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Key words: biodiversity, molecular ecology, nomenclature, taxonomy, Zygomycetes.

Letters

Photochemical reflectance index (PRI) and remote sensing of plant CO_2 uptake

The emerging consistency of the relationship between photochemical reflectance index (PRI) and light use efficiency (LUE) offers promising prospects for continuous global monitoring of plant primary productivity from space.

An accurate continuous quantification of the role of terrestrial ecosystems as carbon (C) sinks constitutes a key issue in the face of ongoing disturbance and climate change. Current tools for continuous monitoring ecosystem C uptake include eddy covariance and remote sensing. Eddy covariance is currently the only direct way to assess C flux of whole ecosystems with high temporal resolution. Nevertheless, eddy covariance towers can effectively measure a single 'point' over flat and uniform terrain, usually on the order of a few square kilometers or less (Baldocchi, 2003). Remote sensing has, instead, the ability to extend the spatial coverage of C flux observations beyond a fixed point. One of the most promising approaches is the use of the PRI as we comment in this perspective letter.

The standard reflectance indices currently mostly used such as the normalized difference vegetation index (NDVI) allow the assessment of the green plant biomass and green leaf area of the ecosystems, and therefore the absorbed light and plant photosynthetic capacity (Gamon *et al*., 1995). However, directly detecting how much of this capacity is actually realized at daily and seasonal scales is a much more challenging goal, especially when NDVI-like indices do not scale with CO_2 uptake, a quite common situation in many ecosystems. Now, this challenge appears to be solvable by using the PRI. This index was defined at the leaf and canopy levels in the early 1990s to assess the efficiency of a plant's use of absorbed photosynthetic active radiation (APAR) for photosynthesis (LUE) (Gamon *et al*., 1992; Peñuelas *et al*., 1995). PRI calculated from the data of satellite imaging spectrometers is currently being increasingly applied at the ecosystem level (Rahman *et al*., 2004; Drolet *et al*., 2008; Garbulsky *et al*., 2008, 2011; Goerner *et al*., 2009; Xie *et al*., 2009; Coops *et al*., 2010; Hilker *et al*., 2010), opening the possibility of highly improving the accuracy of the remote sensing estimation of the spatial and temporal variation in gross CO_2 uptake by vegetation, which is crucial for the monitoring of global C cycle.

The uncertainty of how much of the CO_2 fixation capacity of vegetation is realized in practice comes from the great variability of LUE between plants, environmental conditions, and ecosystems (Garbulsky *et al*., 2010). Consequently, NDVI can be a poor indicator of temporal variation in CO_2 fluxes, particularly for evergreen species subjected to periodic or seasonal downregulation of photosynthesis despite continued light absorption. Many older models used NDVI assuming a constant LUE (Myneni *et al*., 1995) or derived it from literature values by biome (Ruimy *et al*., 1994). A more accurate approach consisting of downregulating the maximum efficiency by biome using climatic variables, like vapor pressure deficit and temperature, as surrogates for photosynthetic stresses is now mostly used to estimate biospheric CO_2 uptake (Running *et al*., 2004; Zhao & Running, 2010). However, this approach still suffers because vapor pressure deficit and temperature alone are not always good surrogates of reduced efficiency or are not available with sufficient accuracy (Heinsch *et al*., 2006; Garbulsky *et al*., 2010).

Now actual estimations of the LUE are becoming accessible through the measurement of the PRI. This reflectance index is based on the short-term reversible xanthophyll pigment changes accompanying plant stress (Gamon *et al*., 1990; Peñuelas *et al*., 1994). These changes are linked to the dissipation of excess absorbed energy that cannot be processed through photosynthesis, and therefore reduces LUE (Demmig-Adams, 1990). Since these pigment changes translate into changes in the reflectance at 531 nm and since 570 nm reflectance is instead insensitive to short-term changes in these pigments, the PRI was defined as (R_{531} − R_{570})/(R_{531} + R_{570}), where R indicates reflectance and numbers indicate wavelength in nanometers (Gamon *et al.*,1992; Peñuelas *et al.*, 1995). Furthermore, the relationship with LUE is reinforced by the fact that PRI also measures the relative reflectance on either side of the green reflectance 'hump' (550 nm), that is, the reflectance in the blue (chlorophyll and carotenoids absorption) region of the spectrum relative to the reflectance in the red (chlorophyll absorption only) region. Consequently, it also behaves as an index of the chlorophyll/carotenoid ratios and therefore of the photosynthetic activities associated with their changes with leaf development, aging or stress at longer term (Peñuelas *et al.*, 1997; Sims & Gamon, 2002; Filella *et al.*, 2009).

At the leaf and canopy levels, the PRI has been extensively found adequate to estimate LUE and thus photosynthetic performance, that is gross primary productivity (GPP), and its use has been extended increasingly in the last few years both in natural and seminatural vegetation and in crops (Garbulsky *et al.*, 2011). The results of these studies confirm an exponential relationship between LUE and PRI over a wide range of species and conditions (Fig. 1a), hence suggesting that the overall photosynthetic system is often sufficiently regulated to maintain consistent relationships between the pigment, morphological and physiological changes linked to PRI and the changes in CO_2 fixation (Gamon *et al.*, 1997; Garbulsky *et al.*, 2011).

