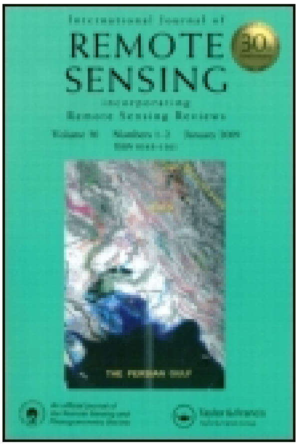

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Leaf and stand-level carbon uptake of a Mediterranean forest estimated using the satellite-derived reflectance indices EVI and PRI

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Various aspects of global environmental change affect plant photosynthesis, the primary carbon input in ecosystems. Thus, accurate methods of measuring plant photosynthesis are important. Remotely sensed spectral indices can monitor in detail the green biomass of ecosystems, which provides a measure of potential photosynthetic capacity. In evergreen vegetation types, however, such as Mediterranean forests, the amount of green biomass changes little during the growing season and, therefore, changes in green biomass are not responsible for changes in photosynthetic rates in those forests. This study examined the net photosynthetic rates and the diametric increment of stems in a Mediterranean forest dominated by *Quercus ilex* using three spectral indices (normalized difference vegetation index (NDVI), enhanced vegetation index (EVI), and photochemical reflectance index (PRI)) derived from Moderate Resolution Imaging Spectroradiometer (MODIS) sensors. Average annual EVI accounted for 83% of the variability of the diametric increment of *Q. ilex* stems over a 10 year period. NDVI was marginally correlated with the diametric increment of stems. This study was the first to identify a significant correlation between net photosynthetic rates and radiation use efficiency at the leaf level using PRI derived from satellite data analysed at the ecosystem level. These results suggest that each spectral index provided different and complementary information about ecosystem carbon uptake in a Mediterranean *Q. ilex* forest.

1. Introduction

Carbon uptake and primary productivity are essential processes that are central to the Earth's carbon cycle and moreover are integrative of the entire ecosystem functioning. Ground measurements of carbon uptake and primary productivity in specific locations are fundamental for assigning biological meaning to the spectral data derived from satellite-based remote sensors, which can be used to generate ecological information in a geographical context. Spectral indices derived from remotely sensed data are valuable in the study of the structure and functioning of terrestrial vegetation (Peñuelas and Filella 1998). The normalized difference vegetation index (NDVI), the most widely used remotely sensed index, is most often used as an estimator of the fraction of the photosynthetically active radiation (PAR) that is absorbed by the canopy (fPAR; Tucker et al. 1985). The

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enhanced vegetation index (EVI) was developed to reduce the noise produced by the soil background and also to reduce the saturation of the reflectance signal at increasing levels of green biomass, which is commonly associated with the NDVI, and to reduce atmospheric noise (Huete et al. 2002). The photochemical reflectance index (PRI) is a spectral index that can monitor changes in radiation use efficiency (RUE) and affiliated physiological parameters at the leaf, canopy, and ecosystem levels (Gamon, Peñuelas, and Field 1992; Garbulsky et al. 2011; Peñuelas, Filella, and Gamon 1995).

RUE is valuable in understanding carbon uptake in vegetation types that have a constant leaf area index (LAI), such as Mediterranean forests (Ogaya and Peñuelas 2006). The temporal changes in RUE in those forests have been correlated with the ratio of actual to potential evapotranspiration (AET/PET), but neither temperature nor VPD was a predictor of variation in RUE (Garbulsky et al. 2010), which is an assumption of many models (Potter, Klooster, and Brooks 1999; Running et al. 2004). Thus, Mediterranean forests are appropriate habitats in which to test the effectiveness of the PRI to estimate the carbon uptake of the vegetation using RUE. Moreover, global warming and the reductions in precipitation that have been predicted (Solomon et al. 2007) will greatly affect the structure and functioning of Mediterranean forests, likely more so than any other type of forest in Europe (Morales et al. 2005, 2007). Studies have demonstrated the effects of those changes on the ecophysiology (Asensio et al. 2007; Ogaya and Peñuelas, 2003, 2006, 2007), phenology (Peñuelas, Filella, and Comas 2002), and distribution (Peñuelas and Boada 2003; Peñuelas et al. 2007) of Mediterranean forests. In addition, these environmental changes affect the ecosystem services provided by this type of forest, which has been modified considerably by human activities (Schröter et al. 2005).

Remote-sensing data can be used to quantify the spatial variation in forest structure and growth (Waring et al. 2006) and plant stem volume (González Alonso et al. 2006). NDVI (Wang et al. 2004) and EVI (Potter et al. 2007) data can identify temporal variation in the annual productivity of deciduous forests. In evergreen Mediterranean forests, in the absence of ancillary data (Maselli et al. 2009), the NDVI and EVI do not provide good estimates of carbon uptake because they are largely insensitive to the short-term changes in CO_2 uptake that are caused by water stress. For instance, the NDVI in a *Quercus ilex* Mediterranean forest did not detect a massive drought event compared to other types of forest (Lloret et al. 2007). In any case, to evaluate the ability of spectral indices to detect temporal and spatial variations in carbon uptake, simultaneous field measurements of leaf photosynthesis or the eddy covariance of CO_2 fluxes and estimates of biomass in stands are needed.

