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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