



# Relationships between photochemical reflectance index and light-use efficiency in deciduous and evergreen broadleaf forests

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## ABSTRACT

In this study, we evaluate the relationships between the photochemical reflectance index (PRI) and light-use efficiency (LUE) based on eight years of continuous in situ measurements acquired on a half-hourly basis for PRI, NDVI (Normalized Difference Vegetation Index), the main micrometeorological variables and net CO<sub>2</sub> exchange data in two deciduous and evergreen mature forests. More specifically, the objectives of this study include investigating the daily, seasonal, and interannual variations of PRI and LUE; linking PRI variations to the main influencing meteorological and eco-physiological variables; and evaluating the performance of PRI as a remote-sensing proxy of LUE under different environmental conditions. The data analysis was performed at different time scales within the season using moving temporal windows and between years. On a seasonal scale, statistical analyses revealed positive relationships between PRI and absorbed photosynthetically active radiation (aPAR) and negative relationships between PRI and LUE. Over shorter periods of a few days, the signs of these relationships remained unchanged; however, their correlations were strongly improved. The highest correlations were most often observed over periods characterized by clear or slightly overcast skies. However, all the periods of clear skies did not involve improvements in the relations of PRI vs. aPAR or PRI vs. LUE. Temporal variations of the intercept (called PRI<sub>0</sub> in this study) of PRI vs. aPAR regressions suggest the presence of a temporal trend that may reflect seasonal changes of the biochemical characteristics of the canopy. Regardless of the cause of this trend, it is important to note that once PRI<sub>0</sub> was subtracted from the measured PRI, the correlations between the corrected PRI and LUE for each year were significantly improved, and a stable multi-year model was obtained. Nevertheless, further studies are required to explain the temporal changes of PRI<sub>0</sub> during the season and to develop a more accurate disentangling approach that would make PRI-based remote-sensing of ecosystem light-use efficiency less sensitive to confounding factors related to spatial and temporal changes in the structural and biochemical properties of the canopy.

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## 1. Introduction

Forests are subjected to climate events with different intensities. Severe droughts can cause significant effects such as leaf discoloration, leaf browning, and early leaf loss (Bréda, Huc, Granier, & Dreyer, 2006; Carnicer et al., 2011). These effects may lead to a decrease of forest productivity and a higher vulnerability to fire and to the proliferation of devastating opportunistic pathogens in the following years (La Porta et al., 2008). Under moderate water, temperature, or light stress, these effects are not as significant; however, the physiological state of the trees, the water use and carbon exchanges may be significantly affected. Under such environmental conditions, the available energy exceeds the capacity of the utilization of light in photosynthesis and the excess of

energy is dissipated as fluorescence and heat according to many mechanisms, which are grouped under the generic term of non-photochemical quenching (NPQ) (as opposed to the photochemical processes involved in photosynthesis). The most important mechanism involved in NPQ processes is associated with changes in the composition of carotenoid pools known as the xanthophyll cycle (Demmig-Adams & Adams, 1996; Jahns & Holzwarth, 2012; Ort, 2001; Yamamoto, 2006). Changes in the concentration of xanthophylls are accompanied by changes in reflectance at approximately 531 nm (Gamon, Peñuelas, & Field, 1992; Gamon, Serrano, & Surfus, 1997). Gamon et al. (1992, 1997) developed the photochemical reflectance index (PRI) using the narrow-band reflectance at 531 nm and a reference band at 570 nm – assumed to be insensitive to variations in the concentrations of xanthophylls – and suggested using this index as a remotely sensed proxy to track changes in the xanthophyll cycle pigment content at the leaf scale and to predict the light-use efficiency (LUE) for many herbaceous and woody species (Gamon & Surfus, 1999; Sims & Gamon, 2002).

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Remote sensing is a powerful tool that provides important information concerning the structure and functioning of forest ecosystems due to its unique potential in terms of spatial and temporal resolutions. The potential use of this tool was mainly evaluated to monitor temporal changes of the forest canopy structure when these changes are accompanied by significant variations in the amount of green leaf biomass or in the chlorophyll content. However, there are still limited studies that focus on the evaluation of remote sensing to monitor the ecophysiological responses at the canopy scale. It may be noted that LUE-based models of gross primary production (GPP) (Hilker et al., 2008) such as the MODIS GPP model (Turner et al., 2006), Glo-PEM (Prince & Goward, 1995) and CASA (Potter et al., 1993) applied at regional and global scales using remote-sensing data do not explicitly account for the large variations in LUE at short time scales. In the MODIS-based GPP approach, a constant biome-specific maximum LUE is used and short-term temporal variations of this parameter are implicitly considered using modulation factors that depend only on the VPD (vapor pressure deficit) and air temperature. This type of modulation may be insufficient to account for the effects of the soil water deficit on GPP because meteorological and edaphic factors are decoupled at short time scales (Hwang et al., 2008; Pan, Birdsey, Hom, McCullough, & Clark, 2006; Turner et al., 2005). The explicit consideration of these effects in the model may be necessary, as suggested by Gebremichael and Barros (2006) and Mu et al. (2007).