We hypothesized that the spectral indices NDVI, EVI, and PRI can be used to estimate carbon uptake at different temporal scales (annual, seasonal, and daily) because they differ in their capacity to detect changes in the ecophysiological state of vegetation. The first objective of this study is to test that hypothesis by evaluating the correlations between ecophysiological variables at the stand level in a Mediterranean forest and the spectral indices derived from Moderate Resolution Imaging Soectroradiometer (MODIS) sensors. The second objective is to identify the biological relevance of the information provided by those spectral indices. In addition, the study investigated the effect of precipitation on annual carbon uptake in water-limited Mediterranean forests.

2. Materials and methods

The study was carried out in a natural Holm oak forest in the Prades Mountains, Catalonia, Spain (41.3408° N, 1.0378° E), in the northeastern Iberian peninsula, where average annual precipitation is 610 mm and average temperature is 12.2°C (1999–2009). Since about 1950, the forest has been undisturbed (Ogaya and Peñuelas 2007). Today, a 4–8 m-high broadleaf evergreen forest is highly dominated by *Q. ilex* L. (8633 tree stems ha^{-1}, 89 Mg ha^{-1}). Tall shrubs are the predominant vegetation in the understory, specifically, *Phillyrea latifolia* L. (3600 tree stems ha^{-1}, 14 Mg ha^{-1}), and *Arbutus unedo* L. (2200 tree stems ha^{-1}, 9 Mg ha^{-1}). The forest had a very dense multi-stem crown (16,616 tree stems ha^{-1}, 115 Mg ha^{-1}). In addition, other evergreen species that are well adapted to dry conditions (*Erica arborea* L., *Juniperus oxycedrus* L., *Cistus albidus* L.) were present. Average LAI was 4. Ten plots that had similar dominance and height of *Q. ilex* vegetation were established within a ~100 ha section of the forest. Within the plots, the variables that are associated with the ecophysiological performance of *Q. ilex* and the soil characteristics were measured. Foliar gas exchange, PAR absorption, and soil temperature and moisture were measured about once per month between 23 March 2006 and 8 August 2008, near midday (1100 – 1400 h) on non-cloudy days. Between 2000 and 2010, the stem diameters of individual *Q. ilex* were measured within four 150 m^2 plots. We evaluated the 10 plots as representative samples of the Prades forest using the surface reflectance of the seven Landsat 5 imagery bands. We performed a spatial analysis based on Landsat 5 imagery in order to evaluate the representativeness of our 10 sites in the whole pixel. We compared the reflectance for the seven bands of the 10 Landsat pixels (900 m^2 each) to that of all of the pixels ($n > 1000$) included in the Prades forest area analysed by the MODIS data and to check whether our 10 sites were representative of the whole MODIS pixels. We did this analysis for one Landsat cloud-free image acquired on 9 September 2007, downloaded from the US Geological Survey (USGS) website (glovis.usgs.gov; courtesy of the USGS).

2.1. Gas exchange measurements

Under clear-sky conditions, gas exchange was measured in the sun leaves (from the upper layer of the canopy, fully exposed to the sun, and south-facing) and the shade leaves (from the lower layers of the canopy) of *Q. ilex*. The net CO_2 uptake rates of four plants per plot were measured (at midday) using a portable gas exchange system, ADC4, and a PLC4B chamber (ADC Inc., Hoddesdon, Hertfordshire, UK).

2.2. Photosynthetically active radiation absorbed by the canopy

To estimate the radiation absorbed by the canopy, we used a PAR ceptormeter (SF-80, Decagon, Pullman, WA, USA) to measure the incident PAR above the canopy and the PAR below the canopy. To get a measure of the spatial variability of the PAR absorption, in each plot, four measurements were taken below the canopy.

2.3. Soil moisture and temperature

Soil moisture was measured monthly using time domain reflectometry (TDR) (Tektronix 1502C, Beaverton, OR, USA) (Zegelin, White, and Jenkians 1989). Three, 25 cm-long stainless steel cylindrical rods were driven into the soil at a single, randomly selected, location within each plot. To record measurements, the TDR device was connected to the ends of the rods by the interconnecting cable. A 30 cm core sample of topsoil was used to calibrate the soil moisture (volume/volume) readings of the TDR.

2.4. Stem diameter increment

Each winter between 2000 and 2010, in each plot, the circumferences of living stems of all plants that had a diameter >2 cm at a height of 50 cm were measured.

