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Photosynthetic light use efficiency from satellite sensors: From global to Mediterranean vegetation

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ABSTRACT

Recent advances in remote-sensing techniques for light use efficiency (LUE) are providing new possibilities for monitoring carbon uptake by terrestrial vegetation (gross primary production, GPP), in particular for Mediterranean vegetation types. This article reviews the state of the art of two of the most promising approaches for remotely estimating LUE: the use of the photochemical reflectance index (PRI) and the exploitation of the passive chlorophyll fluorescence signal. The theoretical and technical issues that remain before these methods can be implemented for the operational global production of LUE from forthcoming hyperspectral satellite data are identified for future research.

1. Introduction

Photosynthesis is one of the main drivers of many services provided by ecosystems, such as climate regulation, carbon sequestration and storage, the production of food or grassland for livestock (Costanza et al., 1997; de Groot et al., 2002; Naidoo et al., 2008). Detecting photosynthetic rates, i.e. how much of the photosynthetic capacity is actually realized, and gross primary production (GPP), i.e. the expression of the photosynthetic carbon uptake at the ecosystemic level, is essential for evaluating the global carbon cycle for research on climate change.

Traditional remote-sensing techniques, based on leaf area index (LAI) or vegetation indices (VIs) related to greenness, allow the assessment of green plant biomass and therefore the potential photosynthetic capacity of plants (Garbulsky et al., 2013). Techniques based on broadband reflectances in the visible and near-infrared spectra, however, may be insensitive to moderate conditions of stress where leaves remain green but have reduced photosynthetic activity (Gamon et al., 1995; Baret et al., 2007). Stress would be detected only on longer time scales, when prolonged stress causes chlorosis, defoliation or the degradation of canopies (Hilker et al., 2008a).

Evergreen Mediterranean vegetation present small changes in green biomass throughout the growing season and these changes are responsible only for small changes in carbon uptake by terrestrial vegetation. In evergreen Mediterranean forests, in the absence of ancillary data, broadband vegetation indices, including the normalized difference vegetation index (NDVI, Rouse et al., 1974), may not provide good estimates of carbon uptake, because they are largely insensitive to the short-term changes in carbon dioxide (CO_2) caused by water stress (Maselli et al., 2009). Lloret et al. (2007) found that the NDVI failed to detect a massive drought in a Mediterranean Quercus ilex forest compared to other types of forest.

The efficiency of photosynthetic tissues to convert absorbed light into organic compounds, i.e. light use efficiency (LUE) of terrestrial vegetation, is a valuable variable for understanding the overall carbon uptake by terrestrial ecosystems, particularly in Mediterranean forests with nearly constant LAI values (Ogaya and Peñuelas, 2006). A direct remote estimation of LUE is very important for detecting the effects of environmental stress on the uptake of carbon by vegetation that may occur prior to a reduction in leaf area (Garbulsky et al., 2008b). The temporal changes in LUE in Mediterranean forests have been correlated with the ratio of actual to potential evapotranspiration, but neither temperature nor vapor-pressure deficit was a predictor of variation in LUE

Abbreviations: LUE, light use efficiency; GPP, gross primary production; PRI, photochemical reflectance index; LAI, leaf area index; VI, vegetation index; NDVI, normalized difference vegetation index; APAR, absorbed photosynthetically active radiation; PAR, photosynthetically active radiation; fAPAR, fraction of absorbed photosynthetically active radiation; PEM, production efficiency model; MODIS, MODerate resolution Imaging Spectroradiometer; MERIS, MEdium Resolution Imaging Spectrometer.

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(Garbulsky et al., 2010), which is an assumption of many models (Potter et al., 1999; Running et al., 2004).

Many attempts to remotely estimate LUE have been made in recent years. While it is clear that in Mediterranean vegetation types it is particularly important (Garbulsky et al., 2011), some issues related to the scale-change problem remain. These issues include structural, angular and atmospheric effects, and some technical limitations associated with the available satellite instruments and data sets that require further evaluation. This review presents the theoretical background of LUE, the state of the art of different ways of estimating LUE, the recent advances in the available remote-sensing technologies and data but also the remaining issues and the necessary future research.

2. Theoretical background of light use efficiency

Many approaches for estimating photosynthesis and primary production (Field et al., 1995; Running et al., 2004) are based on the LUE model proposed by Monteith (1977), which states that the GPP of a stand of vegetation can be derived from the absorbed photosynthetically active radiation during the period of study (APARdt) and from the efficiency (LUE) with which this APAR is converted into biomass:

$$\mathrm{GPP} = \mathrm{PAR} \times \mathrm{fAPAR} \times \mathrm{LUE} \tag{1}$$

where PAR is the incident photosynthetically active radiation (400–700 nm) reaching the canopy, and fAPAR is the fraction of absorbed PAR.

Solar PAR is greatly attenuated by atmospheric absorption and scattering and may be derived from meteorological but also from satellite data sets (Van Laake and Sánchez-Azofeifa, 2005; Liang et al., 2006; Liu et al., 2008). Different treatments are needed for direct and diffuse PAR components because of their different impacts on primary productivity. Diffuse radiation plays an important role in increasing LUEs by plant canopies and decreasing canopy photosynthetic saturation (Gu et al., 2002; Alton et al., 2007).