The pioneering works of Gamon et al. (Filella, Amaro, Araus, & Peñuelas, 1996; Gamon et al., 1992, 1997; Peñuelas, Filella, & Gamon, 1995) demonstrated that it is possible to track short-term changes in LUE at the leaf and canopy scales by clearly demonstrating the sensitivity of PRI to the photosynthetic activity due to variations in environmental conditions. At the canopy scale, especially above complex structures such as forests, recent studies have reported contrasting results, highlighting the combined effects of exogenous factors, especially solar and viewing angles, and the structural and biochemical attributes of the canopy. Using MODIS bands, Drolet et al. (2005, 2008) observed good relationships between PRI and LUE in the back-scattering direction (relative azimuth angle — difference between the sensor and sun azimuth angles  $< 60^\circ$ ) and under a relative zenith angle (difference between the sensor and sun zenith angles) less than  $10^\circ$  and explained these results based on the lower proportion of shaded leaves compared with the forward-scattering direction. Hall et al. (2008) and Hilker et al. (2009) showed the strong dependency of PRI on within-canopy light conditions and established two distinct relationships between PRI and LUE for sunlit and shaded foliage surfaces, respectively. These authors explained these differences based on the changes in the xanthophyll cycle that lead to the decrease in LUE for the sunlit foliage surface exposed to strong light above a saturating point. Hall et al. (2008) noted that the PRI–LUE relationship is better for a sunlit foliage surface, confirming the findings of Gamon et al. (1997). The effects of illumination and viewing angle on the relationship between MODIS-based PRI and LUE were also highlighted by Goerner, Reichstein, and Rambal (2009). The strongest relationships were obtained for viewing angles close to the nadir and in the range of  $30$ – $40^\circ$  from the zenith. In addition to these factors, Goerner et al. (2009) noted the direct and indirect effects of atmospheric conditions that severely degrade the quality of the PRI signal and introduce bias in the relationships between PRI and LUE by restricting the LUE variability to a narrow range because only cloud-free MODIS images can be used.

The studies cited above highlight the difficulty in assessing the relationships between PRI and LUE at canopy scale. This is due to a multitude of factors that may influence the reflectance in PRI bands directly through the effects of biochemical and structural canopy characteristics, sun-view geometry and atmospheric conditions and indirectly through the xanthophyll cycle and thus canopy photosynthesis (light conditions, soil water content, VPD, temperature, etc.). In addition, it is still more complicated to achieve this task using satellite data because the spatial, temporal, and spectral data of the sensors available onboard spatial platforms are not optimal.

In this study, we evaluate the relationships between PRI and LUE from continuous in situ measurements of PRI and net  $\text{CO}_2$  exchange data acquired on a half-hourly basis in two deciduous and evergreen mature forests in France. Eight years of simultaneous measurements of PRI and carbon fluxes are analyzed in this study. To the best of our knowledge, this data set is the longest time-series data set of in situ PRI measurements. Specifically, the objectives of this study involve the following: (1) investigating the daily, seasonal, and interannual variations of PRI and LUE; (2) linking the PRI variations to major influencing meteorological and eco-physiological variables; and (3) developing an approach for the disentangling the effects of canopy structure and leaf biochemistry that affect the PRI vs. aPAR and PRI vs. LUE relationships on a seasonal scale.

## 2. Materials and methods

### 2.1. Study site

This study was undertaken in two mature forests (FLUXNET site codes: FR-Fon and FR-Pue; [www.fluxnet.ornl.gov](http://www.fluxnet.ornl.gov)) differing in their vegetation types and climates. The first one, located near Fontainebleau ( $48^\circ 28' 35'' \text{N} / 2^\circ 46' 48'' \text{E}$ ) — southeast of Paris, corresponds to a temperate forest representative of the main deciduous broad leaf forest type in Europe. The forest stand is managed as mature deciduous forest occupied by two main overstory species of pedunculate and sessile oaks (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl) and a dense understory of coppiced hornbeam (*Carpinus betulus* L.). The age of the overstory is 150 years, and the average height is approximately 25 m. The leaf area index is approximately  $5.5 \text{ m}^2/\text{m}^2$  on average. The elevation is approximately 90 m (a.s.l.), and the climate is a temperate climate characterized by an average annual temperature of approximately  $11^\circ \text{C}$  and an average annual rainfall of approximately 680 mm.

The second forest, Fr-Pue, the Puéchabon experimental forest, is located in the south of France ( $43^\circ 44' 29'' \text{N} / 3^\circ 35' 45'' \text{E}$ ), 60 km northwest of Montpellier. Puéchabon forest is an evergreen broadleaf forest dominated by a dense overstory of holm oak (*Quercus ilex* L.), the most typical tree of the Mediterranean climate. The age of the stand is 70 years, and the average height is approximately 6 m. The leaf area index is approximately  $2.9 \text{ m}^2/\text{m}^2$ . The elevation is approximately 270 m (a.s.l.), and the climate is Mediterranean with an average annual temperature of  $13.4^\circ \text{C}$  and an average annual rainfall of 907 mm. The climate is characterized by mild and wet winters and hot and dry summers, during which long periods of drought are frequent.

### 2.2. Flux and meteorological data

The available measurements were those usually made using the eddy covariance technique to estimate the net carbon exchange and latent and sensible heat fluxes between the forest ecosystem and the atmosphere. At the study site, these measurements include the net carbon exchange (*NEE*), the evapotranspiration (*ETR*), and the main bioclimatic variables (wind speed, incident, reflected and transmitted radiation, VPD, precipitation, air temperature, etc.). All these variables were recorded in the two forests at a half-hour time step.

The gross primary production (*GPP*) — the total amount of photosynthetic production of organic matter in the ecosystem — was calculated according to the CARBOEUROPE database standards (see Delpierre et al., 2012 for more details):

$$GPP = NEE + ER \quad (1)$$

where *GPP* is the gross primary production, *NEE* is the net ecosystem exchange and *ER* is the ecosystem respiration.

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