2.5. *MODIS data and spectral indices*

The spectral data were gathered by the MODIS sensors on board the Terra and Aqua satellites. The Terra satellite orbits the Earth from north to south in the morning, and the Aqua satellite passes south to north in the afternoon. The analysis was based on the spectral information contained in the pixels that cover the studied area from MODIS band 1 (620–670 nm), band 2 (841–876 nm), band 3 (459–479 nm), and band 11 (526–536 nm). The NDVI and EVI were calculated from the 8 day Terra MOD09A1 product and based on four 250 m × 250 m pixels:

$$\mathrm{NDVI} = \frac{(\text{refl band } 2 - \text{refl band } 1)}{(\text{refl band } 2 + \text{refl band } 1)}, \tag{1}$$

$$\mathrm{EVI} = \frac{2.5\,(\text{refl band } 2 - \text{refl band } 1)}{(\text{refl band } 2 + 6\,\text{refl band } 1 - 7.5\ \text{refl band } 3 + 1)}, \tag{2}$$

where refl refers to reflectance. Most of the data used in the analyses came from the Terra platform (2002–2010) because the data set covered a longer (2 year) period.

The PRI was calculated using the 1 km^2 daily-calibrated reflectance MODIS Aqua L1b (MYD021KM V005) for the pixel that covered the largest portion of the study area:

$$\mathrm{PRI} = \frac{(\text{refl band } 11 - \text{refl band } 1)}{(\text{refl band } 11 + \text{refl band } 1)}. \tag{3}$$

The Aqua PRI probably provided the best estimates of midday RUE because the Aqua platform passed over the study area in the afternoon. To eliminate the effects of atmospheric interference caused, e.g. by clouds, the analyses were based on the PRI data that were collected on cloud-free days and the overpass dates used for the calculation of Aqua NDVI and EVI product (MYD13), which indicates the cloud-free day used for the 16 day product (Huete, Justice, and Van Leeuwen 1999). In addition, low-quality observations, i.e. those that had view zenith angles >40°, were excluded from the analyses.

Mean annual values of the spectral indices were calculated as an annual integration for each of the vegetation growing seasons covered by the NDVI and EVI (2000–2009) and PRI (2003–2008) data. Normally, 46 annual values for NDVI and EVI are available; however, because of the low quality of the data, we only included a lower quantity depending on the year. The mean annual PRI was calculated using 20–23 PRI values depending on each year.

2.6. *Statistical analyses*

The parameters measured in the field and the reflectance indices derived from the MODIS sensors were subjected to regression analyses. Net photosynthetic rates were analysed using a bivariate linear regression, with soil moisture and soil temperature as independent variables. The annual stem diametric increment was regressed against NDVI, EVI, and PRI, with annual precipitation in the same year and in the previous year as independent variables. The statistical analyses were performed using R software (R Development Core Team 2008).

3. Results

The spatial analysis showed that our 10 pixels are a good representation of the whole Prades forest or at least for the MODIS pixel. The dispersion of the data for the seven Landsat

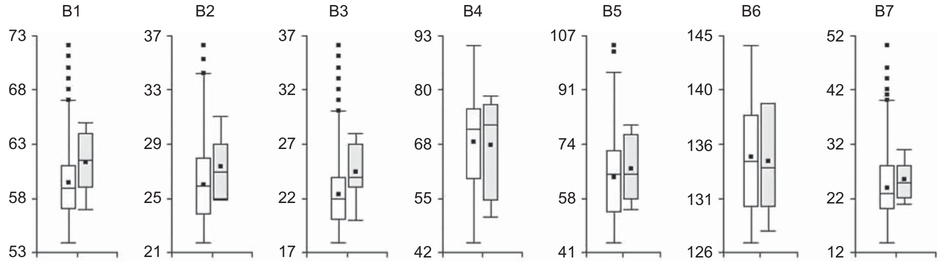

Figure 1. Boxplots for the surface reflectance of the seven Landsat bands of the Prades forest area (white boxes, $n = 1089$) and of the ten plots with ground measurements (grey boxes).

bands for the 10 plots where we measured the ecophysiological variables and that for all the pixels in the area showed a good overlapping (Figure 1).

In the Mediterranean forest in the Prades Mountains, Catalonia, the net photosynthetic rates of *Q. ilex* at the leaf level varied between 0.5 and 15 μmol m^{-2} s^{-1}. The highest rates occurred in spring and the lowest rates occurred in late spring and summer (Figure 2(*a*)). Average absorbed radiation ranged between 80% and 92% (Figure 2(*b*)) and were constant over time (analysis of variance (ANOVA), $p = 0.11$). The highest soil moisture estimates occurred during wet springs (April, May, and June) in 2007 (297 mm precipitation) and 2008 (423 mm), which received, respectively, 30% and 94% more precipitation than the average for the study period (1999–2009) (Figure 2(*c*)). Generally, soil moisture was lowest in summer, and soil temperature was highest in August and lowest in January and February (Figure 2(*d*)).

Throughout the growing season, soil moisture and soil temperature explained a large amount of the variation in leaf-level photosynthesis (Figure 3). In the partial models, soil moisture (positively) accounted for 68% of the variability in photosynthesis, and soil temperature (negatively) accounted for 28% of the variability. Soil temperature and soil moisture were not correlated.

The NDVI ranged between 0.75 and 0.90, but it was constant and almost saturated throughout the growing seasons (Figure 4). Although the highest and lowest values occurred in winter and summer, respectively, the seasonal pattern was subtle. The EVI ranged between 0.2 and 0.5, and it had a pronounced seasonal pattern, with the highest and lowest values in summer and winter, respectively. Between 2000 and 2009, the 8 day NDVI and EVI were negatively correlated ($r = -0.32$; $p < 0.0001$; $n = 416$). The NDVI and the EVI were not correlated with the radiation extinction rate ($p > 0.3$).