In a further step forward, with the availability of the moderate resolution imaging spectroradiometer (MODIS) sensor on TERRA and AQUA satellites, PRI is now increasingly used also at the ecosystem scale by several groups of researchers (Rahman *et al.*, 2004; Drolet *et al.*, 2008; Garbulsky *et al.*, 2008, 2011; Goerner *et al.*, 2009; Xie *et al.*, 2009; Coops *et al.*, 2010; Hilker *et al.*, 2010). These studies show that different biomes and ecosystems with contrasting structural features, environmental constraints, and LUE variability present different parameterization of their LUE–PRI exponential relationships (Goerner *et al.*, 2010; Garbulsky *et al.*, 2011). However, there may be a common relationship for all of them (Garbulsky *et al.*, 2011) (Fig. 1b). These results continue to explore challenging and exciting new ways of soundly assessing gross CO_2 uptake of terrestrial ecosystems, which is essential for a more accurate quantification of the global C cycle and understanding of its variability. PRI, as a proxy of LUE, can be used to complement NDVI, or other proxies of the fraction of APAR, to estimate GPP (Fig. 2). In case no general relationship can be finally established, particular relationships characteristic of the different biomes could be used for each one of them. This way there would be no need of using meteorological data such as minimum temperature and vapor pressure deficit as constraints for a fixed maximum LUE, and therefore a more accurate quantification of processes such as the recent drought effects on C fixation (Filella *et al.*, 2004; Angert *et al.*, 2005; Carnicer *et al.*, 2011) could be obtained solely based in satellite data.

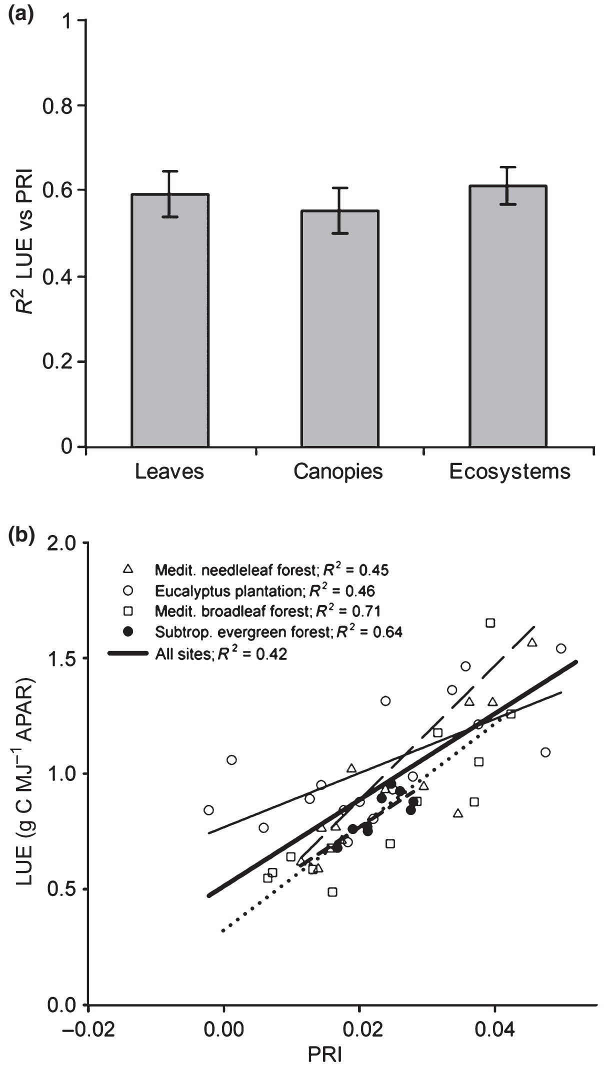

Fig. 1 (a) Coefficients of determination of the relationships (usually exponential) between light use efficiency (LUE) and photochemical reflectance index (PRI) across organizational-spatial scales reported in the available literature. Dispersion bars represent the standard errors. n = 24 studies for leaves, 22 for canopies and 7 for ecosystems. (References for the studies in Garbulsky *et al.*, 2011). (b) Example of ecosystemic seasonal relationships between LUE and PRI during 1 yr for four different forest types: Mediterranean needle leaf forest, Eucalyptus plantation, Mediterranean broadleaf forest, and subtropical evergreen forest. Gross primary productivity (GPP) data were obtained from eddy covariance data of carbon fluxes and absorbed photosynthetic active radiation (APAR) from MODIS (moderate resolution imaging spectroradiometer) data. Daily and midday LUE were well correlated. Details in Garbulsky (2010).

