

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



Kamel Soudani ^{a,*}, Gabriel Hmimina ^a, Eric Dufrière ^b, Daniel Berveiller ^b, Nicolas Delpierre ^a, Jean-Marc Ourcival ^c, Serge Rambal ^c, Richard Joffre ^c

^a University of Paris-Sud, UMR CNRS, AgroParisTech, Université Paris Sud. Laboratoire Ecologie Systématique et Evolution, Faculté des Sciences d'Orsay, France

^b CNRS, UMR CNRS, AgroParisTech, Université Paris Sud. Laboratoire Ecologie Systématique et Evolution, Faculté des Sciences d'Orsay, France

^c CNRS, Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier, France

ARTICLE INFO

Article history:

Received 19 July 2013

Received in revised form 21 January 2014

Accepted 21 January 2014

Available online xxx

Keywords:

Photochemical reflectance index (PRI)

Light use efficiency LUE

Normalized Difference Vegetation Index

(NDVI)

Forests

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 CO₂ 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 PRI₀ 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 PRI₀ 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 PRI₀ 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.

© 2014 Elsevier Inc. All rights reserved.

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).

* Corresponding author. Tel.: +33 1 69 15 56 83.

E-mail address: kamel.soudani@u-psud.fr (K. Soudani).

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° 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 $30\text{--}40^\circ$ 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 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) 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°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°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.

From the expression given in Kumar and Monteith (1981), the GPP can be expressed as:

$$GPP = f_{PAR} \times PAR \times LUE_{maximum} \times \rho \quad (2)$$

where PAR is the incoming photosynthetically active radiation used in the photosynthesis process, f_{PAR} is the fraction of PAR absorbed by the green canopy, $LUE_{maximum}$ is the maximum light-use efficiency, and $\rho \leq 1$ is the reduction factor used to consider the effect of other environmental factors, mainly soil water content, temperature and VPD that control the photosynthesis process.

The parameter $f_{PAR} \times PAR$, called $aPAR$ hereafter, is the absorbed PAR determined using:

$$aPAR = iPAR - rPAR - tPAR \quad (3)$$

where i and r denote the incoming and reflected radiation measured above the canopy, respectively, and t represents the transmitted radiation measured below the canopy. In the expression above, the total amount of $aPAR$ is assumed to be absorbed by leaves, and the portion absorbed by woody parts is assumed to be negligible.

Finally, in this study, the apparent ecosystem light-use efficiency LUE is calculated as:

$$LUE = \frac{GPP}{aPAR} \quad (4)$$

It is important to note that the GPP is not measured directly but is estimated by subtracting the modeled ecosystem respiration (ER) during the day from NEE ; consequently, LUE is subject to two main sources of error—errors inherent in NEE measurements from using the eddy covariance technique and uncertainties in the model predictions of ER during the day. LUE is also subject to uncertainties in radiation measurements, especially those related to sampling of reflected and transmitted PAR due to effects of canopy structure heterogeneity.

2.3. In situ measurements of PRI and NDVI

In each of the two forest sites, measurements of PRI and NDVI were acquired using sensors fixed side-by-side on a mast located approximately 7 m and 5 m from the upper layer of tree crowns in Fontainebleau forest and Puéchabon forest, respectively. For the PRI measurements, we used the model SKR 1800 manufactured by Skye Instruments, Ltd. (Llandrindod Wells, UK). PRI sensors are already used and validated in previous studies (Zarco-Tejada, González-Dugo, & Berni, 2012). NDVI sensors were laboratory-made following the description given in Pontailier, Graham, and Bert (2003) and Soudani et al. (2012). Both the PRI and NDVI sensors facing downward were inclined at an angle of approximately 20° from vertical and oriented to the south to avoid hotspot effects in canopy reflectance when the viewing direction was collinear with the solar direction. The measurements reported in this study were acquired from 2006 to 2011 in Fontainebleau forest and from 2010 to 2011 in Puéchabon forest.

Two PRI sensors were used; one sensor measured the incident solar radiation, while the second sensor simultaneously measured the radiation reflected upward. The PRI sensors measured radiance (or irradiance) in two narrow bands of 10-nm bandwidths centered on 530 nm and 570 nm. The PRI sensor facing downward had a field of view (FOV) of 25°, whereas the sensor facing upward had a cosine-correcting diffuser covering a 180° FOV. The area viewed at the top layer of the canopy was approximately 8 m² in Fontainebleau forest and 4 m² in Puéchabon forest.

In the two forests, a single NDVI sensor measured the radiances above the canopy in the red and near infrared bands, 640–660 nm and 780–920 nm, respectively. The field of view was initially 100° but was collimated to consider viewing constraints encountered at each site.

The area viewed was approximately 100 m² in Fontainebleau forest and 60 m² in Puéchabon forest.

PRI was computed from reflectance (R) according to the following expression:

$$PRI = \frac{R_{[565-575]} - R_{[525-535]}}{R_{[565-575]} + R_{[525-535]}} \quad (5)$$

The NDVI was computed from radiance (Rd) as:

$$NDVI = \frac{Rd_{[780-920]} - Rd_{[640-660]}}{Rd_{[780-920]} + Rd_{[640-660]}} \quad (6)$$

The values between brackets indicate the bandwidths in nanometers. At the two forest sites, the radiances used in the PRI and NDVI calculations are half-hourly average values from radiance measurements scanned every minute and recorded every half hour.

It seems important to note that the formulation of the PRI differs between studies. Many studies use the opposite expression of the Eq. (5). In this study, we referred to the pioneering work of Gamon et al. (1992).

2.4. Statistical data analysis

The statistical data analysis was performed at different time scales within a season using moving temporal windows and between years. In the first analysis, the strength and the direction of the relationships between PRI and the main bioclimatic variables at different time scales were evaluated using the coefficient of determination (R^2). In a second step, and because of the interdependence and the strong and complex interactions between the bioclimatic variables and PRI, the contribution of each variable to the temporal variability of PRI was evaluated using a nonparametric method based on the Random forest machine learning algorithm (Breiman, 2001) using the Random forest package (the R library randomForest – Version 4.6.1). Briefly, for regression analysis, RF is an extension of the tree-based regression method that allows the prediction of a numeric dependent variable from one or more numerical or categorical predictors without any assumptions such as the normality of distributions of the predictors or the form of regression between the dependent variable and the predictors. Starting from the original data (with the root node corresponding to the entire PRI data set in this study), the tree was constructed using binary recursive partitioning of independent variables into subintervals, allowing for smaller deviations between the observed and predicted values of the dependent variable (PRI). Instead of a single tree, RF predicts the dependent variable from a large number of trees (a few hundred) built from subsamples selected in the original data by random sampling with replacement (bootstrap samples of the same size as the original data set). Each subsample was used independently to build a tree. During the building of the tree, all the predictors were not used simultaneously; instead, a second randomization was performed by selecting a random subset of the predictors for each partition. The predictions were averaged over all the trees of RF.

RF also allows the predictive variables to be hierarchized in terms of importance in prediction accuracy. In this study, the importance of each predictive variable was measured as the average decrease in node impurity (Gini index) over all trees in RF due to the introduction of the predictor in the analysis (Breiman, 2001). In addition to this overall measure, the relationships between PRI and the predictive variables were assessed through partial dependence plots, which measure the marginal effect of each predictor on the predicted variable (PRI). An excellent presentation of regression analysis using Random forest with R is given in Berk (2008).

It is important to underline that the purpose of statistical analyses undertaken and results shown in the next sections is not to predict PRI from meteorological and eco-physiological factors but to assess the strength of the relationships between PRI and LUE and to investigate

the effect of each factor on the variability of PRI and on PRI vs. LUE relationships.

3. Results

3.1. Temporal patterns of the NDVI, aPAR, GPP, LUE, and PRI in the two forests

Fig. 1 illustrates the seasonal and interannual variations of the NDVI, aPAR, GPP, LUE, and PRI in 2010 in the two forest stands.

In Fontainebleau forest from 2006 to 2011, the NDVI, aPAR, GPP, LUE, and PRI exhibit similar patterns to that presented in Fig. 1. The temporal pattern of the NDVI indicates the typical seasonal variations of green canopy foliage in deciduous forests. This seasonal dynamic is characterized by two main phases: the leafy season during mid-spring and summer and the dormancy season during late autumn and winter. These two main seasons are separated by two short phases, delimited by two major phenological events: a first phase of budburst, leaf development, and maturation in spring and a second phase of onset of yellowing, senescence, and leaf fall in autumn. On average, over the six available years of NDVI measurements, the NDVI starts to increase on day (day of year) 92 (± 1 day of standard error). The maximum value of the NDVI is reached in the late spring on day 126 (± 4). During the summer, the NDVI is at its maximum level and then starts decreasing on day 276 (± 5) in early autumn at the beginning of leaf yellowing and leaf fall. During this period, the NDVI decreases rapidly until day 330 (± 8). On average, over all the years, the length of the main period of the growing season corresponding to the period of the NDVI plateau is approximately 150 days (± 2 days).