The PRI in the analysed Mediterranean forest presented a distinct seasonal pattern for the analysed period (Figure 5). The highest values (0.26–0.28) occurred in winter and the lowest values (0.09–0.16) occurred in late spring and summer.

Between 2000 and 2009, the annual stem diametric increment of *Q. ilex* in a forest in Catalonia ranged from 0.6 mm year^{-1} in one of the wettest growing seasons to 0.15 mm y^{-1} in one of the driest growing seasons. Precipitation accounted for 48% of the variability in the stem diametric increment. When precipitation in the previous year was added to the model, the model accounted for 66% of the inter-annual variation in the annual stem diametric increment. The average annual EVI explained 83% of the stem diametric increment in *Q. ilex* (Figure 6(*a*)). The average annual NDVI and the stem diametric increment of *Q. ilex* were positively correlated, but they accounted for only 47% of the variance (Figure 6(*b*)). In the period 2003–2009, the average annual PRI accounted for 62% of the

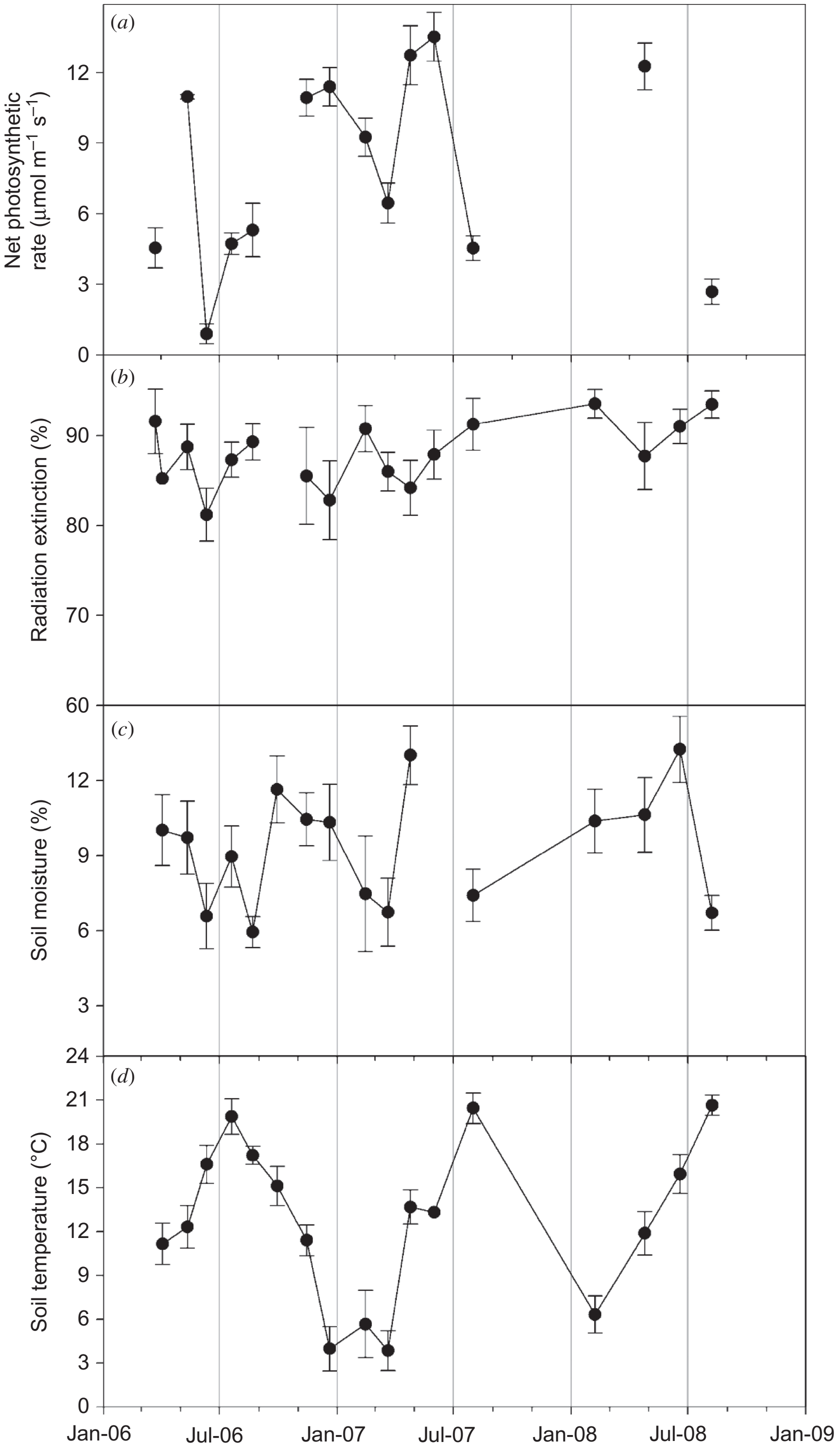

Figure 2. Seasonal variability in (*a*) net photosynthetic rates of *Q. ilex*, (*b*) radiation extinction, (*c*) soil moisture, and (*d*) soil temperature in the Mediterranean forest of the Prades Mountains. Error bars indicate the standard errors of the 10 sites.

