On the remote sensing of the radiation use efficiency and the gross primary productivity of terrestrial vegetation

Martín F. Garbulsky 2010

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Doctoral Thesis

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Juliol 2010

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Ph.D. Thesis in Terrestrial Ecology
Universitat Autònoma de Barcelona

Bellaterra, July 2010

On the remote sensing of the radiation use efficiency and the gross primary productivity of terrestrial vegetation

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Fecha de lectura: 23 de septiembre de 2010

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ABSTRACT

Carbon uptake by vegetation is the largest global CO_2 flux and greatly influences the ecosystem functions. However, its temporal and spatial variability is still not well known and difficult to estimate. Remote sensing techniques can help to better estimate the terrestrial gross primary production (GPP), that is the ecosystem level expression of the photosynthesis process or the rate at which the ecosystem's producers capture CO_2. The main objective of this thesis was to find a way to estimate the spatial and temporal variability of the Radiation Use Efficiency (RUE) at the ecosystem scale and therefore to arrive to more accurate ways to estimate GPP of terrestrial vegetation by means of remotely sensed data. Four specific objectives were addressed in this thesis. The first objective was to examine and synthesize the scientific literature on the relationships between the Photochemical Reflectance Index (PRI), a narrow-band spectral index linked to photosynthetic efficiency, and several ecophysiological variables across a wide range of plant functional types and ecosystems. The second objective was to analyze and synthesize data for the spatial variability of GPP and the spatial and temporal variability of the RUE and its climatic controls for a wide range of vegetation types, from tundra to rain forest. The third objective was to test whether different spectral indices, i.e. PRI, NDVI (Normalized Difference Vegetation Index) and EVI (Enhanced Vegetation Index), derived from the MODerate resolution Imaging Spectroradiometer (MODIS) can be indicators of carbon uptake at different temporal scales by analyzing the relationships between detailed ecophysiological variables at the stand level in a Mediterranean forest. The fourth objective was to assess the use of MODIS PRI as surrogate of RUE in a wide range of vegetation types by using data on carbon uptake of the vegetation derived from eddy covariance towers.

The main conclusions of this thesis are that there is an emerging consistency of the RUE-PRI relationship that suggests a surprising degree of functional convergence of biochemical, physiological and structural components affecting leaf, canopy and ecosystem carbon uptake efficiencies. By complementing the estimations of the fraction of photosynthetically active radiation intercepted by the vegetation (fPAR) PRI enables improved assessment of carbon fluxes at different scales, through the estimation of RUE. A second conclusion supports the idea that the annual functioning of vegetation is more constrained by water availability than by temperature. The spatial variability of annual and maximum RUE can be largely explained by annual precipitation, more than by vegetation type. A third conclusion is that while EVI can estimate annual diametric wood increment, and PRI can estimate daily leaf level net photosynthesis and radiation use efficiency, the role NDVI is more limited as a surrogate of any part of the carbon cycle in this type of forest. Therefore, EVI and PRI are excellent tools for vegetation monitoring of carbon cycle in the Mediterranean forests, the first ones we tested in this thesis. Finally, the PRI derived from freely available satellite information was also found to present significant positive relationship with the RUE for a very wide range of different forest types, even in determined years, the deciduous forests. Overall, this thesis provides a better understanding of the spatial and temporal controls of the RUE and opens the possibility to estimate RUE in real time and, therefore, actual carbon uptake of forests at the ecosystem level using the PRI.

Keywords carbon cycle, Normalized Difference Vegetation Index, Enhanced Vegetation Index, Photochemical Reflectance Index, primary productivity, photosynthesis, remote sensing, climatic controls, eddy covariance, radiation use efficiency, terrestrial vegetation.

Chapter 1
Introduction

The carbon uptake by vegetation is the most important input of carbon from the atmosphere to the ecosystems. Moreover, carbon uptake by vegetation is the most important process balancing the CO_2 concentration in the atmosphere (Canadell et al. 2004). To estimate the carbon uptake by vegetation, namely gross primary productivity (GPP), its temporal and spatial variability and to understand the controls of their changes, has been a central goal of basic and applied ecology (Sala et al. 2000).

Estimations of carbon uptake by vegetation have been derived from diverse methodologies during the last 40 years. Since Lieth (1975) a huge amount of information, methodologies and models have been presented to make more accurate estimations of carbon uptake in space and time. Biomass harvests, frequently used as a proxy for Net Primary Productivity (NPP), eddy covariance fluxes and remote sensing estimations are three of the most used tools from local up to global carbon uptake estimations (Sala et al. 2000). Like any other ecological tool, each one of these techniques has its own advantages and disadvantages.

The estimation of net primary productivity was traditionally and indirectly made by means of biomass harvests. In grasslands or in general those fast turnover ecosystems, i.e. the rate of carbon circulation within the vegetation from growth to senescence, the harvest of green and dead biomass could lead to accurate estimations of aboveground net primary productivity (Sala and Austin 2000). In contrast, in those slow turnover ecosystems (e.g. forests), it is possible to use litterfall techniques but also the measurements of the increments of the woody components, such as diametric increments at breast height, are of widespread use for wood yield assessment. The principal limitation is the impossibility to measure the carbon uptake at a high temporal resolution such as a day.

The development and utilization of the eddy covariance methods emerged as an important and powerful tool for evaluating fluxes of CO_2 between terrestrial ecosystems and the atmosphere, and thus global carbon cycle modelling (Friend et al. 2007) at a very detailed time scale and, nowadays, at a large number of locations over the world (Baldocchi 2003). Using the eddy covariance technique it is possible to measure the Net Ecosystem Exchange and closely estimate the ecosystem respiration (Reco) and consequently the GPP, which is the ecosystem expression of the photosynthesis. This method is based on the fact that the downward and upward turbulent motions of moving air transport CO_2. The three dimensional sensor located above the canopy samples these turbulent motions at a very high frequency to determine the net difference of gas exchanges between the vegetation and the atmosphere. Although the eddy covariance towers are located in a wide range of vegetation types and climate situations with a very detailed temporal resolution, they sample a relative small portion of the landscape, and thus they do not provide a global coverage of carbon fluxes. Moreover, the eddy covariance technique has other requirements, like a flat topography and a minimum wind speed to generate enough turbulence.

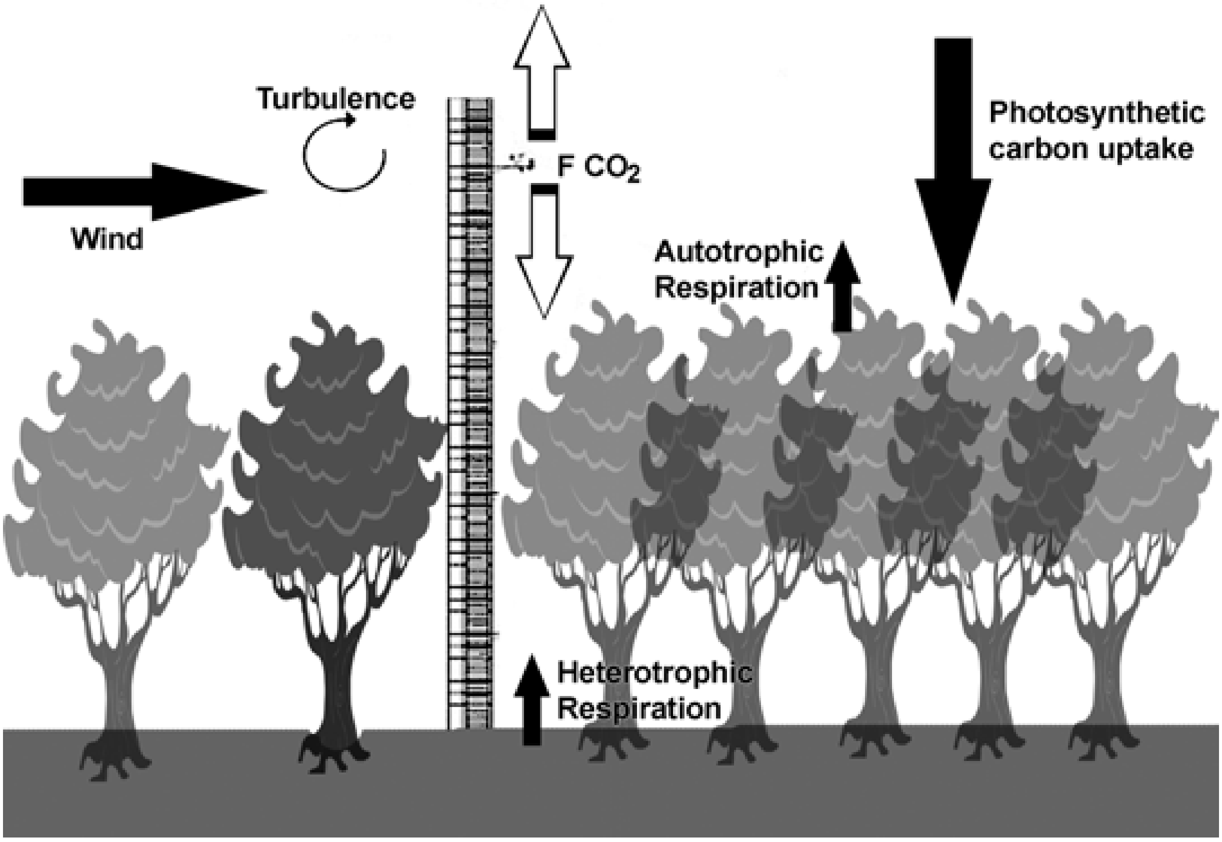


Figure 1. Schematic description of the main ecosystem carbon fluxes and the eddy covariance technique for the measurement of the Net Ecosystem Exchange (NEE).

Remote sensing tools appear as a very interesting complement to make explicit carbon fluxes estimates. Different ground based measurements of carbon uptake by the vegetation have been extrapolated using spectral indices derived from sensors on board of airborne platforms or satellites. The Radiation Use Efficiency (RUE) model (Monteith 1972) proposed that the GPP can be estimated from the radiation absorbed by the vegetation and the RUE term that transforms the absorbed radiation into plant biomass. Satellite information was most frequently used to estimate the fraction of the incident radiation absorbed by the vegetation (FPAR) by means of spectral indices such as the Normalized Difference Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI). They are calculated using the bands located in each side of the sharp order-of-magnitude increase in leaf reflectance between approximately 700 and 750 nm wavelength, referred to as the "red edge (Figure 2). These two indices are calculated from any type of remote sensor (e.g. Landsat, AVHRR, hand held spectroradiometers), with one band located in the near infrared portion (700-1000 nm) and other band in the red portion (600 – 700 nm) of the electromagnetic spectrum. From the reflectance of MODerate resolution Imaging Spectroradiometer (MODIS) sensors bands the vegetation indices are calculated as:

$$NDVI = \frac{(refl.BAND_2 - refl.BAND_1)}{(refl.BAND_2 + refl.BAND_1)}$$

$$EVI = \frac{2.5\,(refl.BAND_2 - refl.BAND_1)}{(refl.BAND_2 + 6\,refl.BAND_1 - 7.5\,refl.BAND_3 + 1)}$$

The Radiation Use Efficiency (RUE) has been a more difficult to estimate and criticized term (Demetriades-Shah et al. 1992). Even more, there is not a clear and operationally available methodology to estimate RUE for different vegetation types and at a reasonable time step. Due to the difficulties to make a direct measurement of RUE, different alternatives have been proposed to remotely estimate it. The xanthophylls cycle is linked to conditions of excess light. If the absorbed photosynthetically active radiation (PAR) exceeds the capacity of the photosynthetic reactions, the xanthophylls cycle pigment violaxanthin is de-epoxidized to zeaxanthin. Therefore, the epoxidation state of the xanthophylls may be a useful indicator of the photosynthetic activity (Gamon et al. 1992; Peñuelas et al. 1995). The Photochemical Reflectance Index (PRI), initially called Physiological Reflectance Index, is a spectral index based on the epoxidation state of the xanthophylls cycle pigments. It is a normalized index based on a band, located at 531 nm, that reflects the conversion of violaxanthin to zeaxanthin, i.e. the epoxidation state of the xanthophyll cycle pigments (EPS). Another band, outside this area, is used to normalize the index for changes in vegetation biomass (Gamon et al. 1992). This band was initially located at 570 nm but since MODIS do not have a band located in that wavelength, now it is still a matter of analysis which reference band can be used. MODIS bands 4 and 12, are the closest, however bands 1, 10 and 13 (Figure 1) are also being analyzed as possible PRI reference bands. Therefore, PRI is calculated as:

$$PRI = \frac{(refl.BAND_{11} - refl.BAND_{REFERENCE})}{(refl.BAND_{11} + refl.BAND_{REFERENCE})}$$

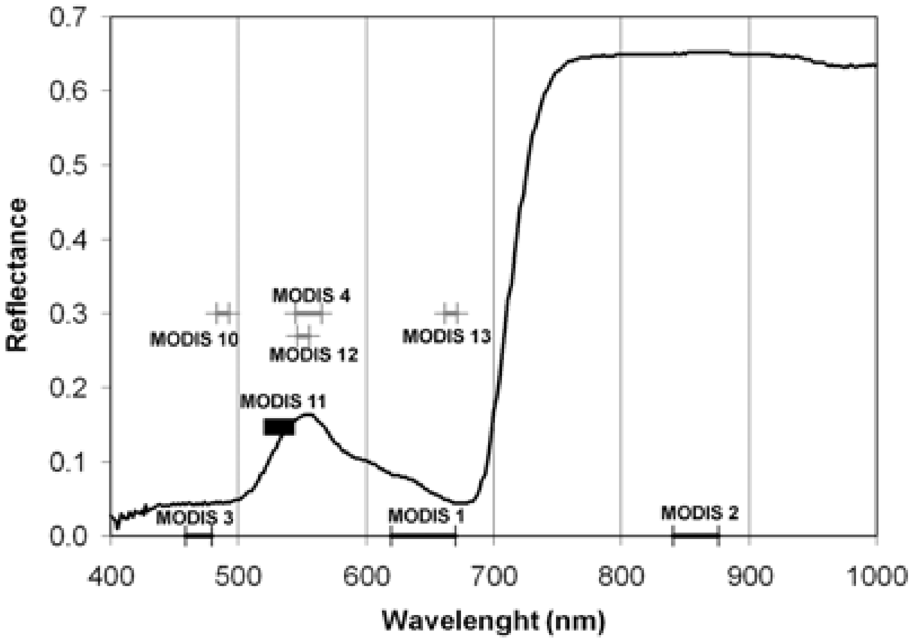


Figure 2. Typical reflectance pattern of green vegetation and the position along the electromagnetic spectrum of MODIS sensor bands used for the calculation of the vegetation indices used in this thesis: Normalized Difference Vegetation Index (NDVI), Enhanced Vegetation Index (EVI) and Photochemical Reflectance Index (PRI).

Several studies presented evidences on the ecological and ecophysiological meaning of the PRI. At the leaf level for a wide range of plant species, the PRI has been proved to be a good estimator of the photosynthetic performance like the chlorophyll fluorescence (Gamon et al. 2005; Guo and Trotter 2004; Peñuelas et al. 1995; Peñuelas et al. 2004; Weng et al. 2006; Winkel et al. 2002). There are also several studies that evaluated the PRI at plant level or high detailed canopy levels (Filella et al. 1996; Filella et al. 2004; Nichol et al. 2006; Trotter et al. 2002). In general, the results of these studies evidence the good performance of the PRI as an estimator of RUE. Low vegetation cover is probably the most important source of noise that hampers a good performance of the PRI (Filella et al. 2004; Nichol et al. 2006; Trotter et al. 2002). At the ecosystem level and using remote sensing images, very few studies on the performance of the PRI as an estimator of the RUE were published before I started this thesis (Drolet et al. 2005; Rahman et al. 2004) but these last years, while conducting this Ph.D. thesis, PRI related analysis has become an area of high and increasing researching activity. The actual remote sensing platforms and sensors do not provide a PRI product ready-to-use and even though MODIS was not specifically designed for estimating RUE from space, it would be of outstanding importance to have an available instrument to easily estimate the spatial and temporal variability of RUE for different vegetation types from space. Because of its high temporal and spectral resolutions, its two different platforms passing daily before and after midday (MODIS Terra and Aqua) and its global coverage, MODIS sensor is currently the most suitable remote sensing tool for a seasonal and global estimate of RUE by means of the PRI.

The main objective of this thesis was to find a way to remotely estimate the spatial and temporal variability of RUE at the ecosystem scale and therefore to arrive to more accurate ways to estimate GPP.

In the first chapter the state of the art of the use of the PRI for the remote estimation of ecophysiological variables is reviewed. The PRI derived from narrow-band spectroradiometers is a spectral index developed in the 1990s (Gamon et al. 1992; Peñuelas et al. 1995) and increasingly being used as an indicator of photosynthetic efficiency. Therefore, in this chapter I examined and synthesized the scientific literature on the relationships between PRI and several ecophysiological variables across a range of plant functional types and ecosystems at the leaf, canopy and ecosystem levels and at the daily and seasonal time scales. The aim was to review the use of PRI as RUE indicator at the leaf, stand and ecosystem scales for different vegetation types and time scales, to identify knowledge gaps and to present perspectives for future research. The final additional aim was to evaluate and construct a general calibration of the relationship of RUE with PRI both at the leaf and ecosystem levels. The review includes the literature reporting the use of the PRI to assess physiological variables related to photosynthetic efficiency such as epoxidation state of xanthophylls (EPS), non photochemical quenching (NPQ), actual photochemical fluorescence yield, RUE derived from gas exchange, and net photosynthesis.

The second chapter presents a global analysis on the controls of gross RUE, the ratio between gross primary productivity (GPP) and the radiation intercepted by terrestrial vegetation, and its spatial and temporal variation. The objectives of this chapter were to analyze and synthesize the spatial variability of GPP and the spatial and temporal variability of RUE and its climatic controls for a wide range of vegetation types, from tundra to rain forest. The analysis is based on a global dataset on photosynthetic carbon uptake and climatic variables from 35 eddy covariance (EC) flux sites spanning between 100 and 2200 mm mean annual rainfall and between -13 and 26°C mean annual temperature. RUE was calculated from the data provided by EC flux sites and remote sensing (MODIS).

The third and fourth chapter presents two evaluations at different scales of the value of the spectral indices derived from satellite MODIS sensors as estimators of the carbon uptake and radiation-use efficiency for Mediterranean forests. Remote sensing techniques such as the widely used reflectance vegetation indices (e.g. NDVI, EVI) allow green plant biomass and therefore plant photosynthetic capacity to be assessed. However, there are vegetation types, such as the Mediterranean forests, in which (a) seasonal variation in green biomass is very low and (b) carbon uptake has important seasonal fluctuations that are mainly determined by water deficits during summer (Rambal et al. 2003) and low temperatures and incident radiation in winter (Ogaya and Peñuelas 2003), which provoke significant periods of very low photosynthesis. In these cases it is important to detect how much of this capacity is actually realized, which is a much more challenging goal, and to understand the controls of the interannual variability. Because of the negligible changes in structure and leaf area index throughout the growing season, it is of great importance in this forest to have accurate measurements of radiation-use efficiency. Particularly, the third chapter of this thesis sought to answer if satellite data can detect the carbon uptake at different time steps of different components of a Mediterranean forest in Tarragona, Spain. The main objective of this study was to give biological meaning to the temporal variability of MODIS spectral indices. Thus it is presented an analysis on the relationships between detailed ecophysiological variables at the stand level with the spectral reflectance derived from satellite sensors. Field data measurements related to carbon uptake and primary productivity were taken between 2000 and 2009 in a Mediterranean forest dominated by *Quercus ilex*. In the fourth chapter, a 5-year analysis of CO_2 fluxes derived from eddy covariance data and MODIS data for a Mediterranean forest in southern Italy provides an ideal opportunity for exploring alternative methods of modeling carbon uptake at the ecosystem level employing satellite-based estimates of RUE. The PRI was evaluated as a surrogate of the temporal variability of RUE.

The last chapter presents an assessment on the use of PRI as surrogate of RUE in a wide range of vegetation types and an evaluation of the use the MODIS PRI to be included in the remote estimations of GPP. Since the different vegetation types dramatically differ in terms of the behavior of seasonality of GPP and radiation absorption, this study evaluated the PRI as a remotely sensed surrogate of the ecosystem RUE in a wide range of vegetation types (grassland, *Eucalyptus* plantation, subtropical and temperate evergreen, Mediterranean broadleaf and needleaf and temperate deciduous forests). I analyzed GPP from eddy covariance data of carbon fluxes and MODIS (MODerate resolution Imaging Spectroradiometer) data.

References

Baldocchi, D. (2003). Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Global Change Biology, 9, 479-492

Canadell, J.G., Ciais, P., Cox, P., & Heimann, M. (2004). Quantifying, understanding and managing the carbon cycle in the next decades. Climatic Change, 67, 147-160

Demetriades-Shah, T.H., Fuchs, M., Kanemasu, E.T., & Flitcroft, I. (1992). A note of caution concerning the relationship between cumulated intercepted solar radiation and crop growth. Agricultural & Forest Meteorology, 58, 193-207

Drolet, G.G., Huemmrich, K.F., Hall, F.G., Middleton, E.M., Black, T.A., Barr, A.G., & Margolis, H.A. (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, 212-224

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

Filella, I., Peñuelas, J., Llorens, L., & Estiarte, M. (2004). Reflectance assessment of seasonal and annual changes in biomass and CO2 uptake of a Mediterranean shrubland submitted to experimental warming and drought. Remote Sensing of Environment, 90, 308-318

Friend, A.D., Arneth, A., Kiang, N.Y., Lomas, M., Ogee, J., Rodenbeck, C., Running, S.W., Santaren, J.-D., Sitch, S., Viovy, N., Ian Woodward, F., & Zaehle, S. (2007). FLUXNET and modelling the global carbon cycle. Global Change Biology, 13, 610-633

Gamon, J.A., Kitajima, K., Mulkey, S.S., Serrano, L., & Wright, S.J. (2005). Diverse optical and photosynthetic properties in a neotropical dry forest during the dry season: Implications for remote estimation of photosynthesis. Biotropica, 37, 547-560

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

Guo, J.M., & Trotter, C.M. (2004). Estimating photosynthetic light-use efficiency using the photochemical reflectance index: variations among species. Functional Plant Biology, 31, 255-265

Lieth, H. (1975). Modeling the primary productivity of the world. In H. Liesth & R.H. Wittaker (Eds.), Primary productivity of the biosphere. (pp. 237-262). New York, USA.: Springer-Verlag

Monteith, J.L. (1972). Solar radiation and productivity in tropical ecosystems. Journal of Applied Ecology, 9, 747-766

Nichol, C.J., Rascher, U., Matsubara, S., & Osmond, B. (2006). Assessing photosynthetic efficiency in an experimental mangrove canopy using remote sensing and chlorophyll fluorescence. Trees-Structure and Function, 20, 9-15

Ogaya, R., & Peñuelas, J. (2003). Comparative seasonal gas exchange and chlorophyll fluorescence of thwo dominant woody species in a Holm Oak Forest. Flora, 198, 132-141

Peñuelas, J., Filella, I., & Gamon, J.A. (1995). Assessment of photosynthetic radiation-use efficiency with spectral reflectance. New Phytologist, 131, 291-296

Peñuelas, J., Munne-Bosch, S., Llusia, J., & Filella, I. (2004). Leaf reflectance and photo- and antioxidant protection in field-grown summer-stressed Phillyrea angustifolia. Optical signals of oxidative stress? New Phytologist, 162, 115-124

Rahman, A.F., Cordova, V.D., Gamon, J.A., Schmid, H.P., & Sims, D.A. (2004). Potential of MODIS ocean bands for estimating CO2 flux from terrestrial vegetation: A novel approach. Geophysical Research Letters. doi:10.1029/2004GL019778, 31

Rambal, S., Ourcival, J.-M., Joffre, R., Mouillot, F., Nouvellon, Y., Reichstein, M., & Rocheteau, A. (2003). Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem: scaling from leaf to canopy. Global Change Biology, 9, 1813-1824

Sala, O.E., & Austin, A.T. (2000). Methods of estimating aboveground net primary productivity. In O.E. Sala, R.B. Jackson, H.A. Mooney & R.W. Howarth (Eds.), Methods in ecosystem science (pp. 31-43). New York: Springer

Sala, O.E., Jackson, R.B., Mooney, H.A., & Howarth, R.W. (2000). Methods in Ecosystem Science. New York.: Springer Verlag

Trotter, G.M., Whitehead, D., & Pinkney, E.J. (2002). The photochemical reflectance index as a measure of photosynthetic light use efficiency for plants with varying foliar nitrogen contents. International Journal of Remote Sensing, 23, 1207-1212

Weng, J.H., Chen, Y.N., & Liao, T.S. (2006). Relationships between chlorophyll fluorescence parameters and photochemical reflectance index of tree species adapted to different temperature regimes. Functional Plant Biology, 33, 241-246

Winkel, T., Methy, M., & Thenot, F. (2002). Radiation use efficiency, chlorophyll fluorescence, and reflectance indices associated with ontogenic changes in water-limited *Chenopodium quinoa* leaves. Photosynthetica, 40, 227-232

Chapter 2

The Photochemical Reflectance Index (PRI) and the remote sensing of leaf, canopy and ecosystem radiation use efficiencies; a review and meta-analysis

ABSTRACT

Traditional remote sensing techniques allow the assessment of green plant biomass, and therefore plant photosynthetic capacity. However, detecting how much of this capacity is actually realized is a more challenging goal. Is it possible to remotely assess actual carbon fluxes? Can this be done at leaf, canopy and ecosystem scales and at different temporal scales? Different approaches can be used to answer these questions. Among them, the Photochemical Reflectance Index (PRI) derived from narrow-band spectroradiometers is a spectral index increasingly being used as an indicator of photosynthetic efficiency. We examined and synthesized the scientific literature on the relationships between PRI and several ecophysiological variables across a range of plant functional types and ecosystems at the leaf, canopy and ecosystem levels and at the daily and seasonal time scales. Our analysis shows that although the strength of these relationships varied across vegetation types, levels of organization and temporal scales, in most reviewed articles PRI was a good predictor of photosynthetic efficiency or related variables with performances at least as good as the widely used NDVI as indicator of green biomass. There are possible confounding factors related to the intensity of the physiological processes linked to the PRI signals, to the structure of the canopies and to the illumination and viewing angles that warrant further studies, and it is expected that the utility of PRI will vary with the ecosystem in question due to contrasting environmental constraints, evolutionary strategies, and radiation use efficiency (RUE; the ratio between carbon uptake and light absorbed by vegetation) variability. Clearly, more research comparing ecosystem responses is warranted. Additionally, like any 2-band index that is affected by multiple factors, the interpretation of PRI can be readily confounded by multiple environmental variables, and further work is needed to understand and constrain these effects. Despite these limitations, this review shows an emerging consistency of the RUE-PRI relationship that suggests a surprising degree of functional convergence of biochemical, physiological and structural components affecting leaf, canopy and ecosystem carbon uptake efficiencies. PRI accounted for 42%, 59% and 62% of the variability of RUE at the leaf, canopy and ecosystem respective levels in unique exponential relationships for all the vegetation types studied. It seems thus that by complementing the estimations of the fraction of photosynthetically active radiation intercepted by the vegetation (FPAR), estimated with NDVI-like indices, PRI enables improved assessment of carbon fluxes in leaves, canopies and many of the ecosystems of the world from ground, airborne and satellite sensors.

Keywords: Radiation Use Efficiency; Gross Primary Productivity; Photochemical Reflectance Index; MODIS.

List of acronyms and abbreviations used in this chapter

MODIS	MODerate resolution Imaging Spectroradiometer
RUE	Radiation Use Efficiency
GPP	Gross Primary Productivity
FPAR	Fraction of the photosynthetic active radiation absorbed by the vegetation
APAR	Absorbed Photosynthetically Active Radiation by green vegetation
NDVI	Normalized Difference Vegetation Index
EVI	Enhanced Vegetation Index
PRI	Photochemical Reflectance Index
FWHM	Full Width of Half Maximum

1. Introduction

A key challenge in arriving at a sustainable world is to better understand biosphere-atmosphere carbon fluxes, which are extremely dynamic in time and space (Le Quere et al. 2009). Several questions remain open. What factors control photosynthetic and respiratory fluxes by terrestrial landscapes? How are these controls and source/sink patterns distributed in time and space? What is the capacity for terrestrial ecosystems to continue functioning as carbon sinks in the face of ongoing disturbance and climate change? Current tools for exploring these questions include eddy covariance and remote sensing. Eddy covariance is currently the only direct way to assess carbon flux of whole ecosystems with high temporal resolution. However, eddy covariance towers can effectively measures a single "point" over flat and uniform terrain, usually on the order of a few hundred squared meters (Baldocchi 2008). Remote sensing has the ability to extend our knowledge of carbon flux in space. Combining remote sensing with eddy covariance in a modeling framework provides a powerful approach for addressing the carbon dynamics of terrestrial ecosystems.

The fraction of photosynthetically active radiation absorbed by the canopy (FPAR) can be estimated from remotely sensed vegetation indices. Vegetation indices, such us the Normalized Difference Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI) are normalized differences between the reflectance in the near infrared and the red regions of the spectrum, which are very often determined from satellite, or aircraft imagery. The FPAR provide a measure of potential and not of actual photosynthesis because of varying synchrony between green canopy development and photosynthetic fluxes across vegetation types (Field et al. 1995, Gamon et al. 1995, Myneni et al. 1995). They even can be empirical estimators of photosynthesis or primary productivity for certain ecosystems because they reflect both recent carbon gain and potential future carbon gain in the absence of constraints on photosynthesis (Field 1991). However, for many ecosystems, considerable uncertainty still remains about how much of this capacity is realized in practice because the radiation use efficiency (RUE) varies significantly between plants, environmental conditions, and ecosystems due to varying environmental constraints (Field et al. 1994, Garbulsky et al. 2010). For example, in many evergreen-dominated ecosystems such as shrublands, Mediterranean or coniferous forests, seasonal or periodic stress events may shut down carbon uptake to near zero (Ogaya and Peñuelas 2003, Asensio et al. 2007) through a process of photosynthetic downregulation, even though in the short term the vegetation continues to absorb light that might otherwise be used for photosynthesis. Consequently, NDVI can be a poor indicator of temporal variation in CO_2 fluxes, particularly for evergreen species subjected to periodic downregulation (Running and Nemani 1988, Gamon et al. 1995). However, it is still a good estimator of the spatial variability of carbon uptake (Garbulsky and Paruelo 2004).

The widely used radiation use efficiency model (Monteith 1977) stated that gross (GPP) or net primary productivity (NPP) of a vegetation stand can be derived from the absorbed photosynthetically active radiation by green vegetation during the period of study (APARdt), the product of FPAR and photosynthetic active radiation (PAR), and from the efficiency (RUE) with which this absorbed radiation is converted into biomass:

$$GPP = \int RUE \times APARdt$$

In various forms, these simple relationships have been the basis for many evaluations of photosynthesis and primary production from the canopy to the global scales (Field et al. 1995, Running et al. 2004). Many models have assumed a constant efficiency (Myneni et al. 1995) or derived this term from literature values by biome (Ruimy et al. 1994). Another approach is to downregulate the maximum efficiency by biome using climatic variables, like vapour pressure deficit (VPD) and temperature, as surrogates for photosynthetic stresses (Running et al. 2004). Because VPD and temperature alone are not always good surrogates of reduced efficiency, meteorologically based methods may not always explain efficiency variation. Many studies show that the efficiency greatly varies in time and space (Runyon et al. 1994, Gamon et al. 1995, Garbulsky et al. 2010) due to periodic environmental and physiological limitations. Factors contributing to this variability, include contrasting functional types (Gamon et al. 1997, Huemmrich et al. 2010), drought and temperature extremes (Landsberg and Waring 1997, Sims et al. 2006a) and nutrient levels (Gamon et al. 1997, Ollinger et al. 2008).

In recent years, this RUE term of the model has been found to be accessible through spectral reflectance, thus opening the possibility of using remote sensing techniques to detect temporal and spatial variations in photosynthetic radiation use efficiency and therefore to improve the temporal and spatial characterization of carbon uptake by vegetation. Different approaches have arisen recently to remotely estimate RUE from a wide variety of wavelengths and sensor types. Among those approaches, the use of land surface temperature derived from thermal wavelengths was successfully tested for a set of 11 different sites distributed only in North America to estimate 16 day GPP, but it would be inadequate for the estimation of GPP in shorter time steps due to the inability to track short-term (e.g. diurnal) physiological variability (Sims et al. 2008). This study included many mesic sites, but did not include many arid or semiarid ecosystems where downregulation due to drought and temperature extremes would likely occur. Consequently, the ability of this approach to capture the full range of variability across biomes, particularly due to short-term stress, remains unclear. An alternate approach links the sun induced chlorophyll fluorescence, derived from an oxygen absorption band located at 760 nm, to the diurnal changes in RUE, but tests of this method have been limited (Damm et al. 2010). Consequently, the full capabilities of these promising approaches are not yet entirely clear.

The detection of the spatial and temporal variations in RUE could also be assessed through the remote sensing of plant pigments. This is a key tool to diagnose a range of plant physiological properties and processes (Peñuelas and Filella 1998, Blackburn 2007). In particular, different studies were conducted during the 1990s at the leaf and close canopy levels using close-range remote sensing from the ground or from low platforms to assess this efficiency parameter RUE based on concurrent xanthophyll pigment changes (Gamon et al. 1990, Gamon et al. 1992, Peñuelas et al. 1994, Peñuelas et al. 1995, Filella et al. 1996, Gamon et al. 1997, Peñuelas et al. 1997a, Peñuelas et al. 1998, Gamon and Surfus 1999). The foundation of this remote sensing approach to estimate the RUE is the de-epoxidation state of the xanthophyll cycle which is linked to heat dissipation (Demmig-Adams and Adams 1996). This is a decay process of excited chlorophyll that competes with and is complementary to photosynthetic electron transport (Niyogi 1999). Since the reflectance at 531 nm is functionally related to the de-epoxidation state of the xanthophyll cycle (Gamon et al. 1990, Gamon et al. 1992, Peñuelas et al. 1995), a Photochemical Reflectance Index (PRI, typically calculated as $[R_{531}-R_{570}]/[R_{531}+R_{570}]$, where R indicates reflectance and numbers indicate wavelength nanometers at the centre of the bands), was developed as a method to remotely assess photosynthetic efficiency using narrowband reflectance (Gamon et al. 1992, Peñuelas et al. 1995). The mechanistic basis for these wavelength selections have been fully explored at the leaf scale (Gamon et al. 1993b), but are more poorly supported at canopy and larger scales, where a variety of alternate wavebands have been used, often based on statistical correlations (Gamon et al. 1992, Inoue et al. 2008) or determined by instrument limitiations (Garbulsky et al. 2008b). The lack of a clear consensus in the literature on the “best” PRI wavelengths, has hindered cross-study comparisons. Consequently, it is not entirely clear if the best wavelengths for measuring this feature at the leaf scale (531, 570 nm) are necessarily the best wavelengths at progressively larger scales, where multiple scattering and other confounding effects may alter the spectral response of the xanthophyll cycle feature, much in the way that pigment absorption peaks can vary depending upon their chemical and scattering medium. More work, therefore, may be needed to determine the ideal PRI algorithm for airborne or space-borne platforms, and these studies have been hampered by the limited availability and high costs of suitable airborne and spaceborne instruments.

Since PRI measures the relative reflectance on either side of the green reflectance "hump" (550 nm), it also compares the reflectance in the blue (chlorophyll and carotenoids absorption) region of the spectrum with the reflectance in the red (chlorophyll absorption only) region. Consequently, it can serve as an index of relative chlorophyll:carotenoid levels, often referred to as bulk pigment ratios or “pool sizes”. Over longer time scales (weeks-months), changes in bulk pigment content and ratios due to leaf development, aging or chronic stress have been reported to play a significant role together with the xanthophyll pigment epoxidation in the PRI signal (Peñuelas et al. 1997a, Gamon et al. 2001, Sims and Gamon 2002, Stylinski et al. 2002). Thus, PRI is also often related to chlorophyll/carotenoid ratios in leaves across a large number of species, ages and conditions (Stylinski et al. 2002, Filella et al. 2009). Therefore, to the extent that photosynthetic activity correlates with changing chlorophyll/carotenoid ratios in response to stress, ontogeny or senescence, PRI may provide an effective measure of relative photosynthetic rates. Together, these responses to de-epoxidation state of the xanthophyll cycle and to chlorophyll/carotenoid ratios ensure that PRI scales with photosynthetic efficiency across a wide range of conditions, species and functional types (Gamon et al. 1992, Peñuelas et al. 1995, Filella et al. 1996, Gamon and Qiu 1999, Stylinski et al. 2002).

Nowadays, the PRI is increasingly being used as an index of photosynthetic performance in general and of RUE in particular in natural and seminatural vegetation (e.g. Peñuelas and Llusia 2002, Asner et al. 2004, Middleton et al. 2009, Mänd et al. 2010) or in crops (e.g. Strachan et al. 2002, Zhou and Wang 2003). The relationships between PRI and different ecophysiological related variables have been tested over a wide range of species, plant functional types, temporal steps and environmental conditions. However, different problems that preclude its generalization to ecosystem scales and its global and operational use as an estimator of RUE have recently been described (Barton and North 2001, Grace et al. 2007). In brief, these problems are related to the interference to the PRI signal produced by other plant pigments not related to photosynthetic efficiency, to the structural differences of the canopies, to varying “background effects” (e.g. soil color, moisture, or shadows) to the different PRI formulations or signals derived from a variety of sensors and to illumination and viewing angles variations. This may help explain why different ecosystems or conditions can appear to have slightly different RUE-PRI responses.

In this study we reviewed the literature reporting the use of the PRI to assess physiological variables related to photosynthetic efficiency such as epoxidation state of xanthophylls (EPS), non photochemical quenching (NPQ), actual photochemical fluorescence yield, RUE derived from gas exchange, and net photosynthesis. Our aim was to analyse the use of PRI as an indicator of RUE at the leaf, stand and ecosystem scales for different vegetation types and time scales, to identify knowledge gaps and to present perspectives for future research. Our final additional aim was to evaluate and construct a general calibration of the relationship of RUE with PRI at the leaf, canopy and ecosystem levels.

2. Methods

We gathered the published articles that reported relationships between remote sensed PRI and any kind of plant physiological variables. This primarily included Science Citation Index articles reporting results at different spatial and temporal scales and from a wide range of plant species or vegetation types. This broad spectrum of studies necessarily included different sensor types, from hand held spectroradiometers to satellite sensors. For each article we registered the main features of the study and the coefficient of determination (R^2) as an indicator of the strength of each presented relationship. For those studies that presented data for PRI and physiological variables but did not present the statistical results of the relationship, we extracted the raw data from the plots, and calculated the statistical results of the relationships ourselves. We analyzed and drew the coefficients of determination of all the correlations using boxplots for each vegetation types (herbaceous, broadleaf, conifers, etc), time scale (daily or seasonal, i.e. changes within seasons and across seasons), and organization level (leaf, canopy –from plant to stand - or ecosystem). In this review, the term “canopy” refers to either a single plant or a monospecific stand, whereas the term “ecosystem” refers to a mixed-species stand. We tested the differences in R^2 between vegetation types using a t test when there were enough cases studied per vegetation type.

We also finally analyzed the overall relationship between RUE and PRI reported in different articles, by plotting in the same x-y graph the points for all the comparable studies together. For this analysis, we selected those articles which presented the plots with all the measured values using the same definition of PRI and similar protocols for the measurements of the variables for the different scales. We evaluated the differences among the slopes and the intercepts of the relationships between RUE and PRI for different vegetation types through analysis of covariance (ANCOVA).

3. Results

We found more than 80 articles published between 1990 and 2009 that reported results on the PRI and its relationship with one or more variables related to photosynthesis performance (Table 1). More than a third part of these studies were published during 2008-09, emphasizing the increasing interest of the scientific community on this subject. These studies were performed at the leaf, the canopy and the ecosystem level and some of them presented more than one relationship, e.g. for different species or different sites. The highest number of relationships reported was for relationships with the effective quantum yield or actual photochemical efficiency ($\Delta F/Fm'$), but the PRI was also linked to several different variables for different spatial and temporal scales: RUE, net CO_2 uptake, NPQ, EPS (or DEPS), the ratio chlorophyll/carotenoids (Table 2). Other less frequent ecophysiological variables reported in the literature were chlorophyll (A+B) content, maximum photosynthesis rate (Amax), steady state value of fluorescence (Fs), and water content.

Table 1. List of studies found in the literature that linked PRI with ecophysiological variables.

Article order by publication date	Year	Reference	Scale	Variance Factor	Species/Vegetation type	Vegetation Type	Sensor	Figure #	Ecophysiological variables
3	1995	(Peñuelas et al. 1995)	Leaves	Hours	*Hedera canariensis*, *Phaseolus vulgaris*, *Rhus ovata/R. integrifolia*, *Heteromeles arbutifolia*, Succulents (*Agave americana, Opuntia ficus-indica* and *Cereus hexagonus*)	Broadleaf	Specrad	1d-4-10 1e	RUE ΔF/Fm’
31	2004	(Evain et al. 2004)	Leaves	Hours	*Vitis vinifera*	Broadleaf	Specrad	1a 1e	NPQ ΔF/Fm’
45	2006	(Weng et al. 2006b)	Leaves	Hours	Mango	Broadleaf	Specrad	1a 1e	NPQ Fv’/Fm’
52	2007	(Rascher et al. 2007)	Leaves	Hours	*Pterocarpus indicus*, *Ceiba pentandra*, *Pachira aquatica*, *Inga sapindoides*	Broadleaf	Specrad	1a 1e	NPQ ΔF/Fm’
64	2008	(Meroni et al. 2008a)	Leaves	Hours	*Populus deltoides* (ozone treatements)	Broadleaf	Specrad	1d-4-10	RUE
41	2006	(Nakaji et al. 2006)	Leaves	Hours	Japanese larch (*Larix kaempferi* Sarg.)	Conifers	Camera	 2b 1d-4-10	Chl Car/Chl RUE
9	1999	(Methy et al. 1999)	Leaves	Hours	Alfalfa	Herbaceous/ Crop	Specrad	1e	ΔF/Fm’
10	1999	(Gamon and Surfus 1999)	Leaves	Hours	Sunflower	Herbaceous/ Crop	Specrad	1c	EPS (ΔPRI)
27	2004	(Guo and Trotter 2004)	Leaves	Hours/ dif species	*Lycopersicon esculentum*, *Populus deltoides* x *P. Nigra*, Evergreen perennials (*Coprosma robusta, Pseudopanax arboreus*) + 3 evergreen perennials	Mixture	Specrad	1a 1b 1d-3c-4-10 1e-3b 1f	NPQ Car/Chl RUE ΔF/Fm’ Net CO$_2$ uptake
2	1994	(Peñuelas et al. 1994)	Leaves	Hours/ Seasonal	Sunflower	Herbaceous/ Crop	Specrad	1c 1d-3f-10 1f -3f	EPS RUE Net CO$_2$ uptake
5	1997	(Peñuelas et al. 1997b)	Leaves	Seasonal	*Quercus ilex / Phillyrea latifolia*	Broadleaf	Specrad	2a 2d-10 2e	NPQ RUE ΔF/Fm’
29	2004	(Peñuelas et al. 2004)	Leaves	Seasonal	*Phillyrea angustifolia*	Broadleaf	Specrad	2f	Net CO2 uptake
63	2008	(Letts et al. 2008)	Leaves	Seasonal	*Populus angustifolia*	Broadleaf	Specrad	2e	ΔF/Fm’
74	2009	(Panigada et al. 2009)	Leaves	Seasonal	*Fagus sylvatica*	Broadleaf	Specrad	2a 2e	NPQ ΔF/Fm’
47	2006	(Weng et al. 2006c)	Leaves	Seasonal	Pinus (*P. taiwanensis, P. armandi* and *P. morrisonicola*), Evergreen trees (*Stranvaesia niitakayamensis, Rhododendron mori* and *Trochodendron aralioides*) and perennial grasses (*Yushania niitakayamensis, Miscanthus transmorrisonensis* and *M. floridulus*)	Conifers	Specrad	3e	Fv’/Fm’

76	2009	(Weng et al. 2009)	Leaves	Seasonal	*Pinus taiwanensis*	Conifers	Specrad	2e	Fv’/Fm’
82	2009	(Filella et al. 2009)	Leaves	Seasonal	*Pinus sylvestris - Quercus ilex*	Conifers	Specrad	2b 2c	DEPS Car/Chl
83	2009	(Busch et al. 2009)	Leaves	Seasonal	*Pinus banksiana*	Conifers	Specrad	2a 2c	NPQ EPS
24	2002	(Winkel et al. 2002)	Leaves	Seasonal	*Chenopodium quinoa*	Herbaceous/ Crop	Specrad	2d-4-10 2e	RUE ΔF/Fm’
26	2002	(Tambussi et al. 2002)	Leaves	Seasonal	Wheat	Herbaceous/ Crop	Specrad	2c	DEPS
35	2005	(Inamullah and Isoda 2005)	Leaves	Seasonal	Soya/cotton	Herbaceous/ Crop	Specrad	2a 2e	NPQ ΔF/Fm’
49	2006	(Chen et al. 2006)	Leaves	Seasonal	Rice	Herbaceous/ Crop	Specrad	2b	Car/Chl
78	2009	(Gerosa et al. 2009)	Leaves	Seasonal	*Phaseolus vulgaris*	Herbaceous/ Crop	Specrad	2e	ΔF/Fm’
42	2006	(Weng et al. 2006a)	Leaves	Seasonal	*Mangifera indica, Podocarpus nagi* and *Alnus formosana*	Mixture	Specrad	2a 2e	ΔF/Fm’ NPQ
54	2007	(Martin et al. 2007)	Leaves	dif populations	*Metrosideros polymorpha*	Broadleaf	Specrad	3a 3b	Car/Chl ΔF/Fm’
38	2005	(Raddi et al. 2005)	Leaves	dif species	Mediterranean forests	Broadleaf	Specrad		NPQ
6	1997	(Gamon et al. 1997)	Leaves	dif species	20 sps (annual, deciduous perennial, and evergreen perennial)/ Cotton	Mixture	Specrad	1e-3b 1d-3c-4-10	ΔF/Fm’ RUE
25	2002	(Sims and Gamon 2002)	Leaves	dif species	53 different species	Mixture	Specrad	3a	Car/Chl
43	2006	(Guo and Trotter 2006)	Leaves	dif species	13 Different species ambient and elevated CO$_2$	Mixture	Specrad	3b 3c-10	ΔF/Fm’ RUE
14	2000	(Stylinski et al. 2000)	Leaves	Leaves	*Quercus pubescens*	Broadleaf	Specrad	 3a	Jmax Car/Chl
15	2000	(Moran et al. 2000)	Leaves	N treatment x light	*Picea engelmannii*	Conifers	Specrad		Chl (A+B)
44	2006	(Inoue and Peñuelas 2006)	Leaves	N x water condition	soybean	Herbaceous/ Crop	Specrad	3c-4-10	RUE
70	2008	(Naumann et al. 2008a)	Leaves	salt concentration	*Myrica cerifera*	Broadleaf	Specrad	3b	ΔF/Fm’
21	2002	(Richardson and Berlyn 2002)	Leaves	Spatial	*Betula papyrifera*	Broadleaf	Specrad	3c	RUE
48	2006	(Asner et al. 2006)	Leaves	Spatial	*Metrosideros polymorpha*	Broadleaf	Specrad		Chl – Car Car/Chl
81	2009	(Martin and Asner 2009)	Leaves	Spatial	*Metrosideros polymorpha*	Broadleaf	Specrad	3a	Car/Chl
17	2001	(Richardson et al. 2001)	Leaves	Spatial	red spruce and balsam fir	Conifers	Specrad	3b	ΔF/Fm’
37	2005	(Whitehead et al. 2005)	Leaves	Spatial x sps	Three different species from six mixed forests	Mixture	Specrad		Amax
12	2000	(Methy 2000)	Leaves /canopy	Hours	*Quercus ilex*	Broadleaf	Specrad	1e 2f	ΔF/Fm’ Net CO$_2$ uptake

1	1992	(Gamon et al. 1992)	Leaves /canopy	Hours	Sunflower	Herbaceous/ Crop	Specrad	1c	EPS RUE
20	2002	(Stylinski et al. 2002)	Leaves /canopy	Seasonal	3 chaparral shrubs (*Quercus berberidifolia, Ceanothus greggii, Adenostoma fasciculamtum*)	Broadleaf	Specrad	3a	ΔF/Fm' Net CO_2 uptake Car/Chl DEPS
33	2005	(Gamon et al. 2005)	Leaves /Plant	Hours	*Anacardium excelsum, Luehea seemanni*	Broadleaf	Specrad		ΔF/Fm'
39	2005	(Dobrowski et al. 2005)	Canopy	Hours	*Vitis vinifera*	Broadleaf	Specrad		Fs
11	2000	(Nichol et al. 2000)	Canopy	Seasonal	Broadleaf deciduous (Aspen - Fen), Conifers (Old jack pine- old black spruce)	Broadleaf	helicopter Specrad	5-7-10	RUE
36	2005	(Serrano and Peñuelas 2005)	Canopy	Seasonal	Mediterranean forest	Broadleaf	Specrad transmittance	5-10	Net CO_2 uptake RUE
40	2006	(Nichol et al. 2006)	Canopy	Seasonal	Mangrove (*Rhizophora* and *Avicennia*)	Broadleaf	Specrad		ΔF/Fm' NPQ
50	2006	(Sims et al. 2006a)	Canopy	Seasonal	Chaparral shrubs	Broadleaf	tram Specrad	5-10	RUE
69	2008	(Peguero-Pina et al. 2008)	Canopy	Seasonal	*Quercus coccifera*	Broadleaf	Specrad		ΔF/Fm' Fs EPS NPQ
75	2009	(Naumann et al. 2009)	Canopy	Seasonal	*Myrica cerifera* and *Iva frutescens*	Broadleaf	airborne spectro		ΔF/Fm'
79	2009	(Cheng et al. 2009)	Canopy	Seasonal	Douglas fir forest	Conifers	Specrad	5-10	RUE
8	1998	(Carter 1998)	Canopy	Seasonal	*Pinus taeda-P. elliotti*	Conifers	Specrad		Amax
18	2002	(Nichol et al. 2002)	Canopy	Seasonal	Boreal forest Siberia	Conifers	Specrad	5-7-10	RUE
34	2005	(Louis et al. 2005)	Canopy	Seasonal	Scots Pine	Conifers	Specrad		Net CO_2 uptake
51	2007	(Nakaji et al. 2007)	Canopy	Seasonal	*Larix kaempferi*	Conifers	Specrad	5-10	RUE
57	2008	(Hall et al. 2008)	Canopy	Seasonal	Douglas fir	Conifers	Specrad	5-7-10	RUE
58	2008	(Hilker et al. 2008)	Canopy	Seasonal	Douglas fir	Conifers	Specrad	5-7-10	RUE
66	2008	(Nakaji et al. 2008)	Canopy	Seasonal	Three sites: *Larix kaempferi, Chamaecyparis obtuse* and *Larix gmelinii x L. kaempferi + Sasa senanensis* and *S. kurilensis*	Conifers	Specrad	5-7-10	RUE
72	2009	(Middleton et al. 2009)	Canopy	Seasonal	Douglas fir	Conifers	Specrad	5-10	RUE
80	2009	(Hilker et al. 2009b)	Canopy	Seasonal	Douglas fir forest	Conifers	Specrad	5-10	RUE
84	2009	(Ac et al. 2009)	Canopy	Hours	Montane grassland	Grassland	Specrad		ΔF/Fm' Chl (A+B)
65	2008	(Meroni et al. 2008b)	Canopy	Seasonal	*Trifolium repens*	Herbaceous/ Crop	Specrad		Fs Net CO_2 uptake
4	1996	(Filella et al. 1996)	Canopy	Hours	Barley	Herbaceous/	Specrad	10	RUE

						Crop			
77	2009	(Wu et al. 2009)	Canopy	Nutrients	wheat	Herbaceous/ Crop	Specrad	6-10	RUE
13	2000	(Peñuelas and Inoue 2000)	Canopy	Seasonal	*Brassica napus*	Herbaceous/ Crop	Specrad		Net CO$_2$ uptake
22	2002	(Strachan et al. 2002)	Canopy	Seasonal	maize (99 and 155 kg N/ha)	Herbaceous/ Crop	Specrad	5-7-10	RUE
56	2008	(Inoue et al. 2008)	Canopy	Seasonal	Rice	Herbaceous/ Crop	Specrad	5-10	RUE
67	2008	(Strachan et al. 2008)	Canopy	Seasonal	maize	Herbaceous/ Crop	Specrad /CASI		GPP
19	2002	(Trotter et al. 2002)	Canopy	dif especies	8 sps	Mixture	Specrad	6-10	RUE
62	2008	(Harris 2008)	Canopy	Seasonal	5 Sphagnum species (*S. tenellum, S. capifolium, S. pulchrum, S. subnitens, S. papillosum*)	Non Higher Plants (Mosses)	Specrad	5-10	ΦPSII
30	2004	(Filella et al. 2004)	Plant/ Canopy	Seasonal	Mediterranean shrubland (*Erica multiflora* and *Globularia alypum*)	Broadleaf	Specrad	 5-10	Net CO$_2$ uptake RUE
68	2008	(Suárez et al. 2008)	Canopy	Spatial	*Olea europea*	Broadleaf	AHS Airborne		Water content
71	2008	(Naumann et al. 2008b)	Canopy	Spatial	*Myrica cerifera*	Broadleaf	airborne Specrad		ΔF/Fm’
16	2001	(Rahman et al. 2001)	Canopy	Spatial	4 sitesx2 dates (3 conifers+1fen)	Conifers	AVIRIS		CO$_2$ uptake
61	2008	(Black and Guo 2008)	Canopy	Spatial	Grassland	Grassland	Specrad		Net CO$_2$ uptake
7	1997	(Peñuelas et al. 1997a)	Canopy	Spatial	aquatic emergent macrophytes	Herbaceous	Specrad	6-10	RUE
46	2006	(Yamano et al. 2006)	Canopy	water stress	soil crusts	Non Higher Plants (Mosses)	Specrad		Fv/Fm
23	2002	(Lovelock and Robinson 2002)	Canopy	water stress	Mosses	Mosses	Specrad		Fv/Fm
53	2007	(Van Gaalen et al. 2007)	Canopy	water stress	*Sphagnum*	Mosses	Specrad		NPQ Water content
73	2009	(Goerner et al. 2009)	Ecosystem	Seasonal	Mediterranean Forests	Broadleaf	MODIS	8-10	RUE
28	2004	(Rahman et al. 2004)	Ecosystem	Seasonal	Broadleaf deciduous forest (Sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron tulipifera*), sassafras (*Sassafras albidium*), white (*Quercus alba*) and black oak (*Q. nigra*)	Broadleaf	MODIS	8-9a-10	RUE
32	2005	(Drolet et al. 2005)	Ecosystem	Seasonal	*Populus tremuloides*	Broadleaf	MODIS	8-9b-10	RUE
55	2008b	(Garbulsky et al. 2008b)	Ecosystem	Seasonal	Mediterranean Forest	Broadleaf	MODIS	8-9a-10	RUE
60	2008a	(Garbulsky et al. 2008a)	Ecosystem	Seasonal	Mediterranean Forests	Broadleaf	MODIS	8-10	RUE
59	2008	(Drolet et al. 2008)	Ecosystem	Seasonal	Boreal coniferous forest	Conifers	MODIS	8-9c-10	RUE

Table 2. Summary of the most common ecophysiological variables linked to PRI, acronyms and methods used in the literature for their estimation.