Seasonal patterns in the aPAR and GPP are similar to those usually observed in temperate deciduous forests and result from the seasonal climatic cycle and phenology. During the nonleafy season, the aPAR records correspond to the radiation absorbed by woody parts. During this period, there is no photosynthesis, and the GPP corresponds mainly to the contribution of herbaceous understory species and also to uncertainties in the modeled GPP estimates. During the leafy season, the GPP is driven by radiation and soil water content because the temperature is usually not a limiting factor during this period.

In Puéchabon forest, the temporal dynamics of the NDVI during the two years of the study are similar. The NDVI temporal variations are significantly dampened compared with those observed in deciduous forests. However, the NDVI decreased significantly, reaching its lowest

value in late April to early May. The decrease in the NDVI corresponds to the period during which the peak of litterfall is reached and also coincides with the slow emergence of a new cohort of leaves. The value of aPAR in Puéchabon forest is, on average, slightly lower than that in Fontainebleau forest during the growing season because of the lower LAI.

Regarding the GPP and LUE, Puéchabon forest experienced severe drought in summer 2010. Indeed, the total annual rainfall was 948 mm and 1157 mm in 2010 and 2011, respectively. However, the contrast between the two years is much more pronounced in the average summer rainfall. During the three summer months of June to August, the total rainfall was 57 mm in 2010 and 154 mm in 2011. The average rainfall during these three months from 1984 to 2011 is 109 mm. Consequently, in comparison with 2011 (data not presented), the GPP in 2010 decreased by approximately 20% during the three months of summer.

In the two forests, the seasonal patterns of PRI and NDVI are similar, emphasizing the control of canopy foliage dynamics on canopy PRI variations. However, in Puéchabon forest, it may be noted that during the GPP decline due to drought during midsummer in 2010, the NDVI remained nearly constant, whereas PRI increased significantly and covered the entire range observed over the entire year.

For the reasons described above and to accurately assess the relationships between PRI and LUE independently of the effects of temporal changes of canopy structural and biochemical characteristics, only the period from days 180 to 255 during the NDVI plateau, which corresponds to the period during which the LAI remains constant near maximum values, is included in the analysis of the PRI data. This period was also selected to avoid the inclusion of data acquired when the leaves were not yet fully mature or senescent because the PRI signal is strongly driven by the effects of temporal variations of leaf pigment pools.

3.2. Assessment of the relationships between PRI and climate meteorological, carbon, and water flux variables at different time scales

Three categories of variables related to climatic conditions and water and carbon fluxes were selected for this analysis: i) aPAR and the ratio of direct-to-total solar radiation (direct/total PAR) above the canopy were used as indicators of the amount of radiation available for photosynthesis and sky conditions; ii) the air vapor pressure deficit (VPD) and the ratio of real evapotranspiration-to-potential evapotranspiration (Etr/Etp) were used as indicators of the evaporative demand of the atmosphere

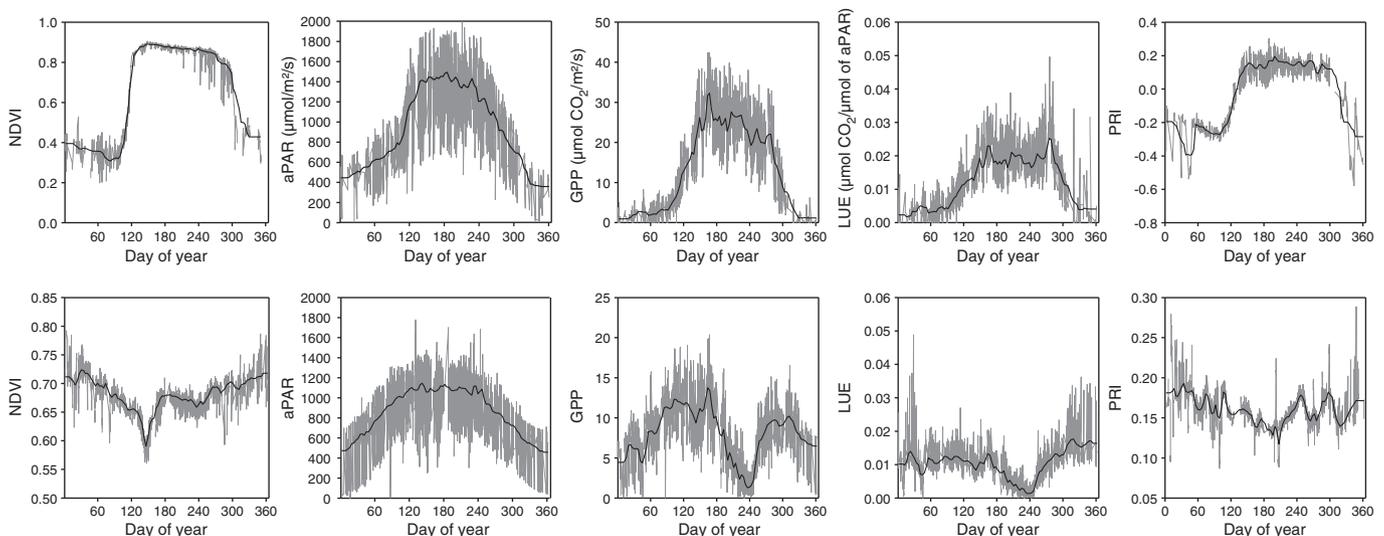


Fig. 1. Seasonal variations in 2010 of NDVI, aPAR, GPP, LUE, and PRI measured every half-hour above a deciduous oak forest canopy (Fontainebleau flux-tower site — upper figures) and above an evergreen holm oak forest canopy (Puéchabon flux-tower site — bottom). The data presented were acquired between 8 h and 18 h TU. Continuous line: smoothed data using a moving average window of approximately ten days.

and water stress; and finally, iii) the GPP and LUE were used as indicators of the amount and apparent quantum yield of photosynthesis.

The relationships between PRI and the variables described above were established on a half-hourly time step basis and during a period of NDVI stability from day 180 to day 255. In addition, to avoid diurnal variations of PRI, only measurements acquired between 10 h and 14 h were selected for analysis.

In Fontainebleau forest, the best coefficients of correlation, shown in Table 1, (in descending order) were observed between the following pairs: PRI vs. aPAR, PRI vs. Direct/total PAR, PRI vs. VPD, PRI vs. LUE, and PRI vs. GPP. The relationships between PRI and Etr/Etp were weaker at both sites. In Puéchabon forest, we observe the same hierarchy of variables correlated to PRI as in Fontainebleau forest, but only for 2011. During 2010, in which drought occurred, the results contrast with those of 2011. The correlations were not significant between PRI and aPAR and were significant between PRI and Etr/Etp, PRI and LUE, and PRI and GPP.

Figs. 2 and 3 illustrate the form of the relationships between PRI and aPAR and between PRI and LUE in the two forests. For each forest site, the relationships are presented for two years, corresponding to the highest and the lowest values of the coefficient of correlation.

Despite the relatively high correlations between PRI vs. aPAR and PRI vs. LUE, these relationships are scattered. At first glance, this scattering may be due to the long period examined in the analysis (days 180–255), as PRI is known to vary at very short time scales. During the period of days 180–255, the structure and ecophysiological functioning of the canopy may have been subjected to changes associated with climatic events and with subtle temporal variations of the biochemical properties of the leaves, although the NDVI remained constant. To account for these considerations, regressions between PRI and aPAR and between PRI and LUE were performed at short-time scales using moving windows within the leafy season – from the beginning of the growing season (including the onset of the NDVI increase in spring – day 126) to the early autumn in Fontainebleau (day 276) and over the entire year (days 1–365) in Puéchabon forest. For both of the studied forests, statistical analyses were conducted for two years (the years mentioned in Figs. 2 and 3), for which the relationships between PRI, aPAR, and LUE on a seasonal scale (day 180 to 255) have the highest and lowest coefficients of correlation. The results are summarized in Figs. 4 and 5, which illustrate the variations of the coefficient of determination (R^2) within a 20-day moving window throughout the season and at different hours of the day at two-hour time intervals. The selection of the size of the moving window is somewhat arbitrary; however, we assume that over 20 days, changes in the leaf biochemical properties are lower than what can be expected over the entire season. We also note that smaller sizes (one and two weeks) were also tested, and the general patterns of R^2 were similar to those observed in Figs. 4 and 5.