Several fAPAR products derived from satellite data sets of moderate resolution on a global scale are already available (e.g. Baret et al., 2013; Gobron et al., 2006; Myneni et al., 2002; Verger et al., 2012). These products are derived using a wide variety of methods of retrieval, ranging from empirical relationships with vegetational indices to more complex physical approaches based on the inversion of radiative transfer models. Validation and intercomparison studies generally show good agreement in the spatial and temporal pattern distribution of fAPAR products but with some differences in the magnitude of products, which are related to the quality and characteristics of satellite input data but also to the inversion-retrieval method and the definition of the product (e.g. Martínez et al., 2013; McCallum et al., 2010; Seixas et al., 2009).

Many production efficiency models (PEMs) assume a constant LUE value (Myneni et al., 1995) or derive this term from published biome-dependent values (Ruimy et al., 1994). Other PEMs consider a potential (maximum) LUE and then downregulate it using meteorological variables, such as vapor-pressure deficit and temperature, as surrogates for photosynthetic stresses (Running et al., 2004). None of these approaches, however, are completely satisfactory. LUE should not be assumed constant but as inherently variable, as recognized by the modeling community (Grace et al., 2007). Considering LUE on the basis of biome classes assumes that interclass variability is greater than intraclass variability, which is often not realistic and fails to reflect the spatial heterogeneity in land cover, stand age, soil type and canopy structure of most biomes (Hilker et al., 2008b). Finally, meteorologically based methods may not always adequately explain variation in efficiency, because vapor-pressure deficit and temperature alone are not always good surrogates of reduced efficiency (Garbulsky et al., 2010). Environmental but also physiological stresses limit photosynthesis and are responsible for the wide variations of LUE in time (diurnal, seasonal and long-term variations) and space (from leaf level to canopy level with variations on local, regional and global scales) (Gamon et al., 1995; Garbulsky et al., 2010; Runyon et al., 1994). The key factors contributing to this variability are contrasting functional types (Gamon et al., 1997; Huemmrich et al., 2010), extremes of drought and temperature (Landsberg and Waring, 1997; Sims et al., 2006) and nutrient levels (Gamon et al., 1997; Ollinger et al., 2008).

Mediterranean forests, in particular, show a very low temporal variability in the estimators of the fAPAR (NDVI and MOD15; cv < 10%) while a high temporal variability for GPP (cv > 35%) and LUE (cv > 48%) for a five-years period (Fig. 1). Therefore a continuous spatiotemporal estimation of LUE on a global scale and particularly for Mediterranean vegetation is thus crucial for improving carbon uptake modeling. Important recent advances in our capacity to remotely estimate LUE have been achieved by using the photochemical reflectance index (PRI) and chlorophyll fluorescence (F).

3. Photochemical reflectance index

3.1. Background

The foundation of this remote-sensing approach for estimating LUE is the de-epoxidation state of the xanthophyll cycle that is linked to heat dissipation in leaves (Demmig-Adams and Adams, 1996). When photochemistry operates at maximal efficiency, excitation is passed mainly to the photoreactions. When the photochemical traps are closed, excitation is lost by a competition between fluorescence and non-radiative dissipative pathways, the latter converting the energy into heat (Fig. 2). Heat dissipation is thus a process of decay of the excited chlorophyll alternative 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, 1992; Peñuelas et al., 1995), the PRI is typically calculated as [R531 − R570]/[R531 + R570] (Peñuelas et al., 1995), where R is reflectance and the numbers represent wavelength in nanometers at the center of the bands). This index was developed to remotely assess photosynthetic efficiency using narrow-band reflectance (Gamon et al., 1992; Peñuelas et al., 1995) (Fig. 3). A series of studies conducted during the 1990s at the leaf and close-canopy levels using close-range remote sensing from the ground or low platforms were able to assess LUE based on the PRI (Filella et al., 1996; Gamon et al., 1990, 1992, 1997; Gamon and Surfus, 1999; Peñuelas et al., 1994, 1995, 1997, 1998).

The PRI measures the relative reflectance on either side of the green reflectance peak (550 nm, Fig. 3), so it also compares the reflectance in the blue (chlorophyll and carotenoid absorption) region of the spectrum with the reflectance in the red (chlorophyll absorption only) region (Peñuelas et al., 2011). Consequently, it can serve as an index of relative carotenoid:chlorophyll levels. Over longer time scales (weeks to months), changes in carotenoid:chlorophyll ratios due to foliar development, aging or chronic stress have been reported to play a significant role together with the xanthophyll pigment epoxidation in the PRI signal (Gamon et al., 2001; Peñuelas et al., 1997; Stylinski et al., 2002). Thus, the PRI is also often related to carotenoid:chlorophyll ratios in leaves across a large number of Mediterranean species, ages and conditions (Filella et al., 2009; Stylinski et al., 2002) and also from remotely sensed data (Stagakis et al., 2010). To the extent that photosynthetic activity correlates with changing chlorophyll:carotenoid ratios in response to stress, ontogeny or senescence, the PRI may thus