Acronym	Full name	Determination methods
	Net CO_2 uptake	Gas exchange at the leaf or stand (eddy covariance) level
RUE	Radiation Use Efficiency	Gas exchange
EPS or DEPS	Epoxidation or De-epoxidation State of the Xanthophylls	Chromatography High Performance Liquid Chromatography (HPLC)
$\Delta F/Fm'$ or $\Phi PSII$	effective quantum yield or actual photochemical efficiency or photochemical efficiency of Photosystem II	Chlorophyll fluorescence
NPQ	Non Photochemical Quenching	Chlorophyll fluorescence
Car / Chl	Carotenoids / Chlorophyll contents	Spectrophotometry HPLC

3.1 Leaf level

3.1.1 Diurnal changes. We found twelve articles that linked the PRI with $\Delta F/Fm'$, NPQ, DEPS (or EPS), ratio chlorophyll/carotenoids and RUE at the leaf scale over short (diurnal) time scales. The largest numbers of relationships was found for $\Delta F/Fm'$ (n=17) and RUE (n=16). The median coefficients of determination for the relationships between PRI and RUE varied between 0.60 and 0.85 and for $\Delta F/Fm'$ varied between 0.62 and 0.82 depending on the vegetation type (Fig. 1d and 1e). Except for chlorophyll/carotenoid levels, which were limited to single study for herbaceous vegetation (Fig. 1b), there were not remarkable differences within the variables among vegetation types. Non-significant relationships for herbaceous plants were reported for the relationship with $\Delta F/Fm'$ and also with NPQ (Fig. 1).

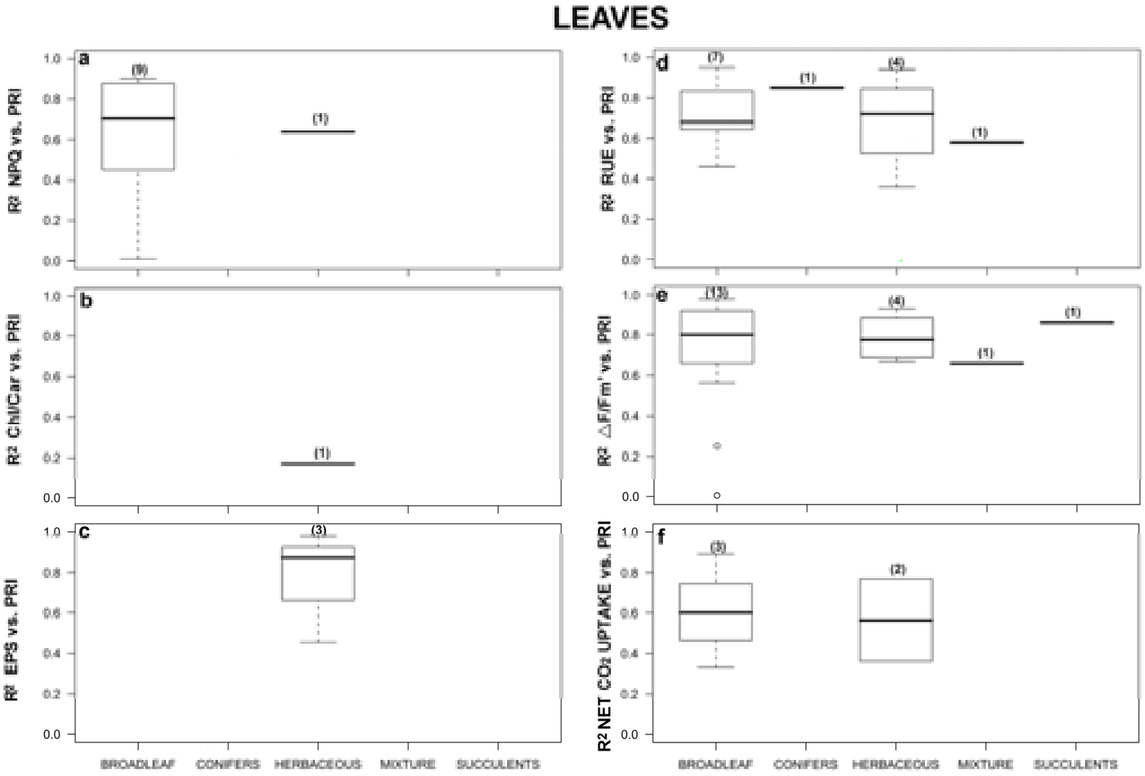


Figure 1. Boxplots for the coefficients of determination for the relationships between the physiological variables: a) Non Phothochemical Quenching (NPQ), b) Chlorophyll/Carotenoid (Chl/Car), c) Epoxidation state of xantophylls (EPS), d) Radiation use efficiency (RUE), e) actual photochemical efficiency (ΔF/Fm’) and f) Net CO_2 uptake, and PRI at the leaf scale and at the short daily time scale. Central lines represent the medians, boxes represent 50% of the data, the whiskers represent the minimum and maximum values and the circles the outliers.The numbers of reported relationships found in the literature are shown in brackets.

3.1.2 Seasonal changes. We found seventeen articles that reported relationships between PRI and ecophysiological variables at the leaf scale over seasonal time scales. Again, the larger number of relationships was found for variables related to quatum yield (ΔF/Fm’ or Fv’/Fm’) with PRI (n=14) and only 6 were found for RUE (Fig. 2d and 2e). PRI accounted for 30 to 80% of the variability of ΔF/Fm’ or Fv’/Fm’ (Fig. 2e). PRI accounted for from 77% of the variability of NPQ in herbaceous leaves and a median of 30% for conifers. A few non-significant relationships were also found between PRI and RUE, NPQ and CO_2 uptake. For broadleaf, conifers and herbaceous species PRI accounted for between 50 and 80% of the temporal variability of Chl/Car and EPS (Fig. 2b and 2c). The R^2 for the relationships between Net CO_2 uptake and PRI was highly variable for broadleaf vegetation, the vegetation type with multiple studies available (Fig. 2f). Three other studies, data not included in figure 2, presented significant relationships with other variables such as total chlorophyll content and PRI (Nakaji et al. 2006, Weng et al. 2009) or also between ΔF/Fm’ and the difference between the PRI measured at predawn and noon (ΔPRI) (Weng et al. 2006a).

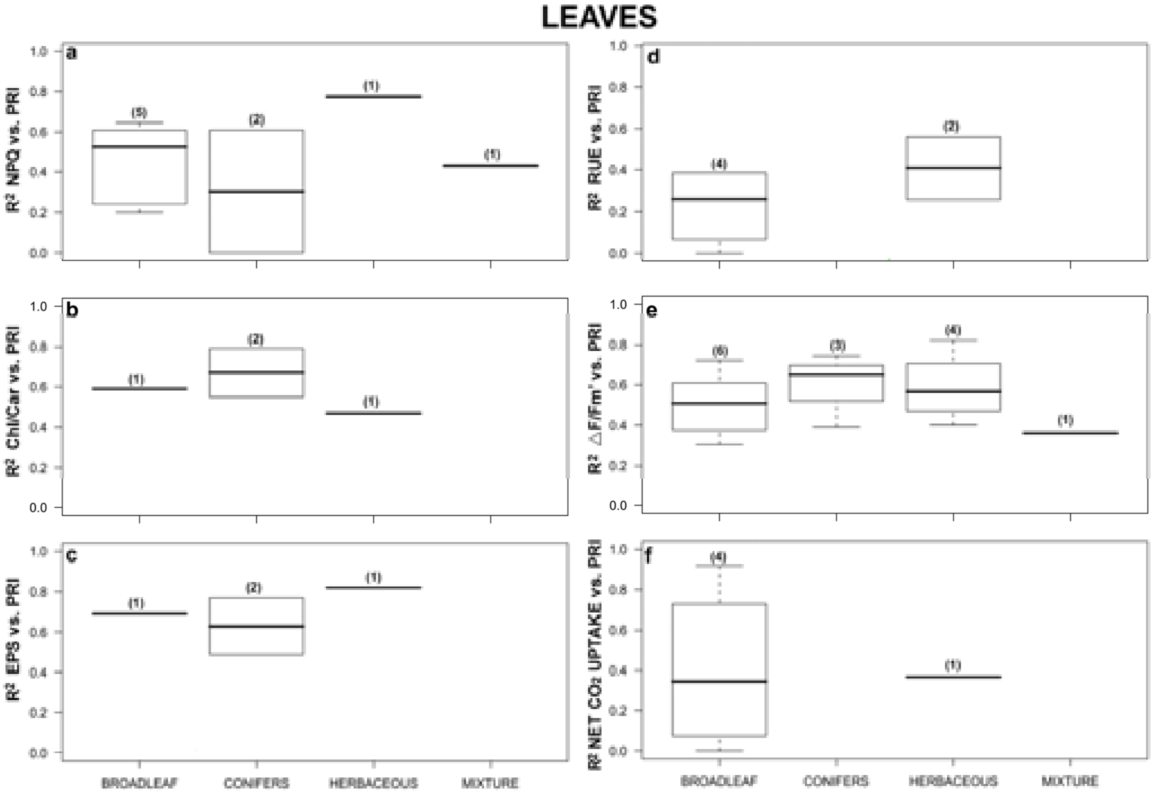


Figure 2. Boxplots of the coefficients of determination (R^2) for the relationships between the ecophysiological variables and PRI at the leaf scale and at the seasonal time scale. Central lines represent the medians, boxes represent 50% of the data, and the whiskers represent the minimum and maximum values.The numbers of reported relationships found in the literature are shown in brackets.

3.1.3 Other factors of change. We also found several studies that presented relationships between PRI and ecophysiological variables at the leaf level when different variance factors (e.g. different species, different populations of a same species or different sites) or different treatments types (e.g. levels of Nitrogen x water availability or salt concentration) were measured in different vegetation types. All but one of these relationships were significant (Fig. 3). Other ecophysiological variables were less frequently tested against PRI. Total chlorophyll content was significantly correlated with PRI (R^2=0.74) when analyzing conifer leaves in a Nitrogen availability experiment (Moran et al. 2000). NPQ was also correlated with PRI (R^2=0.72) in leaves of Mediterranean species (Raddi et al. 2005).

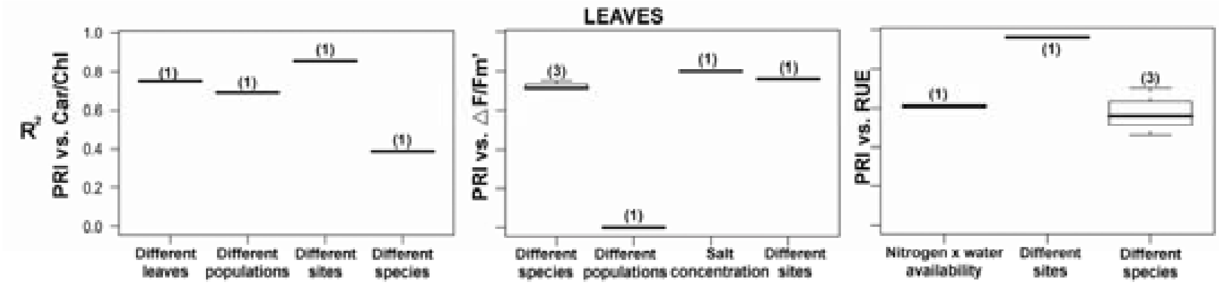


Figure 3. Boxplots of the coefficients of determination of the relationships between physiological variables and PRI at the leaf scale and across different species, sites, leaves, N and water availabilities and salt concentrations. Central lines represent the medians, boxes represent 50% of the data, and the whiskers represent the minimum and maximum values.The numbers of reported relationships found in the literature are shown in brackets.

3.1.4 General relationship at the leaf level. We analyzed the relationships between leaf level photosynthetic RUE and PRI to evaluate if the results reported by different authors are generalizable to different plant types. We reviewed the information reported by different articles that presented relationships between photosynthetic RUE and PRI for determined species (Peñuelas et al. 1995, Gamon et al. 1997, Winkel et al. 2002, Guo and Trotter 2004, Inoue and Peñuelas 2006, Nakaji et al. 2006, Meroni et al. 2008a, Wu et al. 2009). The most common protocol is to use the reflectance of the vegetation of a band centered at 531 nm and a reference band centered at 570 nm. We discarded for this analysis those articles that use other bands to calculated PRI to avoid results not directly comparable . We transformed the PRI values to have all them calculated as PRI=(R531-R570)/(R531+R570). These studies calculated the efficiency as Net photosynthetic exchange/incident photosynthetic photon flux density. The relationships between log RUE and PRI were significant for conifer (R^2=0.41), broadleaf (R^2= 0.58) and herbaceous (R^2= 0.37) species. The slopes between vegetation types did not differ but the intercept for herbaceous species differed from the other two vegetation types. PRI accounted for 42% of the variability of RUE in a unique exponential relationship for all the vegetation types (Fig. 4; R^2=0.42, n=295, $p<0.0001$).

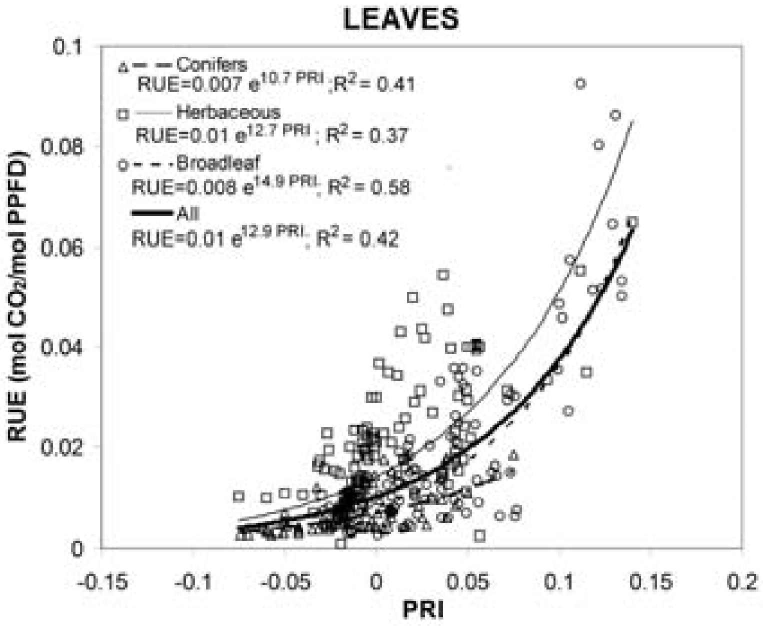


Figure 4. Relationships between leaf scale photosynthetic RUE (RUE = Net photosynthetic rate/incident PPFD) and PRI for broadleaf (Peñuelas et al. 1995, Guo and Trotter 2004, Meroni et al. 2008a), conifers (Nakaji et al. 2006) and herbaceous (Peñuelas et al. 1995, Gamon et al. 1997, Winkel et al. 2002, Guo and Trotter 2004, Inoue and Peñuelas 2006, Wu et al. 2009) plants derived from published results spanning different temporal scales and factors of variances. See Table 1 for details.

3.2 Canopy level

3.2.1 Diurnal changes. We found only a few studies that reported results on the relationships at the canopy (individual plant to stand) level between ecophysiological variables and PRI on the daily course. PRI accounted for 89% of the diurnal changes in photosynthetic efficiency at a sunflower canopy (Gamon et al. 1992). Other studies showed that in a grapevine canopy (Dobrowski et al. 2005), the PRI was significantly correlated to Fs (R^2= 0.32) and in a grassland (Ac et al. 2009) PRI was significantly correlated to the total content of Chl (R^2= 0.63), the Fv/Fm (R^2= 0.55), the Fs (R^2= 0.50) and the ∆F/Fm’ (R^2= 0.47). PRI was also related to diurnal changes in steady state fluorescence and in water stress-related variables, such as stomatal conductance and stem water potential over an olive orchard (Suárez et al. 2008).

3.2.2 Seasonal changes. There is a large quantity of studies on the relationships between ecophysiological variables and PRI illustrating seasonal patterns. These studies include analysis from a part of a growing season to multiple seasons. Most of these studies showed the link between RUE and PRI and presented median R^2 values between 0.4 and 0.75 for broadleaf, conifers, crops and tundra vegetation types. The R^2 for these four vegetation types were not significantly different (t-test, $p<0.05$). The R^2 for shrublands was instead only *ca.* 0.1 which was significantly different to the other vegetation types (Fig. 5).

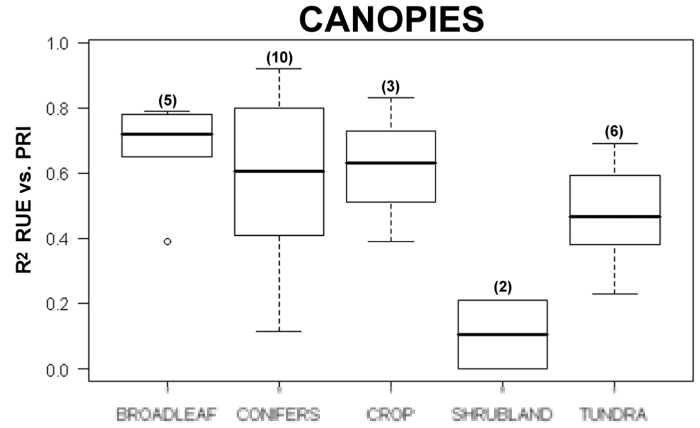


Figure 5. Boxplots of the coefficient of determination for the relationships between RUE and PRI at the canopy scale and at the seasonal time scale. These analyses include mostly studies made on stands of individuals. The R^2 for shrublands is different to the other vegetation types (t-test, $p<0.05$). Central lines represent the medians, boxes represent 50% of the data, whiskers represent the minimum and maximum values and the circles the outliers.The numbers of reported relationships found in the literature are shown in brackets.

3.2.3 Other factors of change At the canopy level and at the seasonal time scale, different type of experiments have reported four significant relationships between canopy RUE and PRI (Fig. 6). PRI was also linked to ecophysiological variables in mosses (Lovelock and Robinson 2002, Van Gaalen et al. 2007, Harris 2008) and soil crusts (Yamano et al. 2006). Those studies showed that PRI links to Fv/Fm (R^2=0.42 - 0.67), to EPS (R^2=0.29), to NPQ (R^2=0.80) and to water content (R^2=0.82). Moreover, other studies analyzing other ecophysiological variables showed that PRI accounted for 46% of the spatial variability of CO_2 uptake for a semiarid grassland and also accounted for 77% of the variability for a coniferous forest across sites and dates (Rahman et al. 2001, Black and Guo 2008).

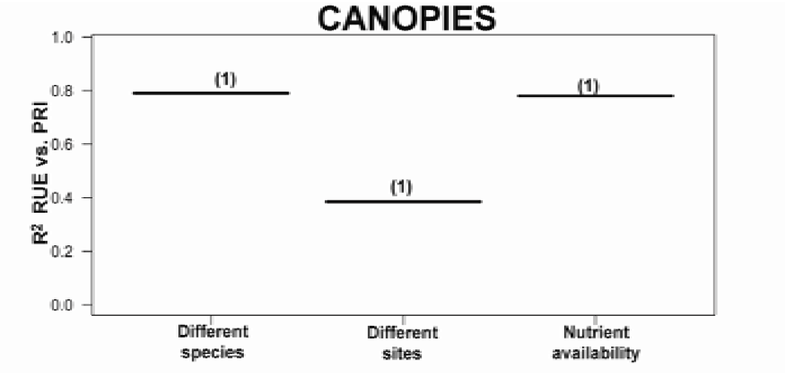


Figure 6. Boxplots of the coefficients of determination of the relationships between RUE and PRI at the canopy scale across different species, nutrient availabilities and sites. These studies are based on reflectance data from hand held spectrometers on stands of wheat with different nutrient availability (Wu et al. 2009), different sites of aquatic vegetation (Peñuelas et al. 1997a) and eight different species (Trotter et al. 2002). The numbers of reported relationships found in the literature are shown in brackets.

3.2.4 General relationship at the canopy level. We analyzed the data provided by those studies that used eddy covariance to estimate RUE togheter with PRI at the canopy level derived from spectroradiometers mounted on different types of platforms. PRI significantly accounted for the variability of RUE for each of the vegetation types (Fig. 7), but the slope and intercept of the relationships log RUE-PRI for conifers significantly differed from the other two vegetation types. When considering all the studies together, the RUE was exponentially related to PRI (Fig. 7), with PRI accounting for 59% of the overall variability of the RUE for all the vegetation types (Fig. 7; R^2=0.42, n=295, p<0.0001).

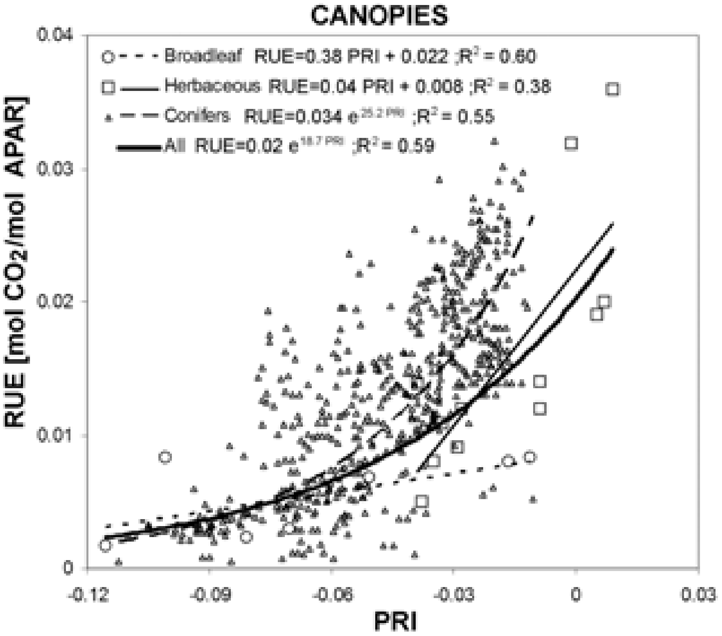


Figure 7. Relationships between eddy covariance derived photosynthetic RUE and PRI for broadleaf (Nichol et al. 2000), conifers (Nichol et al. 2000, Nichol et al. 2002, Hall et al. 2008, Nakaji et al. 2008, Hilker et al. 2009b) and herbaceous vegetation (Strachan et al. 2002) types at the canopy level derived from published results. See table 1 for details. In all the studies RUE=GPP/APAR, but in Nichol et al. (2000, 2002) was calculated as RUE=GPP/incident PAR . The relationship for all the datasets is based on all the data for broadleaf and herbaceous canopies and a random sample of the conifer canopies to equilibrate the number of data of each vegetation type (p<0.001; n=37).

3.3 Ecosystem level

In recent years there have been assessments of whole-ecosystem carbon uptake conducted with simultaneous measurements of reflectance and gas exchange. These ecosystem studies demonstrate significant links between whole-ecosystem fluxes and MODIS PRI. It is worth remembering that MODIS PRI is based, by necessity, on different wavebands than most field studies due to the limited bands available from MODIS. These methods employ a combination of MODIS derived FPAR estimations with eddy covariance at the ecosystem scale in a variety of natural forests including temperate decidous forests (Rahman et al. 2004), deciduous (Drolet et al. 2005) and coniferous (Drolet et al. 2008) boreal forests, and

Mediterranean forests (Garbulsky et al. 2008a, Garbulsky et al. 2008b, Goerner et al. 2009) (Fig. 8).

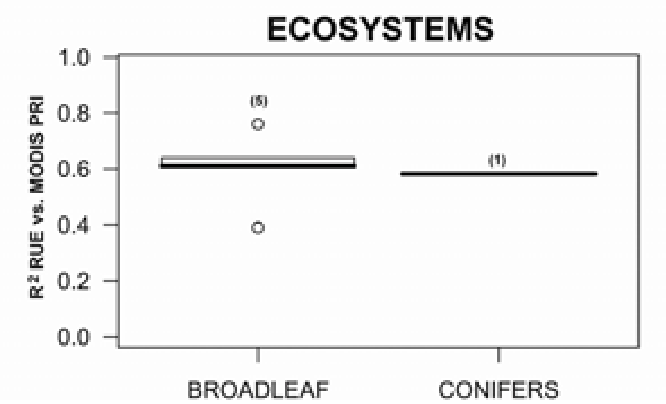


Figure 8. Boxplots of the coefficient of determination for the relationships between RUE and MODIS PRI at the ecosystem scale and at the seasonal time scale. Central lines represent the medians, boxes represent 50% of the data, whiskers represent the minimum and maximum values and the circles are outliers.The numbers of reported relationships found in the literature are shown in brackets.

If PRI is an accurate estimator of RUE, then ecosystem CO_2 uptake could be expressed as

$$CO_2 \text{ uptake} = f\ (\text{PRIxFPAR}) \times \text{PAR}$$

One of the steps needed to arrive at such a generalization of the use of the PRI is to have a general RUE - MODIS PRI relationship that could be used to assess RUE variation for different ecosystem types. We found six studies that present MODIS PRI data as well as concurrent RUE from eddy covariance data and FPAR. In order to build a unique relationship between RUE and MODIS PRI, we selected studies that used the same protocol. The 531 nm band used to calculate the PRI is located in a region of the spectra where the transmission through the atmosphere is very high (Kaufman 1989). Therefore, the signal of the PRI is less affected by atmospheric interferences than other spectral indices like the NDVI, whose bands are located in regions of the spectra much more disturbed by the atmosphere. In fact, it has been demonstrated that the calculation of MODIS PRI without applying atmospheric corrections is an accurate estimator of RUE in different ecosystem types (Drolet et al. 2005, Garbulsky et al. 2008b). From the six studies we finally found only two that presented data on PRI using MODIS bands 11 (526-536 nm) and 12 (546-556 nm) with (Rahman et al. 2004) and without atmospheric correction (Garbulsky et al. 2008b), and transformed both studies to PRI and RUE in mol CO_2/mol photons. Two other studies analyzed data using other bands as references in the formulation of PRI (Drolet et al. 2005, Drolet et al. 2008) could not be used for these analysis because their results are not comparable: they either used band 1 or band 13 as references bands (Fig. 9b and c). This analysis of studies from two different types of forest showed that the seasonal variability of

RUE and MODIS PRI is linked by one unique relationship with PRI accounting for 62% of the variance of RUE (Fig. 9a).

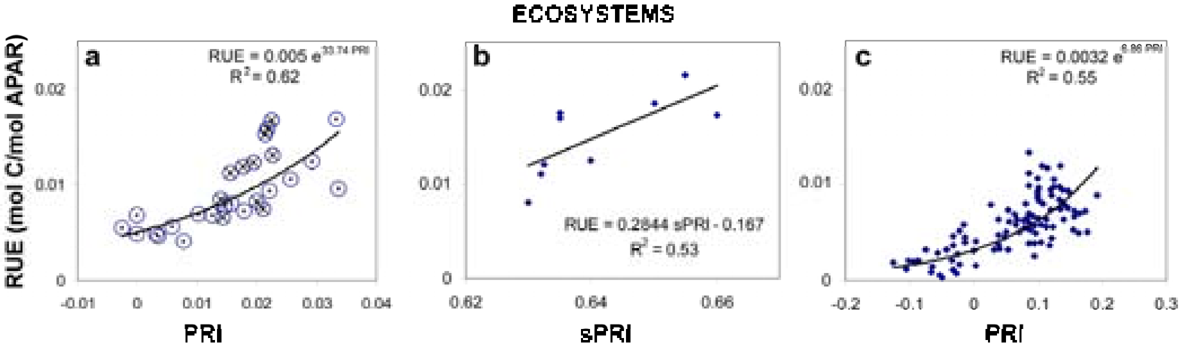


Figure 9. Seasonal relationship between RUE calculated from eddy covariance derived GPP and absorbed PAR (RUE=GPP/APAR) and different formulations of PRI from MODIS data. a) PRI calculated from reflectance in bands 11 and 12 for a Mediterranean forest (Garbulsky et al. 2008b) and a temperate deciduous forest (Rahman et al. 2004). Regression line (circles, n=30) corresponds to a random subset of the points in the Mediterranean forests (dots) and all the points for the temperate decidous forest (crosses) b) Atmospherically corrected sPRI=(1+PRI)/2 calculated from bands 11 and 13 in a boreal deciduous forest (Drolet et al. 2005). c) Atmospherically corrected PRI calculated using band 14 (678 nm) as reference for eight boreal coniferous forests (Drolet et al. 2008). Recalculated and redrawn based on published data.

3.4 RUE-PRI relationships across scales

The relationships between RUE and PRI were generally strong across spatial and temporal scales (Fig. 10). The average coefficients of determination presented the highest values for the daily analysis at the leaf level (Fig. 10). The seasonal analysis at the leaf level presented instead the lowest average values. At the canopy level, daily and seasonal relationships presented similar high coefficients of determination, although we only found one study that presented a daily analysis at the canopy level. The coefficients of determination for the relationships at the leaf and canopy levels for other factors of variation were similar. At the ecosystem level we only found results for seasonal analysis and the average coefficient of determination was higher than the results for the leaf level and similar to the canopy level.

4. Discussion

4.1 PRI assessment of RUE

PRI accounted for a great part of the variability of the ecophysiological variables linked to radiation use efficiency in most vegetation types analyzed in the literature. These results show thus that the PRI is a good spectral index estimator of RUE for leaf, canopy and most ecosystems, and at different temporal scales, from hourly to seasonal. There were only few studies that reflected non-significant relationships between RUE-related ecophysiological variables and PRI. Overall, 86% of the relationships included in this study were significant or accounted for more than 30% of the variability of the ecophysiological variables. The scarce non-significant relationships were particularly frequent when PRI was linked to Net CO_2 uptake or to Amax, not to RUE itself or to its proxy physiological variables (e.g. ΔF/Fm'). We tested the agreement of the RUE-PRI relationships at the foliar (Fig. 4), canopy (Fig. 7) and ecosystem (Fig. 9) levels for different vegetation types derived from different studies in unique general relationships. In those general relationships PRI tends to saturate at increasing RUE and is less sensitive when RUE approaches zero but may be very useful in remote sensing assessment of RUE since they accounted for between 46 and 62% of the total variance of RUE at all spatial scales from leaves to ecosystems.

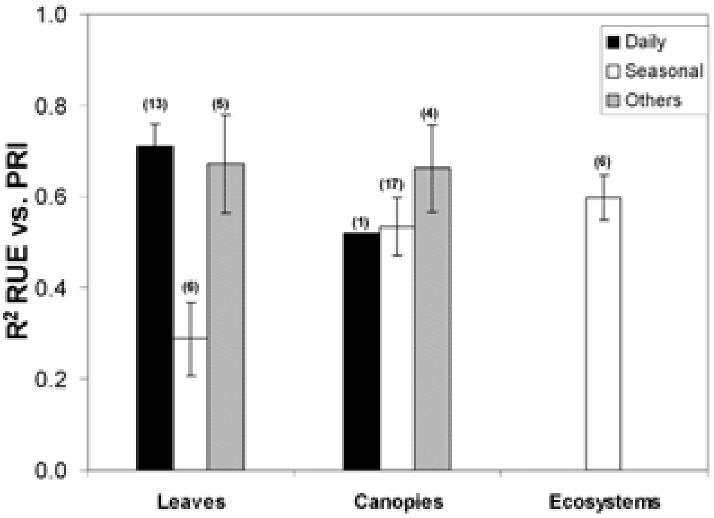


Figure 10. Comparison of the strength of the relationships between RUE and PRI across temporal and spatial scales. Each bar represents the average coefficients of determination for each source of temporal variation (daily or seasonal) or other source of variation (e.g. species or nutrients availability) and spatial scales (leaf, canopy or ecosystem). Dispersion bars represent the standard errors and the numbers of reported relationships are shown in brackets.

Our analysis showed that PRI derived from top-canopy leaves and PRI derived from the whole canopy have been found to be closely linked, at least for relatively closed canopies (Gamon et al. 1992, Filella et al. 1996, Gamon and Qiu 1999, Stylinski et al. 2002). Even more, the average strength of the relationships between RUE and PRI at the seasonal scale is even higher for the canopy-level analyses than for the leaf-level analyses (Fig. 10). The low R^2 value for leaves across seasons, combined with the relatively high correlation between PRI and chlorophyll/carotenoids for leaves (Fig. 2b), can partly be explained by the strong influence of chlorophyll/carotenoid ratios on PRI, particularly as leaves undergo developmental and physiological changes associated with expansion and aging. In some cases, these large pigment changes may confound the RUE-PRI relationship, possibly accounting for the poor R^2 values for leaves across seasons (see Fig. 10). The high strength of the RUE-PRI seasonal relationship at the canopy-level therefore suggests that the optical properties of upper canopy regions can reveal the overall photosynthetic state of the canopy, opening the possibility of assessment of photosynthetic activity at larger scales, i.e. at ecosystem and regional levels. However, at the scale of whole vegetation stands and ecosystems, PRI can also be affected by canopy and stand structure (Barton and North 2001, Hall et al. 2008, Hilker et al. 2008), and it is possible that canopy structural changes (e.g. changing LAI, leaf orientation, or percent vegetation cover) could also be driving seasonal changes in PRI. To confirm the capability of PRI as an ecosystem photosynthetic indicator, appropriate ecosystem-scale methods to sample carbon flux and hyperspectral reflectance simultaneously have been recently, and are still being, developed (e.g. Gamon et al. 2006). Key challenges will be accounting for percent vegetation cover, sun angle and view angle, and background (e.g. soil, shadow, or standing water) effects, all of which are known to complicate PRI interpretation. Structural features, such as the percent of woody or dead canopy material, or the presence of visible soil or other non-green landscape components, can confound the PRI signal as shown for shrublands (Fig. 5, Filella et al. 2004, Sims et al. 2006a). The exact effects of these complexities on the reflectance signature have yet to be fully understood, but several studies showed that PRI can still function as a seasonal photosynthetic indicator at the ecosystem level in closed canopies (Fig. 5) including coniferous forests (Nichol et al. 2000, Rahman et al. 2001, Nichol et al. 2002, Nakaji et al. 2007, Nakaji et al. 2008, Middleton et al. 2009), broadleaf forests (Nichol et al. 2000, Serrano and Peñuelas 2005, Peguero-Pina et al. 2008, Naumann et al. 2009) and crops (Strachan et al. 2002, Inoue et al. 2008). It is interesting to highlight that because of this connection to photosynthetic light regulation, PRI provides a remote assessment of instantaneous photosynthetic radiation-use efficiency (Gamon et al. 1992, Peñuelas et al. 1995, Gamon et al. 1997) not only in higher plants but also in mosses (Lovelock and Robinson 2002, Van Gaalen et al. 2007, Harris 2008). Measurements made on crop canopies have confirmed that by including PRI it is also possible to improve the estimations of GPP (Gitelson et al. 2006, Strachan et al. 2008).

The estimation of radiation use efficiency from remote sensing is a much more recent application than estimations of FPAR. The links between spectral indices such as the NDVI with LAI-FPAR have been studied for much longer time than those of RUE with PRI, and yet, even recent studies do not totally agree over the accuracy of the remote estimations of FPAR, and the confidence of these estimations are not always high (Fensholt et al. 2004, Cohen et al. 2006, Gobron et al. 2006). Even in experiments in highly seasonal ecosystems, the correlation between FPAR and NDVI (Huemmrich et al.) is not much higher (R^2=0.7) than the correlations between RUE and MODIS PRI reviewed in this study. These observations suggest that the use of the PRI, with a much shorter history, to estimate ecophysiological variables of terrestrial vegetation has a great potential to be converted to a good surrogate of RUE, which could, in turn, contribute to improved estimates of photosynthetic carbon gain in the context of current RUE models.

A remarkable finding of this study is that consistent results between PRI and ecosystem carbon uptake efficiency (Fig. 7-9) emerge even though there are a multitude of possible biochemical, ecological, and physical confounding factors operating at several levels of aggregation. At the leaf level, biochemical processes including photorespiration, PSI cyclic electron transport and nitrate reduction can compete with CO_2 fixation for reductant generated by photosynthetic electron transport (Niyogi 1999) and cause PSII efficiency (PRI) and CO_2 assimilation to diverge. There are even other pigment cycles, like those included in the lutein epoxide cycle especially in tropical trees (Matsubara et al. 2008, Esteban et al. 2009) that could also produce noise in the PRI signal. Despite these potential complications, the results summarized here suggest that the overall photosynthetic system is often sufficiently regulated to maintain consistent relationships between PSII processes and CO_2 fixation (Gamon et al. 1997, Stylinski et al. 2002). Seasonally varying pigment levels or ratios also strongly affect PRI (e.g. Stylinski et al. 2002), but, in some cases, this may actually help explain why PRI often works as well as it does, since varying chlorophyll/carotenoid ratios can covary with xanthophyll pigment levels, and this may enhance the ability of PRI to predict RUE. On the other hand, to the extent that pigment ratios are not closely related to RUE, changing pigment ratios would be a confounding variable, as mentioned above. At the ecosystem level, soil and plant respiration might produce significant scatter in the relationship between PRI and carbon uptake because while PRI tracks gross photosynthesis (i.e. direct carbon uptake not including respiratory loss), conventional flux sampling methods provide the net CO_2 flux (i.e. combined photosynthetic carbon gain and respiratory loss) from the sampling area (Moncrieff et al. 1996). Therefore, ecosystem respiration must be estimated, through the extrapolation of night-time values of ecosystem respiration into the daytime (Reichstein et al. 2005), and across latitudinal gradients respiration variation may largely dominate ecosystem carbon balance (Valentini et al. 2000). Soil respiration either may determine a relatively small part of the gas flux for many ecosystems, or it may be scaled to total biomass and thus stand photosynthesis in others (Gamon et al. 2006).Finally, there are also the confounding physical effects of canopy and stand structure (e.g. LAI changes), leaf movement, sun and viewing angles, soil background, and shadows that can significantly influence the PRI signal (Gamon et al. 1995, Barton and North 2001). In particular, recent studies are revealing the extent to which PRI reflectance is affected by sun-target-sensor geometry, and stand structure (Asner 1998, Barton and North 2001, Drolet et al. 2005, Hall et al. 2008, Hilker et al. 2008).

Despite these many potentially confounding factors, the emerging consistency of the PRI-flux relationship suggests a surprising degree of "functional convergence" of biochemical, physiological, and structural components affecting ecosystem carbon fluxes (Field 1991, Stylinski et al. 2002). In other words, ecosystems possess emergent properties that allow us to effectively explore their seemingly complex photosynthetic behavior using surprisingly simple optical sampling methods. Understanding the basis for this convergence, unearthing the "ecophysiological rules" governing these responses, remains a primary goal of current research in these topics.

The coexistence of MODIS TERRA and AQUA data since 2002 offers many novel ways to explore the PRI signal as an ecosystem-scale RUE indicator. The availability of the sensors on board of the two satellites with revisiting time split by two hours increases the viewing and sun angle possibilities. Therefore the use of data provided by both satellites contributes to improve the coverage of backscatter images. These important sources of data have not yet been greatly exploited simultaneously for vegetation studies. We suggest that the analysis of this data could largely improve the assessment of RUE using the available data since 2002. A severe restriction to this has been the fact that the MODIS PRI bands were originally developed for ocean color and have not been routinely processed for land regions. Reprocessing of MODIS data to yield global PRI time series could greatly assist our ability to understand the utility of spaceborne PRI to improve our assessment of ecosystem carbon uptake.

4.2 PRI and RUE standardization

Our results show that, at the present state, there are reasonably consistent general RUE-PRI relationships (Fig. 7-9). Nevertheless, the methodological differences involved in the studies relating PRI with ecophysiological variables, the differences found in the regressions between different vegetation types and the lack of several comparable studies at the ecosystem level (Fig. 9) still hinder the use of a general RUE-PRI relationship without a proper calibration in each case. A primary difference among different studies is in the formulation of the PRI. We found that several formulations are being used to calculate PRI, including different target wavelengths (530 nm, 531 nm or 539 nm), different reference bands, and a contrasting order of the subtraction with the reference band. The use of different wavelengths could have significant impact on PRI’s predictive ability (Inoue et al. 2008). There are probably also scale issues associated with the band selection. PRI using the 570 nm band was useful at a single leaf scale, for which it was originally defined (Gamon et al. 1993b, Peñuelas et al. 1995), but may be less useful at a canopy scale where PRI using the 550 nm band may have a higher predictive ability (Inoue et al. 2008). The use of the sPRI (1+PRI)/2 added even further difficulties in comparing between studies. In the case of PRI derived from MODIS satellite data, bands 10 (488 nm), 12 (551 nm), 13 (667 nm) and 14 (678 nm) have been used as reference bands, rendering the different studies incomparable

On the other hand, the calculation of RUE involved a large set of differences among protocols, e.g. different approaches for carbon uptake estimations, use of total irradiance vs PAR, or total vs. absorbed PAR, and use of different units (MJ or mol), among others. The eddy covariance technique, which is nowadays the most widespread way to measure carbon fluxes at the ecosystem scale, is not free from problems to reach reliable estimates of GPP (e.g. Serrano-Ortiz et al. 2010). For example, at this moment we can not rule out interferences of abiotic or heterotrophic CO_2 fluxes at the ecosystem scale that can surely mask the true RUE-PRI relationship.

A greater availability of ground spectral measurements and technical improvements would help to make the PRI a more accurate estimator of RUE and therefore a more powerful tool. On one side, a ground PRI measurement network coupled to the eddy covariance towers (FLUXNET or others) could provide data for a definite assessment of the utility of the PRI to estimate RUE. This network should be built on the design of a homogeneous sensor for all the sites with the spectral information to calculate a ground based PRI and other vegetation indices, with a field of view similar to the footprint of the tower. An effort in that direction has been advocated by the SpecNet community for several years (Gamon et al. 2006), and is currently being conducted at many flux tower sites. In addition, to overcome the problems related to the eddy covariance technique stated before (e.g. abiotic fluxes, separation of photosynthetic and respiratory fluxes) it would be highly desirable to make concurrent measurements of leaf-level photosynthetic rate and of soil respiration. To determine the photosynthetic contribution to the RUE-PRI relationship, and to clarify the influence of various pigment pools on the PRI, optical measurements coupled with pigment measurements of top-canopy leaves should also be made whenever possible. Finally, long-term studies should also evaluate how structural changes (e.g. due to canopy growth or changing leaf display) might be contributing to the measured PRI signals. Consistent pigment and structural measurements are rarely made in long-term studies, yet they remain essential to fully understand the mechanistic basis of the often high RUE-PRI correlation

On the satellite side, the continued improvement of the spectral resolution provided by the sensors on board of satellite platforms will help to obtain better estimations of PRI. The increase of the spectral (<10 nm) and the spatial (<1 km) resolution of the MODIS current products by fusion techniques with images with higher resolutions (Pohl and Van Genderen 1998, Feng et al. 2006) or the increase of the backscatter view through techniques like the multiple viewing angle of the CHRIS-PROBA satellite (Verrelst et al. 2008) are among the most immediate improvements. The nominal bandwidth of MODIS bands seems broader than the original bands used for the formulation of PRI at the leaf level. However, the FWHM (full width of half maximum) of the MODIS bands are probably not much different from the FWHM of many field sensors that have been used in defining PRI at leaf to stand scales. For example the Spectron (Spectron Engineering, Denver, CO, USA) and UniSpec (PP Systems, Amesbury MA, USA) sensors both have FWHM values of about 10 nm, even though their nominal bandwidth is 2-3 nm (Gamon et al. 1993a, Castro-Esau et al. 2006). So even though the nominal bandwidth is wider, the actual bandwidth is more similar across sensors than it might seem. A full exploration of this topic would require wider availability of airborne and spaceborne hyperspectral sensors (imaging spectrometers), which have been largely unavailable to the broader ecological research community, with the exception of "demonstration" missions (e.g AVIRIS or Hyperion). In the case of the spatial resolution, since most of the eddy covariance towers presently working do not represent an area larger than 1 km^2, and since the footprint varies constantly with windspeed and direction, it is a challenge to produce a satellite-based PRI with a sufficient spatial resolution to match the eddy covariance sampling region. This goal can be achieve by new sensors but also by fusion or simultaneous use of different sources provided by the actual sensors in orbit in order to obtain more information than can be derived from each of the single sensor data alone. In all cases, we advocate a standardization of both RUE (and proxy physiological variables) and PRI measurements and units that allow the comparison of results and the study of possible general relationships. Similarly, careful attention to sun-target-sensor geometry and characterization of stand structure will be needed to fully understand RUE-PRI relationships across ecosystems from contrasting biomes.