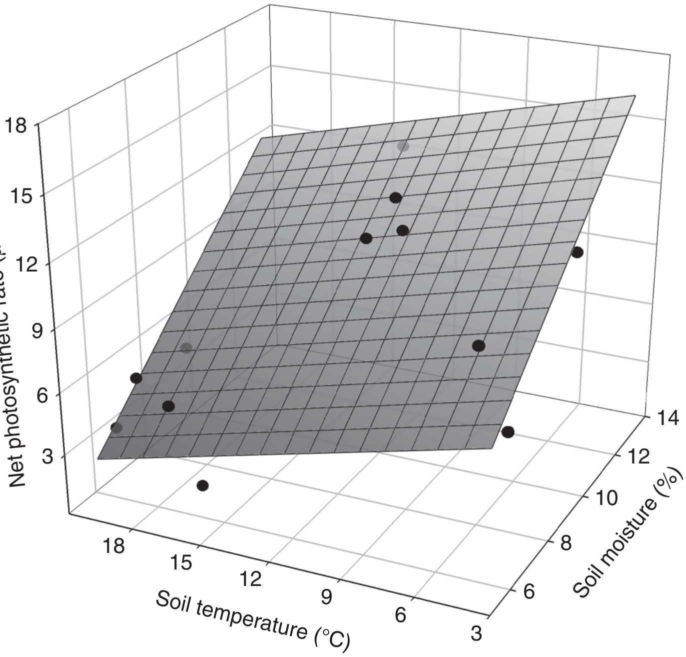

Figure 3. Leaf net photosynthetic rates of *Q. ilex*, soil moisture, and soil temperature in the period 2006–2008 in the Mediterranean forest of the Prades Mountains. The shaded plane indicates the bivariate linear regression ($p < 0.001$, $r^2 = 0.85$; net photosynthetic rate = –0.55 + 1.36 × soil moisture – 0.27 × soil temperature).

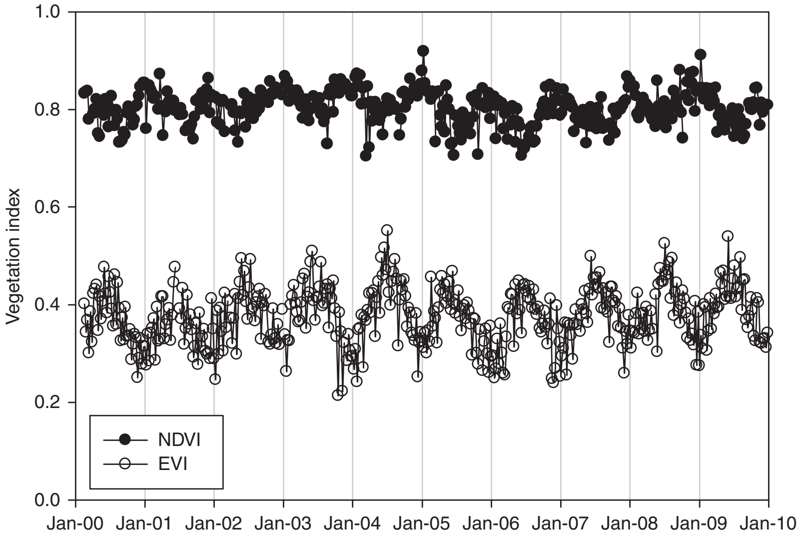

Figure 4. MODIS Terra NDVI and EVI for the Mediterranean forest of the Prades Mountains.

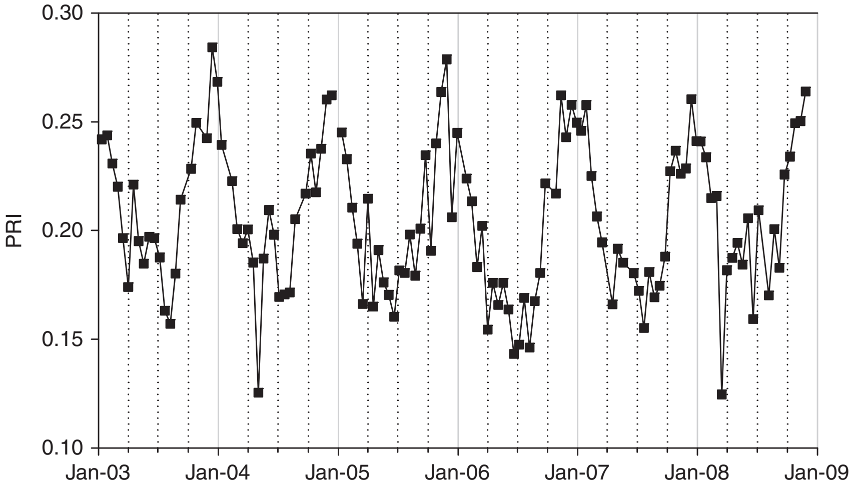

Figure 5. Seasonal pattern of MODIS Aqua PRI for the Mediterranean forest of the Prades Mountains.

