

For the deciduous forest site (US-Me2), the choice of faPAR product does not influence the relationship between observed and modelled LUE. The temporal dynamics of both the MODIS and SeaWiFS faPAR are very similar, Cyclopes faPAR is not available for this site.

The strongest faPAR induced difference in fit between models and observations occurs at the deciduous broad-leaved US-MMS forest. There, using MODIS faPAR results in the best fit. Cyclopes faPAR for US-MMS shows a too gradual decrease in autumn/winter and a too early (but at the same time too slow) increase in spring. In contrast, the SeaWiFS faPAR seems to have too steep increases and decreases and the beginning and end of the growing seasons (data not shown).

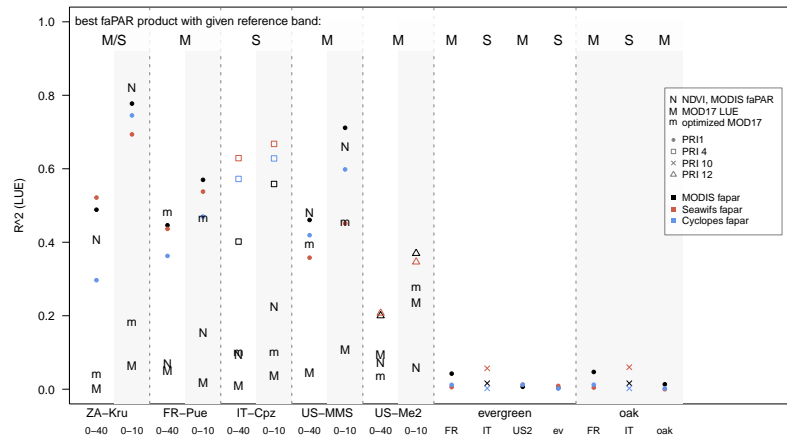


Fig. 4. R^2 of modelled vs. observed LUE using PRI with the best reference band for each site to find out the most suitable faPAR product for each setting. At each site, two ranges of sensor viewing zenith angle are shown: 0–40° and 0–10°. The best faPAR product for a given reference band is denoted with M (MODIS MOD15) and S (JRC SeaWiFS faPAR).

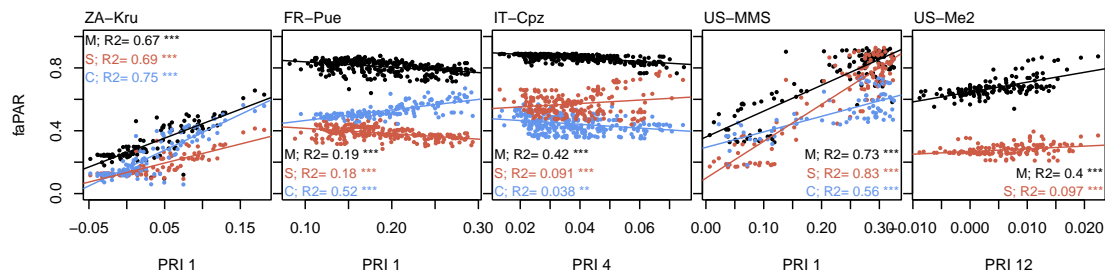


Fig. 5. Scatterplots with R^2 of faPAR from different products (Black: MODIS – M), Red: SeaWiFS – S, Blue: Cyclopes – C) vs. PRI with site-specific most suitable reference band. Significance codes: p value ≤ 0.001 : ***, p value ≤ 0.01 : *

In contrast with the other two faPAR products, Cyclopes faPAR at the ZA-Kru savanna site has a lower amplitude and does not seem to track the beginning and end of the growing season properly (concluded from comparing faPAR and GPP time series, data not shown). This might be the reason of the poor agreement between model and observation for the Cyclopes based LUE. SeaWiFS faPAR captures the length of the growing season for this savanna site well, which might be the reason for the higher agreement when using this faPAR product.

At the FR-Pue evergreen oak forest, both the MODIS and the SeaWiFS faPAR product show hardly any seasonality. This is probably why, despite MODIS faPAR having higher absolute values, choosing one or the other faPAR product has no influence on model fit. Cyclopes faPAR for the FR-Pue site has higher values in winter. The model fit is worse when LUE is based on Cyclopes faPAR.

At the other evergreen oak forest, IT-Cpz, using SeaWiFS faPAR instead of the other faPAR products to calculate in-situ LUE results in a higher agreement with LUE_{PRI} (c.f. Fig. 4). A reason might be that the MODIS faPAR algorithm depends on proper biome classification and biome-specific canopy structures and soil patterns (McCallum et al., 2010).