4.3 Ecosystem-specific PRI performances

Even if we standardize RUE and PRI measurements and calculation, there are still great differences between terrestrial ecosystems in the degree to which any one environmental factor controls photosynthetic rates and therefore on the capability of each vegetation index to estimate structural or functional variables. Therefore, using the available evidence, we find a wide variation in the degree to which FPAR and RUE individually track the dynamics of temporal and spatial patterns of carbon fluxes. Thus the ability to predict fluxes from these indices for different biomes should be quite variable and will depend upon dominant factors affecting photosynthetic carbon flux (Fig 11). For some terrestrial ecosystems, FPAR, estimated from vegetation indexes such as NDVI or EVI, or APAR are good surrogates of GPP (e.g. temperate grasslands). For others, there is indeed a positive correlation between FPAR or APAR and GPP, but a high part of the variance of GPP is yet to be explained (Sims et al. 2006b). For those ecosystems, primarily evergreen-dominated ones, PRI provides a useful index of seasonal carbon fluxes because of its connection with RUE, whereas FPAR would presumably be less useful in this context since FPAR or NDVI of evergreen plants changes little over seasonal time scales (Gamon et al. 1995, Garbulsky et al. 2008b)(Fig. 11). On the contrary, PRI may not be effective in detecting ecosystem flux in ecosystems where FPAR closely follows the seasonal dynamic of CO_2 exchange. This seems to be the case in deciduous ecosystems where photosynthetic fluxes closely track seasonal greening and senescence of the landscape (Sims et al. 2006b) or in the Artic tundra, where net CO_2 uptake is often light limited, or in annual croplands and grasslands where seasonal patterns of temperature or moisture constrain production and carbon flux. In those ecosystems, FPAR scales well with photosynthetic rates and NDVI or EVI are closely tied to seasonal carbon dynamics and thus provide a dominant indicator of ecosystem CO_2 uptake assessment (Sims et al. 2006b). In some other ecosystems, such as shrublands, PRI presented problems for ecosystem gas exchange assessment (Fig. 5), in part due to sun angle effects on discontinuous canopies. In desert areas, or in general in areas with high percentage of bare soil, such as some shrublands, shadows and non photosynthetic or dead material can contribute strongly to the reflectance spectrum, rendering PRI less adequate for the estimation of RUE (Filella et al. 2004, Sims et al. 2006a). Thus, in sparsely vegetated regions, adjustment for percent cover may be needed to yield a useful PRI signal. In tropical areas, the atmospheric interference (e.g. cloudiness, aerosols) are often too high to obtain a good PRI signal and moreover, some field studies on tropical species have indicated that PRI does not scale well with ecophysiological variables, possibly due to the lutein epoxide cycle related reflectance (Martin et al. 2007, Rascher et al. 2007). Other tropical field studies have reported clear correlations between PRI and ecophysiological variables, but these relationships vary between species having different strategies for coping with light stress (Gamon et al. 2005).

The available data, although still scarce for most regions of the world, are beginning to show that the usefulness of PRI relative to the FPAR estimations depends on the particular combination of environmental conditions, radiation use efficiencies, and structural characteristics of the different ecosystems in question. Therefore, an effective application of remote sensing to carbon flux requires an ecological understanding of the environmental controls on carbon flux for these different ecosystems, including the contribution of biotic and abiotic factors to the overall PRI signal. Fortunately, a number of methods exist to help address these topics, including radiative transfer models (Jacquemoud et al. 2009), spectral mixture analysis (Numata et al. 2007), and BRDF (bidirectional reflectance distribution function) methods (Hilker et al. 2009a), and greater integration of these techniques with ecophysiological methods are needed to fully understand the best way to apply the PRI signal.

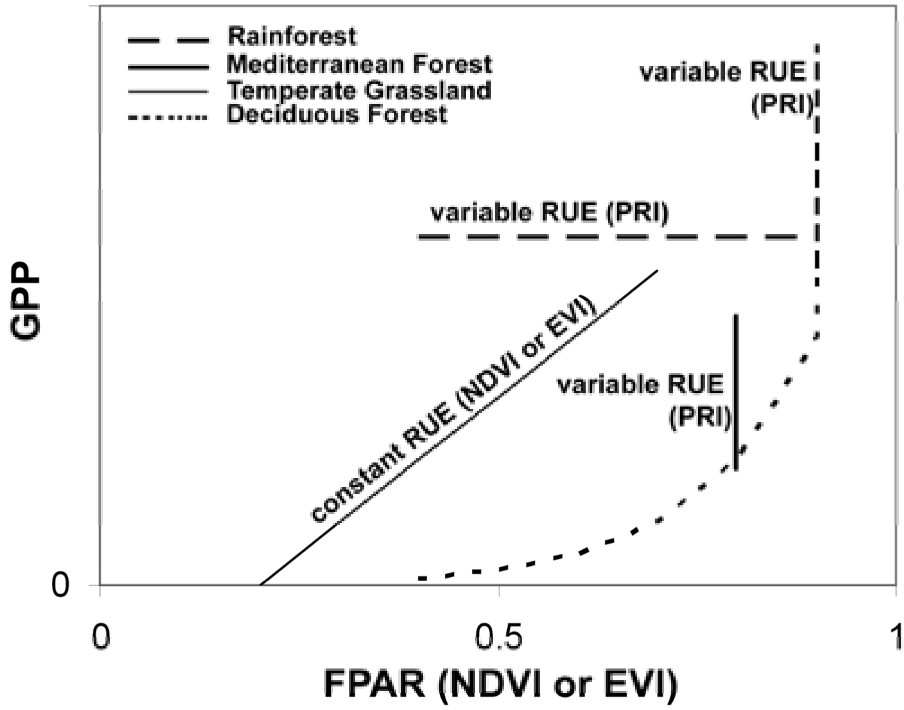


Figure 11. Hypothesized idealized seasonal relationships of GPP to FPAR in ecosystems with contrasting phenologies and GPP dynamics. The suggested best spectral index to estimate RUE is depicted between brackets for each ecosystem type.

5. Concluding remarks

The available evidence shows that the PRI is a reliable estimator of ecophysiological variables closely related to the photosynthetic efficiency at the leaf and canopy levels over a wide range of species, plant functional types and temporal scales. However, there are also some exceptions and differences in the protocols of the studies that generate doubts about the generalization to satellite observable scales. The use of uniform protocols is needed to generate comparable data and at the end a possible general calibration of the relation PRI – RUE. Further studies are also needed to disentangle the several drivers of the PRI signal, and to resolve the potentially confounding factors so that we can improve the assessment of CO_2 fluxes in many different biomes using hyperspectral or narrow-band remote sensing. While flux towers still represent the current standard for ecosystem carbon flux, we must learn to properly calibrate these fluxes against the new remote sensing products if we are to develop reliable remote sampling methods for ecosystem carbon flux. This remains a significant challenge because flux towers sample in time, whereas remotely sensed imagery samples in space (Rahman et al. 2001). To conduct this calibration, we should blend these sampling domains by applying remote sensing aircraft and satellite measurements at the same temporal and spatial scales as flux tower footprint measurements, which is rarely done. Increased acquisition of coordinated flux and optical data from different biomes is thus needed. Additionally, standardized ground-based optical sampling programs at flux towers (Gamon et al. 2006) should be expanded. Once we have properly calibrated the surrogates for FPAR and PRI for different ecosystems, we will be able to apply remote sensing to extrapolate in time and space from tower sites. Although there are currently few space-borne remote sensing instruments of high spectral resolution (note that Hyperion and Chris/Proba are exceptions, but these are demonstration instruments with limited accessibility), this type of data can now be collected from a range of novel helicopter and aircraft instruments (Malenovsky et al. 2009) and from the planned new satellite data. Meanwhile, the 530 nm waveband provided by the satellite-borne MODIS sensor, is starting to be used as a possible RUE indicator at the ecosystem scale across different vegetation types with significant success (Rahman et al. 2004, Drolet et al. 2005, Drolet et al. 2008, Garbulsky et al. 2008a, Garbulsky et al. 2008b, Goerner et al. 2009).

A goal of current studies should be to develop a robust, empirically tested model for ecosystem fluxes driven by a richer degree of remotely sensed information than in the past. This may provide an alternative to complex models that require extensive parameterization and a huge quantity of ground climate data (Running et al. 2004). In this simpler approach, a remote measure of FPAR would be complemented with PRI (a dynamic efficiency factor) to assess the carbon fluxes of the different ecosystems from remote sensing airborne sensors. Since the flux images obtained in this way provide instantaneous maps of gross CO_2 fluxes (Rahman et al. 2001, Fuentes et al. 2006), they have to be extended to daily values. These daily flux estimates could then be integrated throughout the year to derive spatially distributed NPP values for different biomes. This could be achieved with a weekly or biweekly measurement of NDVI and PRI from an aerial or satellite based sensor, combined with estimated daily variations in PRI from calibration sites on the ground. The existing global network of eddy covariance towers (Baldocchi 2008) provides an ideal ground data source for such calibration (Garbulsky et al. 2010).

The advances presented here have established the possibility of combining hyperspectral remote sensing and flux tower data to estimate spatially distributed carbon uptake over large areas, thus, up scaling point tower measurements to the regional scale (Drolet et al. 2008, Hilker et al. 2008). However, any application of the PRI at this regional scale requires very careful attention to a number of potentially confounding factors, many of which are discussed above. An important parallel effort will be to better partition net ecosystem carbon fluxes into their respiratory and photosynthetic components. Particularly if we further understand the ecological rules controlling ecosystem respiration and photosynthesis across multiple ecosystems, we should be able to use these new tools to build a better understanding of global carbon fluxes.

REFERENCES

Ac, A., Z. Malenovsky, J. Hanus, I. Tomaskova, O. Urban, and M. V. Marek. 2009. Near-distance imaging spectroscopy investigating chlorophyll fluorescence and photosynthetic activity of grassland in the daily course. Functional Plant Biology **36**:1006-1015.

Asensio, D., J. Peñuelas, R. Ogaya, and J. Llusià. 2007. Seasonal soil and leaf CO_2 exchanges rates in a Mediterranean holm oak forest and their responses to drought conditions. Atmospheric Environment **41**:2447-2455.

Asner, G. P. 1998. Biophysical and biochemical sources of variability in canopy reflectance. Remote Sensing of Environment **64**:234-253.

Asner, G. P., R. E. Martin, K. M. Carlson, U. Rascher, and P. M. Vitousek. 2006. Vegetation-climate interactions among native and invasive species in Hawaiian rainforest. Ecosystems **9**:1106-1117.

Asner, G. P., D. Nepstad, G. Cardinot, and D. Ray. 2004. Drought stress and carbon uptake in an Amazon forest measured with spaceborne imaging spectroscopy. Proceedings of the National Academy of Sciences of the United States of America **101**:6039-6044.

Baldocchi, D. 2008. Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. Australian Journal of Botany **56**:1-26.

Barton, C. V. M., and P. R. J. North. 2001. Remote sensing of canopy light use efficiency using the photochemical reflectance index - Model and sensitivity analysis. Remote Sensing of Environment **78**:264-273.

Black, S. C., and X. Guo. 2008. Estimation of grassland CO_2 exchange rates using hyperspectral remote sensing techniques. International Journal of Remote Sensing **29**:145 - 155.

Blackburn, G. A. 2007. Hyperspectral remote sensing of plant pigments. Journal of Experimental Botany **58**:855-867.

Busch, F., N. P. A. Hüner, and I. Ensminger. 2009. Biochemical constrains limit the potential of the photochemical reflectance index as a predictor of effective quantum efficiency of photosynthesis during the winter spring transition in Jack pine seedlings. Functional Plant Biology **36**:1016-1026.

Carter, G. A. 1998. Reflectance wavebands and indices for remote estimation of photosynthesis and stomatal conductance in pine canopies. Remote Sensing of Environment **63**:61-72.

Castro-Esau, K. L., G. A. Sanchez-Azofeifa, and B. Rivard. 2006. Comparison of spectral indices obtained using multiple spectroradiometers. Remote Sensing of Environment **103**:276-288.

Chen, W., Q. Zhou, and J. Huang. 2006. Estimating pigment contents in leaves and panicles of rice after milky ripening by hyperspectral vegetation indices. Chinese Journal of Rice Science **20**:434-439.

Cheng, Y. B., E. M. Middleton, T. Hilker, N. C. Coops, T. A. Black, and P. Krishnan. 2009. Dynamics of spectral bio-indicators and their correlations with light use efficiency using directional observations at a Douglas-fir forest. Measurement Science & Technology **20**.

Cohen, W. B., T. K. Maiersperger, D. P. Turner, W. D. Ritts, D. Pflugmacher, R. E. Kennedy, A. Kirschbaum, S. W. Running, M. Costa, and S. T. Gower. 2006. MODIS Land Cover and LAI Collection 4 Product Quality Across Nine Sites in the Western Hemisphere. Ieee Transactions on Geoscience and Remote Sensing **44**:1843-1857.

Damm, A., J. Elbers, A. Erler, B. Gioli, K. Hamdi, R. Hutjes, M. Kosvancova, M. Meroni, F. Miglietta, A. Moersch, J. Moreno, A. Schickling, R. Sonnenschein, T. Udelhoven, S. van der Linden, P. Hostert, and U. Rascher. 2010. Remote sensing of sun-induced fluorescence to improve modeling of diurnal courses of gross primary production (GPP). Global Change Biology **16**:171-186.

Demmig-Adams, B. B., and W. W. Adams. 1996. The role of xanthophyll cycle carotenoids in the protection of photosynthesis. Trends in Plant Science **1**:21-26.

Dobrowski, S. Z., J. C. Pushnik, P. J. Zarco-Tejada, and S. L. Ustin. 2005. Simple reflectance indices track heat and water stress-induced changes in steady-state chlorophyll fluorescence at the canopy scale. Remote Sensing of Environment **97**:403-414.

Drolet, G. G., K. F. Huemmrich, F. G. Hall, E. M. Middleton, T. A. Black, A. G. Barr, and H. A. Margolis. 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**:212-224.

Drolet, G. G., E. M. Middleton, K. F. Huemmrich, F. G. Hall, B. D. Amiro, A. G. Barr, T. A. Black, J. H. McCaughey, and H. A. Margolis. 2008. Regional mapping of gross light-use efficiency using MODIS spectral indices. Remote Sensing of Environment **112**:3064-3078.

Esteban, R., J. M. Olano, J. Castresana, B. Fernández-Marín, A. Hernández, J. M. Becerril, and J. I. García-Plazaola. 2009. Distribution and evolutionary trends of photoprotective isoprenoids (xanthophylls and tocopherols) within the plant kingdom. Physiologia Plantarum **135**:379-389.

Evain, S., J. Flexas, and I. Moya. 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.

Feng, G., J. Masek, M. Schwaller, and F. Hall. 2006. On the blending of the Landsat and MODIS surface reflectance: predicting daily Landsat surface reflectance. Geoscience and Remote Sensing, IEEE Transactions on **44**:2207-2218.

Fensholt, R., I. Sandholt, and M. S. Rasmussen. 2004. Evaluation of MODIS LAI, fAPAR and the relation between fAPAR and NDVI in a semi-arid environment using in situ measurements. Remote Sensing of Environment **91**:490-507.

Field, C. B. 1991. Ecological scaling of carbon gain to stress and resource availability. Pages 35-65 *in* H. A. Mooney, W. E. Winner, and E. J. Pell, editors. Response of Plants to Multiple stresses. Academic Press.

Field, C. B., J. A. Gamon, and J. Peñuelas. 1994. Remote sensing of photosynthesis. Pages 511-527 *in* E.-D. Schulze and M. M. Caldwell, editors. Ecophysiology of Photosynthesis. Ecological Studies 100. Springer, Berlin, Heidelberg, New York.

Field, C. B., J. T. Randerson, and C. M. Malmstrom. 1995. Global net primary production: Combining ecology and remote sensing. Remote Sensing of Environment **51**:74-88.

Filella, I., T. Amaro, J. L. Araus, and J. Peñuelas. 1996. Relationship between photosynthetic radiation-use efficiency of Barley canopies and the photochemical reflectance index (PRI). Physiologia Plantarum **96**:211-216.

Filella, I., J. Peñuelas, L. Llorens, and M. Estiarte. 2004. Reflectance assessment of seasonal and annual changes in biomass and CO_2 uptake of a Mediterranean shrubland submitted to experimental warming and drought. Remote Sensing of Environment **90**:308-318.

Filella, I., A. Porcar-Castell, S. Munné-Bosch, J. Bäck, M. F. Garbulsky, and J. Peñuelas. 2009. PRI assessment of long-term changes in carotenoids/chlorophyll ratio and short-term changes in de-epoxidation state of the xanthophyll cycle. International Journal of Remote Sensing **30**:4443-4455.

Fuentes, D. A., J. A. Gamon, Y. F. Cheng, H. C. Claudio, H. L. Qiu, Z. Y. Mao, D. A. Sims, A. F. Rahman, W. Oechel, and H. Y. Luo. 2006. Mapping carbon and water vapor fluxes in a chaparral ecosystem using vegetation indices derived from AVIRIS. Remote Sensing of Environment **103**:312-323.

Gamon, J. A., C. B. Field, W. Bilger, O. Björkman, A. Fredeen, and J. Peñuelas. 1990. Remote Sensing of the Xanthophyll Cycle and Chlorophyll Fluorescence in Sunflower Leaves and Canopies. Oecologia **85**:1-7.

Gamon, J. A., C. B. Field, A. L. Fredeen, and S. Thayer. 2001. Assessing photosynthetic downregulation in sunflower stands with an optically-based model. Photosynthesis Research **67**:113-125.

Gamon, J. A., C. B. Field, M. Goulden, K. Griffin, A. Hartley, G. Joel, J. Peñuelas, and R. Valentini. 1995. Relationships between NDVI, canopy structure, and photosynthetic activity in three Californian vegetation types. Ecological Applications **5**:28-41.

Gamon, J. A., C. B. Field, D. A. Roberts, S. L. Ustin, and R. Valentini. 1993a. Functional patterns in an annual grassland during an AVIRIS overflight. Remote Sensing of Environment **44**:239-253.

Gamon, J. A., I. Filella, and J. Peñuelas. 1993b. The dynamic 531-nanometer Δ reflectance signal: a survey of twenty angiosperm species. Pages 172-177 *in* H. Yamamoto and C. Smith, editors. Photosynthetic Responses to the Environment American Society of Plant Physiologists, Rockville.

Gamon, J. A., K. Kitajima, S. S. Mulkey, L. Serrano, and S. J. Wright. 2005. Diverse optical and photosynthetic properties in a neotropical dry forest during the dry season: Implications for remote estimation of photosynthesis. Biotropica **37**:547-560.

Gamon, J. A., J. Peñuelas, and C. B. Field. 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. Remote Sensing of Environment **41**:35-44.

Gamon, J. A., and H.-L. Qiu. 1999. Ecological applications of remote sensing at multiple scales Pages 805-846 *in* F. I. Pugnaire and F. Valladares, editors. Handbook of Functional Plant Ecology. Marcel Dekker, Inc, New York.

Gamon, J. A., A. F. Rahman, D. JL, S. M, and K. F. Huemmrich. 2006. Spectral Network (SpecNet): what is it and why do we need it? Remote Sensing of Environment **103**:227-235.

Gamon, J. A., L. Serrano, and J. S. Surfus. 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., and J. S. Surfus. 1999. Assessing leaf pigment content and activity with a reflectometer. New Phytologist **143**:105-117.

Garbulsky, M. F., and J. M. Paruelo. 2004. Remote sensing of protected areas to derive baseline vegetation functioning characteristics. Journal of Vegetation Science **15**:711-720.

Garbulsky, M. F., J. Peñuelas, J. M. Ourcival, and I. Filella. 2008a. Estimación de la eficiencia del uso de la radiación en bosques mediterráneos a partir de datos MODIS. Uso del Indice de Reflectancia Fotoquímica (PRI). Ecosistemas **17**:89-97.

Garbulsky, M. F., J. Peñuelas, D. Papale, J. Ardö, M. L. Goulden, G. Kiely, A. D. Richardson, E. Rotenberg, E. M. Veenendaal, and I. Filella. 2010. Patterns and controls of the variability of radiation use efficiency and primary productivity across terrestrial ecosystems. Global Ecology and Biogeography **19**:253–267.

Garbulsky, M. F., J. Peñuelas, D. Papale, and I. Filella. 2008b. Remote estimation of carbon dioxide uptake of a Mediterranean forest. Global Change Biology **14**:2860–2867.

Gerosa, G., R. Marzuoli, M. Rossini, C. Panigada, M. Meroni, R. Colombo, F. Faoro, and M. Iriti. 2009. A flux-based assessment of the effects of ozone on foliar injury, photosynthesis, and yield of bean (Phaseolus vulgaris L. cv. Borlotto Nano Lingua di Fuoco) in open-top chambers. Environmental Pollution **157**:1727–1736.

Gitelson, A. A., A. Vina, S. B. Verma, D. C. Rundquist, T. J. Arkebauer, G. Keydan, B. Leavitt, V. Ciganda, G. G. Burba, and A. E. Suyker. 2006. Relationship between gross primary production and chlorophyll content in crops: Implications for the synoptic monitoring of vegetation productivity. Journal of Geophysical Research-Atmospheres **111**.

Gobron, N., B. Pinty, O. Aussedat, J. M. Chen, W. B. Cohen, R. Fensholt, V. Gond, K. F. Huemmrich, T. Lavergne, F. Melin, J. L. Privette, I. Sandholt, M. Taberner, D. P. Turner, M. M. Verstraete, and J. L. Widlowski. 2006. Evaluation of fraction of absorbed photosynthetically active radiation products for different canopy radiation transfer regimes: Methodology and results using Joint Research Center products derived from SeaWiFS against ground-based estimations. Journal of Geophysical Research-Atmospheres **111**.

Goerner, A., M. Reichstein, and S. Rambal. 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.

Grace, J., C. Nichol, M. Disney, P. Lewis, T. Quaife, and P. Bowyer. 2007. Can we measure terrestrial photosynthesis from space directly, using spectral reflectance and fluorescence? Global Change Biology **13**:1484-1497.

Guo, J. M., and C. M. Trotter. 2004. Estimating photosynthetic light-use efficiency using the photochemical reflectance index: variations among species. Functional Plant Biology **31**:255-265.

Guo, J. M., and C. M. Trotter. 2006. Estimating photosynthetic light-use efficiency using the photochemical reflectance index: the effects of short-term exposure to elevated CO2 and low temperature. International Journal of Remote Sensing **27**:4677-4684.

Hall, F. G., T. Hilker, N. C. Coops, A. Lyapustin, K. F. Huemmrich, E. Middleton, H. Margolis, G. Drolet, and T. A. Black. 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.

Harris, A. 2008. Spectral reflectance and photosynthetic properties of Sphagnum mosses exposed to progressive drought. Ecohydrology **1**:35-42.

Hilker, T., N. C. Coops, S. B. Coggins, M. A. Wulder, M. Brown, T. A. Black, Z. Nesic, and D. Lessard. 2009a. Detection of foliage conditions and disturbance from multi-angular high spectral resolution remote sensing. Remote Sensing of Environment **113**:421-434.

Hilker, T., N. C. Coops, F. G. Hall, T. A. Black, M. A. Wulder, Z. Nesic, and P. Krishnan. 2008. Separating physiologically and directionally induced changes in PRI using BRDF models. Remote Sensing of Environment **112**:2777-2788.

Hilker, T., A. Lyapustin, F. G. Hall, Y. Wang, N. C. Coops, G. Drolet, and T. A. Black. 2009b. 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.

Huemmrich, K. F., J. A. Gamon, C. E. Tweedie, S. F. Oberbauer, G. Kinoshita, S. Houston, A. Kuchy, R. D. Hollister, H. Kwon, M. Mano, Y. Harazono, P. J. Webber, and W. C. Oechel. 2010. Remote sensing of tundra gross ecosystem productivity and light use efficiency under varying temperature and moisture conditions. Remote Sensing of Environment **114**:481-489

Inamullah, and A. Isoda. 2005. Adaptive responses of soybean and cotton to water stress II. Changes in CO2 assimilation rate, chlorophyll fluorescence and photochemical reflectance index in relation to leaf temperature. Plant Production Science **8**:131-138.

Inoue, Y., and J. Peñuelas. 2006. Relationship between light use efficiency and photochemical reflectance index in soybean leaves as affected by soil water content. International Journal of Remote Sensing **27**:5109-5114.

Inoue, Y., J. Peñuelas, A. Miyata, and M. Mano. 2008. Normalized difference spectral indices for estimating photosynthetic efficiency and capacity at a canopy scale derived from hyperspectral and CO2 flux measurements in rice. Remote Sensing of Environment **112**:156-172.

Jacquemoud, S., W. Verhoef, F. Baret, C. Bacour, P. J. Zarco-Tejada, G. P. Asner, C. Francois, and S. L. Ustin. 2009. PROSPECT plus SAIL models: A review of use for vegetation characterization. Remote Sensing of Environment **113**:S56-S66.

Kaufman, Y. J. 1989. The atmospheric effect on remote sensing and its correction. Pages 336-428 *in* G. Asrar, editor. Theory and applications of optical remote sensing. John Wiley & Sons, Inc., New York.

Landsberg, J. J., and R. H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. Forest Ecology and Management **95**:209-228.

Le Quere, C., M. R. Raupach, J. G. Canadell, G. Marland, L. Bopp, P. Ciais, T. J. Conway, S. C. Doney, R. A. Feely, P. Foster, P. Friedlingstein, K. Gurney, R. A. Houghton, J. I. House, C. Huntingford, P. E. Levy, M. R. Lomas, J. Majkut, N. Metzl, J. P. Ometto, G. P. Peters, I. C. Prentice, J. T. Randerson, S. W. Running, J. L. Sarmiento, U. Schuster, S. Sitch, T. Takahashi, N. Viovy, G. R. v. d. Werf, and F. I. Woodward. 2009. Trends in the sources and sinks of carbon dioxide. Nature Geoscience **doi:10.1038/ngeo689**.

Letts, M. G., C. A. Phelan, D. R. E. Johnson, and S. B. Rood. 2008. Seasonal photosynthetic gas exchange and leaf reflectance characteristics of male and female cottonwoods in a riparian woodland. Tree Physiology **28**:1037-1048.

Louis, J., A. Ounis, J. M. Ducruet, S. Evain, T. Laurila, T. Thum, M. Aurela, G. Wingsle, L. Alonso, R. Pedros, and I. Moya. 2005. Remote sensing of sunlight-induced chlorophyll fluorescence and reflectance of Scots pine in the boreal forest during spring recovery. Remote Sensing of Environment **96**:37-48.

Lovelock, C. E., and S. A. Robinson. 2002. Surface reflectance properties of Antarctic moss and their relationship to plant species, pigment composition and photosynthetic function. Plant Cell and Environment **25**:1239-1250.

Malenovsky, Z., K. B. Mishra, F. Zemek, U. Rascher, and L. Nedbal. 2009. Scientific and technical challenges in remote sensing of plant canopy reflectance and fluorescence. Journal of Experimental Botany **60**:2987-3004.

Mänd, P., L. Hallik, J. Peñuelas, T. Nilson, P. Duce, B. A. Emmet, C. Beier, M. Estiarte, J. Garadnai, T. Kalapos, I. K. Schmidt, E. Kovács-Láng, P. Prieto, A. Tietema, J. W. Westerveld, and O. Kull. 2010. Responses of the reflectance indices PRI and NDVI to experimental warming and drought in European shrublands along a north-south climatic gradient. Remote Sensing of Environment **114**:626-636.

Martin, R., G. Asner, and L. Sack. 2007. Genetic variation in leaf pigment, optical and photosynthetic function among diverse phenotypes of Metrosideros polymorpha grown in a common garden. Oecologia **151**:387-400.

Martin, R. E., and G. P. Asner. 2009. Leaf Chemical and Optical Properties of Metrosideros polymorpha Across Environmental Gradients in Hawaii. Biotropica **41**:292-301.

Matsubara, S., G. H. Krause, M. Seltmann, A. Virgo, T. A. Kursar, P. Jahns, and K. Winter. 2008. Lutein epoxide cycle, light harvesting and photoprotection in species of the tropical tree genus *Inga*. Plant, Cell & Environment **31**:548-561.

Meroni, M., V. Picchi, M. Rossini, S. Cogliati, C. Panigada, C. Nali, G. Lorenzini, and R. Colombo. 2008a. Leaf level early assessment of ozone injuries by passive fluorescence and photochemical reflectance index. International Journal of Remote Sensing **29**:5409-5422.

Meroni, M., M. Rossini, V. Picchi, C. Panigada, S. Cogliati, C. Nali, and R. Colombo. 2008b. Assessing steady-state fluorescence and PRI from hyperspectral proximal sensing as early indicators of plant stress: The case of ozone exposure. Sensors **8**:1740-1754.

Methy, M. 2000. Analysis of photosynthetic activity at the leaf and canopy levels from reflectance measurements: a case study. Photosynthetica **38**:505-512.

Methy, M., R. Joffre, and S. Rambal. 1999. Remote sensing of canopy photosynthetic performances: Two complementary ways for assessing the photochemical reflectance index. Photosynthetica **37**:239-247.

Middleton, E. M., Y. B. Cheng, T. Hilker, T. A. Black, P. Krishnan, N. C. Coops, and K. F. Huemmrich. 2009. Linking foliage spectral responses to canopy-level ecosystem photosynthetic light-use efficiency at a Douglas-fir forest in Canada. Canadian Journal of Remote Sensing **35**:166-188.

Moncrieff, J. B., Y. Malhi, and R. Leuning. 1996. The propagation of errors in long-term measurements of land-atmosphere fluxes of carbon and water. Global Change Biology **2**:231-240.

Monteith, J. L. 1977. Climate and the efficiency of crop production in Britain. Philosophical Transactions of the Royal Society B: Biological Sciences **281**:277-294.

Moran, J. A., A. K. Mitchell, G. Goodmanson, and K. A. Stockburger. 2000. Differentiation among effects of nitrogen fertilization treatments on conifer seedlings by foliar reflectance: a comparison of methods. Tree Physiology **20**:1113-1120.

Myneni, R. B., S. O. Los, and G. Asrar. 1995. Potential Gross Primary Productivity of

Terrestrial Vegetation from 1982-1990. Geophysical Research Letters **22**:2617-2620.

Nakaji, T., R. Ide, H. Oguma, N. Saigusa, and Y. Fujinuma. 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., R. Ide, K. Takagi, Y. Kosugi, S. Ohkubo, K. N. Nasahara, N. Saigusa, and H. Oguma. 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., H. Oguma, and Y. Fujinuma. 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.

Naumann, J. C., J. E. Anderson, and D. R. Young. 2008a. Linking physiological responses, chlorophyll fluorescence and hyperspectral imagery to detect salinity stress using the physiological reflectance index in the coastal shrub, Myrica cerifera. Remote Sensing of Environment **112**:3865-3875.

Naumann, J. C., D. R. Young, and J. E. Anderson. 2008b. Leaf chlorophyll fluorescence, reflectance, and physiological response to freshwater and saltwater flooding in the evergreen shrub, Myrica cerifera. Environmental and Experimental Botany **63**:402-409.

Naumann, J. C., D. R. Young, and J. E. Anderson. 2009. Spatial variations in salinity stress across a coastal landscape using vegetation indices derived from hyperspectral imagery. Plant Ecology **202**:285-297.

Nichol, C. J., K. F. Huemmrich, T. A. Black, P. G. Jarvis, C. L. Walthall, J. Grace, and F. G. Hall. 2000. Remote sensing of photosynthetic-light-use efficiency of boreal forest. Agricultural and Forest Meteorology **101**:131-142.

Nichol, C. J., J. Lloyd, O. Shibistova, A. Arneth, C. Roser, A. Knohl, S. Matsubara, and J. Grace. 2002. Remote sensing of photosynthetic-light-use efficiency of a Siberian boreal forest. Tellus Series B-Chemical and Physical Meteorology **54**:677-687.

Nichol, C. J., U. Rascher, S. Matsubara, and B. Osmond. 2006. Assessing photosynthetic efficiency in an experimental mangrove canopy using remote sensing and chlorophyll fluorescence. Trees-Structure and Function **20**:9-15.

Niyogi, K. K. 1999. Photoprotection revisited: Genetic and molecular approaches. Annual Review Plant Physiology and Plant Molecular Biology **50**:333-359.

Numata, I., D. A. Roberts, O. A. Chadwick, J. Schimel, F. R. Sampaio, F. C. Leonidas, and J. V. Soares. 2007. Characterization of pasture biophysical properties and the impact of grazing intensity using remotely sensed data. Remote Sensing of Environment **109**:314-327.

Ogaya, R., and J. Peñuelas. 2003. Comparative seasonal gas exchange and chlorophyll fluorescence of thwo dominant woody species in a Holm Oak Forest. Flora **198**:132-141.

Ollinger, S. V., A. D. Richardson, M. E. Martin, D. Y. Hollinger, S. E. Frolking, P. B. Reich, L. C. Plourde, G. G. Katul, J. W. Munger, R. Oren, M. L. Smith, K. T. Paw U, P. V. Bolstad, B. D. Cook, M. C. Day, T. A. Martin, R. K. Monson, and H. P. Schmid. 2008. Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: Functional relations and potential climate feedbacks. Proceedings of the National Academy of Sciences **105**:19336-19341.

Panigada, C., M. Rossini, M. Meroni, R. Marzuoli, G. Gerosa, and R. Colombo. 2009. Indicators of ozone effects on Fagus sylvatica L. by means of spectroradiometric measurements. Rivista Italiana Di Telerilevamento **41**:3-20.

Peguero-Pina, J. J., F. Morales, J. Flexas, E. Gil-Pelegrin, and I. Moya. 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., and I. Filella. 1998. Visible and near-infrared reflectance techniques for diagnosing plant physiological status. Trends in Plant Science **3**:151-156.

Peñuelas, J., I. Filella, and J. A. Gamon. 1995. Assessment of photosynthetic radiation-use efficiency with spectral reflectance. New Phytologist **131**:291-296.

Peñuelas, J., I. Filella, J. A. Gamon, and C. Field. 1997a. Assessing photosynthetic radiation-use efficiency of emergent aquatic vegetation from spectral reflectance. Aquatic Botany **58**:307-315.

Peñuelas, J., I. Filella, J. Llusia, D. Siscart, and J. Piñol. 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., J. A. Gamon, A. L. Fredeen, J. Merino, and C. B. Field. 1994. Reflectance Indexes Associated with Physiological-Changes in Nitrogen-Limited and Water-Limited Sunflower Leaves. Remote Sensing of Environment **48**:135-146.

Peñuelas, J., and Y. Inoue. 2000. Reflectance assessment of canopy CO2 uptake. International Journal of Remote Sensing **21**:3353-3356.

Peñuelas, J., and J. Llusia. 2002. Linking photorespiration, monoterpenes and thermotolerance in Quercus. New Phytologist **155**:227-237.

Peñuelas, J., J. Llusia, J. Pinol, and I. Filella. 1997b. Photochemical reflectance index and leaf photosynthetic radiation-use-efficiency assessment in Mediterranean trees. International Journal of Remote Sensing **18**:2863-2868.

Peñuelas, J., S. Munne-Bosch, J. Llusia, and I. Filella. 2004. Leaf reflectance and photo- and antioxidant protection in field-grown summer-stressed Phillyrea angustifolia. Optical signals of oxidative stress? New Phytologist **162**:115-124.

Pohl, C., and J. L. Van Genderen. 1998. Multisensor image fusion in remote sensing: concepts, methods and applications. International Journal of Remote Sensing **19**:823-854.

Raddi, S., S. Cortes, I. Pippi, and F. Magnani. 2005. Estimation of vegetation photochemical processes: an application of the Photochemical Reflectance Index at the San Rossore test site. *in* Proc. of the 3rd ESA CHRIS/Proba Workshop, Frascati, Italy.

Rahman, A. F., V. D. Cordova, J. A. Gamon, H. P. Schmid, and D. A. Sims. 2004. Potential of MODIS ocean bands for estimating CO_2 flux from terrestrial vegetation: A novel approach. Geophysical Research Letters. doi:10.1029/2004GL019778 **31**.

Rahman, A. F., J. A. Gamon, D. A. Fuentes, D. A. Roberts, and D. Prentiss. 2001. Modeling spatially distributed ecosystem flux of boreal forest using hyperspectral indices from AVIRIS imagery. Journal of Geophysical Research, [Atmospheres] **106**:33579-33591.

Rascher, U., C. J. Nichol, C. Small, and L. Hendricks. 2007. Monitoring spatio-temporal dynamics of photosynthesis with a portable hyperspectral imaging system. Photogrammetric Engineering and Remote Sensing **73**:45-56.

Reichstein, M., Falge E, D. Baldocchi, D. Papale, M. Aubinet, P. Berbigier, C. Bernhofer, N. Buchmann, T. Gilmanov, A. Granier, T. Grünwald, K. Havránková, H. Ilvesniemi, D. Janous, A. Knohl, T. Laurila, A. Lohila, D. Loustau, G. Matteucci, T. Meyers, F. Miglietta, J. Ourcival, J. Pumpanen, S. Rambal, E. Rotenberg, M. Sanz, J. Tenhunen, G. Seufert, F. Vaccari, T. Vesala, D. Yakir, and R. Valentini. 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Global Change Biology **11**:1424 -1439.

Richardson, A. D., and G. P. Berlyn. 2002. Changes in foliar spectral reflectance and chlorophyll fluorescence of four temperate species following branch cutting. Tree Physiology **22**:499-506.

Richardson, A. D., G. P. Berlyn, and T. G. Gregoire. 2001. Spectral reflectance of Picea rubens (Pinaceae) and Abies balsamea (Pinaceae) needles along an elevational gradient, Mt. Moosilauke, New Hampshire, USA. American Journal of Botany **88**:667-676.

Ruimy, A., B. Saugier, and G. Dedieu. 1994. Methodology for the estimation of terrestrial net primary production from remotely sensed data. Journal of Geophysical Research **99**:5263–5283.

Running, S. W., and R. R. Nemani. 1988. Relating seasonal patterns of the AVHRR vegetation index to simulated photosynthesis and transpiration of forests in different climates. Remote Sensing of Environment **24**:347-367.

Running, S. W., R. R. Nemani, F. A. Heinsch, M. Zhao, M. Reeves, and H. Hashimoto. 2004. A continuous satellite-derived measure of global terrestrial primary production. Bioscience **54**:547-560.

Runyon, J., R. H. Waring, S. N. Goward, and J. M. Welles. 1994. Environmental limits on net primary production and light-use efficiency across the Oregon Transect. Ecological Applications **4**:226-237.

Serrano-Ortiz, P., M. Roland, S. Sanchez-Moral, I. A. Janssens, F. Domingo, Y. Goddéris, and A. S. Kowalski. 2010. Hidden, abiotic CO_2 flows and gaseous reservoirs in the terrestrial carbon cycle: Review and perspectives. Agricultural and Forest Meteorology **150**:321-329.

Serrano, L., and J. Peñuelas. 2005. Assessing forest structure and function from spectral transmittance measurements: a case study in a Mediterranean holm oak forest. Tree Physiology **25**:67-74.

Sims, D. A., and J. A. Gamon. 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.

Sims, D. A., H. Luo, S. Hastings, W.C. Oechel, A. F. Rahman, and J. A. Gamon. 2006a. Parallel adjustments in vegetation greenness and ecosystem CO_2 exchange in response to drought in a Southern California chaparral ecosystem. Remote Sensing of Environment **103**:289-303.

Sims, D. A., A. F. Rahman, V. D. Cordova, B. Z. El-Masri, D. D. Baldocchi, P. V. Bolstad, L. B. Flanagan, A. H. Goldstein, D. Y. Hollinger, L. Misson, R. K. Monson, W. C. Oechel, H. P. Schmid, S. C. Wofsy, and L. Xu. 2008. A new model of gross primary productivity for North American ecosystems based solely on the enhanced vegetation index and land surface temperature from MODIS. Remote Sensing of Environment **112**:1633-1646.

Sims, D. A., A. F. Rahman, V. D. Cordova, B. Z. El-Masri, D. D. Baldocchi, L. B. Flanagan, A. H. Goldstein, D. Y. Hollinger, L. Misson, R. K. Monson, W. C. Oechel, H. P. Schmid, S. C. Wofsy, and L. K. Xu. 2006b. On the use of MODIS EVI to assess gross primary productivity of North American ecosystems. Journal of Geophysical Research-Biogeosciences G04015, doi:10.1029/ 2006JG000162 **111**.

Strachan, I. B., E. Pattey, and J. B. Boisvert. 2002. Impact of nitrogen and environmental conditions on corn as detected by hyperspectral reflectance. Remote Sensing of Environment **80**:213-224.

Strachan, I. B., E. Pattey, C. Salustro, and J. R. Miller. 2008. Use of hyperspectral remote sensing to estimate the gross photosynthesis of agricultural fields. Canadian Journal of Remote Sensing **34**:333-341.

Stylinski, C. D., J. A. Gamon, and W. C. Oechel. 2002. Seasonal patterns of reflectance indices, carotenoid pigments and photosynthesis of evergreen chaparral species. Oecologia **131**:366-374.

Stylinski, C. D., W. C. Oechel, J. A. Gamon, D. T. Tissue, F. Miglietta, and A. Raschi. 2000. Effects of lifelong CO_2 enrichment on carboxylation and light utilization of *Quercus pubescens* Willd. examined with gas exchange, biochemistry and optical techniques. Plant Cell and Environment **23**:1353-1362.

Suárez, L., P. J. Zarco-Tejada, G. Sepulcre-Cantó, O. Pérez-Priego, J. R. Miller, J. C. Jiménez-Muñoz, and J. Sobrino. 2008. Assessing canopy PRI for water stress detection with diurnal airborne imagery. Remote Sensing of Environment **112**:560-575.

Tambussi, E. A., J. Casadesus, S. M. Munne-Bosch, and J. L. Araus. 2002. Photoprotection in water-stressed plants of durum wheat (Triticum turgidum var. durum): changes in chlorophyll fluorescence, spectral signature and photosynthetic pigments. Functional Plant Biology **29**:35-44.

Trotter, G. M., D. Whitehead, and E. J. Pinkney. 2002. The photochemical reflectance index as a measure of photosynthetic light use efficiency for plants with varying foliar nitrogen contents. International Journal of Remote Sensing **23**:1207-1212.

Valentini, R., G. Matteucci, A. J. Dolman, E. D. Schulze, C. Rebmann, E. J. Moors, A. Granier, P. Gross, N. O. Jensen, K. Pilegaard, A. Lindroth, A. Grelle, C. Bernhofer, T. Grunwald, M. Aubinet, R. Ceulemans, A. S. Kowalski, T. Vesala, U. Rannik, P. Berbigier, D. Loustau, J. Guomundsson, H. Thorgeirsson, A. Ibrom, K. Morgenstern, R. Clement, J. Moncrieff, L. Montagnani, S. Minerbi, and P. G. Jarvis. 2000. Respiration as the main determinant of carbon balance in European forests. Nature **404**:861-865.

Van Gaalen, K. E., L. B. Flanagan, and D. R. Peddle. 2007. Photosynthesis, chlorophyll fluorescence and spectral reflectance in Sphagnum moss at varying water contents. Oecologia **153**:19-28.

Verrelst, J., M. E. Schaepman, B. Koetz, and M. Kneubuhler. 2008. Angular sensitivity analysis of vegetation indices derived from CHRIS/PROBA data. Remote Sensing of Environment **112**:2341-2353.

Weng, J. H., Y. N. Chen, and T. S. Liao. 2006a. Relationships between chlorophyll fluorescence parameters and photochemical reflectance index of tree species adapted to different temperature regimes. Functional Plant Biology **33**:241-246.

Weng, J. H., L. H. Jhaung, J. Y. Jiang, G. M. Lai, and T. S. Liao. 2006b. Down-regulation of photosystem 2 efficiency and spectral reflectance in mango leaves under very low irradiance and varied chilling treatments. Photosynthetica **44**:248-254.

Weng, J. H., K. M. Lai, T. S. Liao, M. Y. Hwang, and Y. N. Chen. 2009. Relationships of photosynthetic capacity to PSII efficiency and to photochemical reflectance index of Pinus taiwanensis through different seasons at high and low elevations of sub-tropical Taiwan. Trees-Structure and Function **23**:347-356.

Weng, J. H., T. S. Liao, M. Y. Hwang, C. C. Chung, C. P. Lin, and C. H. Chu. 2006c. Seasonal variation in photosystem II efficiency and photochemical reflectance index of evergreen trees and perennial grasses growing at low and high elevations in subtropical Taiwan. Tree Physiology **26**:1097-1104.

Whitehead, D., N. T. Boelman, M. H. Turnbull, K. L. Griffin, D. T. Tissue, M. M. Barbour, J. E. Hunt, S. J. Richardson, and D. A. Peltzer. 2005. Photosynthesis and reflectance indices for rainforest species in ecosystems undergoing progression and retrogression along a soil fertility chronosequence in New Zealand. Oecologia **144**:233-244.

Winkel, T., M. Methy, and F. Thenot. 2002. Radiation use efficiency, chlorophyll fluorescence, and reflectance indices associated with ontogenic changes in water-limited Chenopodium quinoa leaves. Photosynthetica **40**:227-232.

Wu, C. Y., Z. Niu, Q. Tang, and W. J. Huang. 2009. Effects of N, K Fertilization on the Relationship between Photosynthetic Light Use Efficiency and Photochemical Reflectance Index (PRI). Spectroscopy and Spectral Analysis **29**:455-458.

Yamano, H., J. Chen, Y. Zhang, and M. Tamura. 2006. Relating photosynthesis of biological soil crusts with reflectance: preliminary assessment based on a hydration experiment. International Journal of Remote Sensing **27**:5393-5399.

Zhou, Q. F., and J. H. Wang. 2003. Leaf and spike reflectance spectra of rice with contrasting nitrogen supplemental levels. International Journal of Remote Sensing **24**:1587-1593.

Chapter 3

Patterns and controls of the variability of radiation use efficiency and primary productivity across terrestrial ecosystems

ABSTRACT

Aim The controls of gross radiation use efficiency (RUE), the ratio between gross primary productivity (GPP) and the radiation intercepted by terrestrial vegetation, and its spatial and temporal variation are not yet fully understood. Our objectives were to analyse and synthesize the spatial variability of GPP and the spatial and temporal variability of RUE and its climatic controls for a wide range of vegetation types.

Location A global range of sites from tundra to rain forest.

Methods We analysed a global dataset on photosynthetic uptake and climatic variables from 35 eddy covariance (EC) flux sites spanning between 100 and 2200 mm mean annual rainfall and between -13 and 26°C mean annual temperature. RUE was calculated from the data provided by EC flux sites and remote sensing (MODIS).

Results Rainfall and actual evapotranspiration (AET) positively influenced the spatial variation of annual GPP, whereas temperature only influenced the GPP of forests. Annual and maximum RUE were also positively controlled primarily by annual rainfall. The main control parameters of the growth season variation of gross RUE varied for each ecosystem type. Overall, the ratio between actual and potential evapotranspiration and a surrogate for the energy balance explained a greater proportion of the seasonal variation of RUE than the vapour pressure deficit (VPD), AET and precipitation. Temperature was important for determining the intra-annual variability of the RUE at the coldest energy-limited sites.

Main conclusions Our analysis supports the idea that the annual functioning of vegetation that is adapted to its local environment is more constrained by water availability than by temperature. The spatial variability of annual and maximum RUE can be largely explained by annual precipitation, more than by vegetation type. The intra-annual variation of RUE was mainly linked to the energy balance and water availability along the climatic gradient. Furthermore, we showed that intra-annual variation of gross RUE is only weakly influenced by VPD and temperature, contrary to what is frequently assumed. Our results provide a better understanding of the spatial and temporal controls of the RUE and thus could lead to a better estimation of ecosystem carbon fixation and better modelling.

