

Can we measure terrestrial photosynthesis from space directly, using spectral reflectance and fluorescence?

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Abstract

Attempts to estimate photosynthetic rate or gross primary productivity from remotely sensed absorbed solar radiation depend on knowledge of the light use efficiency (LUE). Early models assumed LUE to be constant, but now most researchers try to adjust it for variations in temperature and moisture stress. However, more exact methods are now required. Hyperspectral remote sensing offers the possibility of sensing the changes in the xanthophyll cycle, which is closely coupled to photosynthesis. Several studies have shown that an index (the photochemical reflectance index) based on the reflectance at 531 nm is strongly correlated with the LUE over hours, days and months. A second hyperspectral approach relies on the remote detection of fluorescence, which is a directly related to the efficiency of photosynthesis. We discuss the state of the art of the two approaches. Both have been demonstrated to be effective, but we specify seven conditions required before the methods can become operational.

Keywords: carbon cycle, earth observation, photosynthesis, solar induced fluorescence, xanthophyll cycle

Received 22 May 2006; revised version received 16 August 2006 and accepted 3 January 2007

Introduction

The prospect of measuring photosynthesis from space is an exciting one. We would be able to track the responses of photosynthesis to climatological variables at several scales as climatic warming and CO₂ fertilization gather pace. Global vegetation models (Cramer *et al.*, 2001) have attempted to capture this response, but unless these models are to be informed by measurements of photosynthesis they remain hypothetical. Now it may be technically possible to achieve these measurements from sensors on board satellites. In this article we review the progress towards this goal, and suggest an operational system based on satellite observations and ground-based flux measurements.

Low-resolution spectral sensing of vegetation

Multi-spectral satellite remote sensing of the Earth's surface began in 1972 with the launch of ERTS-1, later renamed LANDSAT 1. It was possible to detect varia-

tions in the leafiness of the land cover from its reflectance measured in broad spectral bands. Rouse *et al.* (1973) proposed a simple index, known as the normalized difference vegetation index (NDVI), based on the reflectance at two wavebands in the red and near infrared parts of the solar spectrum, R_{red} and R_{nir} :

$$\text{NDVI} = \frac{R_{\text{nir}} - R_{\text{red}}}{R_{\text{nir}} + R_{\text{red}}}$$

This index is essentially a measure of 'greenness': it has been used to estimate the leaf area per unit of land area [leaf area index (LAI)] but it bears a near-linear relationship with the fraction of absorbed photosynthetically active radiation (fAPAR) (Myneni & Williams, 1994; Gamon *et al.*, 1995). Multiplying the absorbed radiation by a constant factor known as the Radiation Use Efficiency [RUE (ϵ)] provided a means to estimate the rate of photosynthesis (or biomass accumulation) per land area (Monteith, 1972; Kumar & Monteith, 1982).

This index and other such normalized ratios are known to be affected by topography, variations in viewing and illumination angles, atmospheric influences, and variations in soil brightness (Myneni &

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Williams, 1994) but NDVI has been for many years the Earth-observation workhorse to quantify vegetation amount and radiation absorbed. For example, some authors have shown how NDVI is increasing in the northern hemisphere, and they have deduced that photosynthesis is therefore increasing, probably as a result of climatic warming (Myneni *et al.*, 1997, 1998). Unfortunately, NDVI measures only the 'greenness' of the land cover and not photosynthesis itself; consequently, when ϵ has been determined from careful ground measurements of the rate of increase in biomass and absorbed radiation it is found to be rather variable. In a review of 13 cases published between 1977 and 1985, Cannell *et al.* (1987) found that ϵ varied from 0.8 to 2.1 g biomass for every MJ of solar radiation absorbed. This variation is not surprising as green leaves, in the short-term (hours or days), remain green but reduce photosynthesis when they are stressed. Only at longer time scales, when prolonged stress causes premature senescence or abscission would stress therefore show as a change in NDVI. Undoubtedly, NDVI is especially useful for picking up seasonal and interannual variations in the overall 'condition of the canopy', especially in relation to drought (Lui *et al.*, 1994; Sims *et al.*, 2006), and relating these variations to the capacity of the canopy to photosynthesize.

In fact, the magnitude of ϵ is fundamentally determined by the quantum efficiency of photosynthesis. This is known to be reduced by stress factors, such as extreme temperatures, direct sunlight, or shortage of water and nutrients. Superimposed on this there may be changes in stomatal conductance associated with drought, which will certainly reduce the rate of photosynthesis. Thus, ϵ is inherently variable. The modelling community has responded to the realization that ϵ is not constant by building into their models some degree of environmental dependency of ϵ , making it dependent, for example, on temperature and water vapour pressure deficit (Prince & Goward, 1995; Landsberg & Waring, 1997; Potter & Klooster, 1997; Veroustraete *et al.*, 2002; Running *et al.*, 2004). This pragmatic approach is all very well, and is the basis of the estimation method for daily photosynthesis of global vegetation using the MODIS (moderate resolution imaging spectroradiometer) sensor (Running *et al.*, 2004; Zhao *et al.*, 2005). This method does however have limitations and appears to work less well in arid conditions and in some agricultural sites (Turner *et al.*, 2005). Regular direct measurements of ϵ would make it possible to capture the real variation of photosynthetic efficiency and then to assimilate it into computational schemes such as those used by MODIS. This article reviews progress towards that goal.