3.6 Influence of vegetation structure on the PRI signal

For the deciduous sites (ZA-Kru and US-MMS), the MODIS photochemical reflectance index can be estimated from faPAR (see Fig. 5). The intra-annual changes in MODIS PRI are related to the temporal dynamics of total leaf area.

The fraction of PAR absorbed by the vegetation at the evergreen sites shows little seasonal variation compared to the changes in PRI. Thus, for these sites the changes in PRI cannot be explained by variation in faPAR. This suggests that the changes in PRI in those evergreen sites are more a result of changes in leaf pigment composition rather than structural changes.

3.7 Sensitivity of the different modelled LUEs to seasonal and interannual variability

The modelling approaches detailed in this study (c.f. Sects. 2.3.3, 2.4) differ in how well they are capable of reproducing annual and interannual variations in LUE.

At the evergreen oak site FR-Pue, LUE_{PRI} does capture the seasonal dynamics, including the decline in LUE

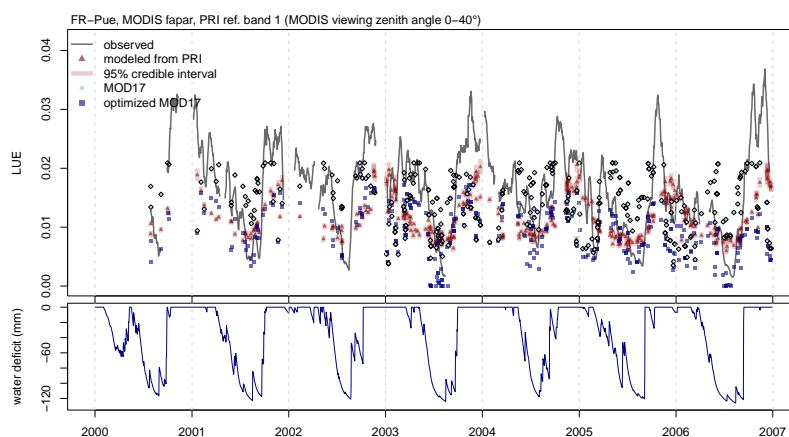


Fig. 6. Top: Time series of observed LUE as 14-day moving average (based on MODIS faPAR) and modelled LUEs (exponential model based on PRI with reference band 1, MOD17, and optimised MOD17) at the FR-Pue site. Bottom: Water deficit in mm (calculated from field capacity and in-situ soil water content measurements).

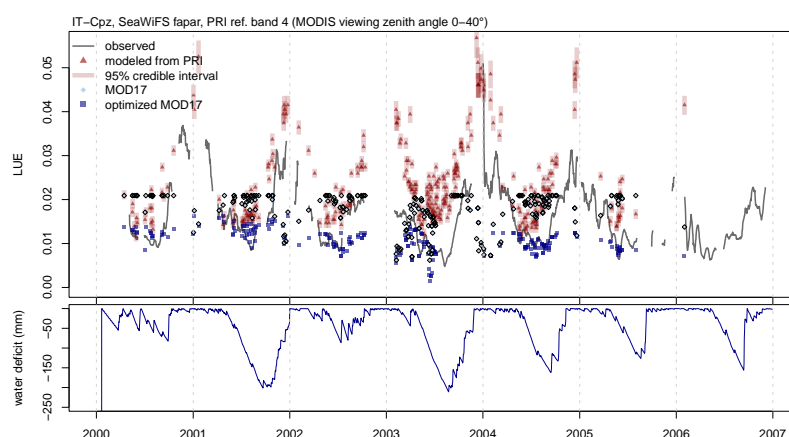


Fig. 7. Top: Time series of observed LUE as 14-day moving average (based on SeaWiFS faPAR) and modelled LUEs (exponential model based on PRI with reference band 4, MOD17, and optimised MOD17) at the IT-Cpz site. Bottom: Water deficit in mm (calculated from water balance).

during summer drought, but not the interannual variability (c.f. Fig. 6). The observed LUE decline in summer is more pronounced during the 2003 heat wave, while the LUE_{PRI_1} amplitude is similar to other years.

LUE_{MOD17} is less capable of capturing the summer depression than the PRI based model. $LUE_{MOD17,opt}$ reproduces the minimum of summer depression well, but the modelled summer depression is much longer than observed.