Keywords Carbon cycle, climatic controls, eddy covariance, gross primary productivity, radiation use efficiency, remote sensing, terrestrial vegetation.

1. INTRODUCTION

At present one of the most important endeavours of ecosystem ecologists is to estimate the photosynthetic carbon uptake by vegetation, its spatial and temporal variability and to understand what controls this variability (Schulze, 2006). Estimates of carbon uptake by terrestrial vegetation at different spatial and temporal scales are often based on the radiation use efficiency (RUE) model (Monteith, 1972). This model proposed that photosynthetic uptake of the vegetation depends on the amount of radiation absorbed by the vegetation and on the efficiency with which the vegetation transforms the absorbed radiation into plant biomass, namely the RUE) (Ruimy *et al.*, 1994):

$$GPP = PAR \times FPAR \times RUE \quad (1)$$

where GPP is the gross primary productivity, PAR is the incident photosynthetically active radiation (400–700 nm), FPAR is the fraction of PAR absorbed by the vegetation, and RUE is the gross radiation use efficiency. The product of PAR and FPAR, namely APAR, is the PAR absorbed by the vegetation. The simplicity of the model makes it attractive and therefore useful for estimating the photosynthetic uptake of vegetation at different spatial and temporal scales. Remote sensing techniques to estimate the photosynthetic uptake of terrestrial vegetation are commonly based on this model because it is possible to estimate FPAR from remotely sensed data (Tucker & Sellers, 1986).

Eddy covariance (EC) methods are an important tool for estimating fluxes of CO2, water and energy at the ecosystem scale, between terrestrial ecosystems and the atmosphere, and, nowadays, for a large number of locations world-wide (Baldocchi, 2008). Moreover, this methodology can be used to measure fluxes in most vegetation types, thus producing comparable datasets between contrasting sites, which constitutes a valuable dataset for validating remote sensing methods (Baldocchi, 2008).

Different studies have assessed the control of the annual carbon uptake by terrestrial vegetation and the components of the RUE model. Annual FPAR for a wide range of biomes from grasslands to rain forests is known to be positively controlled by rainfall (Garbulsky & Paruelo, 2004). The availability of water is also considered to be a main control on carbon uptake (Reichstein *et al.*, 2007). Above-ground net primary productivity (ANPP) is strongly influenced across biomes by actual evapotranspiration (AET; Rosenzweig, 1968; Lieth, 1975) and also by precipitation (Lieth, 1975; Huxman *et al.*, 2004). The controls on the spatial variability of GPP are currently being elucidated. Firstly, Valentini *et al.* (2000) showed that GPP does not depend on latitudinal changes for a wide range of European forests. Later works (Law *et al.*, 2002) showed that the mean annual temperature (MAT) and the site water balance explain much of the variation in GPP across different biomes. Globally, the GPP of forests increases with higher temperatures and precipitation (Luyssaert *et al.*, 2007a). Others suggest that water availability is the main control of GPP for southern European forests, while temperature is considered the most important control for northernmost forests (Reichstein *et al.*, 2007). Along a wide diversity of Asian ecosystems, both precipitation and temperature are considered to be the main determinants of GPP (Kato & Tang, 2008).

The seasonal variability of carbon uptake, as related to FPAR and RUE, depends on the structural and physiological constraints on ecosystem functioning. The ability to estimate the seasonality of photosynthetic uptake of vegetation from leaf area or other surrogates such as FPAR depends on the coupling of the seasonality of absorbed radiation and the photosynthetic RUE to the environmental constraints on plant growth (Bondeau *et al.*, 1999). Strong seasonal and positive coupling of leaf area and photosynthesis occur in vegetation types such as tundra (Boelman *et al.*, 2005), temperate deciduous forests (Waring *et al.*, 1995) and annual crops, where leaf area, PAR and climatic limitations also covary throughout the growing season. Although strong correlation between seasonal changes in FPAR and carbon uptake can occur in some evergreen vegetation (Sims *et al.*, 2006), a lack of seasonal change in FPAR and a low correlation with carbon uptake occurs in many evergreen vegetation types such as rainforests or Mediterranean forests (Sims *et al.*, 2006; Garbulsky *et al.*, 2008).

In contrast to our knowledge of the relationship between carbon uptake and FPAR, RUE is a less well known parameter than the other components of the RUE model, particularly for different vegetation types and along different time-scales. It is certainly the most elusive of the model terms, since it is not possible to measure it directly as it depends on estimates of GPP and absorbed radiation (Gower *et al.*, 1999; Schwalm *et al.*, 2006). In general, vegetation type alone is assumed to be the main control of RUE at the annual scale, but there is a large scatter of RUE values within each vegetation type (Ruimy *et al.*, 1994; Gower *et al.*, 1999). Forest age or management practices, for example, have been described as controls of RUE values at annual scales (Landsberg *et al.*, 1997). Nutritional status, such as foliar nitrogen concentration, could be another driver of spatial and temporal variability in RUE (Mäkelä *et al.*, 2008; Ollinger *et al.*, 2008). However, this may operate mostly at local scales since there is a wide dispersion in the data on the relation between foliar nitrogen concentration and the maximum rate of photosynthesis among different vegetation types (Woodward & Smith, 1995). There is little evidence for relationships between the spatial variability of RUE for different vegetation types and climatic or biogeochemical controls (Turner *et al.*, 2003; Still *et al.*, 2004). Furthermore, a substantial number of those relationships were derived from models rather than using evidence from actual measurements.

At short time-scales (hours to days), environmental stresses (water, temperature) have been shown to modify RUE (Russell *et al.*, 1989). For annual crops, variability in RUE was negatively related to vapour pressure deficit (VPD, Kiniry *et al.*, 1998) and positively related to temperature (Andrade *et al.*, 1993).Variability in RUE was also positively related to temperature in forests (Landsberg & Waring, 1997). For other vegetation types such as shrublands, only a few studies have examined the temporal variation of gross RUE (Sims *et al.*, 2005; Turner *et al.*, 2005), and its biophysical controls are not yet well understood. Nevertheless, several terrestrial models that estimate the seasonality of primary productivity use RUE as an input (Haxeltine & Prentice, 1996; Ruimy *et al.*, 1999). The maximum or potential RUE is set as a constant and is subsequently downregulated by minimum temperature and different estimators of water stress in models that estimate GPP (Potter *et al.*, 1999; Running *et al.*, 2004; Yuan *et al.*, 2007; Mäkelä *et al.*, 2008). Different strategies to define the maximum RUE values and each of the coefficients that account for the stress effects are used to estimate the actual RUE. The maximum RUE is commonly set as a universal invariant across sites and biomes or it is defined for each vegetation type. This assumption of a global constant maximum RUE for different sites within a given biome is far from optimum and is the possible cause of the low performance of the photosynthetic uptake models (Heinsch et al., 2006). The surrogates of water stress to estimate the actual RUE from the downregulation of the maximum RUE vary between models and, as far as we know, to date there has been no evaluation of the different strategies. The possibility of estimating FPAR from several remotely sensed vegetation indices [i.e. the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI)], adds another dimension to the problem.

The EC technique provides an excellent opportunity to test the relationships between carbon uptake and its environmental drivers. In addition, remote sensing data provide a way to gather intercepted radiation from around the globe. In this study we provide evidence about the gross RUE variability estimated from carbon flux data provided by EC flux sites and FPAR estimates from satellite observations in rain forests, deciduous and evergreen forests, grasslands, crops and tundra. The objectives of this study were to analyse and synthesize: (1) the spatial and temporal variability of GPP and RUE for a wide range of vegetation types and from two surrogates for FPAR; and (2) the climatic controls of RUE at global and local scales. We sought to answer whether the spatial variability of mean climatic variables (i. e. precipitation, temperature and AET) are quantitatively more important determinants of the gross RUE than the vegetation types. Furthermore, we hypothesized that the strength of the relationships between temporal variability of gross RUE throughout the growing season and the climatic variables are related to the mean climatic characteristics of the sites.

2. MATERIALS AND METHODS

We analysed EC data of carbon fluxes and FPAR MODIS (Moderate Resolution Imaging Spectroradiometer) Terra data. We synthesized data from 35 sites included in the networks Ameriflux (http://public.ornl.gov/ameriflux/), CarboEurope, CarboAfrica and TCOS-Siberia (http:// gaia.agraria.unitus.it/database/carboeuropeip/). These sites represent different vegetation types distributed throughout Europe, Asia, Africa and America (Table 1, Fig. 1) and cover a great proportion of the global climatic space defined by the range of MAT and mean annual precipitation (MAP). The selected sites comprised homogeneous stands of each vegetation type and were large enough to gather the spectral reflectance of the stand with the satellite images. We discarded sites representing small stands and those adjacent to contrasting land covers (i.e. water bodies, urban) to minimize problems or errors related to tower footprint. Different periods between January 2001 and December 2007 were analysed including at least one complete growing season for each site (Table 1), making a total of 90 growing seasons.

GPP was estimated from the Net Ecosystem Exchange (NEE) fluxes measured at the EC towers with 30′resolution using a standardized partitioning method for all the sites as described by Reichstein *et al.* (2005) and Papale *et al.* (2006). We discarded GPP values lower than 0.1 mmol m^{-2} s^{-1} for our analysis. An average for the 8-day composites of the half-hour values for GPP (gC m^{-2} day^{-1}) and incoming PAR (MJ m^{-2} day^{-1}), derived from the EC tower data, was calculated for days having MODIS FPAR data (MOD15A2). These images consist of an 8-day value at 1-km spatial resolution provided by the MODIS team (Myneni *et al.*, 2002). For all the MODIS data, quality flags were checked to discard low-quality images. The basic temporal resolution of the analysis is 8 days, which corresponds to that of the MOD15A2 images. Theoretically, this represents 46 images per year; however, we obtained fewer than this for each year and site owing to a lack of data or at times the bad quality of the MODIS or the EC data. We defined the 8-day gross RUE as:

$$\text{RUE gC MJ APAR}^{-1}\text{)=GPP}\times\text{FPAR}^{-1}\times\text{PAR}^{-1}\ (2)$$

The average annual RUE was calculated as:

$$\text{annual RUE (gC MJ APAR}^{-1}\text{)=total annual GPP (gC m}^{-2}\text{year}^{-1}\text{]}\times\text{APAR}^{-1}\text{ (MJ m}^{-2}\text{ year}^{-1}\text{) (3)}$$

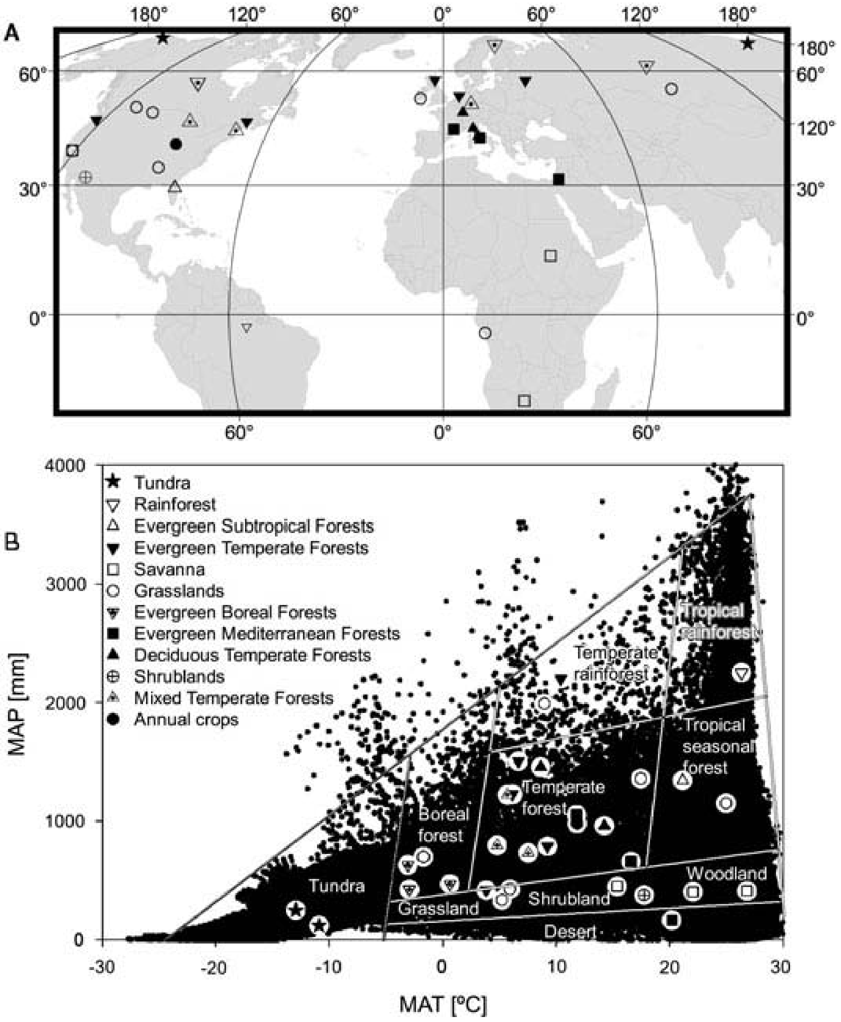


Figure 1 (a) Map of the location of the sites studied (Mollweide projection, central meridian 0°) and (b) their distribution along the climatic space defined by long-term mean annual temperature (MAT) and mean annual precipitation (MAP). The vegetation type symbols represent each site and black points represent 0.5° x 0.5° land pixels from a global climatic database (W. Cramer, pers. comm.; Leemans & Cramer, 1991). Limits between vegetation types are schematic.

To minimize the uncertainties derived from the known quality problems of MODIS FPAR data (e.g. underestimation of winter FPAR in boreal forest; Garrigues *et al.*, 2008) in the calculation of the annual RUE in the northernmost sites (i.e. tundra and boreal sites) we only included GPP and APAR data for the growing season. Since the EVI showed better performance than the MODIS FPAR as an estimator of FPAR for certain vegetation types (Zhang *et al.*, 2006), we also calculated the RUE derived from EVI (RUE EVI), considering EVI = FPAR (Garbulsky *et al.*, 2008). We calculated the EVI from the 8-day MODIS surface reflectance data [MOD09A1 band 1 (620– 670 nm), band 2 (841–876 nm), band 3 (459–479 nm)] as EVI = 2.5 (band 2 -band 1)/(band 2 + 6 band 1 -7.5 band 3 + 1). Finally, we defined the maximum RUE (gC MJ APAR^{-1}) calculated from each FPAR estimator for each site as the maximum gross RUE attained by the vegetation for all the growing seasons analysed. We also calculated the annual GPP/PAR ratio as an overall estimator of the ecosystem efficiency with which the incident radiation is used.

Table 1. Location, main vegetation type, references and standardized climatic features of the sites included in the analysis (MAT: mean annual temperature; MAP: mean annual precipitation). Climatic data derived from the CLIMATE database version 2.1 (W. Cramer, Potsdam, pers. comm., Leemans & Cramer, 1991, http://www.pik-potsdam.de/members/cramer/climate/) and from site measurements (marked with asterisks).

Vegetation	**Site, period analyzed and reference**	**Vegetation category**	**Latitude**	**Longitude**	**MAT (ºC)**	**MAP (mm)**
Tundra	Atqasuk (Alaska, USA) 2006 (Oechel *et al.*, 2000)	Tundra	70° 28' 10.6"	-157° 24' 32"	-10.9	121
Tundra tussock grassland	Cherski (Russia) 2003 (Corradi *et al.*, 2005; Merbold *et al.*, 2009)	Tundra	68º36’53”	161º20’21”	-12.9	249
Mesquite(*Prosopis velutina* Woot.) dominated grassland	Santa Rita mesquite (USA) 2004-05 *(Scott et al., in press)*	Shrubland	31º 48’	-110º 54’	17.7	377*
Grassland northern mixed prairie	Fort Peck- (Montana, USA) 2001-03 (Meyers, 2008b)	Grassland	48º 18’	-105º 6’	5.2	335
Short-grass prairie (dominated by C_3 species) *Stipa comata* Trin. & Rupr, *Koeleria macrantha* (Ledeb.) Schult., *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, *Pascopyrum smithii* (Rydb.) A. Löve;	Lethbridge, (Canada) 2002-03 (Flanagan *et al.*, 2002)	Grassland	49° 42' 33"	-112° 56'24"	5.9	426
Annual C_3 grasses grassland (*Bromus mollis* L., *Taeniatherum asperum* (Sim.) Nevski, *Vulpia megalura* (Nutt.) Rydb., *Trifolium hirtum* All.)	Vaira (USA) 2001 – 02 (Baldocchi *et al.*, 2004)	Grassland	38º 24.42’	-120º 57’	15.3	449
Temperate grassland	Goodwin Creek- (Mississippi USA) 2003 (Meyers, 2008a)	Grassland	34º 15’	-89º 58.2’	17.4	1358
Perennial grassland (*Lolium perenne* L.)	Dripsey (Ireland) 2003 (Byrne *et al.*, 2007; Jaksic *et al.*, 2006)	Grassland	51° 55' 08'' N	8° 45' 04'' W	8.9	1990
Perennial grassland (*Ctenium newtonii* Hack., *Loudetia* sp.)	Tchizalamou (Congo) 2006-07 (Merbold *et al.*, 2008)	Grassland	4° 17' 21'' S	11° 39' 23''	24.9	1150 *

Vegetation	Site, period analyzed and reference	Vegetation category	Latitude	Longitude	MAT ºC	MAP (mm)
Steppe dominated by *Festuca valesiaca* Gaudin, *Koeleria cristata* L., *Stipa krylovi* Roshev., *Cleistogenes squarrosa* Trin., and *Poa botryoides* Trin. ex Griseb	Hakasia steppe (Russia) 2004 (Belelli Marchesini *et al.*, 2007)	Grassland	54º43’30”	90º0’7”	-1.7	699
Savanna dominated by *Quercus douglasii* Hook. & Arn. and *Brachypodium distachyon* (L.) Beauv.	Tonzi (USA) 2002 – 03 (Baldocchi *et al.*, 2004)	Savanna	38º 25.92’	-120º 58.2’	15.3	449
Semiarid Mopane savanna (*Colophospermum mopane* (J,Kirk ex Benth.) J.Kirk ex J.Léonard)	Maun (Botswana) 2000-01 (Veenendaal *et al.*, 2004)	Savanna	23º 33’	-19º54’	22	404
Savanna (*Acacia senegal* Willd., *Aristida pallida* Steud., *Eragrostis tremula* Steud. and *Cenchrus biflorus* Roxb.)	Demokeya (Sudan) 2007 (Sjöström *et al.*, 2009; Ardö *et al.*, 2008)	Savanna	13º16’58”	30º28’42”	26.8	411
Annual crops (corn/soybean)	Bondville, (USA) 2003-05 (Hollinger *et al.*, 2005)	Annual crops	40° 0' 21"	-88° 17' 30"	10.9	973
Broadleaf deciduous. Mediterranean forest (dominated by *Quercus cerris* L.)	Roccarespampani (Italy) 2002-03 (Rey *et al.*, 2002)	Deciduous Temperate Forest	42º 24.48´	11º 55.8´	14.2	961
Broadleaf deciduous temp. forest. (dominated by *Fagus sylvatica* L.)	Hesse (France) 2001-03 (Granier *et al.*, 2002)	Deciduous Temperate Forest	48°40'12"	7° 3'36"	8.6	1453
Mixed broadleaved deciduous, forest dominated by *Fagus sylvatica*	Hainich (Germany) 2002-03 (Kutsch *et al.*, 2008)	Mixed Temperate Forest	51° 04’	10° 27’	7.5	732

Vegetation	**Site, period analyzed and reference**	**Vegetation category**	**Latitude**	**Longitude**	**MAT ºC**	**MAP (mm)**
Old-growth mixed forest (*Acer saccharum* Marshall, *Tilia americana* L., *Tsuga canadensis* (L.) Carrière, *Ostrya virginiana* (Mill.) K.Koch, *Betula alleghaniensis* Britton).	Sylvania (Michigan, USA) 2003 – 05 (Desai *et al.*, 2005)	Mixed Temperate Forest	46° 14' 31.2"	- 89° 20' 51"	4.7	796
Mixed forest dominated by Red Maple (*Acer rubrum* L.), American Beech (*Fagus grandifolia* Ehrh.), Paper Birch (*Betula papyfera* Marsh.) and Eastern Hemlock (*T. canadensis*)	Bartlett Experimental Forest (USA) 2004-05 (Jenkins *et al.*, 2007)	Mixed Temperate Forest	44º 3’ 52”	-71º 17’ 17”	5.6	1222
Scots pine plantation *(Pinus sylvestris* L.)	Loobos (Netherlands) 2001-03 / 05 (Dolman *et al.*, 2002)	Evergreen Temperate Forest	52º 10.08´	5º 44.64´	9.2	788
Conifer forest dominated by red spruce (*Picea rubens* Sarg.) and Eastern hemlock (*T. canadensis*),	Howland Forest (Main Tower, USA) 2000-04 (Hollinger *et al.*, 2004; Hollinger *et al.*, 1999)	Evergreen Temperate Forest	45º 12’ 14”	-68º 44’ 25”	6.1	1226
Conifer plantation dominated by Sitka Spruce (*Picea sitchensis* (Bong.) Carr.)	Griffin (Scotland) 2000-01 (Clement *et al.*, 2003)	Evergreen Temperate Forest	56° 36´ 26" N	3° 47´ 53" W	6.6	1506
Conifer forest dominated by Douglas -fir (*Pseudotsuga menziesii*), Western hemlock (*Tsuga heterophylla*)	Wind River Crane Site (USA) 2000-04 (Chen *et al.*, 2002)	Evergreen Temperate Forest	45º 49’ 13”	-121º 57’ 6”	10.4	2200*
Norway spruce forest (*Picea abies* (L.) H.Karst. 1881)	Fyodorovskoye (Russia) 2002-03 (Milyukova *et al.*, 2002)	Evergreen Temperate forest	56° 27’ 42”	32° 55’ 26”	3.8	418 *
Evergreen coniferous forest Jack pine (*Pinus banksiana* Lamb.), Black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) aspen (*Populus* spp.) and alder (*Alnus* spp.).	UCI 1981 (Canada) 2002 (Goulden *et al.*, 2006)	Evergreen Boreal Forest	55º 51.78’	-98º 29.1’	-2.9	423

Vegetation	**Site, period analyzed and reference**	**Vegetation category**	**Latitude**	**Longitude**	**MAT ºC**	**MAP (mm)**
Evergreen coniferous forest Black spruce, jack pine and aspen.	UCI 1964 burn site (Canada) 2002 (Goulden *et al.*, 2006)	Evergreen Boreal Forest	55º 54.72’	-98º 22.92’	-2.9	423
Needleaf Forest. *Pinus sylvestris* L.	Sodankyla (Finland) 2001 – 03 (Aurela, 2005)	Evergreen Boreal Forest	67° 21' 42.7"	26° 38' 16"	0.6	470
Scots pine forest (*Pinus sylvestris* L.)	Zotino (Russia) 2002 (Tchebakova *et al.*, 2002)	Evergreen Boreal forest	60º44’	89º9’	-3	630
Pinus halepensis Mill. plantation	Yatir (Israel) 2001-02 (Grünzweig *et al.*, 2003; Maseyk *et al.*, 2008)	Evergreen Mediterranean Forest	31º 20.82´	35º 3´	20.2	164
Mediterranean forest (dominated by *Quercus ilex* L.).	Castelporziano (Italy) 2001-05. (Garbulsky *et al.*, 2008)	Evergreen Mediterranean Forest	41º 42´	12º 22´	16.6	658
Mediterranean forest (dominated by *Quercus ilex* L.)	Puechabon (France) 2001-04 (Allard *et al.*, 2008)	Evergreen Mediterranean Forest	43º 44.46´	3º 35.76´	11.8	1054
*Pinus elliottii Engelm.*Needleaf Forest. (new regeneration)	Mize (Florida, USA) 2001-03 (Clark *et al.*, 2004; Gholz & Clark, 2002)	Evergreen Subtropical Forest	29° 45' 53.2"	-82° 14' 41"	21.1	1343
P. elliottii Needleaf Forest. (65 years natural regeneration)	Austin Cary (Florida, USA) 2005 (Clark *et al.*, 2004; Gholz & Clark, 2002; Powell *et al.*, 2008; Powell *et al.*, 2005)	Evergreen Subtropical Forest	29° 44' 17.0"	-82° 13' 7"	21.1	1343
P. elliottii Needleaf Forest (12 years regeneration)	Donaldson (Florida, USA) 2001 – 03 (Clark *et al.*, 2004; Gholz & Clark, 2002; Powell *et al.*, 2008)	Evergreen Subtropical Forest	29° 45' 17.1"	-82° 9' 47"	21.1	1343
Moist tropical forest dominated by large emergent trees (*Manilkara huberi* (Ducke) Chev., *Hymenaea courb*ari L., *Bertholletia excelsa* Humb. & Bonpl., and *Tachigalia* spp.)	Santarem km 67 primary forest (Brazil) 2002 -03 (Saleska *et al.*, 2003)	Rainforest	-2º 54’	-55º	26.3	2252

We analysed the climatic controls of GPP and RUE at the inter-annual and intra-annual scales. For the annual analysis, we calculated the annual value for each of the variables: GPP, gross RUE and maximum gross RUE and the annual precipitation, annual temperature and annual actual evapotranspiration for the corresponding period and long-term MAP and MAT from a global climatic model (W. Cramer, pers. comm., Leemans & Cramer, 1991). ANCOVAs (R Development Core Team, 2008) were used to analyse the contribution of each climatic variable, the vegetation type and their interactions to the spatial variability of RUE.

For the analysis throughout the growing season, we evaluated the controls on the gross RUE by analysing the correlations between RUE and different environmental variables. We averaged the climatic and the flux variables to match the 8-day temporal resolution of the MODIS FPAR and EVI data. We included for this analysis the precipitation and temperature and different estimates of the annual water stress: vapour pressure deficit (VPD), evaporative fraction (EF), potential evapotranspiration (PET), actual evapotranspiration (AET) and the AET/ PET ratio. The VPD was calculated from temperature and relative humidity measurements at the EC towers. EF is a measure of the portion of the available energy used for evapotranspiration and was calculated as LE/(LE + H), where LE is the latent heat (the amount of energy released or absorbed by water during a change of state) and H is the sensible heat flux, both of which are measured at the EC towers. PET was estimated using the Jensen and Haise methodology (Vörösmarty *et al.*, 1998) using air temperature and incident radiation. AET was calculated from the EC LE flux measurements divided by the specific latent heat of vaporization of water. Akaike's information criterion (AIC) was used to select the best correlations between RUE and the environmental variables.

RESULTS

For all sites, there was an appreciable range of long-term MAP (121 mm <MAP <2252 mm) and MAT (-10.9 °C <MAT < 26.3 °C). The mean annual GPP ranged from 122 gC m^{-2} $year^{-1}$ in the tundra site to 3125 gC m^{-2} $year^{-1}$ in the rain forest site.

GPP was positively correlated with MAP, which accounted for 72% of its variance in a logarithmic relationship (Fig. 2a); in contrast, the actual precipitation for the corresponding analysed period accounted only for 56% (P <0.001) of the variance. GPP for all the biomes showed a positive relationship with MAT, with a lower coefficient of determination of 21% (Fig. 2b). In a multiple regression, MAP, MAT and their interaction accounted for 76% of the variability in GPP (GPP =-2615.9 -79.3MAT + 552.4 ln(MAP) + 14.8 ln(MAP)MAT). In contrast, MAT accounted for a great proportion of the spatial variability of GPP when analysing only the subset of the forests sites (GPP = 915.6 + 60.3 MAT; $r^2 = 0.76$; $P < 0.0001$; $n = 18$). When also including the three afforested sites, MAT accounted only for 45% of the variability (GPP = 993 + 49.2 MAT; $r^2 = 0.46$; $P < 0.0001$; n = 21). The relationship between GPP and MAT was also strong when analysing the subset of the northernmost forests (>45° N) with the lowest incoming radiation (GPP = 925.9 + 90.5 MAT; $r^2 = 0.68$; $P < 0.0001$; n = 14). AET also accounted for a high proportion of the variability of GPP for all the sites ($r^2 = 0.70$, Fig. 2c).

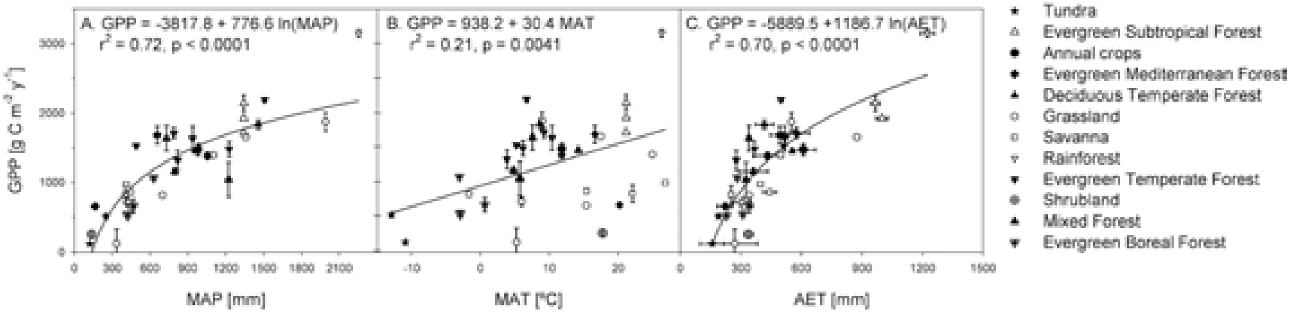


Figure 2 Relationships between gross primary productivity (GPP) and the climate variables. Precipitation (MAP) and temperature (MAT) are long-term annual means from Leemans & Cramer (1991) and actual evapotranspiration derived from eddy covariance towers (AET) is the mean for the studied period. Error bars show the standard errors of GPP and climatic variables for the included growing season for each site.

The average gross annual RUE varied between vegetation types from 0.4 gC MJ^{-1} in the tundra to 1.5 gC MJ^{-1} in the rainforest site (Fig. 3) and the maximum RUE between 0.55 in the tundra and 2.8 gC MJ^{-1} in the annual crops site. Mean and maximum RUE was most variable in grassland. Gross annual RUE varied across vegetation types from 0.34 gC MJ^{-1} in the shrubland to 2.01 gC MJ^{-1} for a grassland site. Gross RUE calculated from EVI presented similar patterns with higher values for both the annual mean and for the maximum RUE (see Appendix 1). Annual RUE EVI was highly correlated with the RUE FPAR across sites ($r = 0.82$, $n = 35$); the correlation was weaker between the maximum RUE EVI and FPAR ($r = 0.52$, $n = 35$).

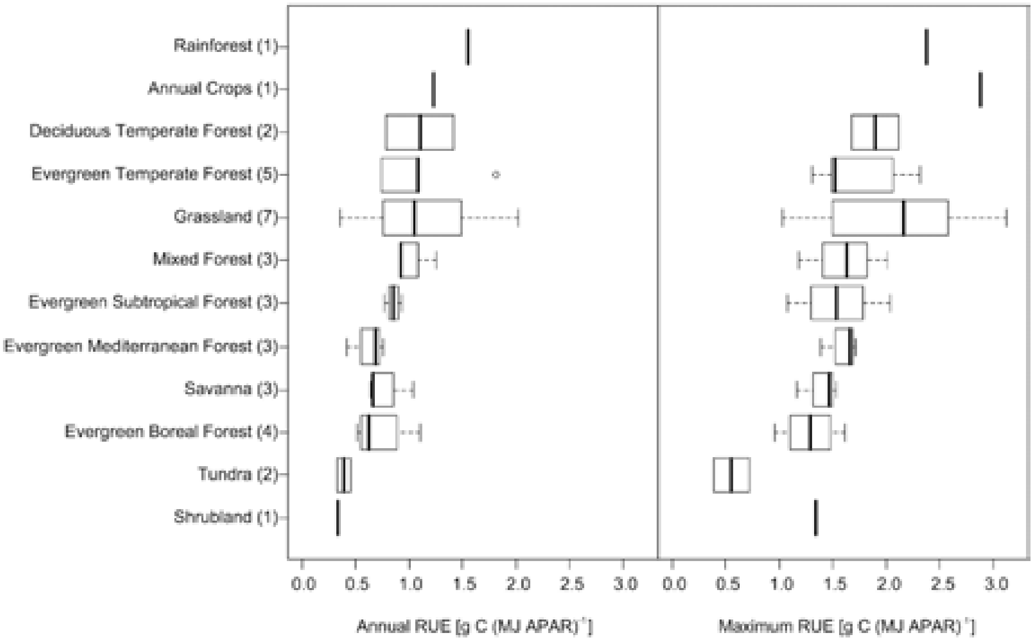


Figure 3 Average gross annual and maximum gross radiation use efficiency (RUE) for the different vegetation types. The numbers of sites included for each vegetation type are shown in brackets. APAR is the product of photosynthetically active radiation (PAR) and the fraction of photosynthetically active radiation absorbed by the vegetation (FPAR). Boxes represent 50% of the data, and the whiskers represent the minimum and maximum values.

MAP accounted for the greatest proportion of the variability of mean RUE FPAR (Table 2). Actual precipitation accounted for a greater proportion of the variability of maximum RUE than long-term MAP. The annual gross RUE was not correlated with temperature and AET accounted for a small part of the spatial variability in RUE (Fig. 4a). The vegetation type and its interaction with the climatic variables did not significantly account for the variability of RUE (Table 2). The relationships between RUE and precipitation did not differ between forests and non-forest sites when considering long-term climate averages or the climate variables for the specific analysed period. RUE was not influenced by temperature, either by interaction of the vegetation type with the climatic variables or by interaction between precipitation and temperature. The dynamics of gross RUE showed a wide range of seasonal patterns between sites. Annual precipitation was the best explanatory variable for maximum RUE (Table 2), which increased along the precipitation gradient (Fig. 4b). Temperature, instead, did not account for any of the variability of maximum RUE. AET explained a smaller portion of the variability than the precipitation (Fig. 4b). Precipitation was also the most important variable to explain the variability of RUE EVI (see Appendix 2); however, precipitation accounted for a lower proportion of the variability of RUE EVI compared with RUE FPAR. Moreover, vegetation type was an important variable to explain the variability of mean and maximum RUE EVI.

The relationships between annual and maximum RUE and the climatic variables were similar to the relationships found using the GPP/PAR ratio, instead of GPP/APAR (data not shown). We also analysed the GPP/PAR ratio as a measure of RUE that provides the overall ecosystem efficiency, instead of the efficiency with which the absorbed radiation is used by the vegetation. The annual mean FPAR accounted for approximately half of the spatial variability of the annual GPP/PAR (results not shown). From the three variables included in the radiation use efficiency model, the FPAR accounted for 62% of the GPP spatial variability. RUE accounted for 53% and the incident PAR did not correlate with GPP (Fig. 5). APAR by itself accounted for 45% of the spatial variability of GPP.

Table 2 Analysis of covariance for mean annual radiation use efficiency (RUE) and maximum RUE across vegetation type (forest, n = 21; non-forest, n = 14) and climatic variables and their interactions: long-term mean annual precipitation (MAP) and long-term mean annual temperature (MAT), and precipitation (precip) and temperature (temp) for the analysed periods.

Mean RUE							Maximum RUE			
Response:	d.f.	Sum of squares	*F* value	*P* value	%*SS*	d.f.	Sum of squares	*F* value	*P* value	%*SS*
Forest	1	0.000	0.002	0.961	0.0	1	0.000	0.000	0.976	0.0
ln(precip)	1	3.215	25.150	<0.0001	46.1	1	7.909	47.986	<0.0001	59.7
temp	1	0.060	0.470	0.499	0.9	1	0.019	0.117	0.734	0.1
Forest x	1	0.009	0.068	0.796	0.1	1	0.095	0.581	0.452	0.7
ln(precip)	1	0.017	0.136	0.715	0.2	1	0.572	3.472	0.073	4.3
Forest x temp	1	0.100	0.784	0.383	1.4	1	0.025	0.156	0.695	0.2
ln(precip) x temp	28	3.579				28	4.615			
Residuals		6.981					13.238			
Total										
Forest	1	0.000	0.003	0.956	0.0	1	0.000	0.000	0.980	0.0
ln(MAP)	1	3.841	37.825	<0.0001	55.0	1	5.091	20.995	<0.0001	38.5
MAT	1	0.004	0.043	0.836	0.1	1	0.530	2.186	0.150	4.0
Forest x ln(MAP)	1	0.288	2.832	0.103	4.1	1	0.578	2.383	0.134	4.4
Forest x MAT	1	0.001	0.005	0.943	0.0	1	0.092	0.380	0.542	0.7
ln(MAP) x MAT	1	0.003	0.026	0.872	0.0	1	0.155	0.639	0.431	1.2
Residuals	28	2.844				28	6.790			
Total		6.981					13.238			

Throughout the growing season, RUE FPAR and RUE EVI had a range of responses to the variability of the environmental factors depending on the site. The coefficients of correlation varied from -0.8 to 0.9 and non-significant correlations, and the slopes of the relationships also varied. Examples of the relationships between RUE FPAR and the environmental variables for contrasting vegetation types can be seen in Fig. 6. The general patterns of the relationships were similar when analysing RUE FPAR or RUE EVI (see Appendix 3). Strong and positive relationships, varying with the environmental variable ($0.77 \leq r \leq 0.95$), were found for the correlations between RUE FPAR and RUE EVI when comparing all the sites.

During the 8-day periods RUE correlated poorly or not at all with precipitation, presumably because of the large buffering provided by antecedent soil water content. There was contrast between the negative effects of within-season temperature and VPD variation on RUE in the warmer sites (i.e. rain forest, savannas, Mediterranean forest and probably subtropical forest) and the positive effects in the cooler ecosystems. Depending on the site, VPD and AET accounted positively or negatively for part of the variation in RUE. MAT accounted for the variability of the temporal relationship between RUE and temperature. In the colder ecosystems, RUE increased with temperature, AET and AET/PET. In the savanna RUE decreased with temperature and increased with AET and AET/PET. In the Mediterranean forest, RUE also decreased with temperature and AET, but increased with AET/PET. EF accounted for the variability of RUE FPAR for the largest number of sites (28 sites) compared with other variables and with the highest coefficient of correlation for 22 of them (see Table S1). AET accounted for the variability of RUE EVI at the greatest number of sites (28 sites), but EF also accounted for a large number of sites (27).

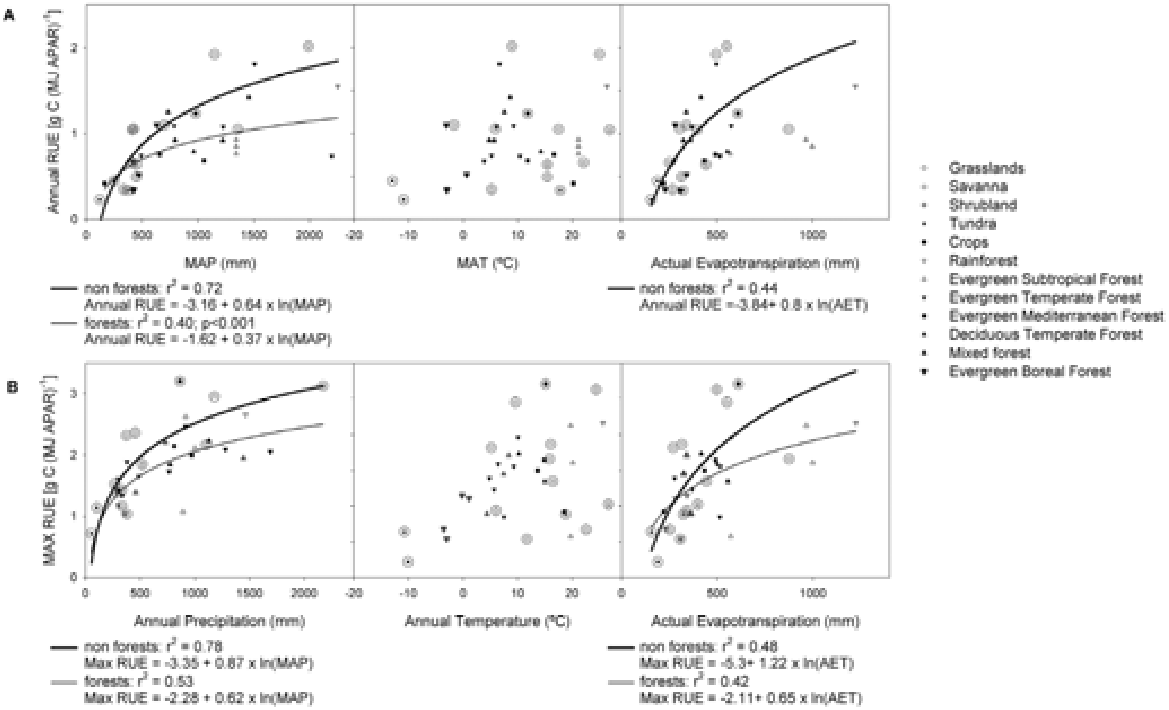


Figure 4 (a) Relationship between annual radiation use efficiency (RUE) and the long-term mean climate variables for forests and non-forest sites. (b) Relationship between the maximum seasonal RUE and the annual climate variables for forests and non-forest sites. Precipitation and temperature data for each site are the mean annual for the periods studied. Circled symbols represent the non-forest sites and thick lines are the regressions for non-forest sites and tiny lines are the regressions for forest sites. Presented relationships are significant *P* <0.01. MAP, mean annual precipitation; MAT, mean annual temperature; AET, actual evapotranspiration.

Overall, EF was the single variable that best explained the variability of RUE FPAR and RUE EVI for all the sites and periods ($P < 0.0001$). However, more complex models, including more than one variable, presented lower AIC values.

DISCUSSION

GPP was primarily related to MAP in our analysis. In accordance with global patterns in ANPP (Huxman *et al.*, 2004) and net primary productivity (NPP, Garbulsky & Paruelo, 2004) GPP is also influenced at a global scale by MAP. We also found that actual evapotranspiration explains a great part of the spatial variability of GPP, in agreement with other previous works (Rosenzweig, 1968; Lieth, 1975). Long-term average climatic conditions, represented by MAP, and not the actual rainfall for the analysed period (<6 years), showed better correlation with GPP. This result is probably evidence for the low capacity of each vegetation type to increase or decrease GPP with changes in water availability at the annual scale, because of the limitations imposed by the structure of the vegetation (e.g. rooting depth, density of meristems).

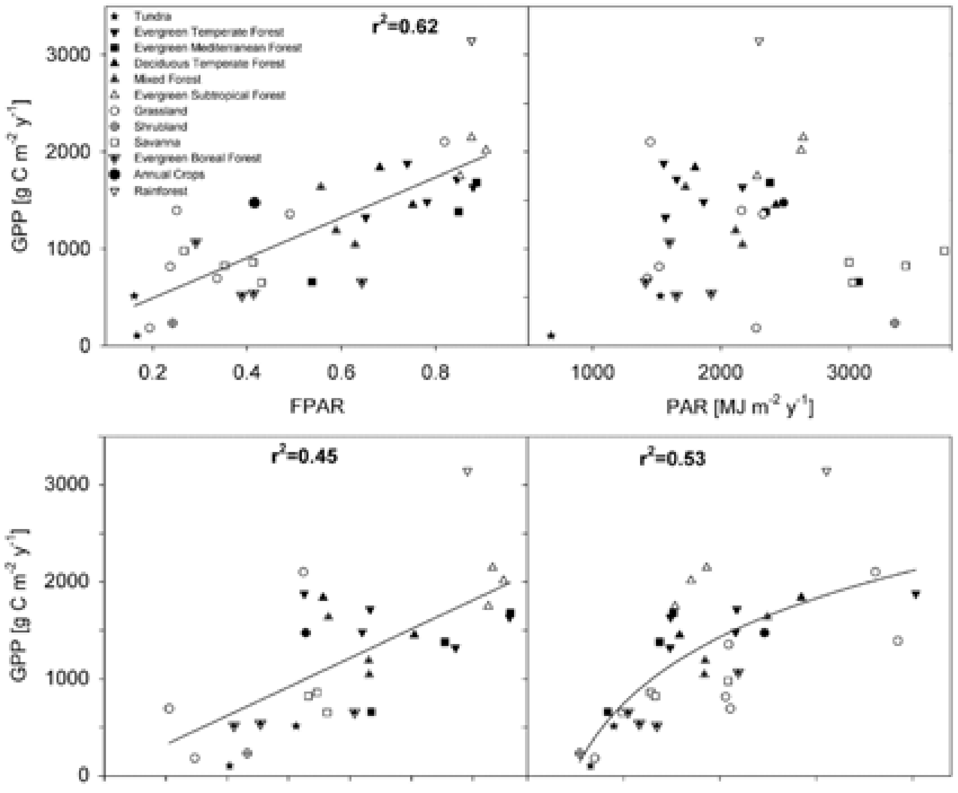


Figure 5 Relationship between average annual gross primary productivity (GPP) and the three components of the radiation use efficiency model: the average annual fraction of photosynthetically active radiation (PAR) absorbed by the vegetation (FPAR), PAR and gross radiation use efficiency (RUE). APAR is the product of photosynthetically active radiation (PAR) and the friction of photosynthetically active radiation absorbed by the vegetation (FPAR).

Previous studies showed a diversity of biotic and abiotic controls of GPP (Valentini *et al.*, 2000; Law *et al.*, 2002; Luyssaert *et al.*, 2007a; Magnani *et al.*, 2007; Reichstein *et al.*, 2007;

Kato & Tang, 2008). Much of the divergence in those results is probably due to the difference in the environmental distribution of the datasets, the successional or disturbance stage of the vegetation and management practices. The correlation between precipitation and temperature of the sites selected in some of the datasets in the published analyses probably led to an overestimation of the actual importance of temperature as a main control of GPP.

Therefore, to decouple the role of temperature and precipitation, we included in our analysis sites with high temperature and low precipitation, and others with low temperature and high precipitation, thus reducing the correlation between MAP and MAT (Fig. 1; n = 35; r^2 = 0.11; P = 0.014). Our results show that water availability is more important than temperature and vegetation type for ecosystem processes along broad biogeographic patterns. Temperature is also an important driver of the GPP when analysing forest biomes and with increasing importance in the coldest and energy-limited forests, as suggested by previous studies (Valentini *et al.*, 2000; Law *et al.*, 2002; Luyssaert *et al.*, 2007a; Magnani *et al.*, 2007; Reichstein *et al.*, 2007). Obviously, our results are sensitive to the partitioning method used to derive GPP from the NEE measured at the EC sites. However, previous works using the same methodology showed that environmental variability is similar when using NEE at midday or midnight (Luyssaert *et al.*, 2007b; Reichstein *et al.*, 2007).

Our results suggest that spatial variability of both the average and maximum gross annual RUE is controlled firstly by precipitation, and secondly by the vegetation type. In general, ecosystems dominated by trees had lower RUE values than the vegetation types dominated by grasses or herbs. For both vegetation types, the annual RUE was primarily related to MAP and the maximum RUE to the yearly precipitation. These results are the first evidence showing that RUE is controlled by climatic factors at global scales. Therefore, our results are important because, although it is well known that climate and global change could affect FPAR (Nemani *et al.*, 2003; Paruelo *et al.*, 2004; Ciais *et al.*, 2005), there is not much evidence about the impact of these changes on the RUE of different vegetation functional types. Previous studies showed the spatial variability of RUE only for ANPP or NPP (Landsberg *et al.*, 1997; Goetz & Prince, 1999; Gower *et al.*, 1999), mainly because of the limitations in estimating RUE for below-ground processes. They suggested that less productive sites, in terms of their NPP, presented lower RUE values (Field *et al.*, 1995; Paruelo *et al.*, 1997), but the relationship with environmental factors was not tested. The variability of annual gross RUE across different biomes in this study was within the range of values observed in previous studies for different ecosystems (Lagergren *et al.*, 2005; Sims *et al.*, 2005; Turner *et al.*, 2005; Schwalm *et al.*, 2006; Li *et al.*, 2008; Mäkelä *et al.*, 2008). In contrast to total annual FPAR, which is positively related to MAP and is not related to temperature (Garbulsky & Paruelo, 2004), the spatial variability of RUE is commonly assigned to vegetation type (Ruimy *et al.*, 1994; Gower et al., 1999) with very few studies linking the RUE with biophysical variables. Annual RUE has been reported to have a positive relationship with mean temperature for a temperature range between -4 and 10°C and for diverse biomes (Schwalm et al., 2006). Our results showed a similar pattern for that tem¬perature range, but with larger data dispersion for warmer areas.