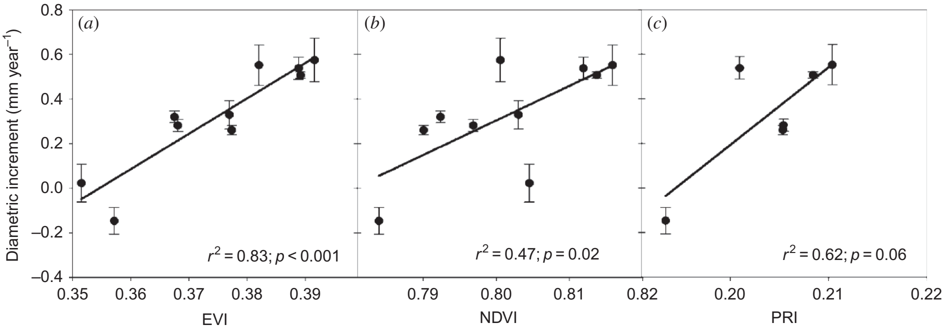

Figure 6. Annual diametric stem increment of *Q. ilex* in the Mediterranean forest of the Prades Mountains and MODIS Terra (*a*) EVI and (*b*) NDVI ($n = 10$), and (*c*) MODIS Aqua PRI ($n = 6$) annual averages for the period 2000–2009.

variability in the stem diametric increment (Figure 6(*c*)). Annual diametric stem increment and EVI did not show a temporal trend along the analysed period (Figure 7).

The temporal variability of leaf RUE and PRI calculated using band 1 as the reference was highly coincident over time (Figure 8). PRI accounted for 36% of the variation in leaf-level net photosynthetic rate (Figure 9(*a*)) and 40% of the variation in RUE (Figure 9(*b*)). Neither net photosynthetic rate nor RUE was correlated with NDVI or EVI (data not shown).

4. Discussion

The contrast in the seasonal patterns of the NDVI and EVI for the oak Mediterranean forest in the Prades Mountains, Spain, demonstrated the differences between the two spectral indices. One of the important differences between the indices is the greater capacity of EVI to amplify the vegetation signal, which improves the sensitivity in high biomass

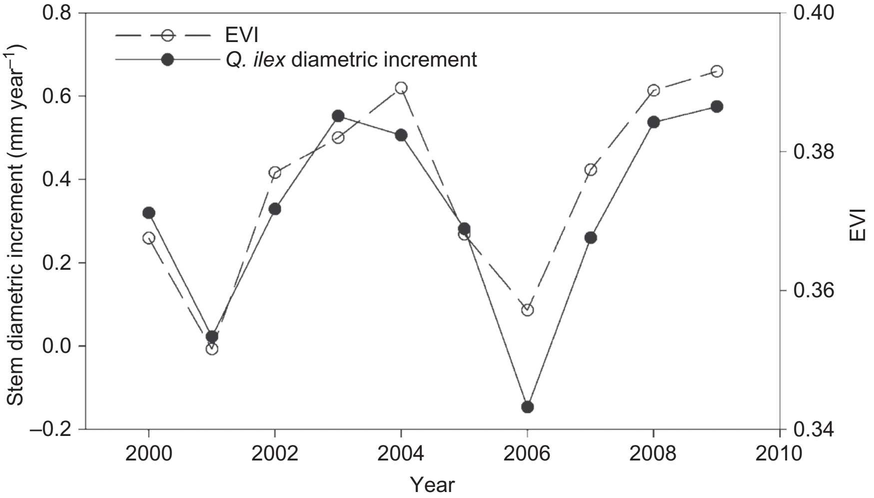

Figure 7. Annual stem diametric increment in *Q. ilex* in the Mediterranean forest of the Prades Mountains and average annual EVI.

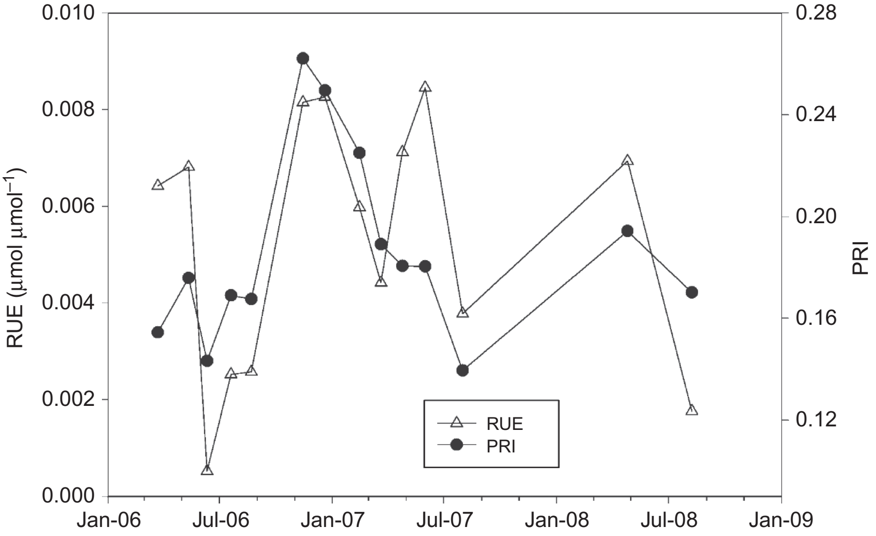

Figure 8. Leaf RUE of *Q. ilex* and the MODIS Aqua PRI in the Mediterranean forest of the Prades Mountains.