In Fontainebleau forest (Fig. 4) and from data acquired in 2010 (highest R^2), significant R^2 values ($P < 0.05$) over the moving window of 20 days at two-hour intervals range between 0.05 and 0.94 for sample sizes varying between 21 and 80 observations, respectively. In 2007

(lowest R^2), significant R^2 values range between 0.04 and 0.89 for sample sizes varying between 29 and 80 observations, respectively.

In Puéchabon forest (Fig. 5) and from the data acquired in 2011 (highest R^2), significant relationships between PRI and aPAR and between PRI and LUE can be observed in winter under clear sky conditions (from day 1 to day 60). Significant relationships were also observed in summer periods, particularly from day 213 to day 265. In 2010, the highest correlations (reaching a peak of 0.9) between PRI and aPAR and between PRI and LUE were observed during two long periods from day 124 to 175 and from day 240 to 300. Between these two periods, from day 175 to 240, which coincides with the period of drought, the relationships between PRI vs. aPAR and PRI vs. LUE were insignificant.

Fig. 6 presents the best regressions observed between PRI and aPAR and between PRI and LUE in 2010 in Fontainebleau forest and in 2011 in Puéchabon forest. In Fontainebleau forest, a maximum R^2 at an hourly time step (0.94) is reached from day 236 to 255. The R^2 value of the PRI vs. LUE relationship over the same period is 0.87. Over this period and when all the data acquired between 10 h and 14 h are pooled, R^2 is approximately 0.76 for PRI vs. aPAR and 0.70 for PRI vs. LUE. In Puéchabon forest, the maximum R^2 (0.93) between PRI and aPAR is reached between days 230 and 249. The maximum R^2 of PRI vs. LUE is approximately 0.92 and is reached between days 213 and 232. In Puéchabon forest from day 230 to 249 and when all the data acquired between 10 h and 14 h are pooled, R^2 is approximately 0.59 for PRI vs. aPAR and PRI vs. LUE.

In conclusion, R^2 between PRI and LUE is less than that between PRI and aPAR, and high correlations between PRI and aPAR do not necessarily imply high correlations between PRI and LUE. Note that the best relationships between PRI and LUE often coincide with periods of clear skies dominated by a high direct-to-total PAR radiation ratio (Figs. 4 & 5).

3.3. Investigating the main drivers of PRI variations and PRI vs. LUE relationships

As underlined in Materials and Methods section, because of both the strong nonlinear interactions and dependencies between different variables, it is difficult to rank the variables in terms of explanatory power of the variability of PRI based on coefficients of correlation (Table 1) that measure the overall linear covariation over the entire range of explanatory variables. Nonlinear technique regression based on Random Forest Regression (RF) analysis is performed using the same dataset used for the statistical correlation analysis summarized in Table 1 (days 180–255, 10 h–14 h) to assess the contribution of the main variables to the variability of PRI. The results are presented in Figs. 7, 8, and 9.

In Fontainebleau forest and using data pooled over the six years of measurements (Fig. 7), the RF regression of PRI on variables presented in Fig. 7b explains approximately 54% of the total variance of PRI (Fig. 7a). aPAR appears to be the most important variable, followed by VPD and the direct/total radiation ratio. LUE, GPP, and Etr/Etp play

Table 1

Pearson's correlation coefficient [r] between PRI and aPAR, direct/total PAR, VPD, Etr/Etp, GPP, and LUE. The value of r was calculated per year during the period of nearly constant NDVI from day 180 to 255, and the measurements were acquired every half-hour between 10 h and 14 h TU. In Fontainebleau forest, because of the small variation between years, the data were pooled over the six years. In Puéchabon forest, to consider the differences between the two years due to drought, the data were analyzed separately for each year. n is the number of observations used in the regression each year. In Fontainebleau, the range (min–max) of n and r is given. ns: not significant ($P > 0.05$).

PRI vs.	aPAR	Direct/total PAR	VPD	Etr/Etp	GPP	LUE
<i>FR Fon</i> (n [581–760])	[0.60–0.74]	[0.51–0.76]	[0.55–0.67]	[–0.00 to –0.30]	[0.14–0.50]	[–0.38 to –0.65]
<i>FR Pue</i> 2010 ($n = 603$)	0.04 ns	0.15	–0.04 ns	–0.33	–0.53	–0.48
2011 ($n = 712$)	0.61	0.65	0.51	–0.12	0.02 ns	–0.53

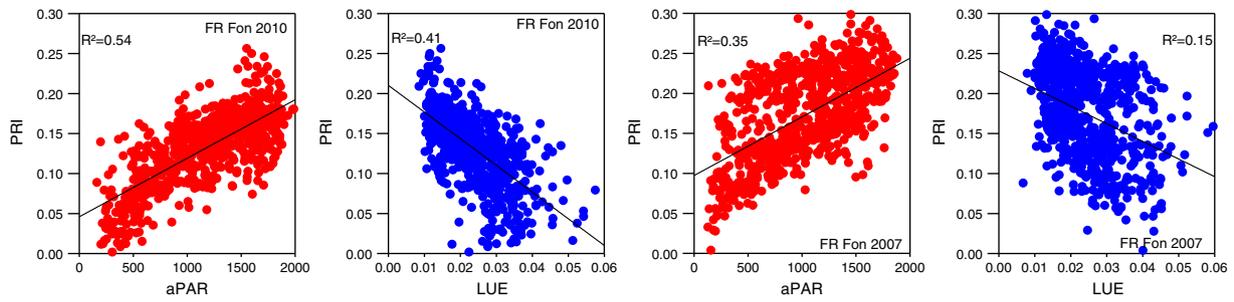


Fig. 2. Relationships between PRI, aPAR, and LUE for 2010 (best correlations) and 2007 (lowest correlations) in Fontainebleau forest. The measurements were acquired every half-hour between 10 h and 14 h TU during a period of nearly constant NDVI from day 180 to 255.

insignificant roles (Fig. 7b). Fig. 7c reveals a monotonic positive relationship between PRI and aPAR over the entire range of aPAR. The relationship between PRI and VPD is also positive; however, a saturation feature is observed at high VPD values. The other variables have insignificant effects on the PRI variation.

In Puéchabon forest, the RF regression was performed separately for the 2010 and 2011 data to consider the contrast between the two years due to the effects of drought. The RF results are presented in Figs. 8 and 9.

The results demonstrate that the hierarchy of the predictive variables computed from variable importance criteria and the form of relationships between these variables and PRI are very different between the two years. In 2010, the year of severe drought, GPP, LUE, and VPD appear to be the most important variables over the entire range of PRI variation. The relationships between PRI and these three variables are negative. In 2011, the results presented in Fig. 9 are quite similar to those obtained in Fontainebleau forest, highlighting a significant effect of the direct/total aPAR on PRI variation. The main variables affecting PRI are aPAR, direct/total PAR, and VPD. These three variables are linearly related to PRI (Fig. 9c). In contrast, the effects of GPP, LUE, and Etr/Etp on PRI are insignificant.

3.4. An approach for disentangling the effects of factors that affect the PRI vs. aPAR and PRI vs. LUE relationships on a seasonal scale

As demonstrated in Figs. 4 and 5, statistically significant “moving window” relationships between PRI and aPAR or PRI and LUE appear or disappear over periods during the leafy season in Fontainebleau forest or during the year in Puéchabon forest. Moreover, even when these relationships are statistically significant, the parameters of regressions vary from one period to another. The temporal variability of the intercept of the linear regression of PRI vs. aPAR is particularly interesting to analyze. Indeed, this parameter corresponds to PRI at very low radiation levels. Because the xanthophyll cycle activity is expected to be negligible at low radiation levels, a large portion of the temporal variability of the intercept throughout the season may be interpreted as being due

to the effects of temporal variations of other factors, particularly the canopy structure and other leaf pigments (e.g. chlorophyll, carotenoid).

Fig. 10 illustrates the temporal variability of intercepts of regressions of PRI vs. aPAR within a moving window of one week in the two studied forests for all the years investigated. We note that the selection of a one-week moving window size is a compromise that we consider adequate for an accurate interpretation of temporal variations in the intercept. If using larger temporal windows, eventual variations in leaf biochemical properties may bias the interpretation of results, whereas narrower temporal windows may artificially increase the temporal variations of the estimates of regression coefficients because of the small sample sizes used.