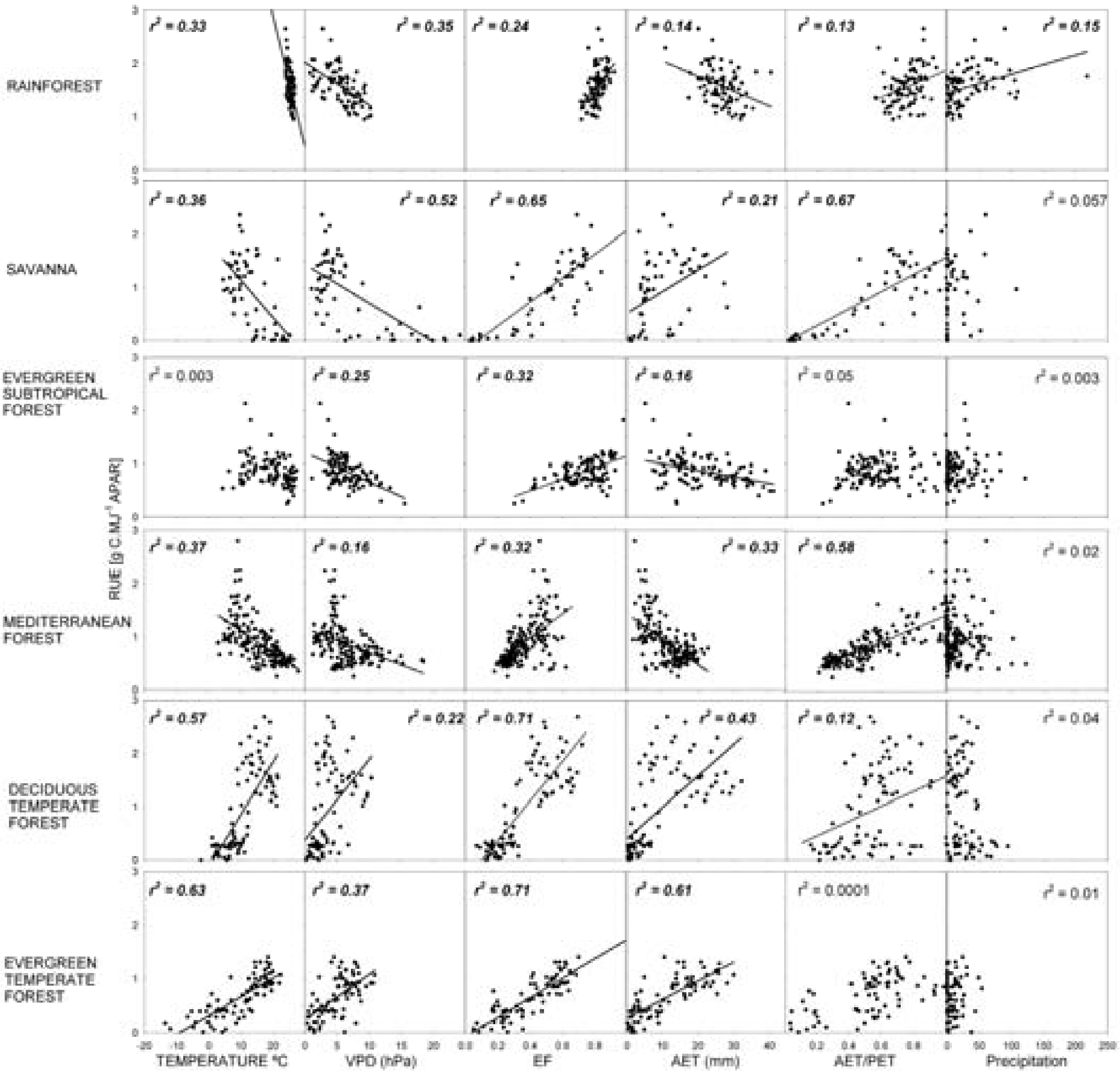


Figure 6. Relationships for 8-day periods between gross radiation use efficiency calculated using the fraction of photosynthetically active radiation absorbed by vegetation (RUE FPAR) and mean temperature, mean vapour pressure deficit (VPD), mean evaporative fraction (EF), sums of actual evapotranspiration (AET), mean ratio of actual evapotranspiration to potential evaporation (AET/PET) and precipitation sums for six contrasting ecosystems. The coefficients of determination (r^2) for signifcant linear relationships (P <0.001), are highlighted in bold.

Our results also demonstrated that the maximum gross RUE is regulated by global climatic patterns determined by precipitation (Fig. 4b). These results are particularly important, for example, with regard to the MODIS methodology (MOD17) for estimating GPP (Heinsch *et* *al.*, 2006). We showed that the maximum RUE varies greatly, not only with vegetation type but also with the precipitation. Moreover, we found that the maximum RUE values for annual crops are higher than for any type of forest, which contradicts the maximum RUE assumptions of the MOD17 methodology. These assumptions were also previously questioned by Turner *et al.* (2003).

The diversity in the annual dynamics of gross RUE is the main factor controlling the differences in the relationships between annual and maximum RUE and precipitation. Sites with similar annual RUE do not necessarily present the same maximum RUE (Fig. 4a,b) because of the differences in the seasonality of GPP and APAR produced by a wide range of environmental constraints. GPP, and therefore RUE, are much more variable in shrubland than in tundra, probably because of the high GPP rates during a short period of reduced water availability in a hot and dry climate, compared with lower GPP rates but a longer growing season in the tundra.

Different algorithms for estimating GPP consider maximum RUE by biome and use the temperature and an estimator of water availability to downregulate this maximum RUE (Running *et al.*, 2004; Yuan *et al.*, 2007). Thus, it is critical to make the correct assessment of the maximum RUE and to determine which are the best variables to use to downregulate that maximum RUE. Relationships of actual RUE with temperature and VPD showed high dispersion, suggesting that considerable noise can be generated with the downregulation of maximum RUE (Fig. 6). In any case the relationships between RUE and temperature and VPD are different for all the sites analysed. Thus, the use of another variable to estimate the water status of the vegetation (e.g. AET/PET, EF) is probably more meaningful for arriving at the best estimate of RUE. It is clear from our analysis that the ability to estimate the seasonality of gross RUE using the variables examined varies with gradients of the environmental factors. These relationships exhibited a high data dispersion and EF is the single best estimator for all the sites. It is important to highlight that whereas temperature influenced the temporal variability of RUE, the spatial variability of temperature did not appear as a main determinant of annual or maximum RUE. These results corroborate the temperature limitation of the RUE only in the coldest sites. For hot humid ecosystems, e.g. rainforest and evergreen subtropical forests, our results suggest that none of the variables analysed are confident surrogates for the actual RUE. In such cases, it would be necessary to analyse other environmental variables as controls of the seasonal variation of gross RUE, such as the ratio of diffuse radiation to the total incident radiation (Law *et al.*, 2002; Knohl & Baldocchi, 2008). Other remote sensing information not included in this analysis, such as the photochemical reflectance index (PRI; Garbulsky *et al.*, 2008) or surface temperature (Sims *et al.*, 2007), are promising new avenues for producing better remote sensed estimations of

RUE and therefore of GPP.

In conclusion, the analysis of carbon uptake estimated by EC fluxes in terrestrial ecosystems over a wide range of latitudes, environments and vegetation types supports the idea that functioning of vegetation that is adapted to its local environment is more constrained by water availability than by temperature. The spatial variability of GPP can be largely explained by precipitation or by AET. Annual gross RUE and maximum gross RUE are positively related to long-term MAP along a wide environmental gradient. These results show that the RUE is globally controlled by climatic constraints and that the ecosystem type plays a secondary role as a control of RUE. Temperature only appears to determine a maximum limit. To date, this is the first study to relate gross RUE estimations based on ground and satellite measurements to global climatic controls.

It represents an important step forward in gross RUE estimation by providing information on a fundamental factor for estimating GPP. Variation of RUE throughout the year, although greatly dispersed, was linked to water availability and temperature depending on the climatic constrains of the ecosystems. Our results showed that EF and AET are the most confident estimators of RUE for all the ecosystems. However, overall, EF was a better estimator of RUE than other surrogates, the VPD and temperature.

REFERENCES

Allard, V., Ourcival, J.M., Rambal, S., Joffre, R. & Rocheteau, A. (2008) Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France. *Global Change Biology*, **14**, 714–725.

Andrade, F.H., Uhart, S.A. & Cirilo, A. (1993) Temperature affects radiation use efficiency in maize. *Field Crops Research*, **32**, 17–25.

Ardö, J., Mölder, M., El-Tahir, B.A. & Elkhidir, H.A. (2008) Seasonal variation of carbon fluxes in a sparse savanna in semi arid Sudan. *Carbon Balance and Management*, **3**,7.

Aurela, M. (2005) Carbon dioxide exchange in subarctic ecosystems measured by a micrometeorological technique. Faculty of Science, Department of Physical Sciences, pp 132. University of Helsinki, Helsinki.

Baldocchi, D. (2008) Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany*, **56**, 1–26.

Baldocchi, D. D., Xu, L. K. & Kiang, N. (2004) How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak-grass savanna and an annual grassland. Agricultural and Forest Meteorology, 123, 13-39.

Belelli Marchesini, L., Papale, D., Reichstein, M., Vuichard, N., Tchebakova, N. & Valentini, R. (2007) Carbon balance assessment of a natural steppe of southern Siberia by multiple constraint approach. *Biogeosciences*, **4**, 581–595.

Boelman, N.T., Stieglitz, M., Griffin, K.L. & Shaver, G.R. (2005) Inter-annual variability of NDVI in response to long-term warming and fertilization in wet sedge and tussock tundra. *Oecologia*, **143**, 588–597.

Bondeau, A., Kicklighter, D.W. & Kaduk, J. (1999) Comparing global models of terrestrial net primary productivity (NPP): importance of vegetation structure on seasonal NPP estimates. *Global Change Biology*, **5**, 35–45.

Byrne, K. A., Kiely, G. & Leahy, P. (2007) Carbon sequestration determined using farm scale carbon balance and eddy covariance. Agriculture Ecosystems & Environment, 121.

Chen, J., Falk, M., Euskirchen, E., Paw U.K.T., Suchanek, T.H., Ustin, S.L., Bond, B.J., Brosofke, K.D., Phillips, N. & Rucheng, B. (2002) Biophysical controls of carbon flows in three successional Douglas-fir stands based upon eddy-covariance measurements. *Tree Physiology*, **22**, 169–177.

Ciais, P., Reichstein, M., Viovy, N., *et al.* (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature*, **437**, 529–533.

Clark, K.L., Gholz, H.L. & Castro, M.S. (2004) Carbon dynamics along a chronosequence of slash pine plantations in north Florida. *Ecological Applications*, **14**, 1154–1171.

Clement, R., Moncrieff, J.B. & Jarvis, P.G. (2003) Net carbon productivity of Sitka spruce forest in Scotland. *Scottish Forestry*, **57**, 5–10.

Corradi, C., Kolle, O., Walter, K., Zimov, S. A. & Schulze, E. D. (2005) Carbon dioxide and methane exchange of a north-east Siberian tussock tundra. Global Change Biology, 11, 1910-1925.

Desai, A.R., Bolstad, P.V., Cook, B.D., Davis, K.J. & Carey, E.V. (2005) Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA. *Agricultural and Forest Meteorology*, **128**, 33–55.

Dolman, A.J., Moors, E.J. & Elbers, J.A. (2002) The carbon uptake of a mid latitude pine forest growing on sandy soil. *Agricultural and Forest Meteorology*, **111**, 157–170.

Field, C.B., Randerson, J.T. & Malmstrom, C.M. (1995) Global net primary production: combining ecology and remote sensing. *Remote Sensing of Environment*, **51**, 74–88.

Flanagan, L.B., Wever, L.A. & Carlson, P.J. (2002) Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Global Change Biology*, **8**, 599–615.

Garbulsky, M.F. & Paruelo, J.M. (2004) Remote sensing of protected areas to derive baseline vegetation functioning characteristics. *Journal of Vegetation Science*, **15**, 711–720.

Garbulsky, M.F., Peñuelas, J., Papale, D. & Filella, I. (2008) Remote estimation of carbon dioxide uptake of a Mediterranean forest. *Global Change Biology*, **14**, 2860–2867.

Garrigues, S., Lacaze, R., Baret, F., Morisette, J.T., Weiss, M., Nickeson, J.E., Fernandes, R., Plummer, S., Shabanov, N.V., Myneni, R.B., Knyazikhin, Y. & Yang, W. (2008) Validation and intercomparison of global leaf area index products derived from remote sensing data. *Journal of Geophysical Research*, **113**, G02028.

Gholz, H. L. & Clark, K. L. (2002) Energy exchange across a chronosequence of slash pine forests in Florida. Agricultural and Forest Meteorology, 112, 87-102.

Goetz, S.J. & Prince, S.D. (1999) Modelling terrestrial carbon exchange and storage: evidence and implications of functional convergence in light-use efficiency. *Advances in Ecological Research*, **28**, 57–92.

Goulden, M.L., Winston, G.C., McMillan, A.M.S., Litvak, M.E., Read, E.L., Rocha, A.V. & Elliot, J.R. (2006) An eddy covariance mesonet to measure the effect of forest age on land– atmosphere exchange. *Global Change Biology*, **12**, 2146–2162.

Gower, S.T., Kucharik, C.J. & Norman, J.M. (1999) Direct and indirect estimation of leaf area index, f(APAR), and net primary production of terrestrial ecosystems. *Remote Sensing of Environment*, **70**, 29–51.

Granier, A., Pilegaard, K. & Jensen, N.O. (2002) Similar net ecosystem exchange of beech stands located in France and Denmark. *Agricultural and Forest Meteorology*, **114**, 75–82.

Grünzweig, J. M., Lin, T., Rotenberg, E., Schwartz, A. & Yakir, D. (2003) Carbon sequestration in arid-land forest. Global Change Biology, 9, 791-799.

Haxeltine, A. & Prentice, I.C. (1996) A general model for the light-use efficiency of primary production. *Functional Ecology*, **10**, 551–561.

Heinsch, F.A., Zhao, M. Running, S.W., *et al.* (2006) Evaluation of remote sensing based terrestrial productivity from MODIS using regional tower eddy flux network observations. *IEEE Transactions on Geoscience and Remote Sensing*, **44**, 1908– 1925.

Hollinger, D. Y., Goltz, S. M., Davidson, E. A., Lee, J. T., Tu, K. & Valentine, H. T. (1999) Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. Global Change Biology, 5, 891-902.

Hollinger, D.Y., Aber, J., Dail, B., Davidson, E.A., Goltz, S.M., Hughes, H., Leclerc, M.Y., Lee, J.T., Richardson, A.D., Rodrigues, C., Scott, N.A., Achuatavarier, D. & Walsh, J. (2004) Spatial and temporal variability in forest–atmosphere CO2 exchange. *Global Change Biology*, **10**, 1689–1706.

Hollinger, S.E., Bernacchi, C.J. & Meyers, T.P. (2005) Carbon budget of mature no-till ecosystem in North Central Region of the United States. *Agricultural and Forest Meteorology*, **130**, 59–69.

Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Weltzin, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Schwinning, S., Small, E.E. & Williams, D.G. (2004) Convergence across biomes to a common rain-use efficiency. *Nature*, **429**, 651–654.

Jaksic, V., Kiely, G., Albertson, J., Oren, R., Katul, G., Leahy, P. & Byrne, K.A. (2006) Net ecosystem exchange of a grassland in contrasting wet and dry years. *Agricultural and Forest Meteorology*, **139**, 323–334.

Jenkins, J.P., Richardson, A.D., Braswell, B.H., Ollinger, S.V., Hollinger, D.Y. & Smith, M.-L. (2007) Refining light-use efficiency calculations for a deciduous forest canopy using simultaneous tower-based carbon flux and radiometric measurements. *Agricultural and Forest Meteorology*, **143**, 64–79.

Kato, T. & Tang, Y. (2008) Spatial variability and major controlling factors of CO2 sink strength in Asian terrestrial ecosystems: evidence from eddy covariance data. *Global Change Biology*, **14**, 2333–2348.

Kiniry, J.R., Landivar, J.A., Witt, M., Gerik, T.J., Cavero, J. & Wade, L.J. (1998) Radiation-use efficiency response to vapor pressure deficit for maize and sorghum. *Field Crops Research*, **56**, 265–270.

Knohl, A. & Baldocchi, D.D. (2008) Effects of diffuse radiation on canopy gas exchange processes in forest ecosystems. *Journal of Geophysical*

Research-Biogeosciences, **113**, G02023, doi: 10.1029/2007JG000663.

Kutsch, W.L., Kolle, O., Rebmann, C., Knohl, A., Ziegler, W. & Schulze, E.-D. (2008) Advection and resulting CO2 exchange uncertainty in a tall forest in central Germany. *Ecological Applications*, **18**, 1391–1405.

Lagergren, F., Eklundh, L., Grelle, A., Lundblad, M., Molder, M., Lankreijer, H. & Lindroth, A. (2005) Net primary production and light use efficiency in a mixed coniferous forest in Sweden. *Plant, Cell and Environment*, **28**, 412–423.

Landsberg, J.J. & Waring, R.H. (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, **95**, 209–228.

Landsberg, J.J., Prince, S.D., Jarvis, P.G., Mcmurtrie, R.E., Luxmoore, R. & Medlyn, B.E. (1997) Energy conversion and use in forests: an analysis of forest production in terms of radiation utilisation efficiency (e). *The use of remote sensing in the modeling of forest productivity* (ed. by H.L. Gholz, K. Nakane, & H. Shimoda), pp. 273–298. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Law, B.E., Falge, E., Gu, L., et al. (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agricultural and Forest Meteorology*, **113**, 97– 120.

Leemans, R. & Cramer, W. (1991) The IIASA database for mean monthly values of temperature, precipitation and cloudiness of a global terrestrial grid. Research Report RR-91–18. International Institute for Applied Systems Analysis (IIASA). Laxenburg, Austria.

Li, S.G., Eugster, W., Asanuma, J., Kotani, A., Davaa, G., Oyunbaatar, D. & Sugita, M. (2008) Response of gross ecosystem productivity, light use efficiency, and water use efficiency of Mongolian steppe to seasonal variations in soil moisture. *Journal of Geophysical Research-Biogeosciences*, **113**, G01019, doi: 10.1029/2006jg000349.

Lieth, H. (1975) Modeling the primary productivity of the world. *Primary productivity of the biosphere* (ed. by H. Lieth and R.H. Whittaker), pp 237–263. Springer-Verlag, New York, USA.

Luyssaert, S., Inglima, I., Jung, M., *et al.* (2007a) CO2 balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biology*, **13**, 2509–2537.

Luyssaert, S., Janssens, I.A., Sulkava, M., Papale, D., Dolman, A.J., Reichstein, M., Hollmen, J., Martin, J.G., Suni, T., Vesala, T., Loustau, D., Law, B.E. & Moors, E.J. (2007b) Photosynthesis drives anomalies in net carbon-exchange of pine forests at different latitudes. *Global Change Biology*, **13**, 2110– 2127.

Magnani, F., Mencuccini, M., Borghetti, M., *et al.* (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 849–851.

Mäkelä, A., Pulkkinen, M., Kolari, P., Lagergren, F., Berbigier, P., Lindroth, A., Loustau, D., Nikinmaa, E., Vesala, T. & Hari, P. (2008) Developing an empirical model of stand GPP with the LUE approach: analysis of eddy covariance data at five contrasting conifer sites in Europe. *Global Change Biology*, **14**, 92–108.

Maseyk, K., Grünzweig, J., Rotenberg, E. & Yakir, D. (2008) Respiration acclimation contributes to high carbon-use efficiency in a seasonally dry pine forest. *Global Change Biology*, **14**, 1553–1567.

Merbold, L., Ardö, J., Arneth, A., *et al.* (2008) Precipitation as driver of carbon fluxes in 11 African ecosystems. *Biogeosciences Discussions*, **5**, 4071–4105.

Merbold, L., Kutsch, W.L., Corradi, C., Kolle, O., Rebmann, C., Stoy, P.C., Zimov, S.A. & Schulze, E.D. (2009) Artificial drainage and associated carbon fluxes (CO2/CH4) in a tundra ecosystem. *Global Change Biology*, **15**, 2599–2614.

Meyers, T. (2008) *L4 eddy covariance data (Fort Peck – Goodwin Creek)*. NOAA/ARL, Atmospheric Turbulence and Diffusion Division, Oak Ridge, TN, USA.

Milyukova, I.M., Kolle, O., Varlagin, A.V., Vygodskaya, N.N., Schulze, E.D. & Lloyd, J. (2002) Carbon balance of a southern taiga spruce stand in European Russia. *Tellus Series B–Chemical and Physical Meteorology*, **54**, 429–442.

Monteith, J.L. (1972) Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology*, **9**, 747– 766.

Myneni, R.B., Hoffman, S., Knyazikhin, Y., Privette, J.L., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G.R., Lotsch, A., Friedl, M., Morisette, J.T., Votava, P., Nemani, R.R. & Running, S.W. (2002) Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sensing of Environment*, **83**, 214–231.

Nemani, R.R., Keeling, C.D., Hashimoto, H., Jolly, W.M., Piper, S.C., Tucker, C.J., Myneni, R.B. & Running, S.W. (2003) Climate-driven increases in global terrestrial net primary production from 1982–1999. *Science*, **300**, 1560– 1563.

Oechel, W.C., Vourlitis, G.L., Hastings, S.J., Zulueta, R.C., Hinzman, L. & Kane, D. (2000) Acclimation of ecosystem CO2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–981.

Ollinger, S.V., Richardson, A.D., Martin, M.E., Hollinger, D.Y., Frolking, S., Reich, P.B., Plourde, L.C., Katul, G., Munger, J.W., Oren, R., Smith, M.-L., Paw U.K.T., Bolstad, P.V., Cook, B., Day, M.C., Martin, T.A., Monson, R.K. & Schmid, H.P. (2008) Canopy nitrogen, carbon assimilation, and albedo in temperate and boreal forests: functional relations and potential climate feedbacks. *Proceedings of the National Academy of Sciences USA*, **105**, 19336–19341.

Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R., Vesala, T. & Yakir, D. (2006) Towards a standardized processing of net ecosystem exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences*, **3**, 571–583.

Paruelo, J.M., Epstein, H.E., Lauenroth, W.K. & Burke, I.C. (1997) ANPP estimates from NDVI for the central grassland region of the United States. *Ecology*, **78**, 953–958.

Paruelo, J.M., Garbulsky, M.F., Guerschman, J.P. & Jobbágy, E.G. (2004) Two decades of normalized difference vegetation index changes in South America: identifying the imprint of global change. *International Journal of Remote Sensing*, **25**, 2793–2806.

Potter, C.S., Klooster, S.A. & Brooks, V. (1999) Interannual variability in terrestrial net primary production: exploration of trends and controls on regional to global scales. *Ecosystems*, **2**, 36–48.

Powell, T. L., Starr, G., Clark, K. L., Martin, T. A. & Gholz, H. L. (2005) Ecosystem and understory water and energy exchange for a mature, naturally regenerated pine flatwoods forest in north Florida. Canadian Journal of Forest Research, 35, 1568-1580.

Powell, T.L., Gholz, H.L., Clark, K.L., Starr, G., Cropper, W.P. & Martin, T.A. (2008) Carbon exchange of a mature, naturally regenerated pine forest in north Florida. *Global Change Biology*, **14**, 2523–2538.

R Development Core Team (2008) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reichstein, M., Falge E, Baldocchi, D., *et al.* (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, **11**, 1424–1439.

Reichstein, M., Papale, D., Valentini, R., Aubinet, M., Bernhofer, C., Knohl, A., Laurila, T., Lindroth, A., Moors, E., Pilegaard, K. & Seufert, G. (2007) Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites. *Geophysical Research Letters*, **34**, L01402, doi:10.1029/ 2006GL027880.

Rey, A., Pegoraro, E., Tedeschi, V., Parri, I.D., Jarvis, P.G. & Valentini, R. (2002) Annual variation in soil respiration and its components in a coppice oak forest in central Italy. *Global Change Biology*, **9**, 851–866.

Rosenzweig, M.L. (1968) Net primary productivity of terrestrial communities: prediction from climatological data. *The American Naturalist*, **102**, 67–74.

Ruimy, A., Kergoat, L. & Bondeau, A. (1999) Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. *Global Change Biology*, **5**, 56–64.

Ruimy, A., Saugier, B. & Dedieu, G. (1994) Methodology for the estimation of terrestrial net primary production from remotely sensed data. *Journal of Geophysical Research*, **99**, 5263–5283.

Running, S.W., Nemani, R.R., Heinsch, F.A., Zhao, M., Reeves, M. & Hashimoto, H. (2004) A continuous satellite-derived measure of global terrestrial primary production. *Bioscience*, **54**, 547–560.

Russell, G., Jarvis, P.G. & Monteith, J.L. (1989) Absorption of radiation by canopies and stand growth. *Plant canopies: their growth, form, and function* (ed. by G. Russell, B. Marshall & P.G. Jarvis), pp. 21–39. Cambridge University Press, Cambridge, UK.

Saleska, S.R., Miller, S.D., Matross, D.M., Goulden, M.L., Wofsy, S.C., Da Rocha, H.R., De Camargo, P.B., Crill, P., Daube, B.C., De Freitas, H.C., Hutyra, L., Keller, M., Kirchhoff, V., Menton, M., Munger, J.W., Hammond Pyle, E., Rice, A.H. & Silva, H. (2003) Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. *Science*, **302**, 1554–1557.

Schulze, E.D. (2006) Biological control of the terrestrial carbon sink. *Biogeosciences*, **3**, 147–166.

Schwalm, C.R., Black, T.A., Amiro, B.D., Altaf Arain, M., Barr, A.G., Bourque, C.P.-A., Dunn, A.L., Flanagan, L.B., Giasson, M.-A., Lafleur, P.M., Margolis, H.A., Mc Caughey, J.H., Orchansky, A.L. & Wofsy, S.C. (2006) Photosynthetic light use efficiency of three biomes across an east–west continentalscale transect in Canada. *Agricultural and Forest Meteorology*, **140**, 269–286.

Scott, R.L., Jenerette, G.D., Potts, D.L., & Huxman, T.E. (2009) Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-enroached semiarid grassland. *Journal of Geophysical Research-Biosciences*, **114**, G04004. doi:10.1029/ 2008JG000900.

Sims, D.A., Luo, H., Hastings, S., Oechel, W.C., Rahman, A.F. & Gamon, J.A. (2006) Parallel adjustments in vegetation greenness and ecosystem CO2 exchange in response to drought in a southern California chaparral ecosystem. *Remote Sensing of Environment*, **103**, 289–303.

Sims, D.A., Rahman, A.F., Cordova, V.D., Baldocchi, D.D., Flanagan, L.B., Goldstein, A.H., Hollinger, D.Y., Misson, L., Monson, R.K., Schmid, H.P., Wofsy, S.C. & Xu, L.K. (2005) Midday values of gross CO2 flux and light use efficiency during satellite overpasses can be used to directly estimate eight-day mean flux. *Agricultural and Forest Meteorology*, **131**, 1–12.

Sims, D.A., Rahman, A.F., Cordova, V.D., El-Masri, B.Z., Baldocchi, D.D., Bolstad, P.V., Flanagan, L.B., Goldstein, A.H., Hollinger, D.Y., Misson, L., Monson, R.K., Oechel, W.C., Schmid, H.P., Wofsy, S.C. & Xu, L. (2007) A new model of gross primary productivity for North American ecosystems based solely on the enhanced vegetation index and land surface temperature from MODIS. *Remote Sensing of Environment*, **112**, 1633–1646.

Sjöström, M., Ardö, J., Eklundh, L., El-Tahir, B. A., El-Khidir, H. A. M., Pilesjö, P. & Seaquist, J. (2009)

Evaluation of satellite based indices for gross primary production estimates in a sparse savanna in the Sudan. Biogeosciences, 6.

Still, C.J., Randerson, J.T. & Fung, I.Y. (2004) Large-scale plant light-use efficiency inferred from the seasonal cycle of atmospheric CO_2. *Global Change Biology*, **10**, 1240–1252.

Tchebakova, N., Kolle, O., Zolotoukhine, D., Arneth, A., Styles, J.M., Vygodskaya, N.N., Schulze, E.D., Shibistova, O. & Lloyd, J. (2002) Inter-annual and seasonal variations of energy and water vapour fluxes above a *Pinus sylvestris* forest in the Siberian middle taiga. *Tellus Series B–Chemical and Physical Meteorology*, **54**, 537–551.

Tucker, C.J. & Sellers, P.J. (1986) Satellite remote-sensing of primary production. *International Journal of Remote Sensing*, **7**, 1395–1416.

Turner, D.P., Gregory, M., Urbanski, S., Wofsy, S.C., Bremer, D., Meyers, T. & Gower, S.T. (2003) A cross-biome comparison of daily light use efficiency for gross primary production. *Global Change Biology*, **9**, 383–395.

Turner, D.P., Ritts, W.D., Cohen, W.B., Maeirsperger, T.K.,L., Gower, S.T., Kirschbaum, A.A., Running, S.W., Zhao, M., Wofsy, S.C., Dunn, A.L., Law, B.E., Campbell, J., Oechel, W.C., Kwon, H.J., Meyers, T.P., Small, E.E., Kurc, S.A. & Gamon, J.A. (2005) Site-level evaluation of satellite-based global terrestrial gross primary production and net primary production monitoring. *Global Change Biology*, **11**, 666– 684.

Valentini, R., Matteucci, G., Dolman, A.J., *et al.* (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

Veenendaal, E.M., Kolle, O. & Lloyd, J. (2004) Seasonal variation in energy fluxes and carbon dioxide exchange for a broadleaved semi-arid savanna (mopane woodland) in southern Africa. *Global Change Biology*, **10**, 318–328.

Vörösmarty, C.J., Federer, C.A. & Schloss, A.L. (1998) Potential evaporation functions compared on US watersheds: possible implications for global-scale water balance and terrestrial ecosystem modeling. *Journal of Hydrology*, **207**, 147–169.

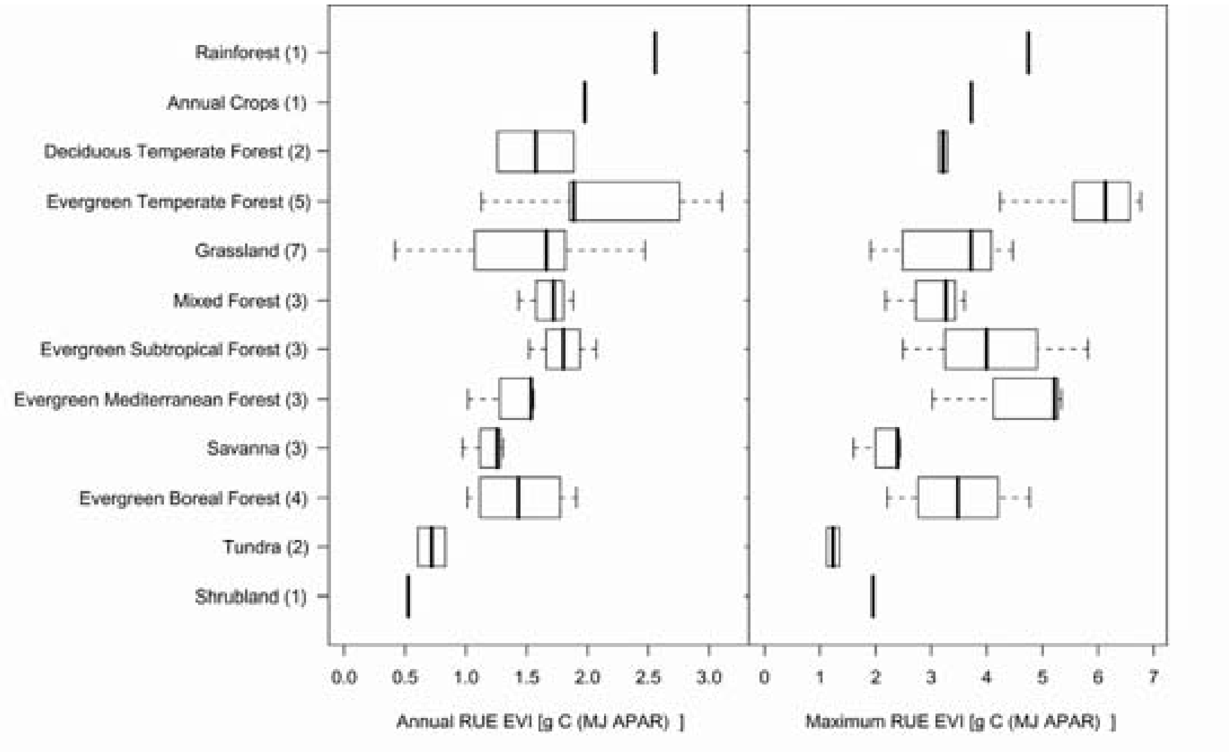
Waring, R.H., Law, B.E., Goulden, M.L., Bassow, S.L., McCreight, R.W., Wofsy, S.C. & Bazzaz, F.A. (1995) Scaling gross ecosystem production at Harvard Forest with remotesensing–acomparison of estimates from a constrained quantum-use efficiency model and eddy-correlation. *Plant Cell and Environment*, **18**, 1201–1213.

Woodward, F.I. & Smith, T.M. (1995) Predictions and measurements of the maximum photosynthetic rate, Amax, at the global scale. *Ecophysiology of photosynthesis* (ed. by E.D. Schulze & M.M. Caldwell), pp 491–509. Springer Verlag, Berlin.

Yuan, W.P., Liu, S., Zhou, G.S., Zhou, G.Y., Tieszen, L.L., Baldocchi, D., Bernhofer, C., Gholz, H., Goldstein, A.H., Goulden, M.L., Hollinger, D.Y., Hu, Y., Law, B.E., Stoy, P.C., Vesala, T., Wofsy, S.C. & other AmeriFlux collaborators (2007) Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes. *Agricultural and Forest Meteorology*, **143**, 189–207.

Zhang, Q.Y., Xiao, X.M., Braswell, B., Linder, E., Ollinger, S., Smith, M.L., Jenkins, J.P., Baret, F., Richardson, A.D., Moore, B. & Minocha, R. (2006) Characterization of seasonal variation of forest canopy in a temperate deciduous broadleaf forest, using daily MODIS data. *Remote Sensing of Environment*, **105**, 189–203.

APPENDIX



Appendix 1. Average gross annual and maximum gross radiation use efficiency (RUE) estimated from the enhanced vegetation index (EVI), as a surrogate for FPAR, for the different vegetation types. The numbers of sites included for each vegetation type are shown in brackets.

Appendix 2. Analysis of Covariance for mean annual radiation use efficiency (RUE) and maximum RUE estimated from the Enhanced Vegetation Index (EVI) across vegetation type (forest; n= 21 and non forest; n= 14) and climatic variables and their interactions: long term Mean annual precipitation (MAP) and long term mean annual temperature (MAT) and Precipitation (Precip) and temperature (Temp) for the analyzed periods.

Response:	RUE EVI					RUE EVI MAX				
	Df	Sum Sq	F value	P value	%SS	Df	Sum Sq	F value	P value	%SS
Forest	1	1.903	7.947	0.009	14.2	1	16.737	12.221	0.001	25.4
ln (precip)	1	4.232	17.675	0.000	31.6	1	9.069	6.622	0.016	13.8
temp	1	0.068	0.283	0.599	0.5	1	0.985	0.719	0.404	1.5
Forest x ln (precip)	1	0.083	0.346	0.561	0.6	1	0.579	0.423	0.521	0.9
Forest x temp	1	0.004	0.017	0.897	0.0	1	0.086	0.063	0.804	0.1
ln (precip) x temp	1	0.392	1.639	0.211	2.9	1	0.019	0.014	0.906	0.0
Residuals	28	6.705				28	38.34			
Total		13.387					65.82			

	Df	Sum Sq	F value	Pr(>F)	%SS	Df	Sum Sq	F value	Pr(>F)	%SS
Forest	1	1.903	7.873	0.009	14.2	1	16.737	13.056	0.001	25.4
ln (MAP)	1	4.680	19.363	0.000	35.0	1	13.076	10.200	0.003	19.9
MAT	1	0.007	0.029	0.865	0.1	1	0.001	0.001	0.977	0.0
Forest x ln (MAP)	1	0.014	0.057	0.814	0.1	1	0.044	0.034	0.854	0.1
Forest x MAT	1	0.000	0.000	0.991	0.0	1	0.037	0.029	0.867	0.1
ln (MAP) x MAT	1	0.016	0.065	0.801	0.1	1	0.030	0.024	0.879	0.0
Residuals	28	6.768				28	35.89			
Total		13.387					65.821			

Appendix 3. Coefficients of correlation for the 8-day period relationships between radiation use efficiency calculated from the fraction of photosynthetically active radiation absorbed by the vegetation (RUE FPAR) and RUE calculated from the enhanced vegetation index (RUE EVI) and seven environmental variables. Significant correlations ($p<0.01$) are marked in bold type. Empty cells are for those cases with lack of data for the environmental variable.

	RUE FPAR							RUE EVI						
Site	Ta	VPD	EF	AET	AET/PET	PRECIP	PET	Ta	VPD	EF	AET	AET/PET	PRECIP	PET
Atqasuq	0.18	0.15	0.25	0.05	-0.19	-0.02	0.09	**0.47**	0.25	0.32	0.07	0.36	**0.45**	0.15
Cherski	**0.73**	**0.74**	0.60	**0.80**	0.35	0.16	**0.77**	**0.73**	0.55	**0.68**	0.58	0.44	0.40	0.58
Santarita	0.23	-0.03	**0.71**	**0.69**	**0.50**	0.28	0.02	0.33	0.07	**0.69**	**0.78**	**0.44**	0.34	0.14
Fort Peck	-0.09	-0.10	**0.53**	**0.39**	**0.36**	0.11	-0.03	**0.33**	0.23	**0.64**	**0.74**	**0.40**	**0.28**	**0.34**
Vaira	**-0.59**	**-0.72**	**0.80**	**0.46**	**0.81**	**0.24**	**-0.62**	**-0.74**	**-0.75**	**0.88**	**0.63**	**0.89**	**0.35**	**-0.65**
Lethbridge	**0.51**	0.30	**0.82**	**0.70**	**0.71**	**0.49**	**0.62**	**0.69**	**0.46**	**0.83**	**0.78**	**0.75**	0.30	**0.72**
Goodwin Creek	0.01	-0.26	0.15	-0.06	0.22	0.29	-0.09	-0.22	-0.41	-0.07	-0.19	0.27	0.17	-0.27
Dripsey	0.06	-0.01	0.39	0.12	-0.01	-0.12	-0.07	-0.29	-0.33		-0.42	0.09	-0.26	-0.44
Tchizalamou	0.04	**-0.45**		0.30	**0.52**	0.09	-0.25		0.03		**0.67**	**0.50**	**0.42**	**0.58**
Hakasia	**0.71**	0.32	**0.71**	**0.74**	0.15	**0.63**	**0.64**	**0.81**	0.46	**0.75**	**0.79**	0.05	**0.69**	**0.75**
Tonzi	**-0.38**	**-0.48**	**0.78**	**0.57**	**0.56**	0.20	-0.17	**-0.41**	**-0.48**	**0.77**	**0.50**	**0.53**	0.19	-0.21
Maun	-0.21	**-0.78**	**0.93**	**0.87**	**0.92**	**0.47**	-0.26	-0.25	**-0.62**	**0.92**	**0.80**	**0.91**	**0.47**	**-0.38**
Demokeya	-0.31	**-0.67**	**0.91**	0.24	0.36	0.38	**0.61**	-0.45	**-0.81**	**0.89**	-0.27	0.14	**0.60**	0.40
Bondville	-0.14	-0.26	**0.30**	0.17	0.24	0.07	-0.06	0.01	-0.21	**0.50**	**0.32**	0.24	0.05	0.05
Roccarrespampani	**0.42**		**0.84**	**0.61**	**0.58**	0.10	0.28	**0.34**		**0.77**	**0.45**	0.70	**0.12**	0.11
Hesse	**0.75**	**0.46**	**0.84**	**0.65**	**0.35**	-0.22	**0.62**	**0.73**	**0.45**	**0.82**	**0.63**	**0.33**	0.02	
Hainich	**0.63**	0.35	**0.77**	**0.61**	0.14	0.15	**0.52**	**0.56**	0.18	**0.73**	**0.55**	0.12	0.28	**0.40**
Sylvania	**0.80**	**0.61**	**0.85**	**0.78**	-0.01	0.12	**0.75**	**0.72**	**0.52**	**0.73**	**0.58**	0.01	0.01	**0.59**
Bartlet	**0.84**	**0.55**	**0.88**	**0.76**	0.12	0.06	**0.79**	**0.86**	**0.56**	**0.86**	**0.75**	0.17	0.08	**0.76**
Loobos	-0.13	**-0.47**	**0.35**	**-0.17**	**0.57**	**0.39**	**-0.42**	**-0.19**	**-0.47**	0.03	**-0.27**	**0.54**	**0.25**	**-0.47**
Howland	**0.85**	**0.63**	**0.86**	**0.71**	**0.46**	0.16	**0.70**	**0.81**	**0.54**	**0.82**	**0.64**	**0.42**	0.21	**0.63**
Griffin	-0.50	-0.52	0.10	**-0.64**	**0.60**	0.39	**-0.64**	-0.28	**-0.57**	-0.06	**-0.59**	**0.12**	0.58	**-0.61**
Wind River creek	-0.30	**-0.42**	0.11	-0.15	0.04	**0.42**	-0.34	**-0.39**	**-0.50**	0.08	**-0.34**	0.17	**0.37**	**-0.46**
Fyodorovskoye	**0.45**	-0.19	**0.83**	**0.48**	**0.55**	**0.43**	0.12	**0.39**	-0.09	**0.82**	**0.52**	**0.38**	0.38	0.16
UCI 1964	0.44	0.71	**0.76**	0.27	0.17	0.56	0.07	**0.74**	**0.82**	**0.82**	**0.65**	**0.54**	0.38	**0.54**
UCI 1981	**0.55**	0.13	**0.79**	0.45	0.52	**0.68**	0.28	**0.81**	**0.59**	**0.90**	**0.67**	**0.67**	**0.82**	**0.65**
Sodankyla	0.61	-0.23	**0.78**	0.42	0.54	0.31	0.06	**0.63**	0.07	0.49	0.32	**0.62**	0.31	0.19

Zotino	**0.67**	0.33	**0.72**	**0.53**	0.39	0.49	0.40	**0.65**	0.24	**0.74**	**0.53**	**0.62**	**0.53**	0.22
Yatir	**-0.76**	**-0.61**	**0.54**	**0.41**	**0.84**	**0.39**	**-0.64**	**-0.83**	**-0.67**	**0.70**	**0.38**	**0.89**	**0.44**	**-0.69**
Castelporziano	**-0.61**	**-0.41**	**0.57**	**-0.58**	**0.77**	0.14	**-0.68**	**-0.65**	**-0.48**	**0.58**	**-0.63**	**0.78**	**0.18**	**-0.72**
Puechabon	**-0.49**	**-0.72**	**0.53**	**-0.16**	**0.67**	**0.27**	**-0.65**	**-0.59**	**-0.75**	**0.29**	**-0.35**	**0.65**	**0.33**	**-0.72**
Mize	**0.17**	**-0.27**	**0.50**	0.14	**0.61**	0.15	**-0.20**	-0.09	**-0.41**	**0.25**	**-0.13**	**0.53**	0.13	-0.41
Austin	0.25	-0.13	**0.34**	0.26	**0.46**		0.13	-0.13	-0.23	**0.07**	-0.10	**0.47**		**-0.27**
Donaldson	0.05	**-0.50**	**0.57**	**-0.41**	0.23	0.06	**-0.52**	**-0.48**	**-0.59**	**0.45**	**-0.45**	**0.40**	**0.03**	-0.67
Santarem	**-0.58**	**-0.59**	**0.48**	**-0.38**	**0.37**	**0.39**	**-0.68**	**-0.70**	**-0.66**	**0.46**	**-0.53**	**0.21**	**0.41**	**-0.75**
# Significant correlations	19	18	28	23	19	11	18	25	20	27	28	23	17	20

Chapter 4

Satellite reflectance indices NDVI, EVI and PRI assess the leaf and stand level carbon uptake of Mediterranean forests from annual to seasonal and daily scales

ABSTRACT

Plant photosynthesis is the primary and most important carbon input to ecosystems. Moreover, it is and it will be affected by the different components of global change. Therefore, it is of outstanding importance to develop accurate tracking tools for the different components of the carbon cycle in ecosystems. Remote sensed spectral indices can closely follow green biomass of ecosystems and thus their potential photosynthetic capacity. However, in evergreen vegetation types such as Mediterranean forests green biomass hardly change throughout growing season and consequently changes in photosynthetic rates are not related to changes in green biomass. This study analyzed the links between different components of the carbon cycle (i.e. net photosynthesis and diametric increment of stems) in a Mediterranean forest dominated by *Quercus ilex* and three spectral indices (NDVI, EVI and PRI) derived from MODIS sensors along several growing seasons. Average annual EVI accounted for 66% of the variability of the annual diametric increment of all the species and 83% of the variability of the diametric increment of the stems of *Q. ilex* alone for a ten-year period. NDVI only marginally correlated with the diametric increment of the stems. We showed for the first time a significant correlation between net photosynthesis and radiation use efficiency at the leaf level with PRI derived from satellite data at the ecosystem level. These results suggest that each spectral index provides different and complementary information for the analysis of ecosystem carbon uptake.

Keywords carbon cycle, Normalized Difference Vegetation Index, Enhanced Vegetation Index, Photochemical Reflectance Index, *Quercus ilex*, primary productivity, photosynthesis, remote sensing

1. INTRODUCTION

Spectral indices derived from remotely sensed data are an extraordinary source of data for the study of the structure and function of terrestrial vegetation (Peñuelas and Filella 1998). The most widely used index is the Normalized Difference Vegetation Index (NDVI) that is traditionally used as an estimator of the fraction of the Photosyntethically Active Radiation (PAR) absorbed by the canopy (FPAR, Tucker et al. 1985). The Enhanced Vegetation Index was later formulated to solve the soil background and saturation problems commonly associated to the NDVI (Huete et al. 2002). The Photochemical Reflectance Index (PRI) is a spectral index that can track changes in the physiological status of the vegetation, particularly the Radiation Use Efficiency (RUE) but also other physiological related variables like the chlorophyll fluorescence at the leaf, canopy and ecosystem levels (Gamon et al. 1992, Peñuelas et al. 1995, Garbulsky et al. submitted).

In ecosystem types with a constant leaf area index, such as the Mediterranean forests (Ogaya and Peñuelas 2006), the RUE is a key variable to understand the carbon uptake. The temporal variability of RUE in these forests was shown to be controlled by the ratio between actual and potential evapotranspiration (AET/PET), but neither temperature nor VPD were good predictors of its variability (Garbulsky et al. 2010) as many models assume. Therefore, Mediterranean forests are good candidates to test the ability of the PRI to estimate the ecophysiological performance and the carbon uptake of the vegetation through the RUE. This test is specially warranted by the fact that the warming and the precipitation decrease projected for the next decades will greatly affect the structure and functioning of Mediterranean forest more than any other forest in Europe (Morales et al. 2005, Morales et al. 2007). Observational and experimental studies are verifying the effects of these changes on the ecophysiology (Ogaya and Peñuelas 2003, 2006, Asensio et al. 2007, Ogaya and Peñuelas 2007) and also on the phenology (Peñuelas et al. 2002) and the distribution Penuelas and Boada 2003 (Peñuelas et al. 2007) of these forests. These changes affect and will affect the ecosystem services provided by these terrestrial ecosystems greatly modified by the human activities (Schröter et al. 2005).

The carbon uptake and the primary productivity are integrative processes crucial to the understanding of the state and health of the ecosystems. The primary productivity is commonly assessed through biomass increment estimations (Sala and Austin 2000). These estimations of primary productivity in particular locations are of key importance to provide biological meaning to the spectral data derived from satellite sensors, that thereafter can be used to spatially spread the ecological information over the landscape. Different average site conditions such as structural characteristics can be estimated through relationships with remote sensing data (Waring et al. 2006). The temporal variation of forest annual productivity can be derived from NDVI (Wang et al. 2004) and EVI (Potter et al. 2007) variability in deciduous forests. However, this is not the case for evergreen Mediterranean forests, due to the limited sensitivity of these spectral indices, NDVI and EVI, to short-term CO_2 uptake changes linked to water stress. In all cases, field measurements of leaf photosynthesis or stand eddy covariance of CO_2 fluxes, but also biomass estimations, are needed to test the ability of spectral indices to estimate short-term variations of carbon uptake.

We hypothesized that different spectral indices can be indicators of carbon uptake at different temporal scales, from days to season and year. Due to the different capacity to react to changes in ecophysiological status of the vegetation, the different spectral indices NDVI, EVI and PRI can become surrogates of ecosystem carbon fluxes at different temporal scales, NDVI and EVI at the annual scale and PRI at the daily and seasonal scale. The objective of this study was to test this hypothesis by analyzing the relationships between detailed ecophysiological variables at the stand level in a Mediterranean forest and these spectral indices derived from MODIS sensor. The final aim was to further provide biological insight on the information provided by spectral indices calculated with MODIS data.