At the other evergreen oak site, IT-Cpz, no distinct interannual variability is observed. The seasonal cycle is captured well by LUE_{PRI_4} (c.f. Fig. 7). Depending on the faPAR product used for the in-situ LUE, LUE is severely over- or underestimated by LUE_{MOD17} , the seasonal cycle is not well reproduced. $LUE_{MOD17,opt}$ shows a dampened seasonal cycle and in general underestimates LUE.

At US-MMS the time series has gaps during cloud cover in winter time, but there are still enough observations and

PRI data to estimate the annual minimum in LUE. There is a peak in observed LUE in summer 2002 that is not reproduced by LUE_{PRI_1} , otherwise the seasonality is tracked well (not shown). LUE_{MOD17} does not match the LUE observations in spring and autumn, while $LUE_{MOD17,opt}$ underestimates the LUE peak in summer.

The evergreen needle-leaf site (US-Me2) possesses a low seasonal variability of LUE. The small fluctuations that are observed are neither well simulated by LUE_{PRI_1} , nor by LUE_{MOD17} or $LUE_{MOD17,opt}$ (not shown).

The short LUE time series of the savanna site is mimicked well by the PRI model, apart from an overestimation in 2002 and some missed nuances (not shown). LUE_{MOD17} and $LUE_{MOD17,opt}$ values underestimate LUE observations, except for the southern-hemisphere winter in 2002, when the observed LUE is low compared to other years.

4 Discussion and conclusions

We conclude that in general estimating LUE at site-level based on PRI reduces uncertainty compared to the other approaches we tested. There is only one set of LUE observations which can be slightly better approximated by an LUE model based on VPD and T_{\min} than by LUE_{PRI}: the 0–40° viewing zenith angle FR-PUE data (c.f. Figs. 3, 4). Note that this LUE is not derived from the standard MOD17 parameters, but from parameters that have been optimised per site and year. This indicates that, at site level, MODIS-based PRI is very competitive as a proxy for light use efficiency.

It is apparent that fine-tuning maximum light use efficiency as well as the VPD and T_{\min} parameters improves the performance of MOD17 type models of LUE (and ultimately GPP). However, our results support the growing body of evidence suggesting that T_{\min} and VPD alone are not sufficient to characterise temporal LUE (and hence GPP) dynamics due to i.e. drought stress (Kanniah et al., 2009; Maselli et al., 2009; Garbulsky et al., 2010a). Soil water availability determines stomatal conductance (Rambal et al., 2003) and hence productivity to a large extent and must be considered in LUE models that constrain a maximum LUE with environmental variables. Soil water estimates are difficult to obtain over larger regions. Estimates derived from remote sensing data are still poor, especially for forests (Guglielmetti et al., 2008). Surrogates of soil water content based on evapotranspiration and precipitation could be a viable alternative Leuning et al. (2005); Coops et al. (2007). Remotely sensed indices of vegetation water content such as the land surface water index (Xiao et al., 2005) or surface temperature might also help to obtain the seasonal variations of LUE in models that determine photosynthetic efficiency from environmental stresses (Hilker et al., 2008c). For these approaches, constraints due to different image acquisition geometries must also be considered.

For the South-African savanna site and the humid subtropical deciduous broad-leaved forest (US-MMS), the accuracy of LUE modelled from NDVI is comparable to that of LUE_{PRI}. At both sites, vegetation greenness and faPAR (as well as leaf area) are intrinsically linked to CO₂ exchange. Hence NDVI and faPAR display similar seasonal dynamics as light use efficiency (Garbulsky et al., 2010b). The PRI signal in general is influenced both by changes in vegetation structure and by changes in pigment composition. Unsurprisingly, the gain in accuracy through using PRI instead of NDVI or faPAR is highest for evergreen sites where changes in LUE are largely unrelated to greenness and changes in leaf area simply because there is little change in greenness over time while LUE varies significantly (see also Running and Nemani, 1988; Gamon et al., 1992; Garbulsky et al., 2010b).

Despite the advantages of using PRI to estimate LUE at site-level, we found no universally applicable light use efficiency model based on MODIS PRI. Models that are opti-

mised for a pool of data from several sites do not perform well.

Plant functional type, even dominant species is not a sufficient criterion to generalise PRI based models. The two sites that are dominated by *Quercus ilex*, FR-Pue and IT-Cpz, seem to have a very different spectral response at comparable LUE levels since their optimal reference bands are 1 (red) and 4 (green). The different behaviour at IT-Cpz might be brought about by a different stand structure, as for example manifested in a higher LAI (c.f. Table 1), as well as higher ground water levels due to the closeness of the sea and hence less water stress (Valentini et al., 1992).