In Fontainebleau forest, Fig. 10 (left) presents the temporal variations of the intercepts of the “moving window” PRI vs. aPAR regressions. At short time scales on the order of a few days, the intercepts vary rapidly and sharply. At the seasonal scale, with the exception of 2006 and 2010, we observe a general tendency for the intercepts to decrease during the season, especially during the period of the NDVI plateau. We also note that interannual intercepts are different at the beginning of the season in the spring and become very close at the end of the season in early autumn. The intercepts become very close except for in 2006.

In Puéchabon forest, Fig. 10 (right) demonstrates that the level of intercepts of PRI vs. aPAR is relatively stable throughout the year and that the range of intercept variations is narrower than in Fontainebleau forest.

As suggested above, a large portion of the temporal variability of the intercept of PRI vs. aPAR (called PRI_0 hereafter) can be interpreted as being due to the effects of temporal variations in the canopy structure and leaf biochemical properties. To disentangle the contribution of these effects from the PRI signal, PRI_0 is subtracted from the PRI observations, and the regressions between the corrected PRI (PRI_c) and aPAR and between PRI_c and LUE are reevaluated. Fig. 11 presents these relationships before and after applying this correction method.

We first note that to assess the relevance of this disentangling method, we extended the period of analysis to include periods during which foliar

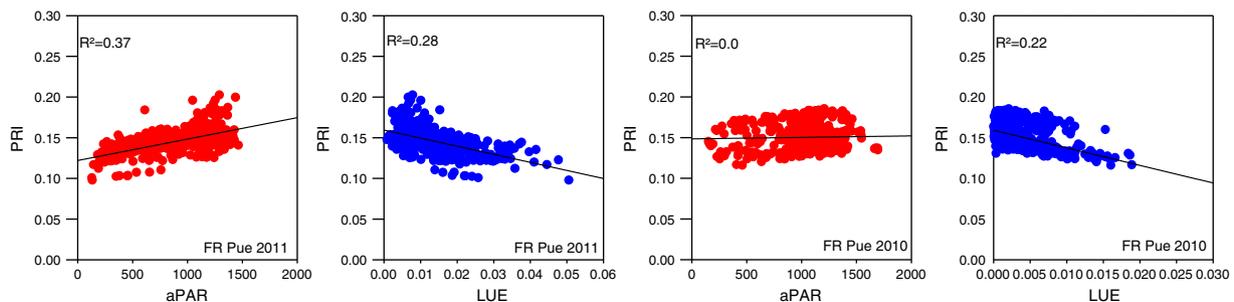


Fig. 3. Relationships between PRI, aPAR, and LUE for 2011 (best correlations) and 2010 (lowest correlations) in Puéchabon forest. The measurements were acquired every half-hour between 10 h and 14 h TU during a period of nearly constant NDVI from day 180 to 255.

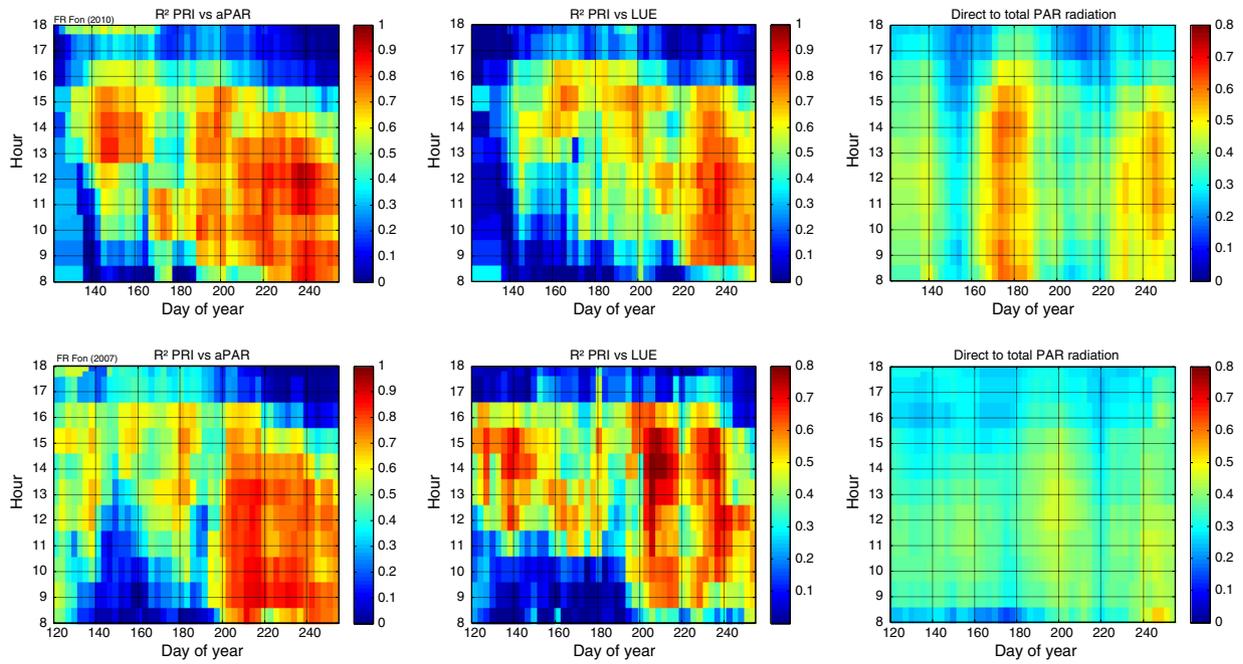


Fig. 4. Images of the temporal variations of the coefficient of determination of the relationships between PRI vs. aPAR and PRI vs. LUE obtained from the measurements acquired in Fontainebleau forest in 2010 (upper three plots: best correlation) and 2007 (lowest correlation). The R^2 values were determined from data acquired separately in two-hour intervals during the day and within a moving window of 20 days over the entire period of the NDVI plateau (days 126–275). The plots on the right correspond to the ratio of direct-to-total PAR radiation.

biochemical properties are supposed to be significantly contrasted. At the Fontainebleau site, the analysis period is from day 130 to day 280, including periods of immature, mature, and early senescent leaves. At the Puéchabon site, we considered the entire year.

For Fontainebleau forest, the disentangling procedure does not provide a significant improvement in the annual PRI vs. aPAR relationships. However, as demonstrated in Fig. 11 (upper), the dispersion around the

general model with pooled data over the six years is reduced, and R^2 increases significantly (from 0.18 to 0.30 after the corrections). Concerning PRI vs. LUE, a notable increase of R^2 was measured for all years (Fig. 11 - bottom). The most important improvement was measured for 2007, for which R^2 increases from 0 to 0.37. The general model has also been significantly improved. R^2 increases from 0.05 to 0.26. As expected, in Puéchabon forest (data not presented), the

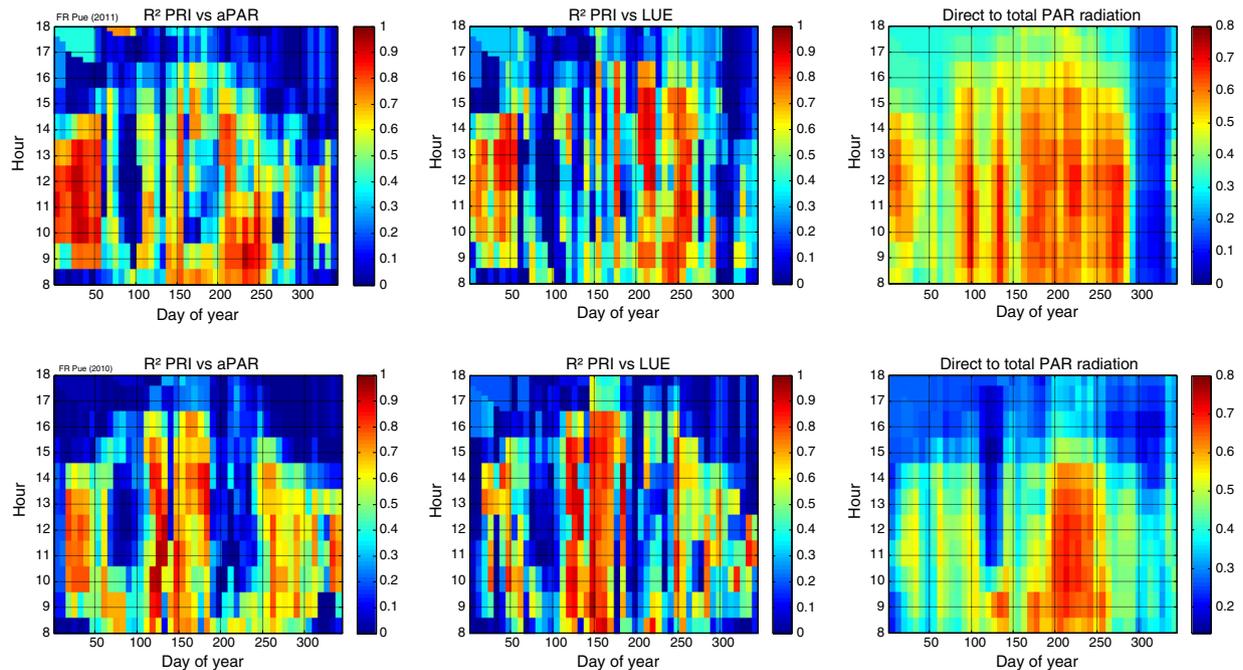


Fig. 5. Images of the temporal variations of the coefficient of determination of the relationships between PRI vs. aPAR and PRI vs. LUE obtained from the measurements acquired in Puéchabon forest in 2011 (upper plots, best correlations) and 2010 (severe drought, low correlations). The R^2 values were determined from data acquired separately in two-hour intervals during the day and within a moving window of 20 days and over the entire year. The plots on the right correspond to the ratio of direct-to-total PAR radiation.