2. MATERIALS AND METHODS

This study was carried out in a natural Holm oak forest at Prades Mountains in Catalunya, NE Spain (41.3408º N, 1.0378º E). Annual average precipitation is 610 mm and average temperature 12.2 ºC (1999-2009). The vegetation is dominated by short broadleaf evergreen trees about 4 m high and tall shrubs. This Holm oak forest has a very dense multi-stem crown (16616 trees ha^{-1}, and 115 Mg ha^{-1}) and it is dominated by *Quercus ilex* L. (8633 trees ha^{-1}, and 89 Mg ha^{-1}), *Phillyrea latifolia* L. (3600 trees ha^{-1}, and 14 Mg ha^{-1}) and *Arbutus unedo* L. (2200 trees ha^{-1}, and 9 Mg ha^{-1}) with presence of other evergreen species well adapted to dry conditions (*Erica arborea* L., *Juniperus oxycedrus* L., *Cistus albidus* L.). Average leaf area index is 4. This forest has been undisturbed approximately since 1950 (Ogaya and Peñuelas 2007).

We selected ten plots with similar vegetation characteristics randomly distributed across an area of approximately 100 ha of the forest. In these plots, we measured different variables related to the ecophysiological performance of *Q. ilex* individuals and soil characteristics. Foliar gas exchange, PAR absorption and soil temperature and moisture measurements were conducted approximately once a month between 23rd March, 2006 and 8th August, 2008 around midday (11 a.m. to 14 p.m.). Stem diameter increment was measured since 2000 to 2010 in four plots.

Gas exchange measurements

Gas exchange was measured in *Q. ilex* leaves of different types. Sun leaves (from the upper layer of the canopy, fully exposed to the sun, and south-facing orientation) and shade leaves (from the lower layers of the canopy) were measured under clear-sky conditions. Net CO_2 uptake rate was measured with a portable gas exchange system ADC4, with a PLC4B chamber (ADC Inc., Hoddesdon, Hertfordshire, UK). Four different plants per plot were measured around the midday.

Photosynthetically active radiation absorbed by the canopy

To estimate the absorbed radiation by the canopy, we used a PAR ceptormeter (SF-80, Decagon, Pullman,WA) and measured the incident PAR above the canopy and the PAR below the canopy. Four measurements were taken below the canopy at each site to have a representation of the spatial variability of the PAR absorption.

Soil moisture and temperature

Soil moisture was measured throughout the experiment by time domain reflectometry (TDR, Tektronix 1502C, Beaverton, OR, USA) (Zegelin et al. 1989). Three stainless steel cylindrical rods, 25 cm long, were permanently fully driven into the soil at one randomly selected place in each plot. The TDR was connected to the ends of the rods in each measurement. We performed a calibration to obtain water content (volume/volume) from the TDR data using the top soil of our site.

Stem diameter

The stem circumference was measured annually since 2000 each winter throughout the study until winter 2010. The measurements were conducted at 50 cm height in all living stems of all the species with a diameter larger than 2 cm at 50 cm height.

MODIS data and reflectance indices

We analyzed data provided by the MODIS sensor on board of Terra and Aqua platforms. The Terra platform orbit around the Earth is timed so that it passes from north to south in the morning, while Aqua passes south to north in the afternoon. We derived three spectral indices from the reflectance data from MODIS $band_1$ (620-670 nm), $band_2$ (841-876 nm), $band_3$ (459-479 nm) and $band_{11}$ (526-536 nm). We calculated the Normalized Difference Vegetation Index (NDVI=(refl $band_2$ - refl $band_1$)/ (refl $band_2$ + refl $band_1$)), the Enhanced Vegetation Index (EVI=2.5 (refl $band_2$ - refl $band_1$)/ (refl $band_2$ +6 refl $band_1$ - 7.5 refl $band_3$+1)) and the Phothochemical Reflectance Index (PRI = (refl $band_{11}$ - refl $band_1$)/ (refl $band_{11}$ + refl $band_1$)). PRI was calculated from calibrated reflectance MODIS Aqua L1b

(MYD021KM V005) for the field measurement days and the overpass dates used for the calculation of NDVI and EVI in the MYD13 product.

Statistical analyses

Regression analyses were conducted between the field measured variables and the reflectance indices calculated from MODIS sensor. Net photosynthesis rates were analyzed by a bivariate linear regression using Soil moisture and Soil temperature as independent variables. The annual stem diametric increment was analyzed using NDVI, EVI, PRI and precipitation of the same year and also the previous year precipitation as independent variables. All the statistical analysis of the data were conducted using R package (R Development Core Team, 2008).

3. RESULTS

Photosynthesis at the leaf level varied between 0.5 and 15 µmol m^{-2} s^{-1}. Maximum values were reached in spring and minimum values in late spring and summer (Figure 1a). Average absorbed radiation values varied between 80 and 92% (Figure 1b) and as expected, were very constant throughout the time with no significant differences between the different measuring dates (ANOVA, p=0.11). Soil moisture maximum values corresponded to two wet springs (April, May and June) in 2007 (297 mm precipitation) and 2008 (423 mm) which correspond to 30% and 94% above the average precipitation for the period 1999-2009 (Figure 1c). Minimum values occurred mainly in summer. Soil temperature showed a clear seasonal pattern with maxima in August and minima in January-February (Figure 1d).

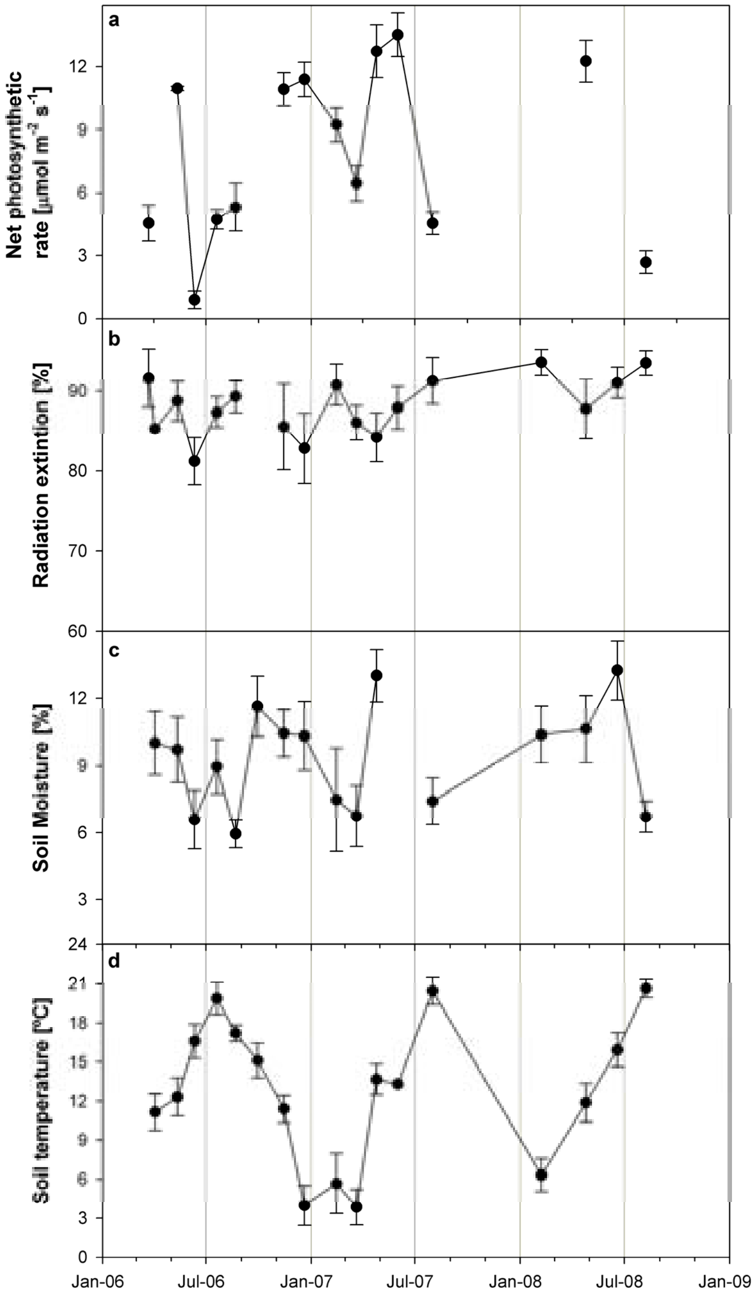


Figure 1. Seasonal variability of a) photosynthesis, b) radiation extinction, c) soil moisture, and d) soil temperature. Error bars are the standard errors for the ten sites.

Soil moisture and temperature accounted for a great part of the variability of leaf level photosynthesis throughout the growing seasons (Figure 2). In the partial models soil moisture positively accounted for 68% of the variability of photosynthesis and soil temperature negatively accounted for 28% of its variability. Soil temperature and moisture were not correlated.

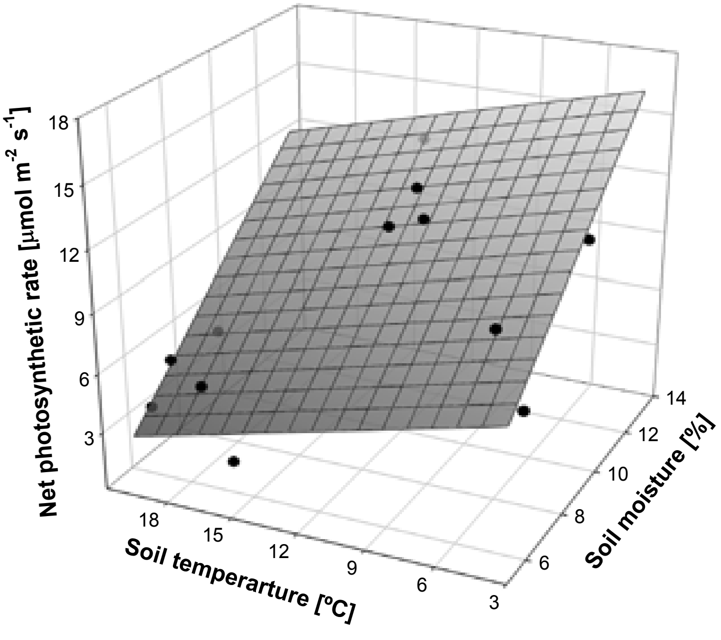


Figure 2. Relationship of leaf level net photosynthetic rates with soil moisture and temperature for the period 2006-2008. Plane shows the bivariate linear regression ($p<0.001$, $r^2 = 0.85$; Photosynthesis = -0.55 + 1.36 Soil moisture - 0.27 Soil temperature)

The NDVI seasonal pattern varied between 0.75 and 0.9 and was constant and almost saturated throughout the growing seasons (Figure 3). Subtle seasonal pattern showed maximum values in winter and minimum in summer. In contrast, the EVI varied between 0.2 and 0.5 and presented a clear seasonal pattern with minimum in winter and maximum in summer. NDVI and EVI 8-day values were negatively correlated for the period 2000-2009 ($r=-0.32$; $p<0.0001$; $n=416$). Neither NDVI nor EVI correlated with the radiation extinction ($p>0.3$).

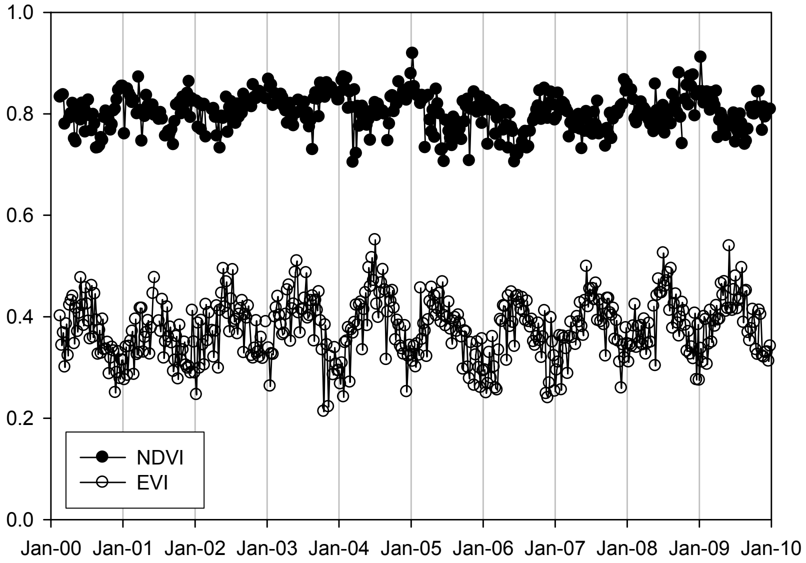


Figure 3. Seasonal patterns of NDVI and EVI derived from MODIS Terra data.

PRI presented a clear seasonal pattern for the analyzed period. Maximum values occurred in winter and varied between 0.26 and 0.28. Minimum occurred between late spring and summer ranging between 0.09 and 0.16.

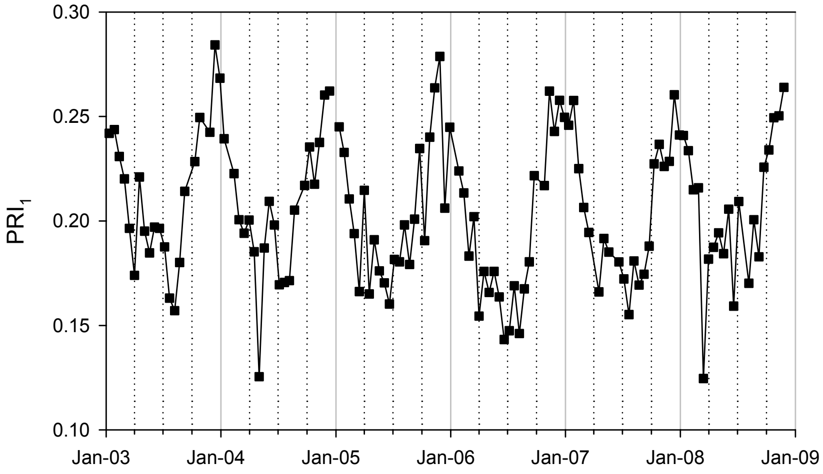


Figure 4. Seasonal patterns of PRI_1 derived from MODIS Aqua data.

The annual diametric increment varied for the ten growing seasons between 2000 and 2009 from 0.6 mm y^{-1} for one of the wettest growing season to a decrease of 0.15 mm y^{-1} for the driest one. Overall, precipitation accounted for 48% of the variability of diametric increment. Including in the model not only the precipitation of the same year but also the previous year precipitation, the model accounted for 66% of the interannual variability in the annual diametric increment. The EVI annual average accounted for 83% of the diametric increment of the *Quercus ilex* individuals (Figure 5a). The NDVI annual average was also correlated to the diametric increment of the *Q. ilex* individuals, but accounting for only 47% of the variance (Figure 5b). The PRI annual average for the period 2003-2009 accounted for 62% of the variability of the diametric increment (Figure 5c). The annual diametric stem increment and the EVI did not show a temporal trend along the analyzed period (Figure 6)

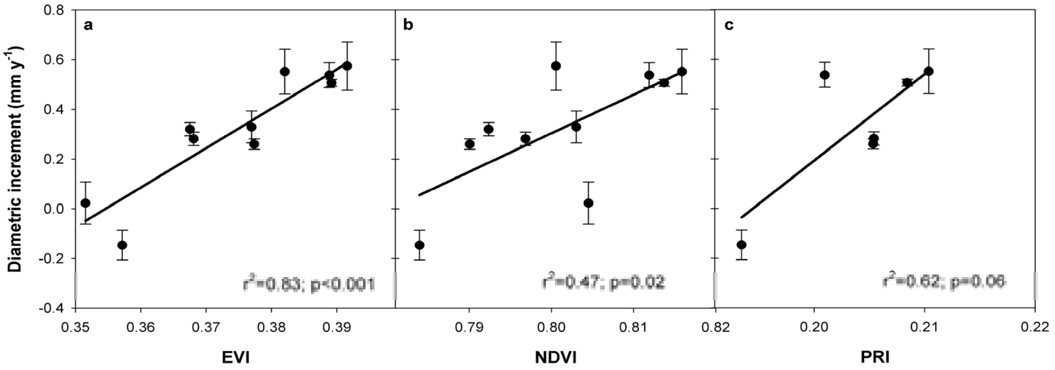


Figure 5. Relationships of the annual diametric stem increment for the dominant species (*Quercus ilex*) with MODIS Terra a) EVI and b) NDVI (n=10) and c) MODIS Aqua PRI (n=6) annual averages for the period 2000-2009.

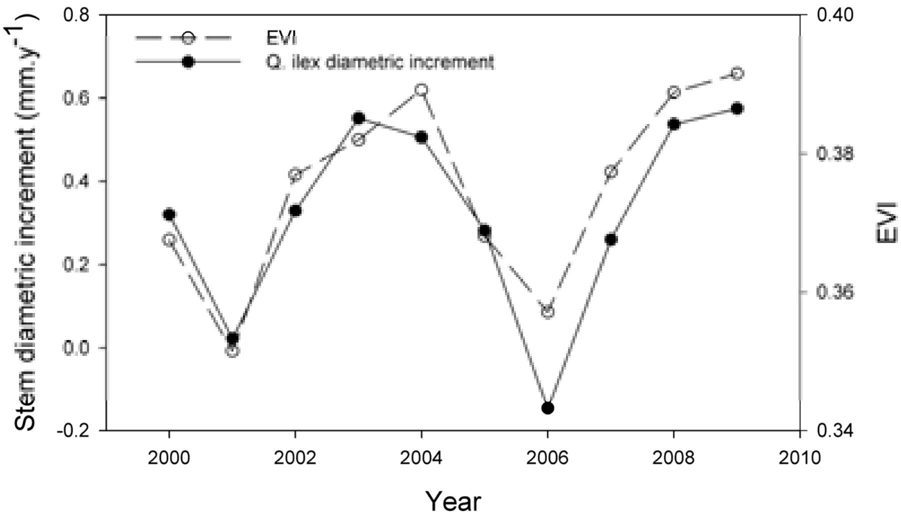


Figure 6. Temporal trends of the annual stem diametric increment of Q. ilex and the annual EVI average.

The PRI calculated using band 1 as reference accounted for 36% of the variability of leaf level net photosynthetic rate (Figure 7a) and 40% of the variability of radiation use efficiency (Figure 7b). There were no significant relationships of net photosynthesis rate neither with radiation use efficiency with NDVI and EVI (data not shown).

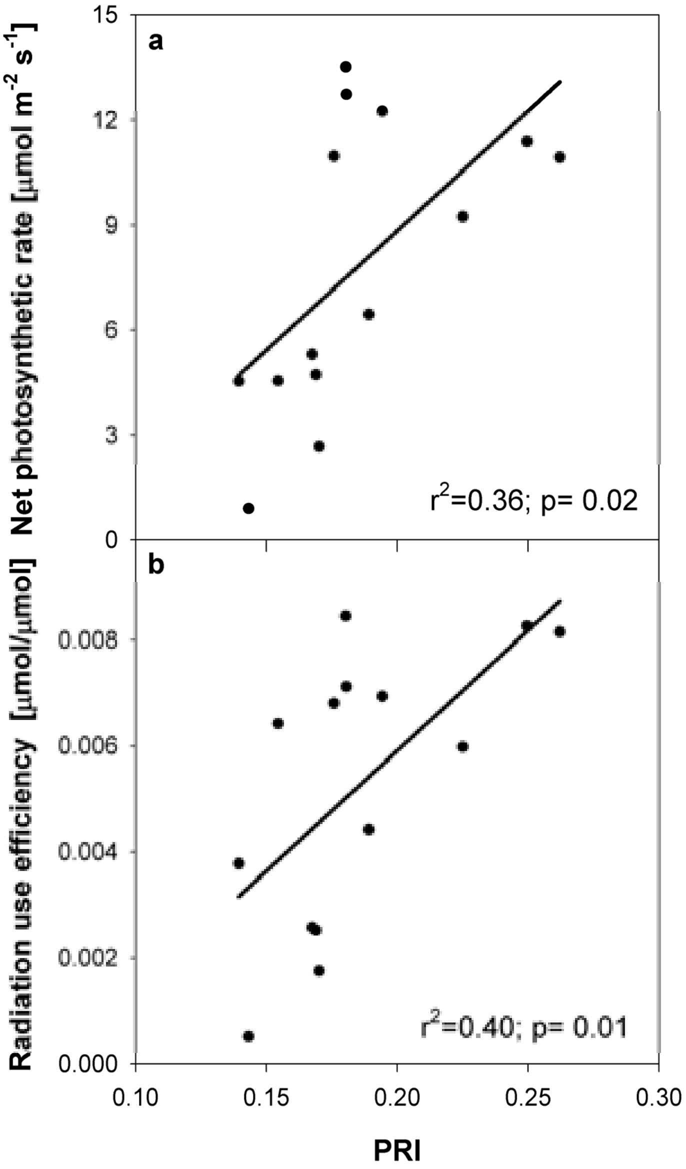


Figure 7. Relationship of leaf level a) net photosynthetic rate and b) radiation use efficiency with MODIS AQUA PRI.

4. DISCUSSION

The contrasting seasonal patterns of NDVI and EVI for this Mediterranean forest evidence the difference between these spectral indices. It is assumed that one of the main differences between both indices is the higher capacity of EVI to enhance the vegetation signal, resulting in an improved sensitivity in high biomass regions and in an improved vegetation monitoring through a de-coupling of the canopy background signal. Another main difference is a reduction in atmosphere influences in EVI (Huete et al. 2002). The results of this study show that the differences between NDVI and EVI go farther since both indices are providing different signals. They even present a temporal negative correlation. We checked this result with data from other Mediterranean forest sites which showed no significant relationships (data not shown), but deciduous type forests did show a significant relationship between NDVI and EVI. Soil is not a major source of noise in this Mediterranean forest due to the very high cover and LAI throughout the year. Moreover radiation extinction, and therefore FPAR, was not related to NDVI nor to EVI. The significant relationships FPAR-NDVI are commonly reported across broad ranges (Myneni and Williams 1994), not for the narrow ranges of FPAR and NDVI measured in this study. In any case, this absence of relationships with FPAR in both indices does not seem to account for the remarkable seasonal differences between EVI and NDVI. Other hypotheses must be posed to explain the differences between NDVI and EVI.

NDVI is probably saturated because of the high and constant values and the high LAI at the Prades site. In contrast, EVI is still sensitive to phenological changes in leaf and canopy color and to changes in the proportions of new and old leaves. New leaves appear in spring with a very pale green color. Although this new cohort of leaves does not represent an effective increment in total LAI because of the simultaneous start of the abscission of old leaves (Ogaya and Peñuelas 2004), it changes the reflectance of the canopy in a detectable way by EVI. In this same line, It had been suggested that while NDVI is an estimator of the FPAR of leaves, EVI estimates FPAR from chlorophyll (Zhang et al. 2005). Also the seasonal differences in pigment content, such as a winter and summer decrease in chlorophyll content (Gratani et al. 1998), could add another partial explanation for the observed differences.

EVI was shown as a good surrogate of the temporal variability of GPP at the ecosystem scale in evergreen needleleaf forest, deciduous broadleaf forest, grassland and woody savanas (Sims et al. 2006), but this does not seem the case for evergreen forest types such as the Mediterranean forest studied here. Neither EVI nor NDVI were good surrogates of leaf level photosynthesis and probably would not be good estimators of ecosystem GPP temporal changes.

However, the average annual EVI presented a better performance than NDVI and PRI as estimator of the annual diametric growth of this Holm oak forest. This better performance of EVI (Figure 5), for a 10 year period, suggests that overall EVI is the best estimator of the annual net primary productivity (NPP). This behavior is due to the saturation of NDVI, to the higher capacity of EVI than NDVI to deal with atmospheric noise and likely to the hypothesized better assessment of annual new leaves flush. In any case, these results are coincident with previous works for other ecosystems showing the good capacity of spectral indices as estimators of annual primary productivity for different vegetation types (Wang et al. 2004, Marsden et al. 2010). Our results, however, are of key importance because we deal with an evergreen forest without a clear growing season.

Notably, PRI also correlated with the stem growth, a variable that integrates the growth of the whole growing season. PRI has been typically correlated with short term variables (Garbulsky et al. submitted), but there were no information on the capacity of PRI to estimate annual integrations of ecosystem performance. The results presented in this study are the first ones that show this type of relationship for a vegetation type with a very flat seasonal pattern of FPAR.

Leaf level photosynthesis was in the range of values already published for this site and species (Asensio et al. 2007). Water availability was the main control of the seasonal variability of photosynthesis, and temperature played a more secondary role in its regulation (Figure 2), what confirms previous results at the ecosystem scale in other Mediterranean forests (Keenan et al. 2010). In contrast to NDVI and EVI that were not related to leaf level photosynthetic rates, PRI significantly estimated leaf level photosynthesis and specially the photosynthetic efficiency. This is in agreement with previous analysis showing that PRI correlates well with different photosynthetic-related variables at the leaf, plant and ecosystem scales for different plant and vegetation types (Garbulsky et al. submitted). Particularly, PRI derived from satellite data has been found to correlate with stand level carbon fluxes derived from eddy covariance towers at boreal (Drolet et al. 2005) and temperate deciduous (Rahman et al. 2004) and Mediterranean (Garbulsky et al. 2008) forests. Carbon fluxes derived from eddy covariance towers provide a wide source of data to scale to remote sensing data. However, there are at least two cautionary remarks in the use of eddy covariance carbon fluxes data: firstly, there is an uncertainty of the eddy covariance GPP data derived from the gap filling and separation of the respiration fluxes processing methods in the order of thousands of g C m^{-2} $year^{-1}$ (Papale et al. 2006, Moffat et al. 2007) that can produce noise in the RUE-PRI relationships and that surely has to be considered; secondly, sites like the one studied here present important slopes that strongly hinder the use of eddy covariance techniques to measure carbon uptake by the vegetation. We here used for our analysis different scales for the remote sensing and the ecophysiological data. We showed for the first time a significant correlation between net photosynthesis and radiation use efficiency at the leaf level with PRI derived from satellite data at the ecosystem level. It is noticeable from our results that a leaf level process could be gathered from satellite information with coarse spatial resolution.

Our results showed thus contrasting and complementary capacities of each of the three spectral indices analyzed for ecological monitoring and for the evaluation of forestry management practices. While EVI can estimate annual diametric wood increment, a surrogate of NPP, and PRI can estimate daily leaf level net photosynthesis and radiation use efficiency, the role NDVI is more limited as a surrogate of any part of the carbon cycle in this type of forest. We conclude that EVI and PRI are excellent tools for vegetation monitoring of carbon cycle in these Mediterranean forests. More studies are warranted in other sites and other vegetation types, particularly for EVI and PRI to make these indices more globally useful as ecological tools to assess primary productivity.

5. REFERENCES

R Development Core Team, 2008. R: A language and environment for statistical computing. *in*. R Foundation for Statistical Computing, Vienna, Austria.

Asensio, D., J. Peñuelas, R. Ogaya, and J. Llusià. 2007. Seasonal soil and leaf CO_2 exchanges rates in a Mediterranean holm oak forest and their responses to drought conditions. Atmospheric Environment **41**:2447-2455.

Drolet, G. G., K. F. Huemmrich, F. G. Hall, E. M. Middleton, T. A. Black, A. G. Barr, and H. A. Margolis. 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**:212-224.

Gamon, J. A., J. Peñuelas, and C. B. Field. 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. Remote Sensing of Environment **41**:35-44.

Garbulsky, M. F., J. Peñuelas, J. A. Gamon, Y. Inoue, and I. Filella. submitted. 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.

Garbulsky, M. F., J. Peñuelas, D. Papale, J. Ardö, M. L. Goulden, G. Kiely, A. D. Richardson, E. Rotenberg, E. M. Veenendaal, and I. Filella. 2010. Patterns and controls of the variability of radiation use efficiency and primary productivity across terrestrial ecosystems. Global Ecology and Biogeography **19**:253–267.

Garbulsky, M. F., J. Peñuelas, D. Papale, and I. Filella. 2008. Remote estimation of carbon dioxide uptake of a Mediterranean forest. Global Change Biology **14**:2860–2867.

Gratani, L., P. Pesoli, and M. F. Crescente. 1998. Relationship between photosynthetic activity and chlorophyll content in an isolated Quercus ilex L. tree during the year. Photosynthetica **35**:445-451.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment **83**:195-213.

Keenan, T., S. Sabate, and C. Gracia. 2010. Soil water stress and coupled photosynthesis-conductance models: Bridging the gap between conflicting reports on the relative roles of stomatal, mesophyll conductance and biochemical limitations to photosynthesis. Agricultural and Forest Meteorology **150**:443-453.

Marsden, C., G. le Maire, J.-L. Stape, D. L. Seen, O. Roupsard, O. Cabral, D. Epron, A. M. N. Lima, and Y. Nouvellon. 2010. Relating MODIS vegetation index time-series with structure, light absorption and stem production of fast-growing Eucalyptus plantations. Forest Ecology and Management **259**:1741-1753.

Moffat, A. M., D. Papale, M. Reichstein, D. Y. Hollinger, A. D. Richardson, A. G. Barr, C. Beckstein, B. H. Braswell, G. Churkina, A. R. Desai, E. Falge, J. H. Gove, M. Heimann, D. Hui, A. J. Jarvis, J. Kattge, A. Noormets, and V. J. Stauch. 2007. Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. Agricultural and Forest Meteorology **147**:209-232.

Morales, P., T. Hickler, D. P. Rowell, B. Smith, and M. T. Sykes. 2007. Changes in European ecosystem productivity and carbon balance driven by regional climate model output. Global Change Biology **13**:108-122.

Morales, P., M. T. Sykes, I. C. Prentice, P. Smith, B. Smith, H. Bugmann, B. Zierl, P. Friedlingstein, N. Viovy, S. Sabaté, A. Sánchez, E. Pla, C. A. Gracia, S. Sitch, A. Arneth, and J. Ogee. 2005. Comparing and evaluating process-based ecosystem model predictions of carbon and water fluxes in major European forest biomes. Global Change Biology **11**:2211-2233.

Myneni, R. B., and D. L. Williams. 1994. On the Relationship between FAPAR and NDVI. Remote Sensing of Environment **49**:200-211.

Ogaya, R., and J. Peñuelas. 2003. Comparative seasonal gas exchange and chlorophyll fluorescence of thwo dominant woody species in a Holm Oak Forest. Flora **198**:132-141.

Ogaya, R., and J. Peñuelas. 2004. Phenological patterns of Quercus ilex, Phillyrea latifolia, and Arbutus unedo growing under a field experimental drought. Ecoscience **11**:263-270.

Ogaya, R., and J. Peñuelas. 2006. Contrasting foliar responses to drought in *Quercus ilex* and *Phillyrea latifolia*. Biologia Plantarum **50**:373-382.

Ogaya, R., and J. Peñuelas. 2007. Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. Plant Ecology **189**:291-299.

Papale, D., M. Reichstein, M. Aubinet, E. Canfora, C. Bernhofer, W. Kutsch, B. Longdoz, S. Rambal, R. Valentini, T. Vesala, and D. Yakir. 2006. Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. Biogeosciences **3**:571-583.

Peñuelas, J., and I. Filella. 1998. Visible and near-infrared reflectance techniques for diagnosing plant physiological status. Trends in Plant Science **3**:151-156.

Peñuelas, J., I. Filella, and P. Comas. 2002. Changed plant and animal life cycles from 1952-2000. Global Change Biology **8**:531-544.

Peñuelas, J., I. Filella, and J. A. Gamon. 1995. Assessment of photosynthetic radiation-use efficiency with spectral reflectance. New Phytologist **131**:291-296.

Peñuelas, J., R. Ogaya, M. Boada, and A. Jump. 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia. Ecography **30**:830-838.

Potter, C. S., P. Gross, V. Genovese, and M. L. Smith. 2007. Net primary productivity of forest stands in New Hampshire estimated from Landsat and MODIS satellite data. Carbon Balance and Management **2**:9.

Rahman, A. F., V. D. Cordova, J. A. Gamon, H. P. Schmid, and D. A. Sims. 2004. Potential of MODIS ocean bands for estimating CO_2 flux from terrestrial vegetation: A novel approach. Geophysical Research Letters. doi:10.1029/ 2004GL019778 **31**.

Sala, O. E., and A. T. Austin. 2000. Methods of estimating aboveground net primary productivity. Pages 31-43 *in* O. E. Sala, R. B. Jackson, H. A. Mooney, and R. W. Howarth, editors. Methods in ecosystem science. Springer, New York.

Schröter, D., W. Cramer, R. Leemans, I. C. Prentice, M. B. Araújo, N. W. Arnell, A. Bondeau, H. Bugmann, T. R. Carter, C. A. Gracia, A. C. de la Vega-Leinert, M. Erhard, F. Ewert, M. Glendining, J. I. House, S. Kankaanpää, R. J. T. Klein, S. Lavorel, M. Lindner, M. J. Metzger, J. Meyer, T. D. Mitchell, I. Reginster, M. Rounsevell, S. Sabaté, S. Sitch, B. Smith, J. Smith, P. Smith, M. T. Sykes, K. Thonicke, W. Thuiller, G. Tuck, S. Zaehle, and B. Zierl. 2005. Ecosystem Service Supply and Vulnerability to Global Change in Europe. Science **310**:1333-1337.

Sims, D. A., A. F. Rahman, V. D. Cordova, B. Z. El-Masri, D. D. Baldocchi, L. B. Flanagan, A. H. Goldstein, D. Y. Hollinger, L. Misson, R. K. Monson, W. C. Oechel, H. P. Schmid, S. C. Wofsy, and L. K. Xu. 2006. On the use of MODIS EVI to assess gross primary productivity of North American ecosystems. Journal of Geophysical Research-Biogeosciences G04015, doi:10.1029/ 2006JG000162 **111**.

Tucker, C. J., C. L. Vanpraet, M. J. Sharman, and G. Vanittersum. 1985. Satellite Remote-Sensing of Total Herbaceous Biomass Production in the Senegalese Sahel - 1980-1984. Remote Sensing of Environment **17**:233-249.

Wang, J., P. M. Rich, K. P. Price, and W. D. Kettle. 2004. Relations between NDVI and tree productivity in the central Great Plains. International Journal of Remote Sensing **25**:3127 - 3138.

Waring, R. H., K. S. Milner, W. M. Jolly, L. Phillips, and D. McWethy. 2006. Assessment of site index and forest growth capacity across the Pacific and Inland Northwest U.S.A. with a MODIS satellite-derived vegetation index. Forest Ecology and Management **228**:285-291.

Zegelin, S. J., I. White, and D. R. Jenkins. 1989. Improved field probes for soil water content and electrical conductivity measurement using time domain reflectometry. Water Resources Research **25**:2367-2376.

Zhang, Q. Y., X. M. Xiao, B. Braswell, E. Linder, F. Baret, and B. Moore. 2005. Estimating light absorption by chlorophyll, leaf and canopy in a deciduous broadleaf forest using MODIS data and a radiative transfer model. Remote Sensing of Environment **99**:357-371.

Chapter 5

Remote estimation of carbon dioxide uptake by a Mediterranean forest

ABSTRACT

The estimation of the carbon balance in ecosystems, regions, and the biosphere is currently one of the main concerns in the study of the ecology of global change. Current remote sensing methodologies for estimating gross primary productivity are not satisfactory because they rely too heavily on (i) the availability of climatic data, (ii) the definition of land-use cover, and (iii) the assumptions of the effects of these two factors on the radiation-use efficiency of vegetation (RUE). A new methodology is urgently needed that will actually assess RUE and overcome the problems associated with the capture of fluctuations in carbon absorption in space and over time. Remote sensing techniques such as the widely used reflectance vegetation indices (e.g. NDVI, EVI) allow green plant biomass and therefore plant photosynthetic capacity to be assessed. However, there are vegetation types, such as the Mediterranean forests, with a very low seasonality of these vegetation indices and a high seasonality of carbon uptake. In these cases it is important to detect how much of this capacity is actually realized, which is a much more challenging goal. The photochemical reflectance index (PRI) derived from freely available satellite information (MODIS sensor) presented for a 5-year analysis for a Mediterranean forest a positive relationship with the RUE. Thus, we show that it is possible to estimate RUE and GPP in real time and therefore actual carbon uptake of Mediterranean forests at ecosystem level using the PRI. This conceptual and technological advancement would avoid the need to rely on the sometimes unreliable maximum RUE.

Keywords: carbon cycle, CO_2 uptake, eddy covariance, Mediterranean forests, MODIS, primary productivity, radiation use efficiency, remote sensing, vegetation

INTRODUCTION

The scientific community is devoting huge amounts of time and resources to assessing the global carbon land-use cover to estimate the radiation-use efficiency budget in a context of climate change (Boisvenue and Running 2006; Ciais et al. 2005; Schulze 2006). Current remote sensing methodologies for estimating gross primary productivity (GPP) mostly depend on absorbed radiation and the efficiency of conversion into carbon-based compounds as proposed in Monteith's (1977) model. Most methodologies rely heavily on (i) the availability of climatic data, (ii) the definition of the vegetation (RUE) and/or (iii) assumptions of the effects of both these previous factors on the RUE. These methodologies are, thus dependent on the availability -of climatic data, the quality of land-cover data, and assumptions regarding RUE (Heinsch et al. 2006).

Scientific work at leaf and plant scales reveals that it is possible to estimate radiation-use efficiency remotely by using a photochemical reflectance index (PRI) (Gamon et al. 1992; Peñuelas et al. 1995; Peñuelas et al. 1997). The PRI derived from a new breed of narrow-band spectroradiometers are increasingly being used as photosynthetic performance indicators at ecosystem level (Asner et al. 2004; Nakaji et al. 2006). By complementing the NDVI estimation of green biomass – and, therefore, of potential productivity (Gamon et al. 1995) – with PRI it is now possible to improve assessments from airborne sensors of the carbon uptake in many of the world's ecosystems (Nichol et al. 2002; Nichol et al. 2006; Rahman et al. 2001). The global coverage of satellites has dramatically improved our capacity to extend PRI-based estimation of RUE and carbon fluxes to all areas of the globe. However, the highly interesting possibilities offered by satellite images are still little used and under evaluation (Drolet et al. 2005; Rahman et al. 2004). GPP estimations for ecosystems with low seasonality in their radiation absorption (e.g. evergreen forests) but high seasonality in their carbon absorption could especially benefit from this approach. In other ecosystems, where high seasonality in the leaf-area index is the main driver of carbon absorption, the traditional NDVI (Tucker et al. 1985) or EVI (Sims et al. 2006b) approach seems robust enough for arriving at a good estimation of the GPP (Sims et al. 2006a).

We evaluated the value of the PRI derived from satellite MODIS sensors as an estimator of the radiation-use efficiency for a Mediterranean forest in which (a) seasonal variation in radiation absorption (green biomass) is very low and (b) carbon absorption has important seasonal fluctuations that are mainly determined by water deficits during summer (Rambal et al. 2003) and low temperatures and incident radiation in winter (Ogaya and Peñuelas 2003), which provoke significant periods of very low photosynthesis. Because of the negligible changes in structure and leaf area index and thus in radiation absorption, it is of great importance in this forest to have accurate measurements of radiation-use efficiency. Thus, this forest study provides an ideal opportunity for exploring alternative methods of modelling carbon absorption employing satellite-based estimates of RUE.

MATERIALS AND METHODS

We analyzed eddy covariance data of carbon fluxes and MODIS (Moderate Resolution Imaging Spectroradiometer) remote sensing data for the period January 2001–December 2005 in the Mediterranean forests of Castelporziano in central Italy (41º 42'18.90" latitude, 12º 22'34.00" longitude). Climate is Mediterranean-type, with 828 mm mean annual rainfall over the sample period occurring mainly during autumn and winter. The mean annual temperature is 14.8 ºC for the same period. The vegetation is a 10 m tall broadleaf evergreen forest mainly dominated by holm oak (*Quercus ilex*) (Tirone et al. 2003) and a leaf area index of 3.5 m^2m^{-2} (Reichstein et al. 2002).

We used the PRI as a remotely sensed estimator of the RUE in the model proposed by (Monteith 1977).

$$GPP = APAR \times RUE; \quad [1]$$

thus

$$RUE = GPP/APAR; \quad [2]$$

where RUE is the radiation-use efficiency, GPP is the GPP, and APAR is the PAR (incident photosynthetic active radiation) absorbed by the vegetation, as calculated by the product of PAR derived from the eddy covariance tower data and FPAR (the fraction of the PAR absorbed by the canopy). We evaluated three alternative estimators of the FPAR: the normalized difference vegetation index [NDVI = (band 2 - band 1)/(band 2 + band 1)], the Enhanced Vegetation Index [EVI = 2.5 (band 2 - band 1)/ (band 2 + 6 band 1–7.5 band 3 + 1)], both derived from MODIS surface reflectance data [MOD09A1 band 1 (620– 670 nm), band 2 (841–876 nm), band 3 (459–479 nm)], and the MODIS FPAR product (MOD15A2) (Myneni et al. 2002). From NDVI and EVI data we calculated the FPAR as FPAR(NDVI) = 1.24 NDVI 0.168 (Sims et al. 2005) and FPAR(EVI) = EVI (Xiao et al. 2005).

The GPP was estimated from the total CO_2 fluxes from the eddy covariance tower (Valentini et al. 2007). We used the current methodology to process the eddy covariance data: CO_2 flux data was u* filtered and ecosystem respiration and storage estimated (Papale et al. 2006; Reichstein et al. 2005) from climate data at 30-min resolution. We performed our analysis including and excluding the gap filled eddy covariance data (Reichstein et al. 2005), in order to reduce the uncertainty associated with gap filling errors produced by the Marginal

Distribution Sampling methodology.

An average of the GPP and PAR half-hour values was used for days having MODIS surface reflectance data (MOD09A1). The MOD09A1 images consist of 8-day composites constructed from the daily surface reflectance for specific dates. The NDVI and the EVI were calculated from those images and assigned to those dates. We tested the correspondence between the daily and the 8-day GPP averages, and we found a high correlation between them ($r = 0.93$) and the slope of the relationship was not different from the 1:1 relationship, although the intercept was different ($P<0.001$). Thus, the temporal resolution of the analysis is 8 days, which corresponds to that of the MOD09A1 and MOD15A2 data. Theoretically, this represents 46 periods per year; however, because of a lack of or a low quality of the remote sensing data or the tower data, we only obtained complete data for 32–39 periods per year. For all the MODIS data, quality flags were checked to discard low quality images.

To calculate the PRI [PRI = (band 11band 12)/(band 11 1 band 12)], we extracted the MODIS daily-calibrated radiance (MODIS Terra L1b – MOD021KM V005) for bands 11 (526–536 nm) and 12 (546–556 nm) for the pixels (nominal 1 km 1 km) that included the tower. Images were co-registered and we used the data of the 3x3 pixel window centered in the tower coordinates. By visual inspection of the images we also eliminated for the analysis the images that were not totally filtered by the MODIS cloud algorithm. We used for the calculation the same specific dates as for the NDVI and EVI calculations. Because the available MODIS surface reflectance data is not corrected for atmospheric effects for bands 11 and 12, we used the available calibrated radiances for those bands. The atmospheric effects on bands 11 and 12 are similar because they are positioned closely together in the spectrum (Vermote et al. 2002; Vermote et al. 1997). Thus, we considered that a normalized spectral index, such as the PRI, would not be affected by using the calibrated radiances with or without atmospheric correction for its calculation. We evaluated the PRI as a seasonal estimator of the RUE [Eqn (2)] by linear and nonlinear correlations of the complete dataset. In order to test the stability of the model, we also evaluated the correlations for each of the 5 single years.

We estimated GPP based on Eqn (1) using PRI and FPAR(MOD15) as surrogates for RUE and FPAR, respectively. To parameterize the relationship between PRI and RUE, we bootstrapped 30 times to generate different exponential models by random splitting the data into smaller datasets of the average sample size of a year ($n = 23$). To estimate RUE, we applied to the PRI data the average for the parameters of the 30 models. Finally, we compared the GPP from the eddy covariance tower against our final GPP estimates and the estimations regularly made by the MODIS team (Heinsch et al. 2003, MOD17A2, version

4.8). We evaluated both methodologies using PAR data estimated from incoming shortwave radiation derived from the global climate model for 2001–2004 [GEOS-4, Data Assimilation Office (DAO)] included in the MODIS GPP product.

Results

GPP ranged from 2 to 9 gCm^{-2} day^{-1} (Fig. 1a), with minimum values occurring mainly in winter and local minima in summer. Radiation absorption, as estimated from NDVI, EVI and FPAR(MOD15), appeared very stable throughout the year (Fig. 1b). The RUE, estimated from tower PAR data and FPAR(MOD15) ranged between 0.3 and 2.2 $gCMJ^{-1}$. Minimum values occurred in summer and maximum values in winter or spring (Fig. 1c). The seasonality of the PRI was similar to that of the RUE throughout the study period. For most of the analyzed years, the PRI was a good reflection of seasonal changes in the timing and magnitude of RUE (Fig. 1c). However, a different scaling between RUE and PRI is evident for winter 2004–2005 and during the last months in 2005. During the last part of 2005 there was scarce RUE data because of the low reliability of the GPP coming from available eddy covariance data. The temporal coefficients of variation were higher for PRI (70%) and RUE (43%) than for the three estimators of FPAR (NDVI, EVI and MOD15) for the analyzed period (4%, 14% and 3%, respectively).

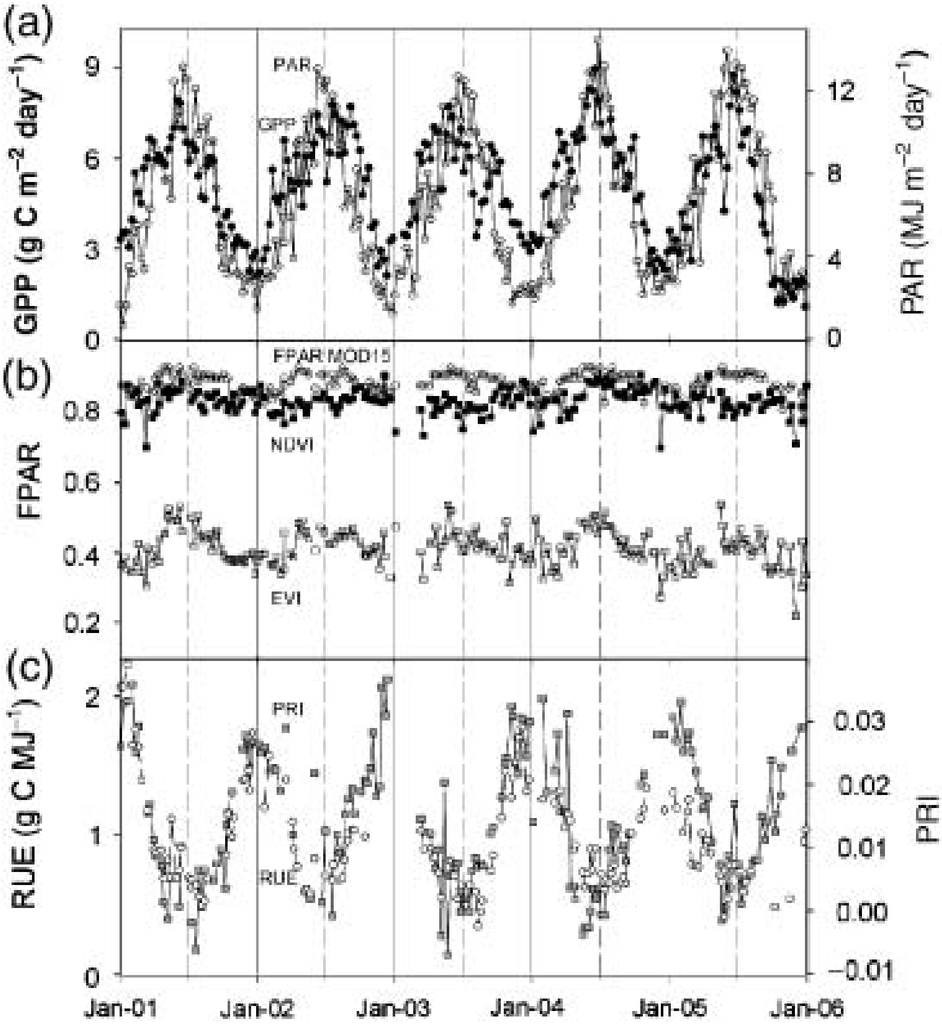


Figure 1 Seasonal course of daily biophysical variables (2001– 2005). (a) Gross primary productivity (GPP; open circles) and photosynthetic active radiation (PAR; black circles) derived from the eddy covariance tower, (b) seasonal dynamics of FPAR derived from: normalized difference vegetation index (NDVI; black squares), enhanced vegetation index (EVI; open squares), and FPAR(MOD15; open triangles) and (c) RUE estimated from FPAR(MOD15) and PAR from the tower (circles) and photochemical reflectance index (PRI; gray squares)

Incident PAR data derived from the tower and that from NASA DAO presented important differences (RMSE = 1.9 MJ m^{-2} day^{-1}). The most important differences occurred during the summer, when the tower PAR data were underestimated by the NASA DAO dataset (Fig. 2). On the contrary, values in the lower end of the gradient tend to be overestimated by the NASA DAO dataset.

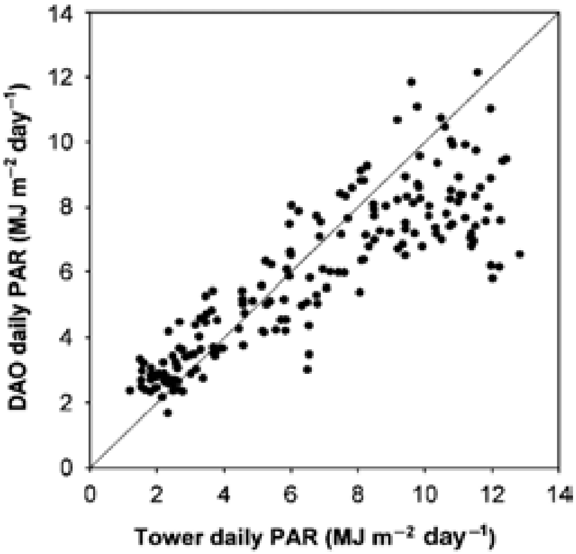


Figure 2 Comparison of the 8-day mean incident radiation measured at the tower site and estimated by the global GEOS-4 model for the 11pixel in Castelporziano for 2001–2004.