regions through a decoupling of the canopy background signal and a reduction in atmosphere influences (Huete et al. 2002). Furthermore, our study demonstrated that NDVI and EVI provide seasonally different signals and they even present a temporal negative correlation. Data from other two Mediterranean forest sites also showed a significant difference in the signals, because the two MODIS indices (NDVI and EVI) were not correlated for 8 year analysis in both sites (Castelporziano, Italy and Puechabon, France: $R^2 < 0.01$, $p > 0.1$). The relationship between NDVI and EVI for a wide range of contrasting vegetation types is significant when analysing the data altogether (Huete et al. 2002). The strength

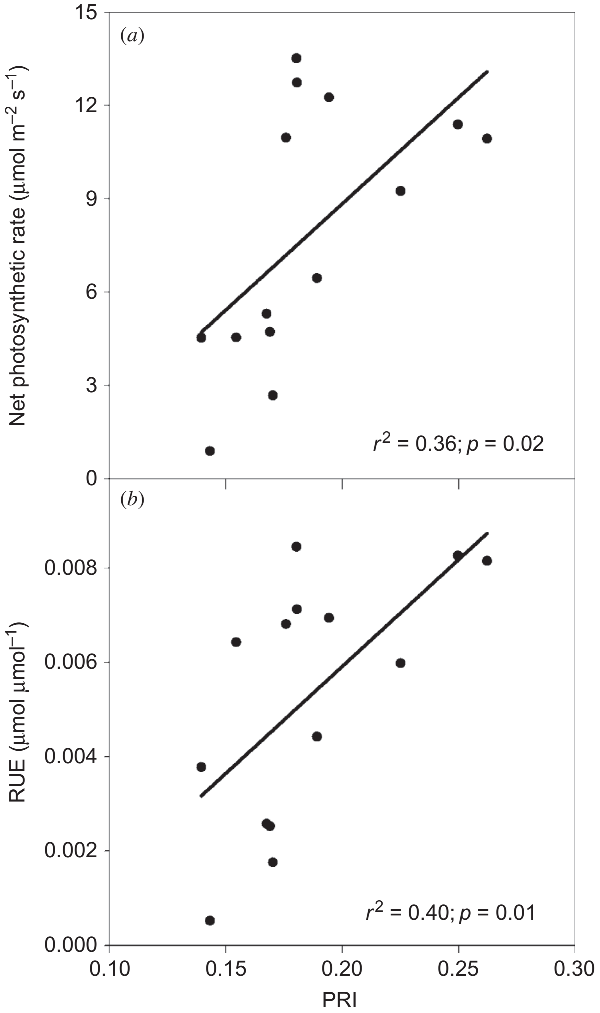

Figure 9. Relationships of leaf-level (*a*) net photosynthetic rates and (*b*) RUE of *Q. ilex* and MODIS Aqua PRI in the Mediterranean forests of the Prades Mountains between 2006 and 2008.

of the correlation between NDVI and EVI differs among vegetation types of the same data set, from non-significant ($r < 0.2$) in an evergreen forest in the Cascade Mountains, USA, to highly significant ($r < 0.99$) in the Uyuni Salt Flats, Bolivia. The coefficient of variation of the vegetation indices reflects the strength of the correlation.

In the Mediterranean forest in Catalonia, soil reflectance does not contribute much noise to the analyses because of the very high vegetation cover and LAI throughout the year. Furthermore, the radiation extinction rate and, therefore, fPAR are not correlated with NDVI or EVI. Typically, significant correlations between fPAR and NDVI are found in data sets that include a range of values that are greater than those encountered in our study (c.f. Myneni and Williams 1994). That said, the absence of correlations between fPAR and the two indices did not explain the remarkable seasonal differences between EVI and NDVI.

In the forest in the Prades Mountains, the NDVI was probably saturated because the LAI was consistently high. In contrast, the EVI was sensitive to phenological changes in the colour of leaves and the canopy, and changes in the proportions of new and old leaves. In spring, new leaves appear very pale green; however, the new cohort did not lead to a net increase in total LAI because the abscission of old leaves occurred simultaneously (Ogaya and Peñuelas 2004), which changed the reflectance of the canopy such that it was detectable by EVI. It had been suggested that, while the NDVI is an estimate of the fPAR of leaves, the EVI estimates fPAR based on chlorophyll content (Zhang et al. 2005). In addition, seasonal changes in the concentrations of pigments, such as a winter and summer decrease in chlorophyll content, might have contributed to the differences observed between the spectral indices. In one study, leaf chlorophyll content (chl a + chl b) in *Q. ilex* was 50% lower in summer and 64% lower in winter than in spring (Gratani, Pesoli, and Crescente 1998).