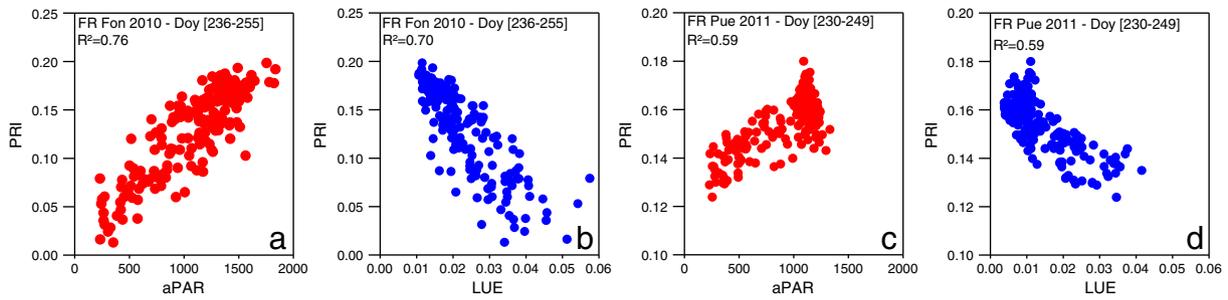


Fig. 6. Illustrations of best correlations between PRI and aPAR and between PRI and LUE in Fontainebleau forest and in Puéchabon forest. The data used were acquired between 10 h and 14 h during the period of maximum R^2 given between brackets.

correction procedure does not improve the relationships between PRI vs. aPAR or PRI vs. LUE because of the small variations of PRI_0 during the year (Fig. 10 - right).

4. Discussion

At the seasonal scale (Fig. 1), the temporal patterns of PRI and NDVI are similar, indicating that the temporal changes of PRI are primarily controlled by the seasonal phenology that modifies both the leaf area and biochemical properties of the canopies. Fig. 1 also demonstrates that during periods of stable total canopy leaf area during summer, the short-term variations in PRI are greater than those in NDVI, suggesting that these two indices are relatively independent.

At the seasonal scale, from day 180 to day 255 (Figs. 2 and 3), our results indicate positive and significant relationships between PRI and aPAR in Fontainebleau forest over the six years of the study and in Puéchabon forest in 2011. These results are consistent with previous studies at both the leaf (Gamon et al., 1997; Peñuelas, Filella, Llusia, Siscart, & Piñol, 1998) and canopy (Evain, Flexas, & Moya, 2004; Peguero-Pina, Morales, Flexas, Gil-Pelegrin, & Moya, 2008) scales. These studies emphasized the strong dependence of PRI on radiation across a wide range of species and hydric conditions. Although the physiological mechanisms involved are complex and not fully understood (Demmig-Adams & Adams, 2006; Holt et al., 2005), the increase of PRI when absorbed PAR increases is explained by the decrease in reflectance at 531 nm due to an increase in light absorption associated with the conversion of violaxanthin into antheraxanthin and zeaxanthin pigments (Gamon et al., 1997).

In contrast, the PRI vs. LUE relationships are negative (Figs. 2 & 3). At the leaf scale, Gamon et al. (1997) and Peñuelas, Llusia, Piñol, and Filella (1997, 1998) have demonstrated negative relationships between PRI and LUE and between PRI and the photochemical efficiency of PSII. At the canopy scale and in mature forests, the works of Nichol et al.

(2000, 2002), Nakaji, Ide, Oguma, Saigusa, and Fujinuma (2007, 2006); Nakaji, Oguma, and Fujinuma (2006); Nakaji et al. (2008), Wu, Niu, Tang, and Huang (2010), Goerner et al. (2011), and the review of Garbalsky, Peñuelas, Gamon, Inoue, and Filella (2011) support a negative relationship between PRI and LUE.

Although significant, the PRI vs. aPAR and PRI vs. LUE relationships at the seasonal scale are scattered and vary from one year to another (Figs. 2 and 3). Over shorter periods within the 20-day moving window, the signs of these relationships remain unchanged (positive for PRI vs. aPAR and negative for PRI vs. LUE); however, the correlations are significantly improved (Figs. 4, 5, and 6). The highest correlations are most often observed over periods characterized by clear or slightly overcast skies. However, all the periods of clear skies do not involve improvements in the PRI vs. aPAR or PRI vs. LUE relationships. This finding is especially highlighted during the drought from day 175 to 240 in 2010 in Puéchabon forest (Fig. 5). During this period, the PRI vs. aPAR or PRI vs. LUE relationships are mostly nonsignificant, even though the weather is dominated by clear skies. Note also that during this period of drought, PRI increased, NDVI remained stable, and LUE has consequently been significantly reduced (Fig. 1).

These findings highlight the complexity of the nature of the relations that link PRI to bio-meteorological factors (GPP, LUE, aPAR, VPD, sky conditions, etc.). This complexity is illustrated from regression analyses using the Random forests approach in Table 1 and Figs. 7, 8, and 9. In Fontainebleau (Fig. 7) over the six years of the study and in Puéchabon in 2011 (Fig. 9), PRI appears to be correlated to radiation and sky conditions, whereas in Puéchabon forest in 2010 (Fig. 8), which was characterized by a severe summer drought, PRI is essentially correlated to GPP. This result leads us to suggest that under non-water-stressed conditions, significant PRI vs. LUE relationships are mainly under the control of the incident radiation. This control is more pronounced under clear or slightly covered skies because of a greater range of variations of PRI, aPAR, and GPP and thus of LUE. Under stable overcast sky

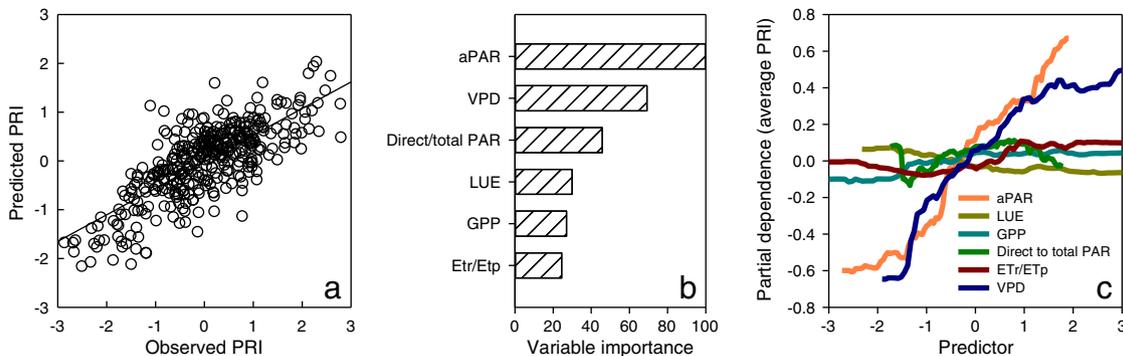


Fig. 7. a: Observed vs. Predicted PRI from RF regression in Fontainebleau forest established based on a validation sample composed of 10% of the entire sample that was randomly selected ($R^2 = 0.54$, $RMS = 0.45$). The data were pooled over the six years – days 180–255 between 10 and 14 h. b: Rank of importance (in % of the importance of the predictor ranked first) based on RF regression of the predictor variables in determining PRI. c: Partial dependence describing the marginal effect of each variable on PRI. The x-axis is the considered variable, and the y-axis is the average value of PRI obtained by fixing the values of X, whereas the other predictors are not fixed (All the variables – PRI and predictors – are centered and reduced).