The PRI presented significant linear and exponential relationships with RUE for the whole analyzed period. The exponential regression accounted for a slightly greater proportion of the variability (r = 0.78) than the linear one (r = 0.76; Fig.3). The NDVI was not correlated with the RUE (r = 0.09) and the EVI presented a negative correlation with RUE (r= -0.42). In order to reduce uncertainties associated with seasonal changes in incident radiation or the view zenith angle, we also tested the ability of the PRI to estimate the RUE splitting the data into high and low incident radiation (i.e. PAR>7MJm^{-2} day^{-1} or PAR<7MJm^{-2} day^{-1}). For both cases, PRI positively correlated with RUE (r = 0.25, n = 73, P<0.0001 and r = 0.50, n = 57, P<0.0001), and presented similar slopes (P = 0.51) but different intercepts (P<0.001).

PRI and the RUE also presented positive relationships when analyzed for each single year. However, slopes and intercepts varied for certain years, regardless of whether RUE was estimated from NDVI or from EVI (data not shown). The strength of the relationships varied between years (0.68 < r < 0.89). Also, the slopes of these relationships presented interannual variability, with lower values for 2004 and 2005 than those for the other three analyzed years. The slopes of these relationships were negatively correlated with the total annual precipitation for the period 2001–2005 (r =0.92; n = 5; P<0.05).

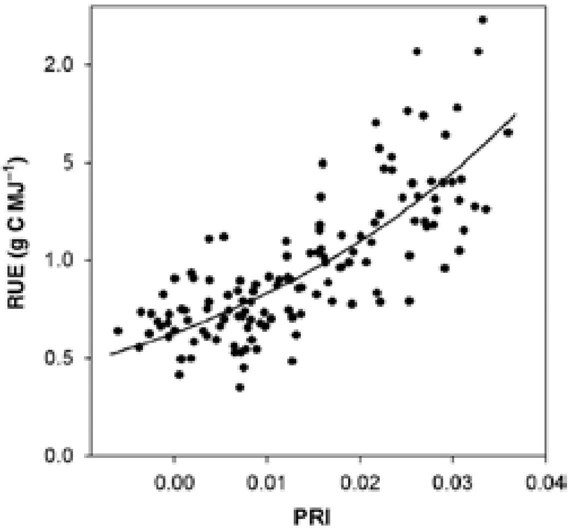


Figure 3 Seasonal relationships between RUE and MODIS PRI for 2001–2005 (r =0.78; P<0.0001; RUE = 0.63 $e^{(27.76\ PRI)}$; F =205.58; n =131).

The use of an exponential estimation of the RUE by means of the PRI for a subset of the data and the application of this relationship to the rest of the data together with DAO PAR data and FPAR(MOD15) strongly improved the MODIS NASA GPP estimate for 2001– 2004 (Fig. 4). The use of PRI significantly reduced the error in the estimate of the 8-day GPP measured in the flux tower when compared with the MODIS NASA GPP product (MODIS17) based on the FPAR product and the RUE estimate based on the maximum ecosystem RUE, the VPD, and the minimum temperature.

Discussion

In this study we provide evidence that the PRI is a reliable estimator of RUE at ecosystem level in Mediterranean forests. Therefore, a real time estimation of carbon uptake can be carried out at Mediterranean forests, and probably in other vegetation types with a low seasonality of leaf area change. Recent work showed that a model based on EVI and surface temperature worked well in many ecosystems, but not so well in a Mediterranean type ecosystem subjected to prolonged drought and large swings in RUE (Sims et al. 2008). The presented methodology relies on the basis of freely available remote sensing data that complements traditional well-established vegetation indices such as the EVI or the NDVI with the PRI. Our results may thus be of great importance and have multiple applications such as the estimation of the productivity (CO_2 fixation) of Mediterranean forests or the detection of the effects of climatic change on vegetation that may occur before leaf-area reduction. But these results provide not only a significant technological improvement but also an important conceptual advance because they show that optical signals incorporate information on vegetation physiological performance (photosynthetic rates linked to changes in pigment ratios) at an ecosystem scale. Our results warrant thus a generalized study of PRI performance in multiple ecosystems and conditions in order to confirm the high expectations raised by the results we present here.

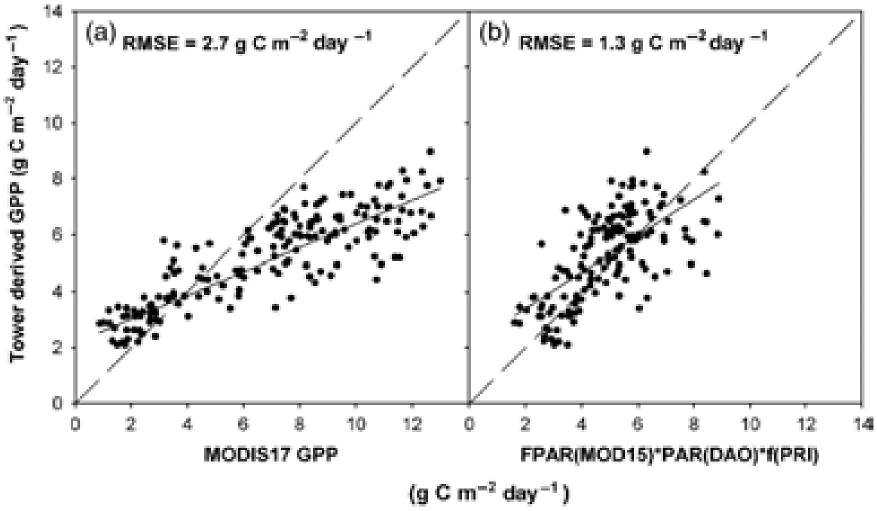


Figure 4 Seasonal relationships between the daily GPP estimated from eddy covariance data and from remote sensing for 2001–2004. (a) MODIS17 GPP derived from FPAR(MOD15), climate data, and a RUE estimate based on the maximum ecosystem RUE, the VPD, and the minimum temperature, and (b) GPP derived from the novel approach suggested here based on FPAR(MOD15), PAR from DAO, and PRI. Black lines are the linear regression between datasets and dotted lines are the 1 : 1 relationships. Root mean square error (RMSE) is indicated for each estimation

We tested the exponential and the linear PRI-RUE relationships. Both options were significant for the whole and the partial datasets. The coefficients of correlation in both types of models were similar for the 5 years dataset analysis, although the exponential regression accounted for a slightly greater proportion of the variability (r = 0.78) than the linear one (r = 0.76; Fig. 3). The relationships also slightly varied for the different years. We presented the nonlinear model because the previous experimental studies at the leaf level showed a saturation of the PRI at high photosynthetic RUE values (e.g. Gamon et al. 1997; Peñuelas et al. 1995) more than linear relationships (e.g. Nakaji et al. 2006; Peñuelas et al. 1997). At the ecosystem level, the available scarce evidence showed linear relationships (e.g. Drolet et al. 2005; Nichol et al. 2002), although a low number of data points were included for much of those linear regression analyses.

We found that the PRI-RUE relationship varied between years and that this variation was partially explained by annual precipitation. There was a decrease in the slope for 2004 and 2005 that can be explained by a reduction in RUE due to lower GPP values during the winters 2004–2005 and 2005–2006, without a reduction in PRI. We hypothesize that this decrease in the slope could be partially explained by the lower respiration rates estimated from temperature and nighttime fluxes for those periods. The lower respiration rates could be a result of the particular climatic conditions of the year (Reichstein et al. 2002) or could also be due to the low quality of the GPP estimations in periods of high rainfall with possible underestimations of the ecosystem respiration. It would be of high interest to analyze databases for longer periods in the next future and to complement the eddy covariance measures with leaf level CO_2 fluxes to rule out this kind of problems. Within years, the comparison of the PRI-RUE relationship showed stability of the slope between periods with low and high incident PAR, indicating that PRI is a good estimator of RUE independently of the seasonal changes in incident PAR.

The up-scaling of the previous work at leaf and plant level (Gamon et al. 1995; Gamon and Qiu 1999; Peñuelas et al. 1995; Peñuelas et al. 1997) to the 1 km x 1 km pixel level was successful for the studied Mediterranean forest, despite a number of a priori expected problems. Unlike greenness vegetation indices, which are mainly related to the red-edge reflectance of the vegetation, the PRI has a very low signal. Nevertheless, despite this low signal and the coarse spatial resolution of MODIS images, the PRI produced a very accurate signal of RUE presumably based on a leaf-level process related to the dissipation of radiation excess by plants and consequent xanthophyll pigment epoxidation. It is also likely that PRI scales with seasonal pigment changes (e.g. carotenoids/chlorophyll a ratio) and other related photosynthetic processes with stronger signals (Filella et al. 2004; Sims and Gamon 2002). Further studies are warranted to improve our understanding of which of these possibilities (xanthophylls cycle or pigment ratios) are primarily driving the seasonal changes in the MODIS PRI signal.

A second possible problem relates to the temporal matching between data from the carbon flux and the satellite spectral data. The MODIS Terra platform passes over in the morning and thus may not capture the full day gas exchange performance. For example, it may miss the afternoon decrease in carbon uptake as a result of summer drought. However, previous work in Mediterranean ecosystems suggest that seasonal down-regulation of carbon absorption due to chronic moisture or temperature stress is perhaps more significant than diurnal patterns (Allard et al. 2008; Xu and Baldocchi 2004), thus the morning overpasses used here should work fine as seasonal indicators of RUE. In any case, it would be interesting to address, by means of experimental tests, the importance of the time of the day for reflectance measurements to estimate PRI at ecosystem scales.

Furthermore, there are still a number of problems regarding the use of this data, above all associated with computational difficulties when performing atmospheric corrections. Corrected reflectances from MODIS are available only for seven out of its 36 bands, and the corrected data for constructing narrow-band spectral indexes such as the PRI are not available yet. Our data suggests that this problem can be overcome by using a normalized reflectance index, PRI, based on spectral bands closely located in the green portion of the electromagnetic spectrum, in order to make correction unnecessary. Therefore, this fact makes the data and the calculations available for everybody by accessing the MODIS data webpage. Previous work (Drolet et al. 2005) also provides evidence that atmospheric correction for close wavelengths is not always necessary.

A fourth issue is that the consistent relationship between ground and satellite data was found despite the fact that soil and plant respiration may produce a significant scatter in the relationship between PRI and carbon uptake. This is due to the fact that while PRI tracks gross photosynthesis (i.e. direct carbon uptake not including respiratory loss), conventional flux sampling methods provide the net CO_2 flux (i.e. combined photosynthetic carbon gain and respiratory loss) from the sampling area and ecosystem respiration is estimated from environmental variables (temperature and water availability) and extrapolation of night-time values of ecosystem respiration into the daytime (Reichstein et al. 2005).

Another issue is related to georegistration problems and to the low spatial resolution of the MODIS PRI. The use of a high number of images with the possible lack of coregistration between them is a problem when comparing a single pixel with the tower data. To reduce the noise derived from these problems we used a large enough Mediterranean forest site (42.5 km^2) to get the reflectance signal with a 1 km^2 MODIS pixel. These problems would be reduced using higher spatial resolution data, from present satellites and those coming in the future.

Finally, there are also the confounding physical effects of canopy structure, leaf movement, sun angle, and soil background that may also significantly influence the PRI signal (Gamon et al. 1992). Areas with low vegetation cover would present problems when using this methodology (Filella et al. 2004; Sims et al. 2006a). The higher leaf area index in Castelporziano compared with other Mediterranean forests could account for the higher strength of the relationship between PRI and RUE in this site. Moreover, the strong PRI–RUE relationship in this closed-canopy stand is also supported by previous studies that experimentally showed for a diversity of closed-canopy stands the close relationship of stand-level PRI with leaf level PRI (Gamon and Qiu 1999).

In any case, it is necessary to check our results in other homogeneous Mediterranean forests larger enough to place the MODIS 1 km^2 pixel, and to examine a range of ecosystems to reveal whether the utility of the PRI to assess carbon uptake will vary with the ecosystem in question due to contrasting environmental constraints, ecophysiological strategies, and light-use efficiencies. A comprehension of ecophysiological principles will be needed to fully reveal these patterns and it is likely that new remote-sensing approaches incorporating PRI will contribute to this understanding.

REFERENCES

Allard, V., Ourcival, J.M., Rambal, S., Joffre, R., & Rocheteau, A. (2008). Seasonal and annual variation of carbon exchange in an evergreen Mediterranean forest in southern France. *Global Change Biology, 14*, 714-725

Asner, G.P., Nepstad, D., Cardinot, G., & Ray, D. (2004). Drought stress and carbon uptake in an Amazon forest measured with spaceborne imaging spectroscopy. *Proceedings of the National Academy of Sciences of the United States of America, 101*, 6039-6044

Boisvenue, C., & Running, S.W. (2006). Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Global Change Biology, 12*, 862-882

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., & Valentini, R. (2005). Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature, 437*, 529-533

Drolet, G.G., Huemmrich, K.F., Hall, F.G., Middleton, E.M., Black, T.A., Barr, A.G., & Margolis, H.A. (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*, 212-224

Filella, I., Peñuelas, J., Llorens, L., & Estiarte, M. (2004). Reflectance assessment of seasonal and annual changes in biomass and CO_2 uptake of a Mediterranean shrubland submitted to experimental warming and drought. *Remote Sensing of Environment, 90*, 308-318

Gamon, J.A., Field, C.B., Goulden, M., Griffin, K., Hartley, A., Joel, G., Peñuelas, J., & Valentini, R. (1995). Relationships between NDVI, canopy structure, and photosynthetic activity in three Californian vegetation types. *Ecological Applications, 5*, 28-41

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., & Qiu, H.-L. (1999). Ecological applications of remote sensing at multiple scales In F.I. Pugnaire & F. Valladares (Eds.), *Handbook of Functional Plant Ecology* (pp. 805-846). New York: Marcel Dekker, Inc

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

Heinsch, F.A., M. Zhao, S. W. Running, J. S. Kimball, R. R. Nemani, K. J. Davis, P. V. Bolstad, B. D. Cook, A. R. Desai, D. M. Ricciuto, B. E. Law, W. C. Oechel, H. J. Kwon, H. Luo, S. C. Wofsy, A. L. Dunn, J. W. Munger, D. D. Baldocchi, L. Xu, D. Y. Hollinger, A. D. Richardson, P. C. Stoy, M. B. S. Siqueira, R. K. Monson, S. P. Burns, & Flanagan, L.B. (2006). Evaluation of remote sensing based terrestrial productivity from MODIS using regional tower eddy flux network observations. *Ieee Transactions on Geoscience and Remote Sensing, 44*, 1908-1925

Heinsch, F.A., Reeves, M., Votava, P., Kang, S., Milesi, C., Zhao, M., Glassy, J., Jolly, W.M., Loehman, R., Bowker, C.F., Kimball, J.S., Nemani, R.R., & Running, S.W. (2003). User's Guide GPP and NPP (MOD17A2/A3) Products NASA MODIS Land Algorithm. In, *User's Guide GPP and NPP (MOD17A2/A3) Products NASA MODIS Land Algorithm* (p. 57). Missoula, MT: University of Montana

Monteith, J.L. (1977). Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society B: Biological Sciences, 281*, 277-294

Myneni, R.B., Hoffman, S., Knyazikhin, Y., Privette, J.L., Glassy, J., Tian, Y., Wang, Y., Song, X., Zhang, Y., Smith, G.R., Lotsch, A., Friedl, M., Morisette, J.T., Votava, P., Nemani, R.R., & Running, S.W. (2002). Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. *Remote Sensing of Environment, 83*, 214-231

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., Lloyd, J., Shibistova, O., Arneth, A., Roser, C., Knohl, A., Matsubara, S., & Grace, J. (2002). Remote sensing of photosynthetic-light-use efficiency of a Siberian boreal forest. *Tellus Series B-Chemical and Physical Meteorology, 54*, 677-687

Nichol, C.J., Rascher, U., Matsubara, S., & Osmond, B. (2006). Assessing photosynthetic efficiency in an experimental mangrove canopy using remote sensing and chlorophyll fluorescence. *Trees-Structure and Function, 20*, 9-15

Ogaya, R., & Peñuelas, J. (2003). Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany, 50*, 137-148

Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R., Vesala, T., & Yakir, D. (2006). Towards a standardized processing of Net Ecosystem

Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences, 3*, 571-583

Peñuelas, J., Filella, I., & Gamon, J.A. (1995). Assessment of photosynthetic radiation-use efficiency with spectral reflectance. *New Phytologist, 131*, 291-296

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

Rahman, A.F., Cordova, V.D., Gamon, J.A., Schmid, H.P., & Sims, D.A. (2004). Potential of MODIS ocean bands for estimating CO_2 flux from terrestrial vegetation: A novel approach. *Geophysical Research Letters. doi:10.1029/ 2004GL019778, 31*

Rahman, A.F., Gamon, J.A., Fuentes, D.A., Roberts, D.A., & Prentiss, D. (2001). Modeling spatially distributed ecosystem flux of boreal forest using hyperspectral indices from AVIRIS imagery. *Journal of Geophysical Research, [Atmospheres], 106*, 33579-33591

Rambal, S., Ourcival, J.-M., Joffre, R., Mouillot, F., Nouvellon, Y., Reichstein, M., & Rocheteau, A. (2003). Drought controls over conductance and assimilation of a Mediterranean evergreen ecosystem: scaling from leaf to canopy. *Global Change Biology, 9*, 1813-1824

Reichstein, M., Falge E, D. Baldocchi, D. Papale, M. Aubinet, P. Berbigier, C. Bernhofer, N. Buchmann, T. Gilmanov, A. Granier, T. Grünwald, K. Havránková, H. Ilvesniemi, D. Janous, A. Knohl, T. Laurila, A. Lohila, D. Loustau, G. Matteucci, T. Meyers, F. Miglietta, J. Ourcival, J. Pumpanen, S. Rambal, E. Rotenberg, M. Sanz, J. Tenhunen, G. Seufert, F. Vaccari, T. Vesala, Yakir, D., & Valentini, R. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology, 11*, 1424 -1439

Reichstein, M., Tenhunen, J.D., Roupsard, O., Ourcival, J.M., Rambal, S., Dore, S., & Valentini, R. (2002). Ecosystem respiration in two Mediterranean evergreen Holm Oak forests: drought effects and decomposition dynamics. *Functional Ecology, 16*, 27-39

Schulze, E.D. (2006). Biological control of the terrestrial carbon sink. *Biogeosciences, 3*, 147-166

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

Sims, D.A., H. Luo, S. Hastings, W.C. Oechel, Rahman, A.F., & Gamon, J.A. (2006a). Parallel adjustments in vegetation greenness and ecosystem CO_2 exchange in response to drought in a Southern California chaparral ecosystem. *Remote Sensing of Environment, 103*, 289-303

Sims, D.A., Rahman, A.F., Cordova, V.D., Baldocchi, D.D., Flanagan, L.B., Goldstein, A.H., Hollinger, D.Y., Misson, L., Monson, R.K., Schmid, H.P., Wofsy, S.C., & Xu, L.K. (2005). Midday values of gross CO_2 flux and light use efficiency during satellite overpasses can be used to directly estimate eight-day mean flux. *Agricultural and Forest Meteorology, 131*, 1-12

Sims, D.A., Rahman, A.F., Cordova, V.D., El-Masri, B.Z., Baldocchi, D.D., Bolstad, P.V., Flanagan, L.B., Goldstein, A.H., Hollinger, D.Y., Misson, L., Monson, R.K., Oechel, W.C., Schmid, H.P., Wofsy, S.C., & Xu, L. (2008). A new model of gross primary productivity for North American ecosystems based solely on the enhanced vegetation index and land surface temperature from MODIS. *Remote Sensing of Environment, 112*, 1633-1646

Sims, D.A., Rahman, A.F., Cordova, V.D., El-Masri, B.Z., Baldocchi, D.D., Flanagan, L.B., Goldstein, A.H., Hollinger, D.Y., Misson, L., Monson, R.K., Oechel, W.C., Schmid, H.P., Wofsy, S.C., & Xu, L.K. (2006b). On the use of MODIS EVI to assess gross primary productivity of North American ecosystems. *Journal of Geophysical Research-Biogeosciences G04015, doi:10.1029/ 2006JG000162, 111*

Tirone, G., S. Dore, G. Matteucci, S. Greco, & Valentini, R. (2003). Evergreen Mediterranean Forests: Carbon and Water Fluxes, Balances, Ecological and Ecophysiological Determinants. In R. Valentini (Ed.), *Fluxes of Carbon, Water and Energy of European Forests. Ecological Studies 163* (pp. 125-150). Berlin: Springer

Tucker, C.J., Vanpraet, C.L., Sharman, M.J., & Vanittersum, G. (1985). Satellite Remote-Sensing of Total Herbaceous Biomass Production in the Senegalese Sahel - 1980-1984. *Remote Sensing of Environment, 17*, 233-249

Valentini, R., Arriga, N., Mazzenga, F., & Stefani, P. (2007). Level 4 dataset CEIP_EC_L4_ITCpz_v01 in CarboeuropeIP Ecosystem Component Database http://gaia.agraria.unitus.it/database

Vermote, E.F., El Saleous, N.Z., & Justice, C.O. (2002). Atmospheric correction of MODIS data in the visible to middle infrared: first results. *Remote Sensing of Environment, 83*, 97-111

Vermote, E.F., Tanré, D., Deuzé, J.L., Herman, M., & Morcrette, J.J. (1997). Second simulation of the satellite signal in the solar spectrum, 6S: an overview. *Ieee Transactions on Geoscience and Remote Sensing, 35*, 675-686

Xiao, X.M., Zhang, Q.Y., Hollinger, D., Aber, J., & Moore, B. (2005). Modeling gross primary production of an evergreen needleleaf forest using MODIS and climate data. *Ecological Applications, 15*, 954-969

Xu, L., & Baldocchi, D.D. (2004). Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. *Agricultural and Forest Meteorology, 123*, 79-96

Chapter 6

Photochemical Reflectance Index (PRI) can estimate seasonal variations of ecosystem gross radiation use efficiency across different vegetation types

ABSTRACT

The estimation of carbon uptake by vegetation is a critical challenge in the quantification of the carbon cycle. The Radiation Use Efficiency (RUE) model proposed that the Gross Primary Productivity (GPP) can be estimated from the radiation absorbed by the vegetation and the RUE term that transforms the absorbed radiation into plant biomass. Satellite information is most frequently used to estimate the fraction of the incident photosynthetically active radiation absorbed by the vegetation (fPAR) using spectral indices such as the Enhanced Vegetation Index (EVI). Remotely sensed estimation of RUE could also make it independent from ground climatic data. The Photochemical Reflectance Index (PRI) is a normalized spectral index based on the reflectance of the vegetation of narrow bands centered in 531 nm, and has been shown to correlate with the variations of the RUE in leaves and plants. We aimed here to study the possibility to scale up the estimation of RUE to ecosystem level. We evaluated the PRI as a remotely sensed surrogate of the ecosystem RUE in a wide range of vegetation types (grassland, *Eucalyptus* plantation, subtropical and temperate evergreen, Mediterranean broadleaf and needleaf and temperate deciduous forests). We analyzed GPP from eddy covariance data of carbon fluxes and related it to MODIS (MODerate resolution Imaging Spectroradiometer) data. PRI_4 was calculated using MODIS band 4 (545-555 nm) as reference band and PRI_1 using band 1 (620-670 nm). EVI reasonably estimated GPP only for deciduous sites and APAR significantly improved the estimation of daily GPP. Daily and midday RUE were well correlated and the values of RUE for the seven sites presented in general a good agreement with previous studies. RUE presented positive relationship with PRI in all different sites except in grasslands. For single years PRI_1 or PRI_4 accounted for 45 to 80% of the variability of RUE depending on the site. The best estimations of RUE by PRI occurred in the sites with the most constant values of fPAR. PRI_4 showed the best correlation with RUE in the subtropical needleleaf forest, in the *Eucalyptus* plantation, and in the Mediterranean broadleaf and needleleaf forests. PRI_1 was better surrogate of RUE in the temperate deciduous forest and in the temperate evergreen forest. In the temperate deciduous forest, the strength of the RUE-PRI relationship greatly varied between years. In more temperate deciduous forests PRI emerged as useful complement to estimate GPP at least in years with changes in GPP without changes in biomass. These results show thus that it is possible to estimate RUE and GPP in real time in most ecosystems by using PRI or a combination of EVI and PRI. Moreover, the use of PRI could directly assess the changes in RUE or in photosynthetic performance previous to more drastic decays in leaf area or other structural parameters.

Keywords: gross primary productivity, carbon cycle, spectral indices, Normalized Difference Vegetation Index, Enhanced Vegetation Index

INTRODUCTION

The estimation and prediction of carbon uptake by the vegetation is a critical challenge in quantifying the carbon cycle (Canadell et al. 2004). Many models to estimate carbon uptake, its spatial and temporal variability, are derived from the radiation use efficiency (RUE) model (Monteith 1972, Monteith 1977), which proposed that the carbon uptake can be estimated from the radiation absorbed by the vegetation and the RUE term that transforms the absorbed radiation into photosynthates (Ruimy et al. 1994). This model is very simple and has been widely applied to globally estimate primary productivity for different vegetation types (e.g. Field et al. 1995, Running et al. 2004). However, there are still many uncertainties which mainly result from the inaccurate estimation of each of the variables involved in the model.

Remote sensing tools emerged in the early 1980s as a very interesting complement to make explicit carbon fluxes estimates made with other techniques (Sellers 1985, Tucker and Sellers 1986). Different ground based measurements of carbon uptake by the vegetation have been extrapolated in time and space using spectral indices derived from sensors on board of satellites or airborne platforms. Satellite information was most frequently used to estimate the fraction of the photosynthetically active radiation absorbed by the vegetation (fPAR) by means of spectral indices such as the Normalized Difference Vegetation Index (NDVI) (Sellers 1985, Myneni et al. 2002) or the Enhanced Vegetation Index (EVI) (Huete et al. 2002). Evidences from different vegetation types show that carbon uptake can be estimated directly and solely from spectral indices that estimate radiation absorption (fPAR). Several works showed that temporal or spatial variability of carbon uptake of vegetation scales with the NDVI (e.g. Box et al. 1989, Paruelo et al. 1997) and more recently also with the EVI (e.g. Xiao et al. 2004a, Xiao et al. 2004b, Rahman et al. 2005, Xiao et al. 2005, Sims et al. 2006, Olofsson et al. 2008, Sjöström et al. 2009, chapter 4). In general, these studies showed that EVI by itself is a good surrogate of temporal changes in GPP derived from eddy covariance towers, although there are still several unresolved questions on this matter, like the different GPP-EVI relationships between leaf expansion and senescence in deciduous forest (Nagai et al. 2010). Although different time and spatial scales are represented in these studies, the success of the seasonal estimations depends on the coupling of the seasonality of leaf area with the photosynthesis rate (Sims et al. 2006). For evergreen vegetation types, the strength of the relationships between GPP and EVI is generally lower than in deciduous vegetation types, since changes in GPP are related to physiological related processes and not related to changes in leaf area. The product fPAR times the photosynthetically active radiation, namely APAR, was also positively related with GPP for different vegetation types at a daily time step (Turner et al. 2003). The type of the relationships varied with the vegetation type from linear to hyperbolic, saturating at high levels of APAR, meaning that the RUE decreases at high levels of APAR.

Among the variables of the RUE model, RUE itself has been the most difficult variable to estimate. The most common way to estimate RUE is by assuming the relationships with climatic variables such as vapor pressure deficit (VPD) and temperature (Heinsch et al. 2006). This is probably the most clear and operationally available methodology to globally estimate RUE for different vegetation types and at a reasonable time step, but these relationships have been demonstrated to be weak (Garbulsky et al. 2010). One of the most promising ways to make these estimations independent from climatic data is to remotely estimate RUE. The Photochemical Reflectance Index (PRI) is a normalized spectral index that was related to spatial and temporal variations of the RUE (Gamon et al. 1992, Peñuelas et al. 1995) and was proposed as a possible way to scale up the changes in the RUE from leaves to ecosystems (Garbulsky et al. submitted). At the ecosystem level, there are multiple evidences showing that the PRI derived from MODIS can be used to accurately infer the seasonal and spatial changes of RUE for different vegetation types including Mediterranean forests (Garbulsky et al. 2008, Goerner et al. 2009), temperate deciduous forest (Rahman et al. 2004) and deciduous (Drolet et al. 2005) and coniferous (Drolet et al. 2008) boreal forests. Even though MODIS was not specifically designed for estimating RUE from space, the precedent references demonstrated that it is possible to use a MODIS PRI to infer the spatial and seasonal distribution of RUE for different forest types and demonstrated the enormous potential of MODIS data. Different problems that preclude its generalization to ecosystem scales and its global and operational use as an estimator of RUE have recently been reviewed (Garbulsky et al. submitted). These problems are related to the interference to the PRI signal produced by other plant pigments not related to photosynthetic efficiency, to the structural differences of the canopies, to varying “background effects” (e.g. soil color, moisture, or shadows) to the different PRI formulations or signals derived from a variety of sensors and to illumination and viewing angles variations. This latter point is of significant importance to arrive to a reliable PRI signal. Additional observational studies are crucial for identifying a number of remaining issues, e.g. the behavior of PRI in other biomes (Hilker et al. 2008) before we can operationally produce RUE estimates from satellite platforms.

The main objective of this study was to analyze the links between the intra and interannual carbon uptake of vegetation estimated by the eddy covariance technique for a wide diversity of vegetation types and the spectral indices of the vegetation derived from the MODerate resolution Imaging Spectroradiometer (MODIS). Since different vegetation types dramatically differ in terms of the behavior of seasonality of GPP and radiation absorption, we analyzed the importance of each one of the terms of the RUE model (PAR, EVI, as a surrogate of fPAR, and RUE) for a wide diversity of vegetation functional types. The available data are beginning to show that the usefulness of PRI to estimate RUE depends on the particular combination of environmental conditions, radiation use efficiencies, and structural characteristics of the different vegetation types in question. We hypothesized that the PRI would have ecosystem-specific performances depending on the degree to which any one environmental factor controls photosynthetic rates. Therefore we expected a wide variation in the degree to which fPAR and RUE are individually important to track the dynamics of temporal and spatial patterns of carbon fluxes for different ecosystem types. The ability to predict fluxes from these indices for different biomes should be thus quite variable and would depend upon dominant factors affecting photosynthetic carbon flux.

The specific objectives of this study were,

1) to describe the seasonal variations of GPP estimations derived from one widely used estimator of fPAR, that is EVI, along a diversity of vegetation types,

2) to assess the relative importance of each of the components of the RUE model (i.e. PAR, fPAR, APAR and RUE) to estimate GPP in different ecosystems, and

3) to evaluate the MODIS PRI as a remotely sensed estimator of the seasonal variability of ecosystem gross RUE in a range of vegetation types with contrasting seasonality in the fPAR, APAR and GPP.

The final objective was to generate an operationally simple way to use the available data to increase the accuracy of GPP estimations, particularly in those ecosystems with low seasonal changes in the fPAR.

MATERIALS AND METHODS

We gathered data from seven sites having eddy covariance data for a wide range of vegetation types and climatic conditions. The selected sites are included in the Ameriflux (http://public.ornl.gov/ameriflux/) or CarboEurope (http://gaia.agraria.unitus.it/database/carboeuropeip/) networks. These sites represent a wide range of vegetation types distributed throughout Europe and America (Table 1). The selected sites comprised homogeneous stands of each vegetation type and were large enough to gather the spectral reflectance of the stand with the satellite images. Different periods between January 2003 and December 2008 were analyzed including at least two complete growing seasons for each site (Table 1).

GPP was estimated from the Net Ecosystem Exchange (NEE) fluxes measured at the EC towers with 30 min resolution using a standardized partitioning method for all the sites as described by Reichstein et al. (2005) and Papale et al. (2006). We discarded GPP values lower than 0.1 µmol $m^{-2}s^{-1}$ for our analysis. An average for the specific day of the composites of the half-hour values for GPP (g C m^{-2} day^{-1}) and incoming PAR (MJ m^{-2} day^{-1}), derived from the EC tower data, was calculated for days having MODIS AQUA vegetation indices data (MYD13Q1). These images consist of a 16-day value at 250-m spatial resolution (Huete et al. 2002). For all the MODIS data, quality flags were checked to discard low-quality images. The basic temporal resolution of the analysis is 16 days, which corresponds to that of the MYD13Q1 data. Theoretically, this represents 23 images per year; however, we obtained fewer images for each year and site owing to a lack or to a bad quality of the MODIS or the EC data. We defined the daily gross RUE as:

$$\text{RUE (g C MJ APAR}^{-1}\text{)=GPP} \times \text{fPAR}^{-1} \times \text{PAR}^{-1} \quad (1)$$

A daily average of the GPP and PAR half-hour values was used for days having MODIS AQUA NDVI and EVI data (MYD13). We used the NDVI and EVI from the 16-day MODIS products. NDVI was used as an estimator for fPAR for the RUE calculation. We firstly evaluated the capacity of EVI and EVI*PAR as estimators of GPP temporal variability for a daily and a midday (from 1 to 3 pm) averages for each site. We used the data for the specific day of the MYD13Q1 MODIS product.

Table 1 Main vegetation type, analyzed period, location and reference for the sites included in the analysis.

Vegetation type	Site and analyzed period	Lat	Long	Reference
Evergreen subtropical needleleaf forest dominated by *Pinus elliotti*	Donaldson, USA 2003-04	29° 45' 17.1"	-82° 9' 47"	(Powell et al. 2008)
Eucalyptus globulus plantation	Espirra, Portugal 2003-05	38º 38' 21.7"	-8º36'6.48"	(Rodrigues et al. 2005, Pereira et al. 2007)
Mediterranean Evergreen broadleaf forest dominated by *Quercus ilex*	Castelporziano, Italy 2003-05	41º 42´	12º 22´	(Garbulsky et al. 2008)
Deciduous temperate forest dominated by *Quercus cerris*	Roccarrespampani, Italy 2003-08	42º 24.48´	11º 55.8´	(Rey et al. 2002)
Mediterranean Evergreen needleleaf forest dominated by *Pinus halepensis*	San Rossore, Italy 2003-04	43º43'40.29",	10º17'3.99"	
Evergreen temperate forest dominated by *Picea rubens* and *Tsuga canadensis*	Howland forest, USA 2003-05	45º 12’ 14”	-68º 44’ 25”	(Hollinger et al. 2004)
Grassland (mixed prairie)	Fort Peck, USA 2003-06	48º 18’	-105º 6’	(Meyers 2008)

We calculated the PRI = (band 11- ref band)/(band 11 + ref band), from the MODIS Aqua daily calibrated radiances (MYD for bands 11 (526-536 nm) and reference bands 1 (620–670 nm) and 4 (545 - 565 nm) for the pixels that included the towers. Band 4 is located in a similar position but is broader than band 12 (546-556 nm), which was previously used to calculated PRI (Garbulsky et al. 2008). We evaluated the PRI using band 1 (PRI_1) and band 4 (PRI_4) as references as seasonal estimators of the RUE (Eq 1) by linear relationships.

The viewing and solar geometry can heavily impact on PRI signal. Therefore, we used the view and solar zenith angle and the relative azimuth angles from the MODIS geolocation product for AQUA images to analyze their impact on the PRI signal. Pixels with viewing zenith angles higher than 45º were discarded for our analysis. We performed multiple regressions between the daily and midday RUE as dependent variable and PRI_1, PRI_4 and the angles as independent ones. For those sites with more than one year data, we also included the year as a factor in an Analysis of Covariance (ANCOVA) to test if the relationships between RUE and PRI are stable throughout the different growing seasons. All the statistical analysis were performed with R package (R Development Core Team, 2008).

RESULTS

The temporal variability of daily GPP was in general poorly estimated by EVI for the analyzed sites except in the temperate deciduous forest. The relationships between the daily averages GPP with EVI varied between non significant relationships in the Eucalyptus plantation and the subtropical evergreen forest to relationships with a coefficient of determination of 0.78 in the deciduous temperate forest (figure 1). Even a slightly negative relationship resulted for the Mediterranean needleleaf forest. All the relationships between daily GPP and EVI*PAR were positive and significant, and the coefficient of determination varied from 0.11 to 0.79.

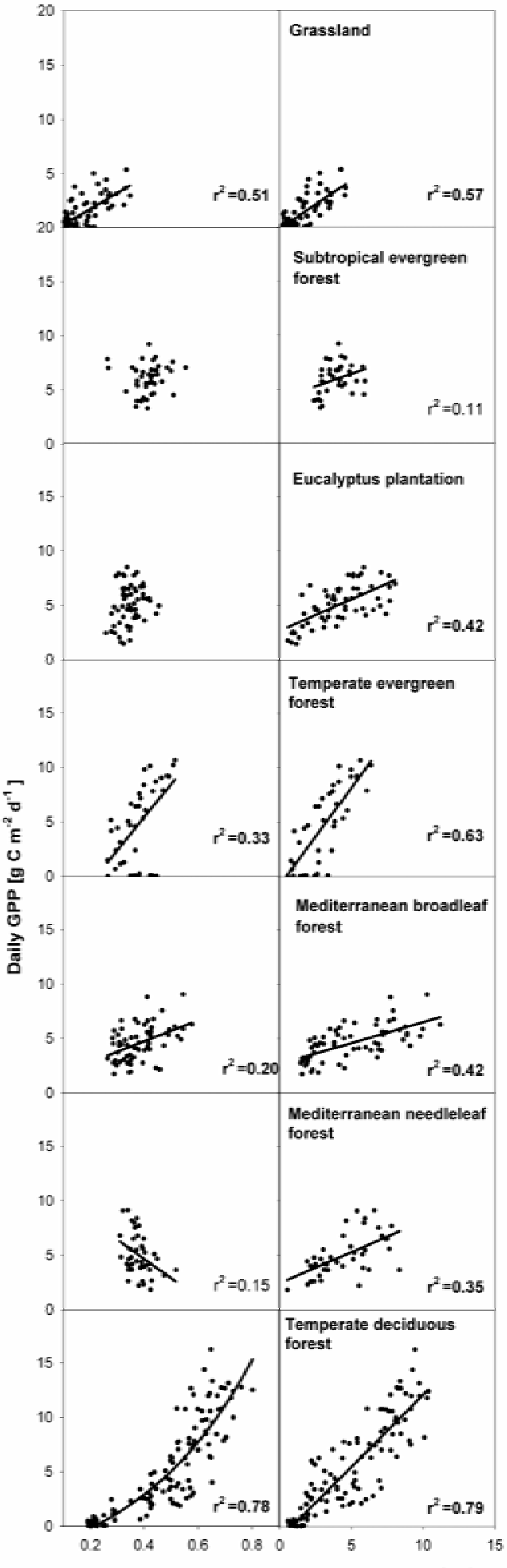


Figure 1. Relationships of daily GPP with EVI and EVI*PAR for the whole growing seasons in seven sites with contrasting vegetation types. Regression lines are significant ($p<0.1$) and those marked in bold type are highly significant ($p<0.0001$).

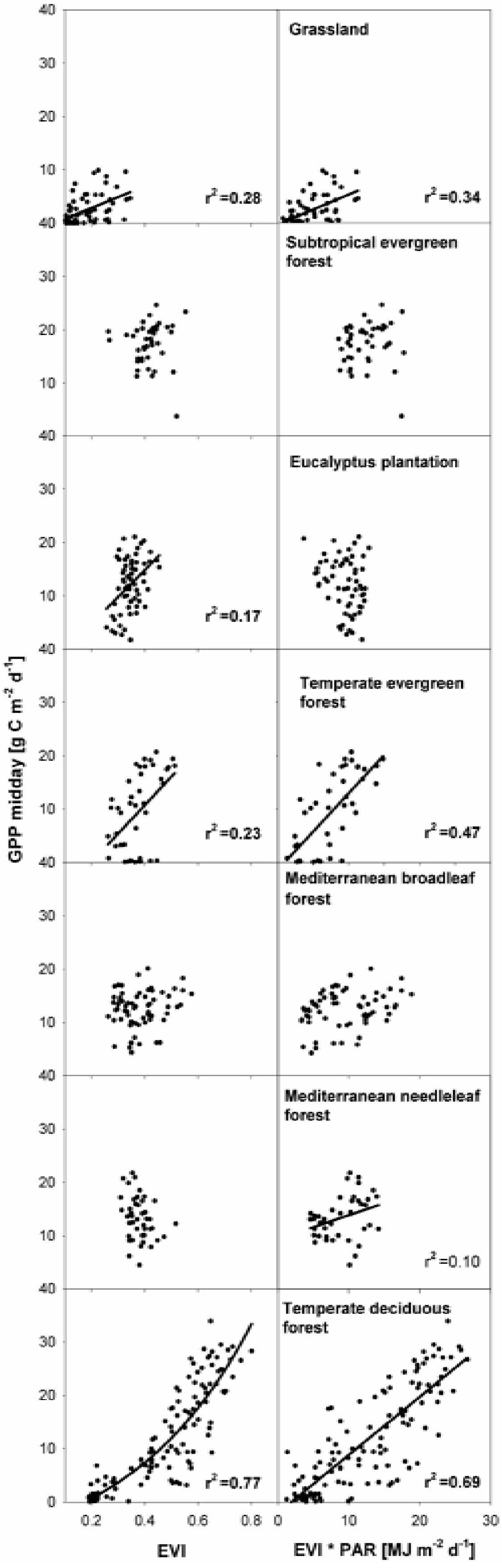


Figure 2. Relationships of midday (1 to 3 p.m.) GPP with fPAR and APAR in seven sites with contrasting vegetation types. Regression lines are significant ($p<0.1$) and those marked in bold type are highly significant ($p<0.0001$).

The strength of the relationships between midday GPP and EVI was also very variable for the seven analyzed sites. The relationships between midday GPP and EVI varied from non significant relationships in the Mediterranean broadleaf, needleaf and the subtropical needleaf forests to relationships with coefficient of determination of 0.77 in the deciduous temperate forest (figure 2). The strength of the relationships between midday GPP and EVI*PAR were also very variable ($0.10 < R^2 < 0.69$) and for three of the sites the relationships were non significant.

Daily and midday GPP were highly correlated ($0.60 > R^2 > 0.95$). Gross Radiation use efficiency (RUE) varied across sites and along the growing seasons. In general the daily RUE or the midday RUE were similar (t test, $p>0.2$) and highly correlated ($0.68 > R^2 > 0.95$) for all the sites (figure 3).

The Photochemical Reflectance Index (PRI) derived from MODIS Aqua satellite varied throughout the growing seasons (Figure 4). PRI_4 and PRI_1 range values differed for each of the sites but in some cases were parallel (e.g. *Eucalyptus plantation* and Mediterranean needleleaf forest). Seasonal patterns also differed between sites. Maximum PRI_4 and PRI_1 seasonal values occurred in winter in the Mediterranean forests while in the temperate evergreen forest maximum PRI_1 occurred in summer.

In general PRI_1 and PRI_4 were significantly related to RUE for all the sites (Table 2). Only for the grassland site PRI did not accounted for the variability of RUE. The view and sun angles accounted for part of the variability of RUE in several sites, but there was no consistent pattern. Between them, the sun zenith angle was most frequently the one accounting for more variability of the RUE. The relative azimuth angle (sun azimuth – view azimuth) significantly accounted for the variability of RUE only in the *Eucalyptus* plantation. In the *Eucalyptus* plantation and the Mediterranean broadleaf forest RUE-PRI relationships significantly differed between years.

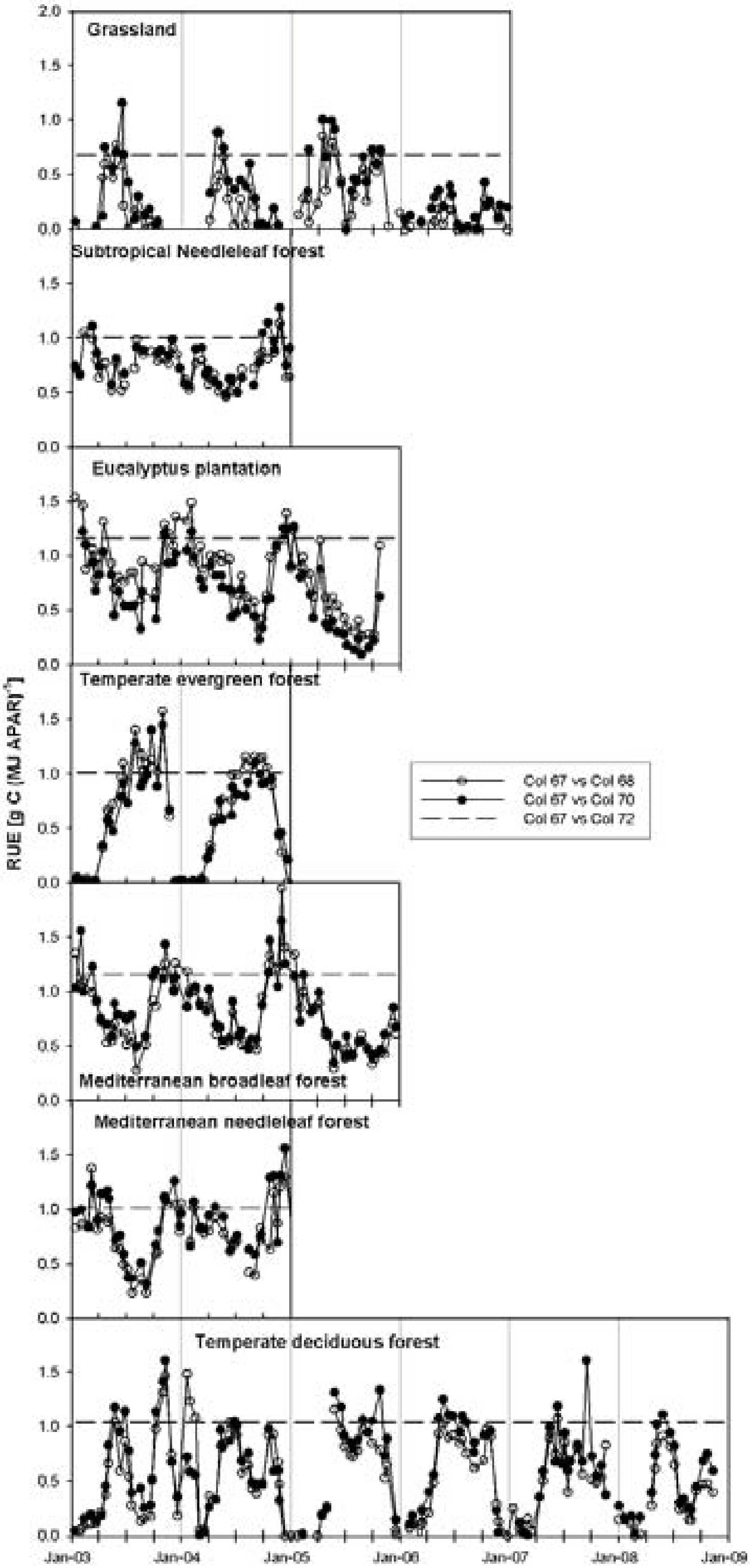


Figure 3. Seasonal variations of daily and midday radiation use efficiencies (RUE) for seven sites with contrasting vegetation types. Dashed lines are the maximum radiation use efficiency used in the MODIS GPP algorithm for each vegetation type: grassland, evergreen needleleaf forest, evergreen and deciduous broadleaf forest.