In the Prades Mountains, the EVI was a good indicator of the temporal variation in gross primary production (GPP) at the ecosystem scale. In evergreen needleleaf forests, deciduous broadleaf forests, grasslands, and woody savannas in North America (Sims et al. 2006), and in shrublands, corplands, grasslands, woodlands, and wooded grasslands in Africa (Sjöström et al. 2011), the EVI was correlated with GPP. That was not apparent, however, in some types of evergreen forests such as this Mediterranean forest. The EVI and the NDVI were not good indicators of leaf photosynthetic rates and, probably, they would not be helpful in identifying changes in ecosystem GPP as suggested for other Mediterranean forests in Italy (Garbulsky et al. 2008).

The average annual EVI was more strongly correlated with the annual stem diametric increment in the *Q. ilex* forest than the NDVI or the PRI. This better performance of EVI (Figures 5 and 6), for a 10 year period, suggests that, overall, EVI was the best indicator of annual net primary productivity (NPP). Other factors included the saturation of the NDVI and the greater capacity of the EVI to reduce the atmospheric noise, and probably the assessment of the annual flush of new leaves can explain these results. 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 (Marsden et al. 2010; Wang et al. 2004). Our results, however, are of key importance because we deal with an evergreen forest without a clear seasonal variation in the leaf area.

Water availability is an important factor in ecosystem function, e.g. loss of foliage, dieback, and the emissions of volatile organic compounds in Mediterranean forests (Lloret, Siscart, and Dalmases 2004; Peñuelas and Llusià 2001). In the oak forest in the Prades Mountains, current-year and previous-year precipitations were significantly positively correlated with stem diametric increment. In addition, the drought in southeastern Europe in 2003 did not affect the growth of this Mediterranean forest (Figure 6), but it affected the other types of forests in the region (Lloret et al. 2007), as was also seen in the crown condition trends (Carnicer et al. 2011).

Notably, in this oak forest in Catalonia, PRI and stem diametric increment, which reflect growth over the entire season, were positively correlated. Typically, the PRI is correlated with short-term variability of ecophysiological variables (Garbulsky et al. 2011), but our study has demonstrated the capacity for the average annual PRI to measure the annual ecosystem performance for a vegetation type in which fPAR does not vary seasonally.

The leaf-level photosynthetic rates of *Q. ilex* in this Mediterranean forest were in the range of values known for this site and species (Asensio et al. 2007). Changes in the availability of water were the main causes of the seasonal variation in photosynthesis, and temperature was a secondary factor (Figure 2), which has been observed at the ecosystem scale in other Mediterranean forests (Keenan, Sabate, and Gracia 2010). Unlike the NDVI and the EVI, which were not correlated with leaf-level photosynthetic rates, PRI accurately reflected leaf-level photosynthetic rates and, especially, photosynthetic efficiency. Other studies have shown that PRI was strongly correlated with various photosynthesis-related variables at the leaf, plant, and ecosystem scales in various plant and vegetation functional types (Garbulsky et al. 2011). In particular, the PRI derived from satellite data can be correlated with the stand-level carbon fluxes detected by eddy covariance towers in boreal (Drolet et al. 2005), temperate deciduous (Rahman et al. 2004), and Mediterranean (Garbulsky et al. 2008) forests. Carbon fluxes derived from eddy covariance towers provide a powerful database to scale to remote-sensing data. However, caveats for the use of eddy covariance carbon flux data include uncertainty in the eddy covariance GPP data derived from the gap filling and separation of the respiration flux processing methods. This uncertainty ranges well below 100 g C m^{-2} $year^{-1}$ (Moffat et al. 2007; Papale et al. 2006) and can produce noise in the correlations between RUE and PRI. Moreover, sites such as the one studied here in mountainous areas hinder the effectiveness of using eddy covariance to measure the carbon uptake of vegetation. We showed for the first time a significant correlation between net photosynthesis and RUE 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.

In the oak forest in Catalonia, Spain, the three spectral indices differed in their potential benefits to ecological monitoring and the evaluation of forestry management practices. As we hypothesized, the three spectral indices are different in their capacity to detect changes in the ecophysiological state of vegetation. The EVI can estimate annual stem diametric increment, a surrogate of NPP, and PRI can estimate daily leaf-level net photosynthesis and RUE. The NDVI is more limited in its capacity to reflect any component of the carbon cycle in Mediterranean forests. We conclude that EVI and PRI are highly suited to vegetation monitoring of carbon cycle in these Mediterranean forests. More studies are warranted in other sites and other vegetation types, particularly for the EVI and the PRI to make these indices more globally useful as ecological tools to assess primary productivity. In addition, we also concluded that the *Q. ilex* forest we analysed relies on the actual precipitation to capture carbon, and also on a memory effect derived from the water conditions of the previous year.

Our final conclusions were that (1) PRI was a good surrogate of RUE at the leaf level and EVI of annual diametric increment in a Mediterranean forest; (2) in contrast, NDVI presented no clear relationships with the measured ecophysiological variables; and (3) current-year precipitation, but also previous-year precipitation, controlled plant CO_2 fixing.

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