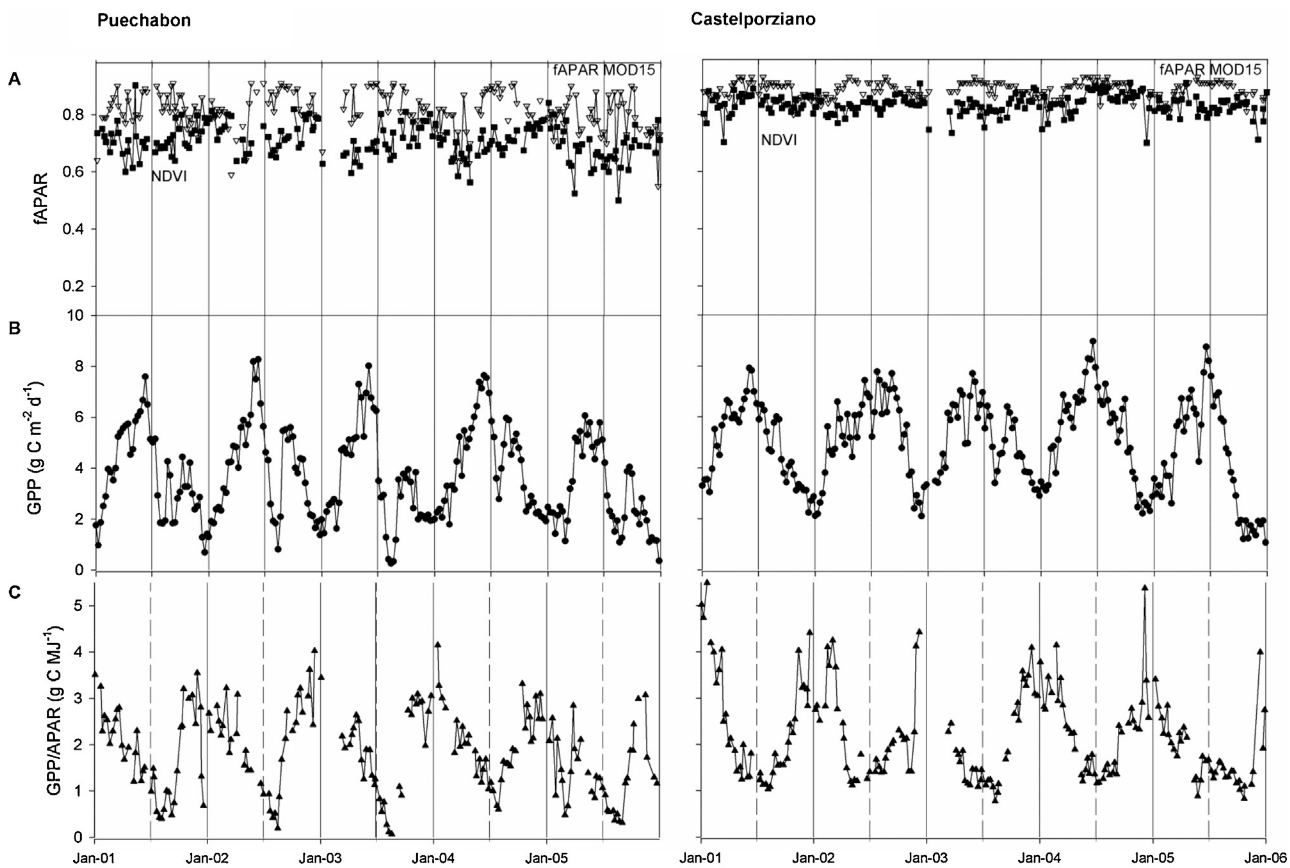

Fig. 1. Seasonal variation of (A) fAPAR surrogates (NDVI and MODIS fAPAR: MOD15), (B) Gross primary productivity (GPP) and (C) GPP/APAR as an estimator of light use efficiency at two Mediterranean forests: Puechabon, France and Castelporziano, Italy (2001–2005).
Source: Redrawn from Garbulsky et al. (2008a).

provide an effective measure of relative photosynthetic rates. Seasonally varying pigment levels also strongly affect the PRI, which may help to explain why the PRI often works as well as it does seasonally to predict LUE (Garbulsky et al., 2011).

The relationships described above indicate that the PRI could significantly improve the global and regional monitoring of CO_2 uptake by terrestrial ecosystems. The relationships have been found mostly on leaf and canopy scales (Garbulsky et al., 2011). In recent years, however, several ecosystemic studies have also demonstrated significant links between whole ecosystemic fluxes and the MODIS (MODerate resolution Imaging Spectroradiometer) PRI in a variety of natural forests, including temperate deciduous

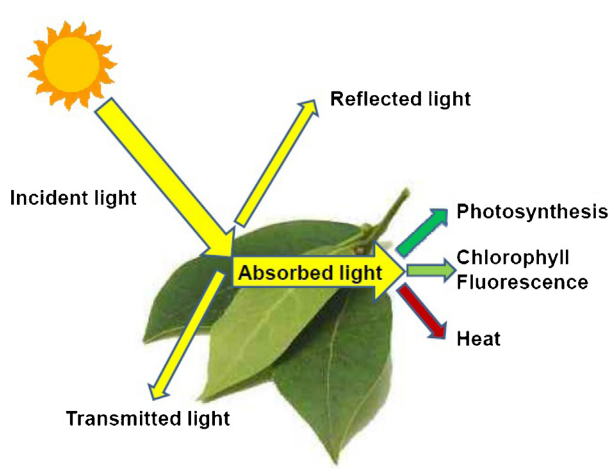

Fig. 2. Incident sunlight on leaves and the fate of complementary pathways after interception. Light absorbed by chlorophyll can be used to drive photochemistry, a process that can use up to 80% of the absorbed radiation. Energy can alternatively be lost as fluorescence (0.5–2% of absorbed radiation) or as heat (18–98%).