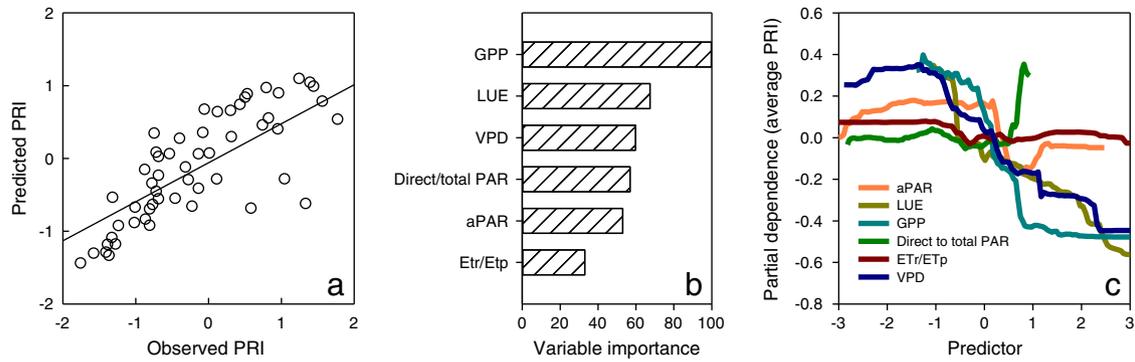


Fig. 8. a: Observed vs. Predicted PRI from RF regression in Puéchabon forest (2010) established based on a validation sample composed of 10% of the entire sample that was randomly selected data (overall $R^2 = 0.61$, $RMS = 0.39$). b: Rank of importance (in % of the importance of the predictor ranked first) based on RF regression of the predictor variables in determining PRI. c: Partial dependence describing the marginal effect of each variable on PRI. The x-axis is the considered variable, and the y-axis is the average value of PRI obtained by fixing the values of X, whereas the other predictors are not fixed (All the variables – PRI and predictors – are centered and reduced).

conditions, the range of variability of these variables appears to be less important, which may partially explain the lack of statistical significance of the PRI vs. aPAR and PRI vs. LUE relationships. Under water-limited conditions, the decline of the strength of the relationship between PRI and LUE in Puéchabon forest is difficult to explain; however, from a statistical point of view, the small variations of LUE observed during the drought period may be a relevant reason (Fig. 1). In other words, in addition to physiological mechanisms that directly control PRI, small variations of LUE under severe stress conditions may explain the loss of the PRI vs. LUE relationship due to an insufficient signal-to-noise ratio.

The seasonal and interannual variability of PRI and thus the relationships between PRI, aPAR, and LUE are highly dependent on canopy foliage and on leaf pigment content. The dependency of PRI on canopy foliage dynamics can be clearly observed in Fig. 1, which illustrates the similar seasonal patterns of PRI and NDVI. Strong relations between PRI and the leaf area index (LAI) and between PRI and the chlorophyll content have been established in previous studies (Garrity, Eitel, & Vierling, 2011; Hmimina, Dufrene, & Soudani, 2014; Rahimzadeh-Bajgiran, Munehiro, & Omasa, 2012). Therefore, the relationships between PRI and LUE established over the entire season or for different years, such as those established using MODIS data (Drolet et al., 2005; Drolet et al., 2008; Hilker et al., 2010), are expected to be significantly affected by temporal changes in the structural and biochemical properties of the canopy.

Approaches such as those developed by Rahimzadeh-Bajgiran et al. (2012), who have developed a new spectral index that combines PRI

and another spectral index as an indicator of chlorophyll content, may be used to explicitly consider the effects of temporal changes of chlorophyll content on PRI vs. LUE relationships. In our study, we suggest a different approach. Fig. 10 illustrates the variation in the intercept (PRI_0) of the PRI vs. aPAR relationships, suggesting the possible presence of a temporal tendency that may reflect changes in structural and biochemical characteristics of the canopy. Because the amount of canopy foliage is likely constant, as suggested by the stability of NDVI during this period, this tendency can be explained by changes in the biochemical properties of the canopy, as observed in previous studies (Gond, de Pury, Veroustraete, & Ceulemans, 1999). Regardless of the cause of this tendency, it is important to note that once PRI_0 is subtracted from the measured PRI, the relationships between the corrected PRI and LUE for each year are significantly improved, and a stable multi-year model can be obtained. Nevertheless, further experimental studies are required to explain the temporal changes of PRI_0 during the season and to develop a more accurate disentangling approach to make PRI-based remote-sensing of leaf and ecosystem light-use efficiency less sensitive to spatial and temporal changes in the canopy structure and chlorophyll content.

5. Conclusions

Our study highlights the strong dependency between PRI and two categories of factors. At the seasonal scale, the temporal dynamics of PRI is primarily controlled by the phenology and the temporal dynamics of the structural and biochemical characteristics of the canopy. Thus, from this point of view, PRI is similar to other spectral indices sensitive

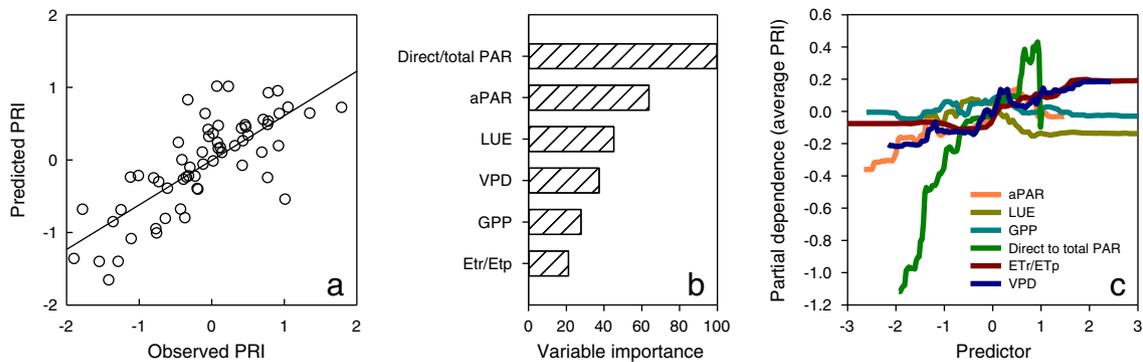


Fig. 9. a: Observed vs. Predicted PRI from RF regression in Puéchabon forest (2011) established based on a validation sample composed of 10% of the entire sample that was randomly selected ($R^2 = 0.56$, $RMS = 0.44$). b: The rank of importance (in % of the importance of the predictor ranked first) based on RF regression of the predictor variables in determining PRI. c: Partial dependence describing the marginal effect of each variable on PRI when all the other variables are fixed. The x-axis is the considered variable, and the y-axis is the average value of PRI obtained by fixing the values of X, whereas the other predictors are not fixed (all the variables – PRI and predictors – are centered and reduced).

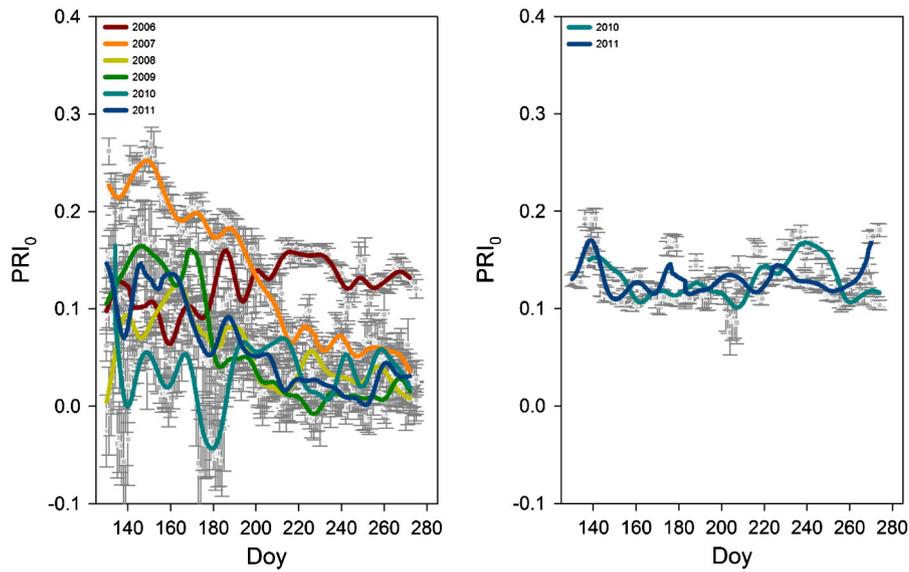


Fig. 10. Variation of the intercept of the regression of PRI on aPAR in Fontainebleau forest (left) and in Puéchabon forest (right) within a 6-day moving window. The intercepts and errors determined from regressions are presented in gray. The continuous lines are the intercepts interpolated for each day using weighted smoothing splines. The weights are proportional to R^2 .