There are different problems that still may preclude the generalization of PRI use to ecosystem and biospheric scales and its global and operational use as an estimator of LUE

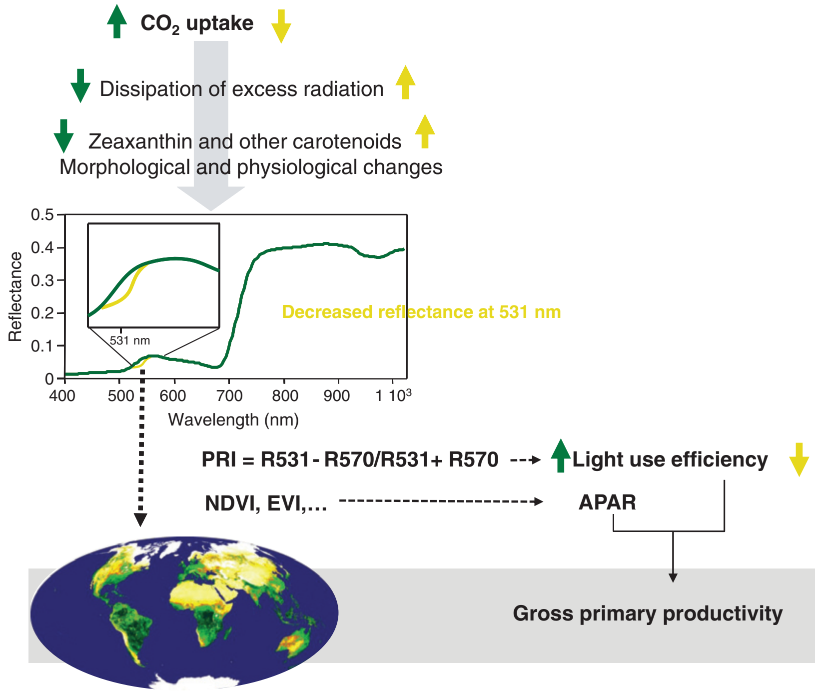

Fig. 2 Recent progress in remote sensing of gross CO$_2$ uptake in terrestrial ecosystems from leaf to regional scales by using the photochemical reflectance index (PRI) offers great prospects of significantly improving the monitoring of the CO$_2$ uptake of the terrestrial ecosystems globally and regionally. Daily global snapshots like this one where dark green shows greater productivity, pale green, medium productivity and yellow shows little or no production, now obtained with normalized difference vegetation index (NDVI)-like indices could be greatly improved with PRI complementary algorithms to more accurately monitor the terrestrial biosphere CO$_2$ uptake through the assessment of light use efficiency (LUE). Dark green colors for the arrows, reflectance spectrum and map indicate the conditions and sites with high gross primary productivity (GPP) while the yellow–pale green colors indicate the conditions and sites with low GPP. Credit for this MODIS-based image: NASA Earth Observatory. http://visibleearth.nasa.gov/.

(Grace *et al.*, 2007). In brief, these problems are related to the structural differences of the canopies, to varying 'background effects' (e.g. soil color, moisture, shadows, or presence of other nongreen landscape components) or to the different reflectance signals derived from illumination and viewing angles variations (Filella *et al.*, 2004; Sims *et al.*, 2006; Hilker *et al.*, 2010). Because of that, PRI may be more broadly applicable and portable across climatically and structurally different biome types when the differences in canopy structure are known (Hilker *et al.*, 2010). However, the emerging consistency of the relationship between PRI, LUE and ecosystem CO$_2$ uptake increasingly found in these studies (Xie *et al.*, 2009; Garbulsky *et al.*, 2011) (Fig. 1) suggests a surprising degree of 'functional convergence' of biochemical, physiological, and structural components affecting ecosystem C fluxes (Field, 1991). In other words, ecosystems possess emergent properties that may end up allowing us to effectively explore their seemingly complex photosynthetic behavior using surprisingly simple optical sampling methods such as measurement of PRI. Understanding the basis for this convergence, unearthing the 'ecophysiological rules' governing these responses, remains a primary goal of current ecophysiological research. Meanwhile, what is more important for the pragmatic empirical remote sensing of CO$_2$ uptake, PRI, especially from near-nadir satellite observations (Goerner *et al.*, 2010) and with multiangle atmospheric correction (Lyapustin & Wang, 2009; Hilker *et al.*, 2010) can become an excellent tool for continuous global monitoring of GPP (Fig. 2) which is essential to follow the C sequestration under changing climate. The launching of new image spectrometers, such as the NASA HyspIRI or the German EnMAP, will allow the calculation of PRI at even 30 m resolution offering thus great potential. The remote sensing of solar induced fluorescence in future European Space Agency (ESA) satellite missions can further complement PRI data and enhance the accuracy of the assessment of CO$_2$ uptake in terrestrial ecosystems.

Acknowledgements

Funding provided by the Spanish Government projects CGL2006-04025/BOS, CGC2010-17172 and Consolider Ingenio Montes (CSD2008-00040), and by the Catalan Government project SGR 2009-458.

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Key words: CO_2 uptake, global monitoring, gross primary productivity, light use efficiency (LUE), MODIS (moderate resolution imaging spectroradiometer), normalized difference vegetation index (NDVI), photochemical reflectance index (PRI), remote sensing.