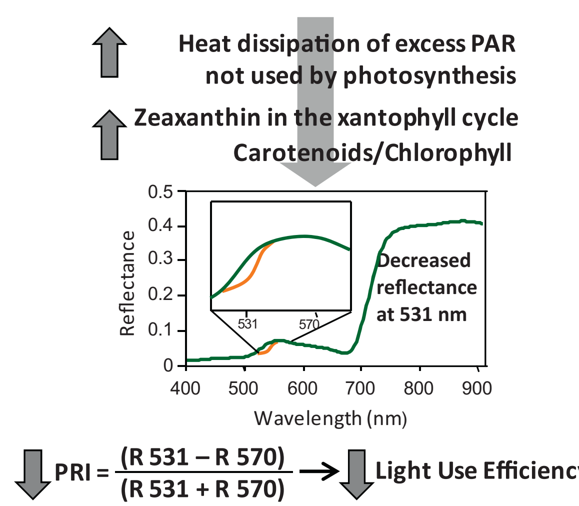

Fig. 3. The pigment-cycle approach to remotely sense gross LUE in terrestrial vegetation by means of the photochemical reflectance index (PRI). The remote sensing of the xanthophyll cycle provides a surrogate for estimating the dissipation of excess radiation not used for photosynthesis from leaves to primary productivity on regional scales. Light gray colors for the arrows and reflectance spectrum are indicative of conditions with excess radiation and therefore low LUE, while the green spectrum indicates the conditions with high LUE.

Table 1
Current and future satellite tools for estimating photosynthetic efficiency from plant pigments.

Satellite	Sensor	Launching/service period	Reference	Main features of the data
Earth Observing-1 (EO-1)	Hyperion	November 2000	http://eo1.gsfc.nasa.gov/	Descending polar orbit with an equatorial crossing time at 10:03. High-resolution hyperspectral imager with 220 spectral bands (from 400 to 2500 nm) at 30-m resolution with a revisit period of 16 days
PROBA	CHRIS	22 October 2001	https://earth.esa.int/web/guest/missions/esa-operational-eo-missions/proba	Sun-synchronous orbit with a revisit period of 7 days. Depending on the setting mode, spatial resolution is 18 m or 34 m at the nadir setting. Along track narrow-band spectrometric observations of the PRI of up to five angles
TERRA – AQUA	MODerate resolution Imaging Spectroradiometer (MODIS)	TERRA: January 2000 AQUA: May 2002	http://modis.gsfc.nasa.gov/	The same sensor on two satellites. Two revisits a day (morning and afternoon) for 16 spectral bands from 400 to 1000 nm at 250, 500 and 1000 m spatial resolution and 10 nm bandwidth
ADvanced Earth Observing Satellite II (ADEOS-2)	GLobal Imager (GLI)	December 2002–October 2003	http://sharaku.eorc.jaxa.jp/ADEOS2/	Six 250-m resolution channels and 30 other 1-km resolution channels, with a revisit period of 4 days
Environmental Mapping and Analysis Program (EnMAP)	HyperSpectral Imager (HSI)	Planned for 2015	http://www.enmap.org/	Sun-synchronous orbit with a revisit period of 4 days, a spatial resolution of 30 m × 30 m and 94 bands between 420 and 1000 nm
Hyperspectral Infrared Imager (HyspIRI)	VSWIR	Currently at the study stage	http://hyspiri.jpl.nasa.gov/	380–2500 nm in 10 nm contiguous bands with a spatial resolution of 60 m at nadir and a revisit period of 19 days

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,b; Goerner et al., 2009, 2011) (Fig. 4).

3.2. Satellite missions and data sets

The satellite-borne MODIS sensor, which has provided global data since 2000, has so far been the best tool for testing the utility of the PRI at the ecosystemic level. The 530 nm (526–536) waveband has successfully monitored LUE at the ecosystemic scale across different types of vegetation (Drolet et al., 2005, 2008; Garbulsky et al., 2008a,b; Goerner et al., 2009; Rahman et al., 2004). A few space-borne remote-sensing instruments currently provide high spectral resolution (e.g. Hyperion and CHRIS/PROBA). New missions are planned and novel instruments carried by helicopter and aircraft also provide data (Malenovsky et al., 2009). Forthcoming sensors (Table 1) are expected to provide better data for estimating LUE from space. The launching of new image spectrometers, such as the HyspIRI by NASA or the EnMAP project lead by the German Aerospace Centre (DLR), will allow the calculation of the PRI at high spatial resolution and will offer promising perspectives for LUE estimation.