to canopy structure such as the NDVI and to some other spectral biochemical indices sensitive to leaf chlorophyll and carotenoid contents. At a shorter temporal scale – a few days – PRI has a wider dynamic range than NDVI and is mainly controlled by solar radiation and sky conditions. PRI increases when absorbed radiation increases and decreases rapidly in response to cloud cover. PRI is inversely correlated to light-use efficiency. At a short time scale, the relationships between

PRI and LUE may be very significant. At seasonal and interannual scales, these relationships are more scattered, which may be partially due to seasonal changes in structural and biochemical properties of the canopy. Consequently, the relationships between LUE and PRI using satellite data such as MODIS should be interpreted with extreme caution. In our study, the intercepts of PRI vs. aPAR regressions established over short periods of a few days were interpreted as estimates of PRI at very low

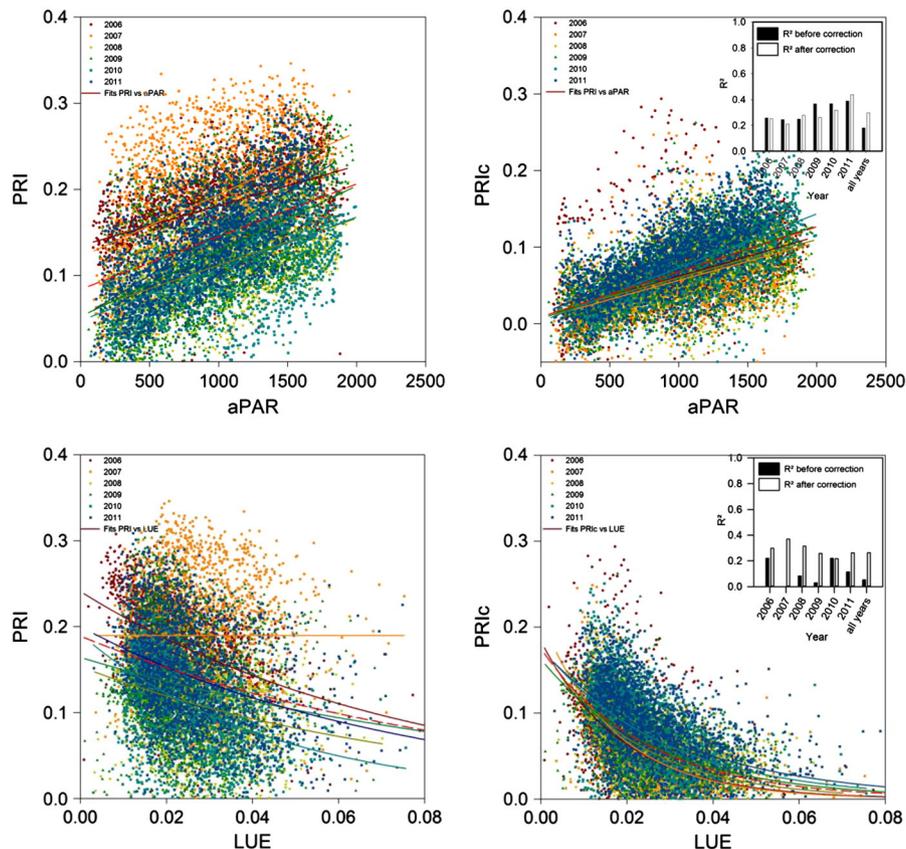


Fig. 11. Relationships between PRI and aPAR (upper) and between PRI and LUE (bottom) in Fontainebleau forest. On the left and on the right, the relationships before and after correction (PRic) by subtracting PRI_0 from PRI observations are presented, respectively. Insets represent R^2 of fits before correction (vertical black bars) and after correction (vertical white bars). The continuous curves represent the regression lines for each year. The short dashed curve in red represents the general model using data pooled over all the years.

incident radiation and called PRI_0 . The temporal changes of PRI_0 were used as indicators of temporal changes of the canopy state independent of the effects of radiation on the physiological mechanisms that control PRI. After subtraction of PRI_0 from the measured PRI, significant improvements in the corrected PRI vs. LUE relationships were observed. This approach of PRI correction must be studied in depth because it constitutes a very interesting method of considering the effects of temporal changes of canopy biochemical properties on PRI vs. LUE relationships at seasonal scales.

Acknowledgments

The authors thank GIP ECOFOR and SOERE F-ORE-T (Systèmes d'observation et d'expérimentation pour la recherche en environnement). We would like to express our profound gratitude to Jean Yves Pontailier, Laurent Vanbostal and all other persons involved in the data collection process. We are also very grateful for thorough and helpful comments from the reviewers of the manuscript.