The optimal reference bands we determined (MODIS bands 1, 4, 12) fall within the spectral regions identified by Middleton et al. (2009); Cheng et al. (2009) as useful PRI reference wavelengths in a study on foliar LUE in a Douglas fir stand. Middleton et al. (2009) also showed that a PRI based on the relatively broad spectral bands of MODIS (10 nm) correlates well with PRI values derived from 3 nm wide bands. The results of our analysis suggest that the usability of different reference wavelength might depend on species composition and stand structure. The first study on PRI by Gamon et al. (1992) pointed out that no single reference wavelength suited all purposes equally well (e.g. tracking LUE in unstressed and water stressed sunflowers). The review by Garbulsky et al. (2010b) points out that the optical properties of the canopy are influenced – apart from species and environmental conditions – by the fraction of dead and woody biomass, vegetation density and spectral properties of the soil, all of which can affect the suitability of reference bands. The present study adds to the body of knowledge showing that 570 nm is not the only reference bands suitable for PRI. A data base encompassing more sites with a diversity of functional and structural traits would be desirable to arrive at a final conclusion in this regard.

To increase the amount of data useful for a parameter estimation, it would be helpful to include more heterogeneous sites in future analysis. A footprint climatology assessment such as described by Chen et al. (2009) in combination with multi-angular high spectral resolution measurements (Hilker et al., 2008b) would be valuable for optimising model parameters in these cases. The impact of the sun's position on the PRI-LUE relationships in this study should be limited by the similar data acquisition times (c.f. Fig. 1). Nevertheless, a follow on-study should consider the sensor angle relative to the position of the sun to obtain certainty on the influence of the image acquisition geometry on the PRI-LUE relationship.

Using only PRI values for near-nadir satellite observations does improve the accuracy of LUE predictions compared to using the whole range of viewing angles, or observations binned in off-nadir 10° wide bands of viewing zenith angle. In a boreal setting, modelling LUE only based on PRI derived from backscatter reflectance also explained LUE_{obs} variance better than when using observations combined (Drolet et al.,

2005, 2008). This is an indirect way of tackling the dependence of reflectance on viewing geometry. When looking from different angles, different fractions of e.g. tree canopy, understorey/grass, and soil will be visible to the sensor and result in a variation of surface reflection. Excluding off-nadir observations reduces this effect. For example, the validity of the more densely vegetated and homogeneous FR-Pue site is less effected by viewing angle than the savanna site where the contribution of trees to the signal by MODIS is more dependent on viewing angle. Another reason why near nadir data might have a better correspondence with in-situ LUE is a smaller atmospheric effect on PRI/NDVI due to the shorter Earth surface-satellite distance at small viewing zenith angles. The drawback of excluding part of the data is of course that the temporal coverage might become inadequate. Hilker et al. (2009) found that most of the directional effects on the LUE-PRI relationship can be attributed to atmospheric scattering. The standard single orbit algorithms such as 6S (Vermote et al., 1997) cannot compensate for this atmospheric disturbance. MAIAC, a generic aerosol-surface retrieval algorithm recently developed for MODIS (Lyapustin and Wang, 2009) showed promising results for detecting subtle changes in narrow waveband indices such as PRI (Hilker et al., 2009).

Another promising approach seems to be the consideration of shadow fraction in PRI-based estimations of PRI. Ground-based pilot studies have been very successful in doing so (Hall et al., 2008; Hilker et al., 2009). The fraction of shaded/sunlit parts of the canopy has an important influence on the light use efficiency of vegetation and not just the PRI signal. However, which fraction of sunlit leaves is seen by a satellite depends on the position of the sensor relative to the canopy and the sun as well as the canopy structure. If the vegetation structure is not well known, uncertainty remains whether changes in PRI are due to a different position of the sensor or due to actual changes in LUE. For space-borne PRI studies, multi-angular acquisitions, taken within a short time period in which LUE is constant, are necessary (Coops et al., 2010).

Future research directions to improve the knowledge on PRI could include the development of physically-based models that predict reflectance changes at 531 nm. Innovations in this regard must allow leaf optical properties to vary with leaf-level illumination conditions and base the computation of reflectance changes on down-regulation of photosynthesis (Coops et al., 2010).

In summary, when calibrated at site level a model based on MODIS PRI gives better or at least as good estimates of ecosystem light use efficiency as the other approaches we tested. In this study, an universally applicable model relating LUE to MODIS PRI across different sites could not be found.

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