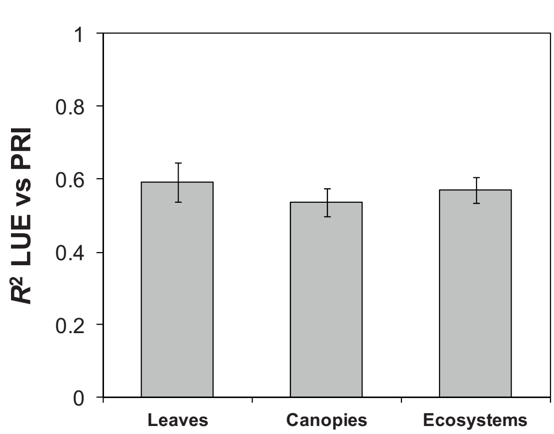

Fig. 4. Average strength of the relationships between LUE and the PRI across organizational scales (leaf, canopy or ecosystem). The bars represent the coefficients of determination for daily and seasonal time scales and variation related to spatial variation, different species or nutrient availabilities. The error bars represent standard errors (24 studies for leaves, 28 for canopies and 17 for ecosystems).

3.3. Cautionary remarks

Several questions remain for a generalization of the use of the PRI at ecosystemic scales for the global estimation of LUE (Grace et al., 2007; Garbulsky et al., 2011). Multiple biochemical, ecological, and physical confounding factors operating at several levels of aggregation in the LUE-PRI relationship are apparent from a review of the literature (Garbulsky et al., 2011). At the leaf level, biochemical processes such as photorespiration, cyclic electron transport of photosystem I (PSI) and nitrate reduction can compete with CO_2 fixation for reductants generated by photosynthetic electron transport (Niyogi, 1999) and cause the divergence of photosystem II (PSII) efficiency (PRI) and CO_2 assimilation. Other pigment cycles, including the lutein epoxide cycle (Esteban et al., 2009; Matsubara et al., 2008), could also produce noise in the PRI signal. Despite these potential complications, the overall photosynthetic system may often be sufficiently regulated to maintain consistent relationships between PSII processes and CO_2 fixation (Gamon et al., 1997; Stylinski et al., 2002).

At the canopy level, the problems are related to different factors that affect the reflectance and are not appropriately considered in PRI computation. These factors include background effects (e.g. soil color, moisture, shadows or the presence of other non-green components of the landscape), structural effects (e.g. leaf movement and changes in LAI or in the distributions of leaf angles) and directional effects associated with changes in illumination and viewing angles (Filella et al., 2004; Sims et al., 2006; Hilker et al., 2010) that determine the pattern of shadows and may significantly influence the PRI signal (Gamon et al., 1995; Asner, 1998; Barton and North, 2001; Drolet et al., 2005; Hall et al., 2008; Hilker et al., 2008a). Recent advances have demonstrated the feasibility of techniques for multiangle correction of these structural disturbances for the continuous monitoring of CO_2 sequestration (Lyapustin and Wang, 2009; Hilker et al., 2010).

The consistency of the relationships among the PRI, LUE and CO_2 uptake increasingly reported in different studies across ecosystems (Garbulsky et al., 2011; Peñuelas et al., 2011; Hilker et al., 2011) suggests a high degree of functional convergence of biochemical, physiological and structural components affecting ecosystemic C fluxes between types of ecosystems (Field, 1991). The complex photosynthetic behavior of emergent ecosystemic properties may be explored using this simple index PRI. Understanding the basis for this convergence and finding the ecophysiological principles governing these responses remain a primary goal of current research.

The generation of comparable data for the transferability of PRI-LUE relationships requires the use of uniform protocols (Peñuelas et al., 2011). Further studies are also needed to disentangle the several drivers of the PRI signal and to resolve the potentially confounding factors for improving the assessment of CO_2 fluxes in many different biomes using hyperspectral or narrow-band remote sensing. In this sense, advances in modeling and standardization of the biome or vegetation appear necessary.

4. Chlorophyll fluorescence

Significant advancements have recently been made in estimating LUE and carbon uptake from chlorophyll fluorescence viewed from space. Remote sensing from space of fluorescence from terrestrial vegetation is of great interest because it can provide global information on the functional status of vegetation, including LUE and global primary production. Global retrieval of solar-induced fluorescence emitted by terrestrial vegetation is beginning to provide an alternative approach for measuring photosynthetic efficiency.

Available evidences show that the leaf level maximal chlorophyll fluorescence in Mediterranean species is sensitive to the summer stress in response to drought but also in winter in response to cold stress (Gratani et al., 2000; Oliveira and Peñuelas, 2004; Llorens et al., 2003; Ogaya and Peñuelas, 2003; Bellot et al., 2004; Prieto et al., 2009). Moreover, long term studies showed that chlorophyll fluorescence in Mediterranean *Quercus ilex* and *Phyllerea latifolia*, a tree and a shrub respectively, reflect simulated climate change in temperature and water (Ogaya et al., 2011). All these are encouraging results stimulate the idea that the use of remotely sensed fluorescence could provide a powerful tool particularly in Mediterranean vegetation types.