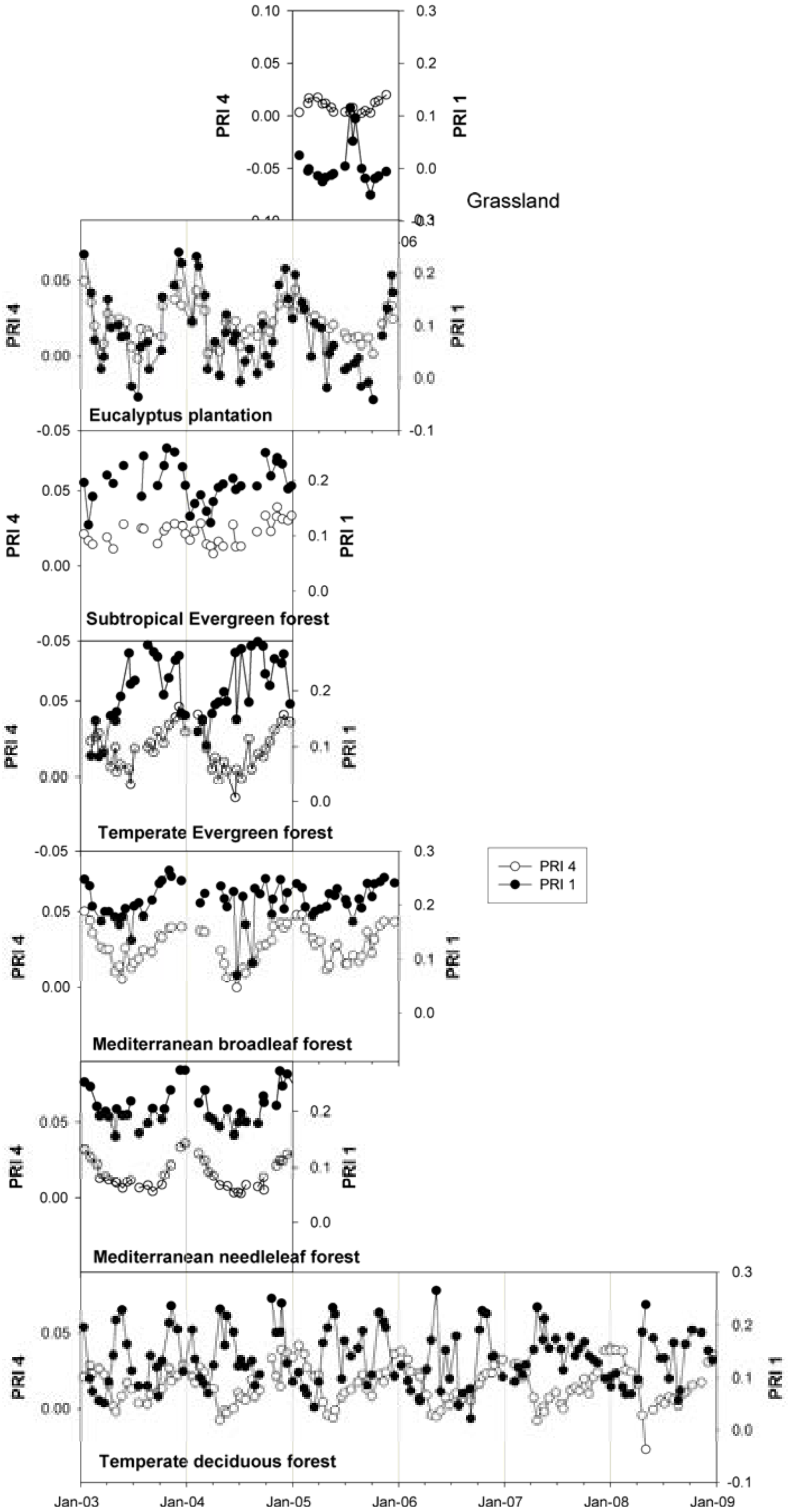


Figure 4. Seasonal variations of the MODIS Aqua Photochemical Reflectance Index (PRI) calculated using bands 4 and 1 as reference bands in seven sites with contrasting vegetation types.

Table 2. Multiple linear relationships between RUE and PRI, zenith and azimuth angles and year for each site. Bold type coefficients are significant ($p< 0.01$).

	RUE daily		RUE midday	
	PRI_1	PRI_4	PRI_1	PRI_4
Grassland				
PRI_1	0.038		0.136	
PRI_4		0.006		0.030
Sun zenith angle	0.195	**0.126**	0.125	0.017
View zenith angle	0.094	0.043	0.046	0.025
relative azimuth angle	0.001	0.000	0.005	0.006
Subtropical evergreen forest				
PRI_1	**0.284**		**0.258**	
PRI_4		**0.364**		**0.212**
sun zenith angle	**0.175**	0.026	0.093	0.021
view zenith angle	0.022	0.000	0.004	0.023
relative azimuth angle	0.010	0.011	0.016	0.005
year	0.009	0.003	0.009	0.058
Eucalyptus plantation				
PRI_1	**0.474**		**0.478**	
PRI_4		**0.351**		**0.346**
sun zenith angle	0.012	**0.041**	**0.046**	**0.095**
view zenith angle	0.000	0.000	0.000	0.001
relative azimuth angle	**0.039**	**0.056**	**0.041**	**0.056**
year	**0.089**	**0.132**	**0.053**	**0.085**
Evergreen temperate forest				
PRI_1	**0.467**		**0.434**	
PRI_4		0.058		0.050
sun zenith angle	**0.094**	**0.116**	**0.087**	**0.120**
view zenith angle	0.005	**0.129**	0.001	**0.145**
relative azimuth angle	0.002	0.072	0.004	0.018
year	0.022	0.006	0.000	0.003
Mediterranean broadleaf forest				
PRI_1	0.018		**0.031**	
PRI_4		**0.260**		**0.330**
sun zenith angle	**0.427**	**0.146**	**0.514**	**0.182**
view zenith angle	0.027	0.021	0.007	0.003
relative azimuth angle	0.009	0.011	0.002	0.002
year	**0.130**	**0.144**	**0.054**	**0.062**
Mediterranean needleaf forest				
PRI_1	**0.132**		**0.201**	
PRI_4		**0.265**		**0.309**
sun zenith angle	**0.118**	0.008	**0.137**	0.037
view zenith angle	0.000	0.007	0.000	0.002
relative azimuth angle	0.003	0.002	0.000	0.001
year	0.005	0.012	0.037	0.049
Temperate deciduous forest				
PRI_1	**0.216**		**0.261**	
PRI_4		**0.207**		**0.215**
sun zenith angle	**0.144**	0.013	**0.139**	0.014
view zenith angle	0.000	0.005	0.000	0.005
relative azimuth angle	0.000	0.003	0.000	0.004
year	0.008	0.004	**0.026**	0.021

When filtering the data by sun-view geometry, PRI_4 accounted for a great part of the variability of RUE for single years in the more perennial sites (Fig. 5a). PRI_4 did not account for the variability of RUE in any of the Temperate forests (Fig. 5b). PRI_1 also accounted for the variability of RUE in the Mediterranean needleleaf forest, in the *Eucalyptus* plantation, in the subtropical evergreen forest (Fig. 5d), and moreover in the temperate deciduous and the temperate evergreen forests (Fig. 5e). Neither PRI_4 (Fig. 5c) nor PRI_1 (Fig. 5f) accounted for the variability of RUE in the grassland site.

Even for those vegetation types with significant relationships between GPP and EVI APAR such as the temperate deciduous forest, RUE estimation by PRI can provide a significant improvement complementing the estimation of GPP. In the temperate deciduous forest, we found a high interannual variability of the relationships between GPP, RUE and the spectral indices. When the data was split for the different years, the strength of relationships between GPP and EVI were highly variable. The coefficient of determination for the relationship between GPP and EVI APAR varied for the temperate deciduous forest between 0.42 and 0.91 for the six analyzed years (Figure 6). The strength of the relationship between RUE and PRI changed even more between years, with coefficients of determination that ranged from 0.06 to 0.6, and there was a significant negative correlation between the coefficients of determination of this relationship GPP-EVI APAR with those of the relationship RUE-PRI ($R^2=0.69$; $p<0.05$; $n=6$, Fig. 6).

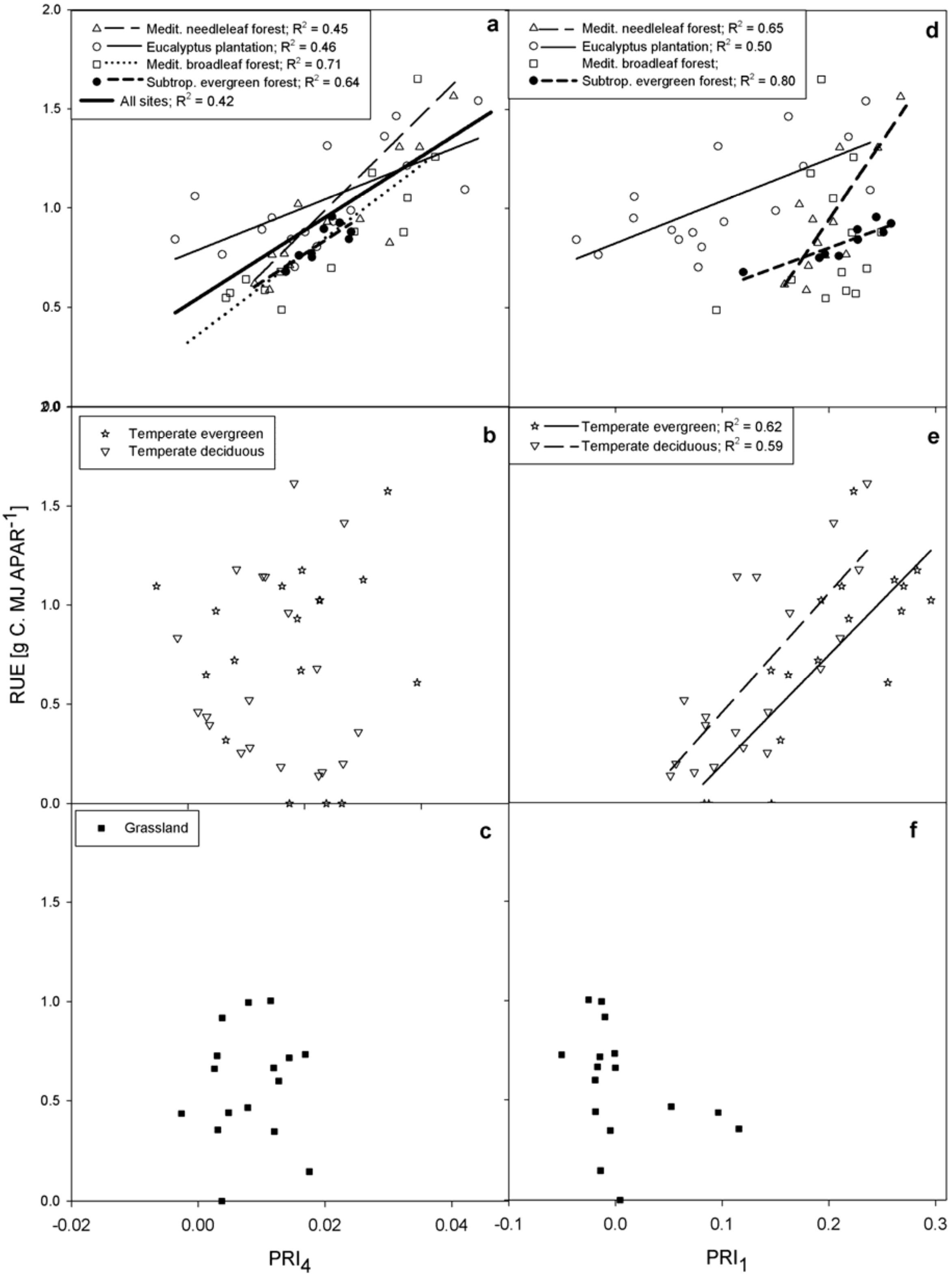


Figure 5. Seasonal relationships between RUE and PRI for one selected year for each one of the seven vegetation types studied. Linear regressions are significant ($p<0.01$).

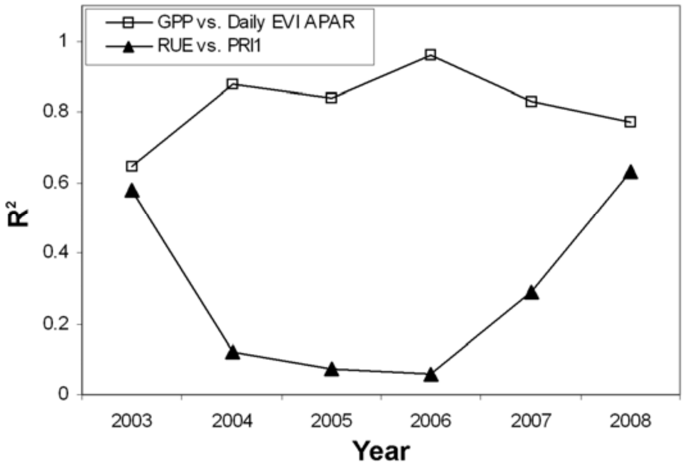


Figure 6. Interannual variability of the relationships between daily GPP and EVI APAR and between RUE and PRI for the temperate deciduous forest.

These results show that PRI is a good surrogate for RUE, and thereof that it can be included in the RUE model to estimate GPP. Particularly, in those ecosystems where EVI or APAR did not account for a significant proportion of the variability of GPP, an estimation of RUE by means of PRI could derive in a better estimation of GPP. For example, in the Mediterranean needleleaf forest neither EVI nor APAR explained a significant part of the temporal variability of GPP (Fig.1, 2, 7a and 7b). The inclusion of PRI_4 as a surrogate of RUE for this site significantly increased the accuracy of the estimated GPP (Fig. 7c). GPP derived from eddy covariance and GPP estimated by EVI and PRI were highly correlated.

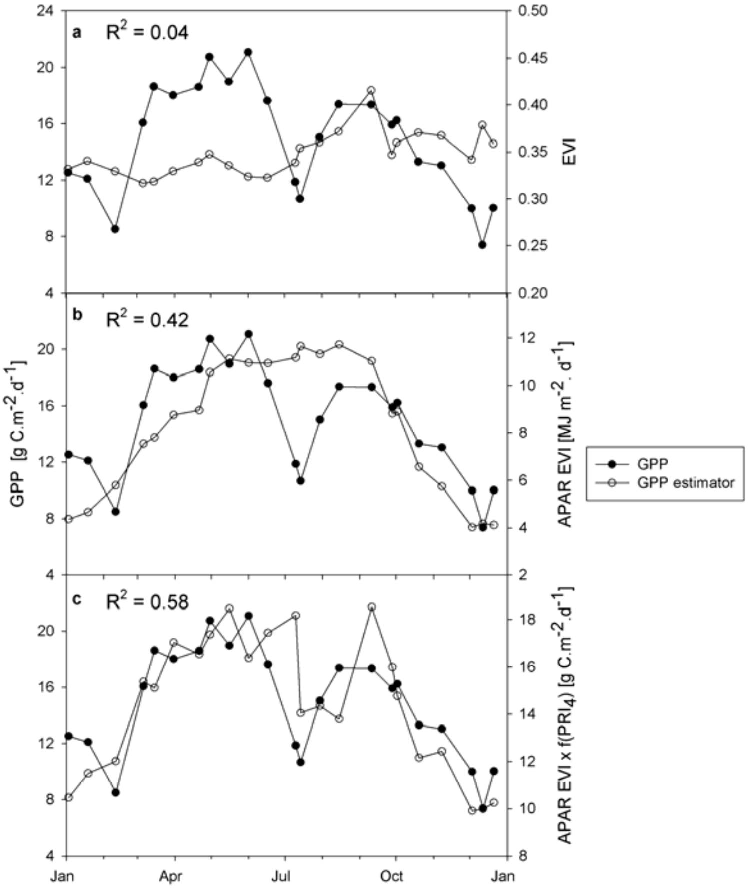


Figure 7. Time course of GPP and three surrogates for GPP for the Mediterranean needleleaf forest: a) EVI, b) APAR and c) APAR x f(PRI). The coefficients of correlation (R^2) are for the relationships between the variables plotted in each panel.

DISCUSSION

EVI and EVI APAR were overall poor estimators of seasonal GPP derived from eddy covariance both for the daily average (Fig. 1) and the midday average (Fig. 2). Regressions were consistently high only for the temperate deciduous forest and with lower coefficients of determinations for the grassland and the temperate evergreen forest site. The other evergreen sites presented non significant relationships or relationships with very low coefficient of determination. The use of EVI APAR instead of only EVI generally increased the R^2 for the average daily GPP in all the sites and in some cases also for the midday GPP. These results complement but also show some disagreement to previous results that showed that EVI is a reliable estimator of the temporal variability of GPP for a wide range of vegetation types (Sims et al. 2006). We specifically selected several evergreen sites to test the capacity of the EVI and the APAR to estimate the temporal variability of carbon uptake. Evergreen vegetation types (i.e. boreal forests, rainforest, and Mediterranean forest) cover a huge part of the globe and therefore the inclusion of a remote estimator of RUE, such as the PRI, in the GPP calculation could contribute to increase the accuracy of the estimation for these vegetation types. In the deciduous vegetation types, the use of the PRI should probably be limited to assess the decrease of photosynthetic rates during the part of the year with high and constant fPAR.

The calculation of RUE was well correlated when considering the complete day or only the midday hours (1 to 3 p.m.) for all the analyzed sites (Fig. 3). This result is important considering the highly temporal variability of the RUE during the day and throughout the growing seasons and it is in agreement with previous works (Sims et al. 2005). It is important, however, to note that the use of a shorter period of time to calculate RUE produce more variability due to the short-term variation in cloudiness and therefore in incident PAR and carbon uptake. The PRI is at least in part a reflection of the short term variability of RUE (Peñuelas et al. 1995), thus the noise produced by short term variation in GPP and incident PAR in the eddy covariance data might reduce the strength of the relationships when using the data for midday only.

The values of RUE for the sites included in our analysis presented in general a good agreement with previous studies. Different algorithms to estimate GPP depend on the maximum RUE. In particular, the MODIS GPP algorithm (Heinsch et al. 2003), which provide global estimations of GPP, uses a constant maximum RUE for each of the eleven biome types predefined in the methodology. Our results are evidencing that we can expect higher maximum values, for certain biomes, than those assumed in the MODIS GPP algorithm (Fig. 3). Maximum differences between our results and the proposed maxima in the MODIS GPP algorithm were found for the winter in Mediterranean broadleaf forest. Although the difference was up to 60% higher than that proposed as maximum for the evergreen broadleaf biome, this difference occurred in winter, a period of the year with low GPP; therefore the impact on the annual GPP estimation is likely small. In contrast, maximum RUE for the temperate evergreen forest was in summer 50% higher than those proposed by the MODIS GPP algorithm; thus it is expected a high impact on the GPP estimation because it is the period of highest photosynthetic activity. Maximum RUE values for subtropical needleaf forest ranged, in contrast, close to the maximum RUE proposed by the MODIS GPP algorithm. The estimation of fPAR involved in the calculation of RUE could explain probably part of the differences, but there is a general trend that confirms that RUE could reach higher values than those propose by the MODIS GPP algorithm. Our results are coincident with previous analysis that showed also higher RUE values for boreal forests (Drolet et al. 2008) and also globally for a wide range of biomes (Garbulsky et al. 2010). The logic behind the MODIS GPP algorithm assumes a link between eleven biome types and the maximum RUE. In each one of the biomes there is a wide range of vegetation types, including different species and also a wide range of environmental conditions, what is probably a big limitation already assumed by the authors (Heinsch et al. 2003).

We found significant relationships between RUE and PRI for all the forest sites. However, it is worth to note that the capabilities of PRI_1 and PRI_4 as surrogates of RUE varied between sites (Table 2). For selected years, PRI_4 was better surrogate of RUE in the subtropical needleleaf forest, in the *Eucalyptus* plantation, and in the Mediterranean broadleaf and needleleaf forests (Fig. 5a). PRI_1 was clearly better surrogate of RUE in the temperate deciduous forest and in the temperate evergreen forest (Fig. 5e), but also presented a good performance in other three sites where PRI_4 also correlated with RUE (Fig. 5d). As expected, because of the high seasonal changes in biomass and the low leaf area and therefore the interfering soil signal, none of the formulations of the PRI tracked the variability of RUE for the grassland site (Fig. 5c and f). The lack of a MODIS band located in 570 nm to use as a reference band as originally suggested (Gamon et al. 1992), motivated the analysis of other alternative reference bands. Previous studies tested the use of different reference bands for the calculation of PRI and showed that various wave lengths could be successfully used (Drolet et al. 2005, Drolet et al. 2008, Goerner et al. 2009). Our results and the previous available data suggest that there is probably a link between the characteristics of each vegetation type (e.g. canopy structure, leaf type, dominant pigment signals) that control the success of each reference band. MODIS band 1 (620– 670 nm) is probably tracking a greater part of the changes in green biomass compared to band 4 (545 - 565 nm). This could be one of the reasons of the success of PRI_1 in the sites with higher seasonality such as the temperate forest.

The relationships of RUE and PRI_4 (Fig. 5a) and of RUE and PRI_1 for the temperate forests (Fig. 5e) presented a remarkable degree of coincidence among sites. Previous analyses of the relationships between RUE and PRI at the leaf and canopy levels (Garbulsky et al. submitted) showed a high degree of agreement between different vegetation types and showed a common relationship, but the small number of existing studies precluded a similar analysis using satellite data at the ecosystem level. The results of this study show that a unique RUE-PRI relationship may exist also at the ecosystem level at least, for those vegetation types with low changes in green biomass throughout the year, in spite of the differences in the wide range of vegetation types, canopy structures, leaves types and pigment contents that affect the PRI signal. This is certainly an important step forward in the effort to reach a spatial generalization in the use of MODIS data to estimate RUE and therefore GPP.

The strength of the relationships between GPP and the APAR surrogates varied between years, at least for the temperate deciduous forest, the site with the longest dataset (Fig. 6). The environmental conditions of each growing season made the strength of the relationships variable, evidencing that there is “room” to improve the remote sensing estimations of GPP even in the more deciduous sites, such as the temperate deciduous forest sites. We proposed in our original hypothesis that due to the high seasonal variability of the green biomass in these sites GPP would correlate well with EVI or APAR, in the way that was previously informed for deciduous forest (Sims et al. 2006). However, our analysis of the interannual variability of the strength of the GPP-EVI relationship showed that there are years with a very low coefficient of determination and therefore a lower confidence in the relationship. Notably, the strength of the relationship RUE-PRI varies between years in the opposite sense than the GPP-EVI. This result is evidencing the high capacity of PRI in those years when the EVI is not as good estimator of changes in GPP, probably because they are not related to a reduction in the leaf area of the canopy but to a decrease in summer GPP and therefore in RUE. PRI emerges thus as an useful complement to estimate GPP even in temperate deciduous forests, at least of those changes in GPP not accompanied by changes in biomass.

It is in evergreen forests where PRI appears as a very useful and consistent complement to estimate RUE and GPP. The inclusion of the PRI as a surrogate of RUE in the Mediterranean needleleaf forest improved the estimation of GPP (Fig. 7) in comparison to the use of EVI or APAR. The availability of the MODIS sensors data allowed for the first time to have PRI data for RUE studies available globally, for a time period covering several growing seasons and at a reasonably time step. This data together with the eddy covariance data made possible the publication of several studies showing the relationships between RUE and PRI at the ecosystem scale for single stands of vegetation or for similar vegetation types (Rahman et al. 2004, Garbulsky et al. 2008, Goerner et al. 2009). However, other studies showed no significant relationships for the temporal variability between PRI and RUE, but showed a significant relationship for the spatial variability (Drolet et al. 2008). Although these studies were made for different forest types there is yet a lack of a common methodology to use the PRI without a proper calibration for other sites. Our results showed for the first time the variability in the relationships RUE-PRI for a wide range of vegetation types using the same methodology. Therefore, we are evidencing the differences of the capabilities of PRI between vegetation types and the relative lower importance of the viewing and sun geometry of the images. If this is the case, an effective application of remote sensing to carbon flux requires an ecological understanding of the environmental controls on carbon uptake for these different ecosystems, including the contribution of biotic and abiotic factors to the overall PRI signal. We tested here the data provided by the MODIS sensor on board the Aqua satellite. PRI Aqua seems to have good relationships with RUE, and moreover PRI Aqua probably has a greater sensibility to changes in RUE compared to Terra platform, probably because the later overpass of the Aqua, closer to midday. In any case, these results warrant further investigation to test the capacity of both data sources.

We conclude that the PRI derived from freely available satellite information presented significant positive relationship with the RUE for the different forest sites, including in determined years for the most deciduous sites. The PRI can directly assess the changes in RUE previous to more drastic decays in leaf area or other structural parameters, as seen in the deciduous temperate forest. Therefore, our results open the possibility to estimate RUE in real time and therefore actual carbon uptake of forests at ecosystem level using the PRI. Our results, however, warrant further research to extend the analysis to a more extended time series and to assess the controls of the different performance of PRI across sites.

REFERENCES

R Development Core Team, 2008. R: A language and environment for statistical computing. *in*. R Foundation for Statistical Computing, Vienna, Austria.

Box, E. O., B. N. Holben, and V. Kalb. 1989. Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO_2 flux. Vegetatio **80**:71-89.

Canadell, J. G., P. Ciais, P. Cox, and M. Heimann. 2004. Quantifying, understanding and managing the carbon cycle in the next decades. Climatic Change **67**:147-160.

Drolet, G. G., K. F. Huemmrich, F. G. Hall, E. M. Middleton, T. A. Black, A. G. Barr, and H. A. Margolis. 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**:212-224.

Drolet, G. G., E. M. Middleton, K. F. Huemmrich, F. G. Hall, B. D. Amiro, A. G. Barr, T. A. Black, J. H. McCaughey, and H. A. Margolis. 2008. Regional mapping of gross light-use efficiency using MODIS spectral indices. Remote Sensing of Environment **112**:3064-3078.

Field, C. B., J. T. Randerson, and C. M. Malmstrom. 1995. Global net primary production: Combining ecology and remote sensing. Remote Sensing of Environment **51**:74-88.

Gamon, J. A., J. Peñuelas, and C. B. Field. 1992. A narrow-waveband spectral index that tracks diurnal changes in photosynthetic efficiency. Remote Sensing of Environment **41**:35-44.

Garbulsky, M. F., J. Peñuelas, J. A. Gamon, Y. Inoue, and I. Filella. submitted. 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.

Garbulsky, M. F., J. Peñuelas, D. Papale, J. Ardö, M. L. Goulden, G. Kiely, A. D. Richardson, E. Rotenberg, E. M. Veenendaal, and I. Filella. 2010. Patterns and controls of the variability of radiation use efficiency and primary productivity across terrestrial ecosystems. Global Ecology and Biogeography **19**:253–267.

Garbulsky, M. F., J. Peñuelas, D. Papale, and I. Filella. 2008. Remote estimation of carbon dioxide uptake of a Mediterranean forest. Global Change Biology **14**:2860–2867.

Goerner, A., M. Reichstein, and S. Rambal. 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.

Heinsch, F. A., M. Zhao, S. W. Running, J. S. Kimball, R. R. Nemani, K. J. Davis, P. V. Bolstad, B. D. Cook, A. R. Desai, D. M. Ricciuto, B. E. Law, W. C. Oechel, H. J. Kwon, H. Luo, S. C. Wofsy, A. L. Dunn, J. W. Munger, D. D. Baldocchi, L. Xu, D. Y. Hollinger, A. D. Richardson, P. C. Stoy, M. B. S. Siqueira, R. K. Monson, S. P. Burns, and L. B. Flanagan. 2006. Evaluation of remote sensing based terrestrial productivity from MODIS using regional tower eddy flux network observations. Ieee Transactions on Geoscience and Remote Sensing **44**:1908-1925.

Heinsch, F. A., M. Reeves, P. Votava, S. Kang, C. Milesi, M. Zhao, J. Glassy, W. M. Jolly, R. Loehman, C. F. Bowker, J. S. Kimball, R. R. Nemani, and S. W. Running. 2003. User's Guide GPP and NPP (MOD17A2/A3) Products NASA MODIS Land Algorithm. Pages 57 *in* User's Guide GPP and NPP (MOD17A2/A3) Products NASA MODIS Land Algorithm. University of Montana, Missoula, MT.

Hilker, T., N. C. Coops, M. A. Wulder, T. A. Black, and R. D. Guy. 2008. The use of remote sensing in light use efficiency based models of gross primary production: A review of current status and future requirements. Science of The Total Environment **404**:411-423.

Hollinger, D. Y., J. Aber, B. Dail, E. A. Davidson, S. M. Goltz, H. Hughes, M. Y. Leclerc, J. T. Lee, A. D. Richardson, C. Rodrigues, N. A. Scott, D. Achuatavarier, and J. Walsh. 2004. Spatial and temporal variability in forest-atmosphere CO_2 exchange. Global Change Biology **10**:1689-1706.

Huete, A., K. Didan, T. Miura, E. P. Rodriguez, X. Gao, and L. G. Ferreira. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment **83**:195-213.

Meyers, T. 2008. Fort Peck L4 eddy covariance data. *in*. NOAA/ARL, Atmospheric Turbulence and Diffusion Division, Oak Ridge, TN, USA.

Monteith, J. L. 1972. Solar radiation and productivity in tropical ecosystems. Journal of Applied Ecology **9**:747-766.

Monteith, J. L. 1977. Climate and the efficiency of crop production in Britain. Philosophical Transactions of the Royal Society B: Biological Sciences **281**:277-294.

Myneni, R. B., S. Hoffman, Y. Knyazikhin, J. L. Privette, J. Glassy, Y. Tian, Y. Wang, X. Song, Y. Zhang, G. R. Smith, A. Lotsch, M. Friedl, J. T. Morisette, P. Votava, R. R. Nemani, and S. W. Running. 2002. Global products of vegetation leaf area and fraction absorbed PAR from year one of MODIS data. Remote Sensing of Environment **83**:214-231.

Nagai, S., N. Saigusa, H. Muraoka, and K. Nasahara. 2010. What makes the satellite-based EVI–GPP relationship unclear in a deciduous broad-leaved forest? Ecological Research **25**:359-365.

Olofsson, P., F. Lagergren, A. Lindroth, J. Lindström, L. Klemedtsson, W. Kutsch, and L. Eklundh. 2008. Towards operational remote sensing of forest carbon balance across Northern Europe. Biogeosciences **5**:817-232.

Papale, D., M. Reichstein, M. Aubinet, E. Canfora, C. Bernhofer, W. Kutsch, B. Longdoz, S. Rambal, R. Valentini, T. Vesala, and D. Yakir. 2006. Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. Biogeosciences **3**:571-583.

Paruelo, J. M., H. E. Epstein, W. K. Lauenroth, and I. C. Burke. 1997. ANPP estimates from NDVI for the Central Grassland Region of the United States. Ecology **78**:953-958.

Peñuelas, J., I. Filella, and J. A. Gamon. 1995. Assessment of photosynthetic radiation-use efficiency with spectral reflectance. New Phytologist **131**:291-296.

Pereira, J. S., J. A. Mateus, L. M. Aires, G. Pita, C. Pio, J. S. David, V. Andrade, J. Banza, T. S. David, T. A. Paço, and A. Rodrigues. 2007. Net ecosystem carbon exchange in three contrasting Mediterranean ecosystems – the effect of drought. Biogeosciences **4**:791-802.

Powell, T. L., H. L. Gholz, K. L. Clark, G. Starr, W. P. C. Jr, and T. A. Martin. 2008. Carbon exchange of a mature, naturally regenerated pine forest in north Florida. Global Change Biology **14**:2523-2538.

Rahman, A. F., V. D. Cordova, J. A. Gamon, H. P. Schmid, and D. A. Sims. 2004. Potential of MODIS ocean bands for estimating CO_2 flux from terrestrial vegetation: A novel approach. Geophysical Research Letters. doi:10.1029/ 2004GL019778 **31**.

Rahman, A. F., D. A. Sims, V. D. Cordova, and B. Z. El-Masri. 2005. Potential of MODIS EVI and surface temperature for directly estimating per-pixel ecosystem C fluxes. Geophysical Research Letters **32**.

Reichstein, M., Falge E, D. Baldocchi, D. Papale, M. Aubinet, P. Berbigier, C. Bernhofer, N. Buchmann, T. Gilmanov, A. Granier, T. Grünwald, K. Havránková, H. Ilvesniemi, D. Janous, A. Knohl, T. Laurila, A. Lohila, D. Loustau, G. Matteucci, T. Meyers, F. Miglietta, J. Ourcival, J. Pumpanen, S. Rambal, E. Rotenberg, M. Sanz, J. Tenhunen, G. Seufert, F. Vaccari, T. Vesala, D. Yakir, and R. Valentini. 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Global Change Biology **11**:1424 - 1439.

Rey, A., E. Pegoraro, V. Tedeschi, I. d. Parri, P. G. Jarvis, and R. Valentini. 2002. Annual variation in soil respiration and its components in a coppice oak forest in central Italy. Global Change Biology **9**:851-866.

Rodrigues, A., G. Pita, and J. Mateus. 2005. Turbulent Fluxes of Carbon Dioxide and Water Vapour Over an Eucalyptus Forest in Portugal. Silva Lusitana **13**:169-180.

Ruimy, A., B. Saugier, and G. Dedieu. 1994. Methodology for the estimation of terrestrial net primary production from remotely sensed data. Journal of Geophysical Research **99**:5263–5283.

Running, S. W., R. R. Nemani, F. A. Heinsch, M. Zhao, M. Reeves, and H. Hashimoto. 2004. A continuous satellite-derived measure of global terrestrial primary production. Bioscience **54**:547-560.

Sellers, P. J. 1985. Canopy reflectance, photosynthesis and transpiration. International Journal of Remote Sensing **6**:1335-1372.

Sims, D. A., A. F. Rahman, V. D. Cordova, D. D. Baldocchi, L. B. Flanagan, A. H. Goldstein, D. Y. Hollinger, L. Misson, R. K. Monson, H. P. Schmid, S. C. Wofsy, and L. K. Xu. 2005. Midday values of gross CO_2 flux and light use efficiency during satellite overpasses can be used to directly estimate eight-day mean flux. Agricultural and Forest Meteorology **131**:1-12.

Sims, D. A., A. F. Rahman, V. D. Cordova, B. Z. El-Masri, D. D. Baldocchi, L. B. Flanagan, A. H. Goldstein, D. Y. Hollinger, L. Misson, R. K. Monson, W. C. Oechel, H. P. Schmid, S. C. Wofsy, and L. K. Xu. 2006. On the use of MODIS EVI to assess gross primary productivity of North American ecosystems. Journal of Geophysical Research-Biogeosciences G04015, doi:10.1029/ 2006JG000162 **111**.

Sjöström, M., J. Ardö, L. Eklundh, B. A. El-Tahir, H. A. M. El-Khidir, P. Pilesjö, and J. Seaquist. 2009. Evaluation of satellite based indices for gross primary production estimates in a sparse savanna in the Sudan. Biogeosciences **6**.

Tucker, C. J., and P. J. Sellers. 1986. Satellite Remote-Sensing of Primary Production. International Journal of Remote Sensing **7**:1395-1416.

Turner, D. P., M. Gregory, S. Urbanski, S. C. Wofsy, D. Bremer, T. Meyers, and S. T. Gower. 2003. A cross-biome comparison of daily light use efficiency for gross primary production. Global Change Biology **9**:383-395.

Xiao, X., J. Aber, Q. Zhang, B. Moore III, D. Hollinger, M. Goltz, and E. A. Davidson. 2004a. Satellite-based modeling of gross primary production in an evergreen needleleaf forest. Remote Sensing of Environment **89**:519-534.

Xiao, X. M., Q. Y. Zhang, B. Braswell, S. Urbanski, S. Boles, S. Wofsy, M. Berrien, and D. Ojima. 2004b. Modeling gross primary production of temperate deciduous broadleaf forest using satellite images and climate data. Remote Sensing of Environment **91**:256-270.

Xiao, X. M., Q. Y. Zhang, D. Hollinger, J. Aber, and B. Moore. 2005. Modeling gross primary production of an evergreen needleleaf forest using MODIS and climate data. Ecological Applications **15**:954-969.

7. Final Conclusions

This final chapter highlights the main questions of each chapter and the main findings. Finally, I conclude on the main objective of my research and present some ideas on how to go further and continue with my research.

CHAPTER 2: Can the PRI detect ecophysiological changes of plant at different organizational levels and temporal scales?

In this chapter I showed the results of a wide revision of scientific literature on the relationships between ecophysiological variables and PRI. Although the strength of the relationships between ecophysiological variables and PRI varied across vegetation types, levels of organization and temporal scales, in most reviewed articles PRI was a good predictor of photosynthetic efficiency or related variables with performances at least as good as the widely used NDVI as indicator of green biomass. There are possible confounding factors related to the physiological intensity of the PRI signals, to the structure of the canopies and to the illumination and viewing angles that warrant further studies, and it is expected that the utility of PRI will vary with the ecosystem in question due to contrasting environmental constraints, evolutionary strategies, and RUE variability. Additionally, like any 2-band index that is affected by multiple factors, the interpretation of PRI can be readily confounded by multiple environmental variables, and further work is needed to understand and constrain these effects. Despite these limitations, this review shows an emerging consistency of the RUE-PRI relationship that suggests a surprising degree of functional convergence of biochemical, physiological and structural components affecting leaf, canopy and ecosystem carbon fluxes. It seems thus that by complementing the estimations of the fraction of photosynthetically active radiation intercepted by the vegetation (FPAR), estimated with NDVI-like indices, PRI makes now already possible to improve the assessment of carbon fluxes in leaves, canopies and many of the ecosystems of the world from ground, airborne and satellite sensors.

This chapter was submitted for its publication to Remote Sensing of Environment. Garbulsky, M.F., J. Peñuelas, J. Gamon, Y. Inoue and I. Filella.

CHAPTER 3: What are the environmental controls of the GPP and the RUE at global scales?

Rainfall and actual evapotranspiration (AET) positively influenced the spatial variation of annual GPP, whereas temperature only influenced the GPP of forests. Annual and maximum RUE were also positively controlled primarily by annual rainfall. The main control parameters of the growth season variation of gross RUE varied for each ecosystem type. Overall, the ratio between actual and potential evapotranspiration and a surrogate for the energy balance explained a greater proportion of the seasonal variation of RUE than the vapour pressure deficit (VPD), AET and precipitation. Temperature was important for determining the intra-annual variability of the RUE at the coldest energy-limited sites. Our analysis supports the idea that the annual functioning of vegetation that is adapted to its local environment is more constrained by water availability than by temperature. The spatial variability of annual and maximum RUE can be largely explained by annual precipitation, more than by vegetation type. The intra-annual variation of RUE was mainly linked to the energy balance and water availability along the climatic gradient. Furthermore, we showed that intra-annual variation of gross RUE is only weakly influenced by VPD and temperature, contrary to what is frequently assumed. Our results provide a better understanding of the spatial and temporal controls of the RUE and thus could lead to a better estimation of ecosystem carbon fixation and better modelling.

This chapter was recently published: Garbulsky, M.F., J. Peñuelas, D. Papale, J. Ardö, M.L. Goulden, G. Kiely, A.D. Richardson, E. Rotenberg, E.M. Veenendaal and I. Filella 2010. Global Ecology & Biogeography. 19: 253–267.

CHAPTER 4. What are the relationships between ecophysiological variables at the stand level in a Mediterranean forest and the NDVI, EVI and PRI?

The contrasting seasonal patterns of NDVI and EVI for the Mediterranean forest evidence the difference between these spectral indices. For the analyzed Mediterranean forest nor EVI neither NDVI are good surrogates of leaf level photosynthesis and probably would not be good estimators of GPP. The better performance of EVI compared to NDVI and PRI as an estimator of diametric growth for a 10 year period suggests that overall EVI is a better estimator of the annual net primary productivity. It is also interesting that PRI correlated with a variable that integrates the growth of the whole growing season. PRI has been typically correlated with short term variables, but there were no information of the capacity of PRI to estimate annual integrations of ecosystem performance. The results presented in this study are the first that show this type of relationship for a vegetation type with a very flat seasonal pattern of FPAR. Water availability was the main control of photosynthesis and temperature played a more secondary role in its regulation. In contrast to NDVI and EVI that were not related to leaf level photosynthetic rates PRI significantly estimate leaf level photosynthesis and specially the photosynthetic efficiency. It is shown for the first time a significant correlation between net photosynthesis and radiation use efficiency at the leaf level with PRI derived from satellite data at the ecosystem level. It is noticeable from the results in this chapter that a leaf level process could be gathered from satellite information with coarse spatial resolution. Overall, the results showed in this chapter evidenced the contrasting and complementary capacities of each of the three spectral indices analyzed. While NDVI is an estimator of FPAR, EVI can estimate diametric wood increment, a surrogate of NPP, and PRI is an estimator of leaf level net photosynthesis and radiation use efficiency. We conclude that these three indices are excellent tools for vegetation monitoring with concrete and different biological meaning, at least for Mediterranean forest.

CHAPTER 5: What is the value of the PRI as an estimator of RUE in a Mediterranean forest?

The MODIS PRI derived from freely available satellite information presented for a 5-year analysis for a Mediterranean forest a positive relationship with the RUE. Thus, we show that it is possible to estimate RUE and GPP in real time and therefore actual carbon uptake of Mediterranean forests at ecosystem level using the PRI. This conceptual and technological advancement would avoid the need to rely on the sometimes unreliable maximum RUE. In any case, it is necessary to check our results in other homogeneous Mediterranean forests larger enough to place the MODIS 1 km^2 pixel, and to examine a range of ecosystems to reveal whether the utility of the PRI to assess carbon uptake will vary with the ecosystem in question due to contrasting environmental constraints, ecophysiological strategies, and RUE. A comprehension of ecophysiological principles will be needed to fully reveal these patterns and it is likely that new remote-sensing approaches incorporating PRI will contribute to this understanding.

This chapter was recently published: Garbulsky, M.F., J. Peñuelas, D. Papale and I. Filella 2008. Global Change Biology, 14: 2860–2867.

CHAPTER 6. What is the value of PRI as an estimator of RUE for a wide range of ecosystem types?

Our results showed, in contrast to previous studies, that neither EVI nor EVI x PAR are good estimators of GPP. PRI presented a positive relationship with the RUE in different sites. The more constant the values of fPAR, the higher the strength of the relationship between RUE and PRI. However, sun-target-sensor geometry in some of the sites also presented significant but weaker correlations with RUE. Thus, we show that it is possible to estimate RUE in real time and therefore actual carbon uptake of forests at ecosystem level using the PRI. The use of PRI from freely available satellite information could directly assess the changes in RUE or in photosynthetic performance previous to more drastic decays in leaf area or other structural parameters.

Preliminary results from this chapter were presented at the 1st TERRABITES Symposium - Hamburg, Germany, 9-11 February 2010. Garbulsky, M.F. J. Peñuelas, and I. Filella 2010. Photochemical Reflectance Index (PRI) can estimate seasonal variations of ecosystem gross radiation use efficiency for different forest types.

FURTHER RESEARCH – A ROAD AHEAD

This thesis contributed to our understanding of the temporal and spatial variability of carbon uptake by the terrestrial vegetation and the possibilities to the estimations through remote sensing techniques. Beside the questions that were answered, there are other questions or ideas that came to mind and that are also a result of this thesis and the work behind it. These questions would probably guide my future research. I will briefly summarize several of these ideas:

1. The way to calculate the efficiency in which vegetation transform the radiation in carbon compounds is by itself a matter of discussion. Instead of using the RUE, the ratio between GPP and APAR, the Quantum yield provide a more dynamic relationship between GPP and PAR. In this case it is possible to plot GPP and APAR as independent and dependent variables and examining the slope and looking at dx/dy. The RUE approach take into account a unique moment along the day and assumes that the intercept of the relationship goes to zero, which in many cases it may not and will bias the ratios. On the other hand the derivative tells us the diurnal sensitivity of the system, i.e. with a change in APAR, how much will the GPP change (Gilmanov et al. 2010). This is a partial derivative and could be very instructive for determined vegetation types but for other a low coefficient of variation or a low coefficient of determination between the two variables will tell us other variables are in determining GPP and not only the APAR.
   The slope of the daily relationship between GPP and APAR would be another ecophysiological variable that can link to PRI. This approach could be the extension to the ecosystem scale of the ∆F/Fm’ analyzed at the plant and canopy scales (chapter 2). Using the same data used for this thesis in chapters 3 and 6, the suggested analysis could provide new and a different insight on the interpretation of PRI and its links to the ecophysiology of the photosynthesis.

2. The evaluation of the impacts of the climatic changes on the vegetation functioning is matter of active research nowadays (Paruelo et al. 2004, Reichstein et al. 2007, Zhao and Running 2010). The results in this thesis can greatly contribute to progress in the quality of these evaluations. This thesis showed that PRI is a reliable estimator of RUE. Therefore, these results open the possibility to analyze the medium and long-term patterns of the RUE using the MODIS PRI that can provide data from 2000 up to now. Temporal trends of PRI could be a remote indicator of the actual photosynthesis performance and not the potential photosynthetic capacity as can be analyzed by means of the NDVI. Moreover, it will be interesting to know what are the environmental controls

of the temporal and spatial variability of PRI and therefore to assess the possible impacts of climatic change on RUE and on GPP for different vegetation types.

3. There are other vegetation spectral indices, apart from the PRI, that were used to estimate vegetation stresses such as Moisture stress index MSI; (MSI, Hunt and Rock 1989), normalized difference water index NDWI, (NDWI, Gao 1996), and land surface water index LSWI; (LSWI, Xiao et al. 2002). Although the use of these indices is not well supported by scientific evidences such was shown for the PRI (chapter 2), it will be interesting to compare these different indices to find the best way to estimate RUE or plant stresses at the ecosystem level.

REFERENCES

Gao, B. C. 1996. NDWI: a normalized difference water index for remote sensing of vegetation liquid water from space. Remote Sensing of Environment **58**:257–266.

Gilmanov, T. G., L. Aires, Z. Barcza, V. S. Baron, L. Belelli Marchesini, J. Beringer, D. Billesbach, D. Bonal, J. Bradford, E. Ceschia, D. Cook, C. C., A. Frank, D. Gianelle, C. Gimeno, T. Gruenwald, H. Guo, N. Hanan, L. Haszpra, J. Heilman, A. Jacobs, M. B. Jones, D. A. Johnson, G. Kiely, S. Li, V. Magliulo, E. Moors, Z. Nagy, M. Nasyrov, C. Owensby, K. Pinter, C. Pio, M. Reichstein, M. J. Sanz, R. L. Scott, J. F. Soussana, P. C. Stoy, T. Svejcar, Z. Tuba, and G. Zhou. 2010. Productivity, Respiration, and Light-Response Parameters of World Grassland and Agroecosystems Derived From Flux-Tower Measurements. Rangeland Ecology & Management **63**:16-39.

Hunt, E. R., and B. N. Rock. 1989. Detection of changes in leaf water-content using near-infrared and middle-infrared reflectances Remote Sensing of Environment **30**:43–54.

Paruelo, J. M., M. F. Garbulsky, J. P. Guerschman, and E. G. Jobbagy. 2004. Two decades of Normalized Difference Vegetation Index changes in South America: identifying the imprint of global change. International Journal of Remote Sensing **25**:2793-2806.

Reichstein, M., P. Ciais, D. Papale, R. Valentini, S. Running, N. Viovy, W. Cramer, A. Granier, J. Ogee, V. Allard, M. Aubinet, C. Bernhofer, N. Buchmann, A. Carrara, T. Grunwald, M. Heimann, B. Heinesch, A. Knohl, W. Kutsch, D. Loustau, G. Manca, G. Matteucci, F. Miglietta, J. M. Ourcival, K. Pilegaard, J. Pumpanen, S. Rambal, S. Schaphoff, G. Seufert, J. F. Soussana, M. J. Sanz, T. Vesala, and M. Zhao. 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. Global Change Biology **13**:634-651.

Xiao, X., S. Boles, J. Y. Liu, D. F. Zhuang, and M. L. Liu. 2002. Characterization of forest types in Northeastern China, using multitemporal SPOT-4 VEGETATION sensor data. Remote Sensing of Environment **82**:335–348.

Zhao, M., and S. W. Running. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science **329**:940-943.

Acknowledgments

Mi primer agradecimiento para Josep Peñuelas. Desde el primer contacto vía electrónica me ha demostrado su grandísima generosidad y su grandiosa calidad humana. Más allá de su capacidad de trabajo y haber contribuido en diferentes aspectos para poder llegar a este punto de mi formación, estoy muy contento de haber podido trabajar con él.

A Iolanda Filella por sus ideas y contribuciones que han mejorado diferentes aspectos de esta tesis.

Romà Ogaya fue una persona clave en el desarrollo y la toma de datos a campo. A él, mi enorme agradecimiento por todo el gran trabajo realizado.

A toda la gente del CREAF, particularmente a los compañeros de despacho, que de alguna manera u otra contribuyeron en el trabajo, la convivencia diaria y para resolver diferente clases de problemas.

A Malena, Teo e Irene, que sin ellos a mi lado diariamente, todo esto no tendría ningún sentido.

A todos los visitantes que tuvimos en nuestra casa en Barcelona. Mis padres, hermanos, suegros, sobrinos, cuñados, tíos prestados y amigos, todos ellos nos ayudaron a llevar adelante estos años de vida en Barcelona.

I also gratefully acknowledge the following people, institutions and programs that made possible my work in Barcelona:

- the University of Buenos Aires
- the Commissioner for Universities and Research of the Ministry of Innovation, Universities and Enterprise of the Catalan Government and of the European Social Fund
- the Alβan Programme.
- the Catalan Government (grants SGR2009-458 and SGR2005-00312) and the Spanish Ministry of Education and Science (grants CGL2006-04025/BOS and Consolider - Ingenio MONTES CSD 2008-00040).
- the PIs and managers of the Ameriflux (AmeriFlux Science Team Research grant – US Department of Energy, Terrestrial Carbon Program, award no. DE-FG02-04ER63911), CarboEuropeIP, CarboAfrica, EuroSiberian Carbonflux and TCOS-Siberia projects sites for their research contributions and the eddy covariance data and the Office of Science (BER, US Department of Energy Terrestrial Carbon Processes), the Irish Environmental Protection Agency and the Italy–US bilateral project funded by the Italian Minister of Environment and the Carboitaly FISR project.

And to all the coauthors that contributed to make possible different parts of this thesis.

MUCHAS GRACIAS!