References

- Berk, A.R. (2008). *Statistical learning from a regression perspective*. Springer Verlag 0387775005 (EAN 978-0387775005. P 223 (358 pp.)).
- Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*, 63, 625–644.
- Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., & Peñuelas, J. (2011). Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *PNAS*, 108(4), 1474–1478.
- Delpierre, N., Soudani, K., François, C., Le Maire, G., Bernhofer, C., Kutsch, W., et al. (2012). Quantifying the influence of climate and biological drivers on the interannual variability of carbon exchanges in European forests through process-based modelling. *Agricultural and Forest Meteorology*, 154–155, 99–112.
- Demmig-Adams, B., & Adams, W. W. (1996). The role of xanthophyll cycle carotenoids in the protection of photosynthesis. *Trends in Plant Science*, 1, 21–26.
- Demmig-Adams, B., & Adams, W. W. (2006). Photoprotection in an ecological context: The remarkable complexity of thermal energy dissipation. *New Phytologist*, 172, 11–21.
- Drolet, G. G., Huemmrich, K. F., Hall, F. G., Middleton, E. M., Black, T. A., Barr, A. G., et al. (2005). A MODIS-derived photochemical reflectance index to detect inter-annual variations in the photosynthetic light-use efficiency of a boreal deciduous forest. *Remote Sensing of Environment*, 98(2–3), 212–224.
- Drolet, G. G., Middleton, E. M., Huemmrich, K. F., Hall, F. G., Amiro, B.D., Barr, A. G., et al. (2008). Regional mapping of gross light-use efficiency using MODIS spectral indices. *Remote Sensing of Environment*, 112, 3068–3074.
- Evain, S., Flexas, J., & Moya, I. (2004). A new instrument for passive remote sensing: 2. Measurement of leaf and canopy reflectance changes at 531 nm and their relationship with photosynthesis and chlorophyll fluorescence. *Remote Sensing of Environment*, 91, 175–185.
- Filella, I., Amaro, T., Araus, J. L., & Peñuelas, J. (1996). Relationship between photosynthetic radiation-use efficiency of barley canopies and the photochemical reflectance index (PRI). *Physiologia Plantarum*, 96, 211–216.
- Gamon, J. A., Peñuelas, J., & Field, C. B. (1992). A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. *Remote Sensing of Environment*, 41, 35–44.
- Gamon, J. A., Serrano, L., & Surfus, J. S. (1997). The photochemical reflectance index: An optical indicator of photosynthetic radiation use efficiency across species, functional types, and nutrient levels. *Oecologia*, 112, 492–501.
- Gamon, J. A., & Surfus, J. S. (1999). Assessing leaf pigment content and activity with a reflectometer. *New Phytologist*, 143, 105–117.
- Garbalsky, M. F., Peñuelas, J., Gamon, J. A., Inoue, Y., & Filella, I. (2011). The photochemical reflectance index (PRI) and the remote sensing of leaf, canopy and ecosystem radiation use efficiencies: A review and meta-analysis. *Remote Sensing of Environment*, 115, 281–297.
- Garrity, S. R., Eitel, J. U. H., & Vierling, L. A. (2011). Disentangling the relationships between plant pigments and the photochemical reflectance index reveals a new approach for remote estimation of carotenoid content. *Remote Sensing of Environment*, 115, 628–635.
- Gebremichael, M., & Barros, A. P. (2006). Evaluation of MODIS gross primary productivity (GPP) in tropical monsoon regions. *Remote Sensing of Environment*, 100, 150–166.
- Goerner, A., Reichstein, M., & Rambal, S. (2009). Tracking seasonal drought effects on ecosystem light use efficiency with satellite-based PRI in a Mediterranean forest. *Remote Sensing of Environment*, 113, 1101–1111.
- Goerner, A., Reichstein, M., Tomelleri, E., Hanan, N., Rambal, S., Papale, D., et al. (2011). Remote sensing of ecosystem light use efficiency with MODIS-based PRI. *Biogeosciences*, 8, 189–202.
- Gond, V., de Pury, D.G. G., Veroustraete, F., & Ceulemans, R. (1999). Seasonal variations in leaf area index, leaf chlorophyll, and water content; scaling-up to estimate fAPAR and carbon balance in a multilayer, multispecies temperate forest. *Tree Physiology*, 19, 673–679.
- Hall, F. G., Hilker, T., Coops, N. C., Lyapustin, A., Huemmrich, K. F., Middleton, E., et al. (2008). Multi-angle remote sensing of forest light use efficiency by observing PRI variation with canopy shadow fraction. *Remote Sensing of Environment*, 112, 3201–3211.
- Hilker, T., Coops, N. C., Hall, F. G., Black, T. A., Wulder, M.A., Nescic, Z., et al. (2008). Separating physiologically and directionally induced changes in PRI using BRDF models. *Remote Sensing of Environment*, 112, 2777–2788.
- Hilker, T., Hall, F. G., Coops, N. C., Lyapustin, A., Wang, Y., Nescic, Z., et al. (2010). Remote sensing of photosynthetic light-use efficiency across two forested biomes: Spatial scaling. *Remote Sensing of Environment*, 114, 2863–2874.
- Hilker, T., Lyapustin, A., Hall, F. G., Wang, Y., Coops, N. C., Drolet, G., et al. (2009). An assessment of photosynthetic light use efficiency from space: Modeling the atmospheric and directional impacts on PRI reflectance. *Remote Sensing of Environment*, 113, 2463–2475.
- Hmimina, G., Dufrière, E., & Soudani, K. (2014). Relationship between PRI and leaf ecophysiological and biochemical parameters under two different water statuses: Toward a rapid and efficient correction method using real-time measurements. *Plant, Cell & Environment*, 37(2), 473–487.
- Holt, N. E., Zigmantas, D., Valkunas, L., Li, X. -P., Niyogi, K. K., & Fleming, G. R. (2005). Carotenoid cation formation and the regulation of photosynthetic light harvesting. *Science*, 307, 433–436.
- Hwang, T., Kang, S., Kim, J., Kim, Y., Lee, D., & Band, L. (2008). Evaluating drought effect on MODIS gross primary production (GPP) with an eco-hydrological model in the mountainous forest, East Asia. *Global Change Biology*, 14, 1037–1056.
- Jahns, P., & Holzwarth, A.R. (2012). The role of the xanthophyll cycle and of lutein in photoprotection of photosystem II. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*, 1817, 182–193.
- Kumar, M., & Monteith, J. L. (1981). Remote sensing of crop growth. In H. Smith (Ed.), *Plants and the daylight spectrum* (pp. 133–144). London, New York, Toronto, Sydney, San Francisco: Academic Press.
- La Porta, N., Capretti, P., Thomsen, I., Kasanen, R., Hietala, A., & Weissenberg, K. (2008). Forest pathogens with higher damage potential due to climate change in Europe. *Canadian Journal of Plant Pathology*, 30, 177–195.
- Mu, Q., Zhao, M., Heinsch, F. A., Liu, M., Tian, H., & Running, S. W. (2007). Evaluating water stress controls on primary production in biogeochemical and remote sensing based models. *Journal of Geophysical Research*, 112, G01012.
- Nakaji, T., Ide, R., Oguma, H., Saigusa, N., & Fujinuma, Y. (2007). Utility of spectral vegetation index for estimation of gross CO₂ flux under varied sky conditions. *Remote Sensing of Environment*, 109, 274–284.
- Nakaji, T., Ide, R., Takagi, K., Kosugi, Y., Ohkubo, S., Nasahara, K. N., et al. (2008). Utility of spectral vegetation indices for estimation of light conversion efficiency in coniferous forests in Japan. *Agricultural and Forest Meteorology*, 148, 776–787.
- Nakaji, T., Oguma, H., & Fujinuma, Y. (2006). Seasonal changes in the relationship between photochemical reflectance index and photosynthetic light use efficiency of Japanese larch needles. *International Journal of Remote Sensing*, 27, 493–509.
- Nichol, C. J., Huemmrich, K. F., Black, T. A., Jarvis, P. G., Walthall, C. L., Grace, J., et al. (2000). Remote sensing of photosynthetic-light-use efficiency of boreal forest. *Agricultural and Forest Meteorology*, 101, 131–142.
- Nichol, C. J., Lloyd, J., Shibistova, O., Arneht, A., Roser, C., Knohl, A., et al. (2002). Remote sensing of photosynthetic-light-use efficiency of a Siberian boreal forest. *Tellus*, 54, 677–687.
- Ort, D. R. (2001). When there is too much light. *Plant Physiology*, 125, 29–32.
- Pan, Y., Birdsey, R., Hom, J., McCullough, K., & Clark, K. (2006). Improved estimates of net primary productivity from MODIS satellite data at regional and local scales. *Ecological Applications*, 16, 125–132.
- Peguero-Pina, J., Morales, F. n., Flexas, J., Gil-Pelegrin, E., & Moya, I. (2008). Photochemistry, remotely sensed physiological reflectance index and de-epoxidation state of the xanthophyll cycle in *Quercus coccifera* under intense drought. *Oecologia*, 156, 1–11.
- Peñuelas, J., Filella, I., & Gamon, J. A. (1995). Assessment of photosynthetic radiation-use efficiency with spectral reflectance. *New Phytologist*, 131, 291–296.
- Peñuelas, J., Filella, I., Llusà, J., Siscart, D., & Piñol, J. (1998). Comparative field study of spring and summer leaf gas exchange and photobiology of the Mediterranean trees *Quercus ilex* and *Phillyrea latifolia*. *Journal of Experimental Botany*, 49, 229–238.
- Peñuelas, J., Llusia, J., Piñol, J., & Filella, I. (1997). Photochemical reflectance index and leaf photosynthetic radiation-use-efficiency assessment in Mediterranean trees. *International Journal of Remote Sensing*, 18, 2863–2868.
- Pontailier, J. -Y., Graham, J. H., & Bert, G. D. (2003). Estimation of leaf area index using ground-based remote sensed NDVI measurements: Validation and comparison with two indirect techniques. *Canadian Journal of Remote Sensing*, 26, 381–387.
- Potter, C. S., Randerson, J. T., Field, C. B., Matson, P. A., Vitousek, P.M., Mooney, H. A., et al. (1993). Terrestrial ecosystem production: A process model based on global satellite and surface data. *Global Biogeochemical Cycles*, 7, 811–841.
- Prince, S. D., & Goward, S. N. (1995). Global primary production: A remote sensing approach. *Journal of Biogeography*, 22, 815–835.
- Rahimzadeh-Bajgirani, P., Munehiro, M., & Omasa, K. (2012). Relationships between the photochemical reflectance index (PRI) and chlorophyll fluorescence parameters and plant pigment indices at different leaf growth stages. *Photosynthesis Research*, 113, 261–271.
- Sims, D. A., & Gamon, J. A. (2002). Relationships between leaf pigment content and spectral reflectance across a wide range of species, leaf structures and developmental stages. *Remote Sensing of Environment*, 81, 337–354.
- Soudani, K., Hmimina, G., Delpierre, N., Pontailier, J. -Y., Aubinet, M., Bonal, D., et al. (2012). Ground-based network of NDVI measurements for tracking temporal

- dynamics of canopy structure and vegetation phenology in different biomes. *Remote Sensing of Environment*, 123, 234–245.
- Turner, D. P., Ritts, W. D., Cohen, W. B., Gower, S. T., Running, S. W., Zhao, M., et al. (2006). Evaluation of MODIS NPP and GPP products across multiple biomes. *Remote Sensing of Environment*, 102, 282–292.
- Turner, D. P., Ritts, W. D., Cohen, W. B., Maeirsperger, T. K., Gower, S. T., Kirschbaum, A. A., et al. (2005). Site-level evaluation of satellite-based global terrestrial gross primary production and net primary production monitoring. *Global Change Biology*, 11, 666–684.
- Wu, C., Niu, Z., Tang, Q., & Huang, W. (2010). Revised photochemical reflectance index (PRI) for predicting light use efficiency of wheat in a growth cycle: Validation and comparison. *International Journal of Remote Sensing*, 31, 2911–2924.
- Yamamoto, H. (2006). Functional roles of the major chloroplast lipids in the violaxanthin cycle. *Planta*, 224, 719–724.
- Zarco-Tejada, P. J., González-Dugo, V., & Berni, J. A. J. (2012). Fluorescence, temperature and narrow-band indices acquired from a UAV platform for water stress detection using a micro-hyperspectral imager and a thermal camera. *Remote Sensing of Environment*, 117, 322–337.