4.1. Background

Fluorescence signals originate in the core of the photosynthetic apparatus, where absorbed photosynthetically active radiation (APAR) is converted into chemical energy. Fluorescence is the result of the competition between several pathways for the excitation captured in the antenna (see Section 3 and Fig. 2). Because the yield of fluorescence varies inversely with the fraction of open reaction centers, fluorescence provides a useful tool for investigating photosynthetic processes. A small amount of the light absorbed by chlorophyll in an assimilating leaf can be reemitted (at longer wavelengths) as fluorescence by the chlorophyll molecules of PS II, which adds a weak signal to reflected solar radiation (Fig. 5). Extensive experimental and theoretical studies demonstrate that chlorophyll fluorescence is a proxy to actual photosynthesis and as such is directly related to LUE and CO_2 uptake (Seaton and Walker, 1990). Fluorescence also behaves as an indicator of plant vitality and plant stress, because the emission of fluorescence competes with mechanisms of adaptation/protection activated by plants. Measuring fluorescence can thus provide access to new information about the variables of photosynthetic performance (Maxwell and Johnson, 2000). An advantage of chlorophyll fluorescence over other remotely sensed vegetational information is that it is an emission signal sensitive only to APAR absorbed by chlorophyll and not to non-plant components of a target region.

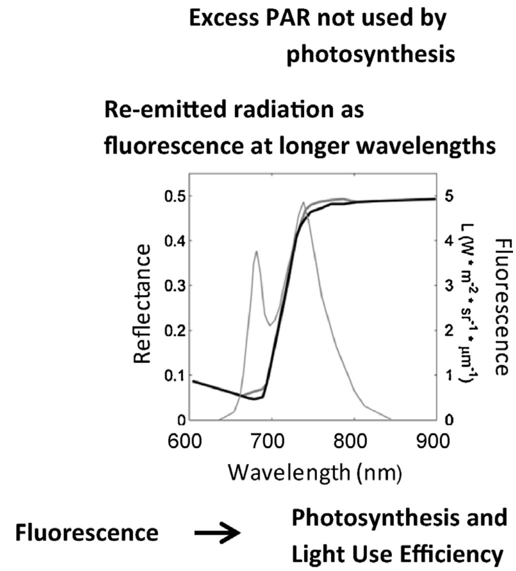

Fig. 5. Fluorescence as an estimator of photosynthesis activity. Fluorescence affects the characteristic canopy reflectance signal in the 400–900 nm spectral range as simulated with the FluorMOD model (Zarco-Tejada et al., 2006). The black line represents the reflectance spectrum without fluorescence effects, and the gray line including fluorescence effects. Superimposed is the fluorescence radiance with two typical peaks at 685 nm and 740 nm.

Improvements in the techniques of measuring fluorescence have made the detection of fluorescence an important tool for basic and applied research in plant physiology (Krause and Weis, 1991). Measurements of chlorophyll fluorescence are traditionally made at the leaf level using an external source of light. Fluorescence yield can be quantified by exposing a leaf to light of defined wavelength and measuring the amount of light re-emitted at longer wavelengths when the light is turned off.

Laboratory methods for measuring active fluorescence signals are not applicable on the scale of ecosystems, and new developments to measure passive chlorophyll fluorescence from space are needed. The signals of solar-induced chlorophyll fluorescence (F) are characterized by peaks in the blue-green (maxima at 440 and 520 nm) and in the red and far-red (maxima at 685 and 740 nm) spectral domains. The magnitudes of the latter two broad peaks with maxima around 685 and 740 nm can be related to photosynthetic efficiency (Fig. 5). Because the magnitude of solar radiation reflected by vegetation and the atmosphere can be 100–150 times more intense than F at the top of the atmosphere, the main challenge to estimate F from remote-sensing passive measurements is to decouple the F signal from the solar radiation (Meroni et al., 2009).

The first documented attempts to discriminate chlorophyll fluorescence from terrestrial vegetation without an artificial source of excitation were performed during the 1970s (Plascyk, 1975), and large steps forward are currently being made (Meroni et al., 2009; Rascher et al., 2009). The remote sensing of chlorophyll fluorescence, though, is a challenging issue and is still in the early stages of development. The F signal can be detected passively in narrow

Table 2
Remote-sensing tools for the assessment of chlorophyll fluorescence from space.

Satellite	Sensor	Launch/in orbit	Reference	Main features of the data
ENVISAT	MEdium Resolution Imaging Spectrometer (MERIS)	From March 2002 to April 2012	http://wdc.dlr.de/sensors/meris/	Spatial resolution of 260 m × 300 m Two channels near the O2-A band centered at 753.8 and 760.6 nm; bandwidths are 7.5 and 3.75 nm, respectively
ENVISAT	SCanning Imaging Absorption spectroMeter for Atmospheric CHartographY (SCIAMACHY)	From March 2002 to April 2012	www.sciamachy.org http://wdc.dlr.de/sensors/sciamachy/	A range of bandwidths of 0.2–0.5 nm from 240 to 1700 nm and from 2000 to 2400 nm, limb vertical 3 km × 132 km, nadir horizontal 32 km × 215 km
GOSAT (Greenhouse gases Observing SATellite)	TANSO Fourier Transform Spectrometer (FTS)	23 January 2009	www.gosat.nies.go.jp	Sun-synchronous orbit with an equatorial crossing time at 13:00, revisiting in 3 days
OCO-2 (Orbiting Carbon Observatory)	Single instrument with three classical grating spectrometers	July 2014	http://oco.jpl.nasa.gov/	Sun-synchronous orbit crossing equator at noon. Three measurement angles
Earth Explorer 8	FLuorescence EXplorer (FLEX) Fluorescence Imaging Spectrometer (FIS)	2018 or later, now in development	http://esamultimedia.esa.int/docs/SP1313-4_FLEX.pdf	Descending sun-synchronous orbit with an equatorial crossing time at 10:00
Geostationary Carbon Process Mapper (GCPM)	Geostationary Fourier Transform Spectrometer (GeoFTS)	In project phase	Key et al. (2012)	Geostationary: 10 times per day at ~4 km × 4 km
TanSat (Chinese carbon dioxide observation satellite)		2015, now in development	Liu et al. (2012)	Sun-synchronous orbit at 13:30 h, with a revisit period shorter than 16 days

absorption lines (≈2–3 nm) of the solar and atmospheric spectrum in which irradiance is strongly reduced, i.e. the Fraunhofer lines. Three main Fraunhofer lines in the visible and near-infrared have been used for estimating F: Hα from hydrogen (H) absorption in the solar atmosphere centered at 656.4 nm and two telluric oxygen (O_2) absorption bands in Earth's atmosphere, namely O_2-B centered at 687 nm and O_2-A at 760 nm. A combination of Fraunhofer lines would allow the measurement of the two main fluorescence bands. The two O_2 bands (A and B) and the Hα bands are considered the most useful (Meroni et al., 2009).

Fluorescence has often been measured from ground-based and airborne instruments, especially during the last decade (Moya et al., 1992; Meroni et al., 2009), but information available from satellites has been very limited. F was first estimated from space (Guanter et al., 2007) using data from the O_2-A absorption band provided by the ENVISAT MEdium Resolution Imaging Spectrometer (MERIS). The MERIS-derived fluorescence correlated well (R^2 = 0.85) with data acquired by the Compact Airborne Spectrographic Imager (CASI-1500) sensor and with ground-based estimates. Recent studies ((Frankenberg et al., 2011a; Joiner et al., 2011), have provided the first results on a global scale from data from the Thermal And Near-infrared Sensor for carbon Observation-Fourier Transform Spectrometer (TANSO-FTS/GOSAT). These two studies used different approaches. Joiner et al. (2011) used one strong Fraunhofer potassium line (K I at 770.1 nm) instead of infilling the O_2-A band. Frankenberg et al. (2011b) extended this single-line approach to the use of two broader spectral windows centered at 757 and 772 nm. This method of retrieval, making use of broader spectral windows containing several Fraunhofer lines, is expected to be less sensitive to instrumental noise than the method based on a single line. Retrievals in two separate windows provide more independent measurements for enhancing the signal-to-noise ratio of the final F determination. Data collected over a span of 22 months have accurately compared F intensity levels and spatial patterns with physically based methods of F retrieval (Guanter et al., 2012).

The current projects for estimating carbon uptake by vegetation with chlorophyll fluorescence from space are thus providing encouraging new results. The retrieval of F signals from space is feasible with the method of Fraunhofer-line retrieval, which is simple, fast and robust and which has been verified with data from the ground, principally data derived from eddy covariance. Fluorescence appears to provide information that is independent of reflectance data. F retrievals from the Greenhouse gases Observing SATellite (GOSAT) and NASA's Orbiting Carbon Observatory-2 (OCO-2) (Table 2), in conjunction with their global atmospheric CO_2 measurements, will provide an exceptional combination of vegetational and atmospheric perspectives on the global carbon budget, constraining our model predictions for future levels of atmospheric CO_2. Most importantly, this method is very insensitive to atmospheric scattering (Frankenberg et al., 2012), being able to sense F even through thin clouds.

4.2. Satellite missions and data sets

In addition to the sensors in orbit at the time of publication, a number of new satellite projects will be able to measure fluorescence from vegetation (Table 2). One of the major and most ambitious projects is the European Space Agency's FLEX (FLuorescence EXplorer) to be put in orbit in 2018. The main instrument is the Fluorescence Imaging Spectrometer (FIS) that will cover the O_2-A (760 nm) and O_2-B (687 nm) absorption lines with a spectral band of 20 nm. The ground spatial resolution at nadir will be 300 m, and the revisiting period will be seven days.

NASA's OCO-2 is another important projected satellite that will be specifically dedicated to the study of atmospheric CO_2 from space. Three high-resolution grating spectrometers (Day et al., 2011), one for each of the O_2-A (757–772 nm), weak CO_2 (1590–1621 nm) and strong CO_2 (2041–2082 nm) bands, will be combined with meteorological observations and ground-based CO_2 measurements to characterize CO_2 sources and sinks on regional scales at monthly intervals for two years at a spatial resolution of 1.29 km × 2.25 km.

The Geostationary Carbon Process Mapper (GCPM) in turn proposes three geostationary platforms. This project aims to measure key atmospheric trace gases and process tracers related to climate change and human activity at high temporal resolution and to generate contiguous maps of CO_2, methane (CH_4), carbon monoxide (CO) and F up to 10 times per day at a spatial resolution of ∼4 km × 4 km from geostationary orbits. These measurements will capture the spatial and temporal variability of the carbon cycle across diurnal, synoptic, seasonal and interannual timescales. The combination of high-resolution mapping and high frequency of measurement will provide quasi-continuous monitoring, effectively eliminating uncertainties of atmospheric transport from source/sink inversion modeling. The CO_2/CH_4/CO/F measurements could also provide the information needed to disentangle natural and anthropogenic contributions to atmospheric carbon concentrations.

4.3. Cautionary remarks

While fluorescence remote sensing of carbon uptake seems promising, the available data still present various problems. The orbiting sensors were designed for measuring greenhouse gases in the atmosphere and for analyzing fluorescence from terrestrial vegetation. These functions are probably the source of many of the actual limitations of the data. The problems related to remote sensing of fluorescence from space, at least with the satellites available in the near future, are the low spatial resolution, limited daily global coverage and frequency of revisits. Another drawback is the lack of data availability from previous years. The SCIAMACHY spectrometer, on board the EnviSat platform, is the only available sensor from the early 2000s that can provide a broad spatial resolution of fluorescence data (30 km × 60 km) (Joiner et al., 2012).

The main limitation at present is probably the scarce knowledge of what remotely sensed fluorescence is actually "telling us" about vegetational functioning. One line of evidence suggests that fluorescence has a positive, biome- and wavelength-dependent correlation with absorbed PAR. Studies at the leaf level and other empirical evidence indicate that fluorescence also correlates positively with LUE in different situations. This relationship, however, is probably not universal across vegetational types, and therefore a biome-dependent scaling from F to GPP would be warranted. The first observations of fluorescence from space are very recent (Frankenberg et al., 2011a,b; Joiner et al., 2011), so ground-based validation of the new data is needed to assess the capability and reliability of this new methodology. Additional research is also needed to disentangle the effects of confounding factors, such as illumination, canopy structure and temporal and spatial resolution of the satellite data, on the relationship between solar-induced fluorescence and photosynthesis.

5. Final considerations

The PRI and fluorescence are thus pragmatic approaches for remotely estimating parameters related to carbon uptake. The PRI was intended to be a surrogate of LUE and fluorescence was originally proposed as a proxy of LUE and was shown to be proportional to GPP. Both the PRI and fluorescence offer good overall performance but have well-known problems associated with the use of remotely sensed vegetational indices (structural, angular, soil background, atmospheric effects, among others), the weakness of the signals and the established biome dependence that hinders an easy generalization for application on a global scale. These problems need to be resolved but are currently being studied by several groups. Resolutions should come soon along with several new sensors specifically designed and devoted to the measurement of these variables.

The main advantages and limitations of both approaches are partially related to the available data from the actual sensors in orbit. The low spatial resolution appears to be a primary limitation of both approaches, but while MODIS can provide PRI data at a resolution of 1 km × 1 km, actual F data have a resolution on the order of tens of km^2. In both cases, the signal-to-noise ratio is a problem, but the estimation of fluorescence seems less dependent than the PRI approach on atmospheric and geometric problems. In particular, for Mediterranean vegetation, it was already shown that the MODIS PRI is a good surrogate for the estimation of LUE in perennial forest (Garbulsky et al., 2008a,b; Goerner et al., 2009; Moreno et al., 2012). However, hand held spectroradiometer estimations of PRI fail to seasonally follow the canopy LUE in Mediterranean shrublands (Filella et al., 2004) probably due to low leaf area and therefore the effect of bare soil in the PRI signal. Further analyses are warranted, using new and forthcoming sensors and platforms, to evaluate the capability of PRI and F to estimate LUE in different Mediterranean vegetation types. In particular in Mediterranean shrublands, sensors with different viewing angles could provide new insights to this elusive vegetation types for the LUE estimation.

A proper calibration of GPP and LUE estimations provided by the new remote-sensing products is warranted and remains a significant challenge. Eddy-covariance towers represent the current standard for ecosystemic carbon-flux estimation of GPP, but flux towers sample over time, whereas remotely sensed imaging samples through space (Rahman et al., 2001), hindering the calibration. To conduct this calibration, we should merge these sampling domains by applying measurements from remote-sensing aircraft and satellites at the same temporal and spatial scales as flux-tower footprint measurements, which is rarely done. Coordinated acquisition of 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. We should properly calibrate the surrogates for LUE for different ecosystems or vegetational types so that we could apply remote sensing to extrapolate in time and space from tower sites.

In conclusion, in spite of the needed improvements in our knowledge and techniques, the available results already indicate a wide and promising avenue for the estimation of LUE of terrestrial vegetation from satellite data, especially if the PRI and F can be standardized for common use in all biomes and ecosystems.

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