Hyperspectral remote sensing

Sensing the xanthophyll cycle

When light exceeds the amount that can be used for photosynthesis (as happens on most days in bright sunshine) or where a stress factor depresses the rate of photosynthesis (for example when bright light and low temperatures are combined, or when drought occurs), energy is diverted from chlorophyll to the xanthophyll cycle, as part of a process known as nonphotochemical quenching (NPQ). This is a protective mechanism, preventing the reaction centres from becoming over-excited and therefore damaged. Dynamic changes in the xanthophyll cycle are accompanied by a reflectance change in a narrow region of the visible spectrum centred at 531 nm (Bilger *et al.*, 1989; Gamon *et al.*, 1992, 1993; Stylinski *et al.*, 2000, 2002; Tambussi *et al.*, 2002). This photoprotective mechanism varies diurnally and also in response to various stress factors acting over longer time scales (Krause & Weis, 1984; Krause, 1988; Demmig-Adams & Adams, 1992; Adams & Demmig-Adams, 1994; Long *et al.*, 1994; Niyogi, 1999; Havaux & Kloppstech, 2001; Hendrickson *et al.*, 2003).

An appropriate reflectance index to detect unequivocally these changes in reflectance requires two narrow wavebands, one centred on 531 nm, which is affected by the de-epoxidation of the xanthophyll pigments, and a reference waveband centred on 570 nm, which remains unaffected by the de-epoxidation reaction (Gamon *et al.*, 1992). The photochemical reflectance index (PRI) is expressed as

$$\text{PRI} = \frac{R_{531} - R_{570}}{R_{531} + R_{570}},$$

where R refers to the narrow-band (± 2 nm) reflectance centred on the stated wavelength. We may note in passing that although the form of the PRI and NDVI expressions are the same, the wavelengths required for NDVI as defined from LANDSAT-TM bands are quite different and therefore the two indices are independent of each other. We may also note that NDVI is a broad-band index and, therefore, easy to measure. PRI on the other hand requires hyperspectral sensors, which have only recently become available aboard satellites (Table 1). MODIS ocean wavebands centred on 531 and 570 nm are 10 nm broad, which is much broader than the ideal for PRI but may nevertheless be useful (Drolet *et al.*, 2005).

Changes in the PRI have been related to RUE or light use efficiency (LUE) (Foyer, 1993; Gamon *et al.*, 1997). Here, it should immediately be noted that not all authors use the same definitions of efficiency and some discussion about definitions is therefore required.

Table 1 Operational hyperspectral imaging spectrometers, their operators and spectral characteristics

Name	Full name	Manufacturer	Operator	Bands	λ range (and full width at half maximum) (nm)
AAHIS	Advanced Airborne Hyperspectral Imaging System	SETS Technology		288	432–832 (6)
AHS	Airborne Hyperspectral Scanner	Daedalus Enterprise Inc.		48	433–12700 (20–1500)
AIP	Airborne Instrument Program	Lockheed	NASA Johnson Space Center		2000–6400
AIS-1	Airborne Imaging Spectrometer	NASA, JPL	NASA, JPL	128	900–2100, 1200–2400 (9.3)
AIS-2	Airborne Imaging Spectrometer	NASA, JPL	NASA, JPL	128	800–1600, 1200–2400 (10.6)
AISA	Airborne Imaging Spectrometer for Applications	Specim Ltd.	Specim Ltd.	286	450–900 (1.56–9.36)
AMS	Airborne Modis Simulator (based on Daedalus AADS-1268)		NASA	50	530–15500
AMSS	Airborne Multispectral Scanner MK-II	Geoscan Pty Ltd.	Geoscan Pty Ltd.	46	500–12 000 (20–590)
ARES	Airborne Remote Earth Sensing	Lockheed	Lockheed	75	2000–6300 (25–70)
ASAS	Advanced Solid State Array Spectroradiometer	NASA	NASA	62	400–1060 (11.5)
ASTER	ASTER Simulator	GER Corp.	JAPEx Geoscience Institute, Tokyo	24	760–12 000 (300–700)
Simulator					
AVIRIS	Airborne Visible/Infrared Imaging Spectrometer	NASA, JPL	NASA, Ames	224	400–2450 (9.4–16)
CAESAR	CCD Airborne Experimental Scanner for Applicators in Remote Sensing	NLR		12	520–780 (10–30)
CASI	Compact Airborne Spectrographic Imager	Itres Research		288	430–870 (2.9)
CHRIS	Compact High Resolution Imaging Spectrometer	Sira Optics UK and BNSC	ESA, through Vaerhart	Up to 63	400–1050 (2.3–12)
CHRISS	Compact High Resolution Imaging Spectrograph Sensor	Science Applications Int. Corp. (SAIC)	SETS Technology, Inc.	40	430–860
CIS	Chinese Imaging Spectrometer	Shanghai Institute of Technical Physics		91	400–12 500 (10–1000)
DAIS	Digital Airborne Imaging Spectrometer	GER Corp.		211	400–12 000 (15–2000)
21115					
DAIS	Digital Airborne Imaging Spectrometer	GER Corp.		37	400–12 000 (20–4000)
3715					
DAIS	Digital Airborne Imaging Spectrometer	GER Corp.	DLR, Germany	79	400–12 000 (15–2000)
7915					
EPS-A	Environmental Probe System	GER Corp.		32	400–12 000 (10-variable)
FLI/PMI	Fluorescence Line Imager/Programmable Multispectral Imager	Moniteq Ltd.	Department of Fisheries and Oceans	228	430–805 (2.5)
FTV/FHSI	Fourier-Transform Visible Hyperspectral Imager	Kestrel Corp., FIT		256	440–1150 (5–10)
GERIS	Geophysical and Environmental Research Imaging Spectrometer	GER Corp.		63	400–2500 (16.5–120)

HRIS		ESA				
HYDICE	Hyperspectral Digital Imagery Collection Experiment	Naval Research Laboratory	ERIM	210	413–2504 (7.6–14.9)	
IISRB	Infrared Imaging Spectrometer	Bomem		1720	3500–5000 (<1.0)	
IMSS	Image Multispectral Sensing	Pacific Advanced Technology		320	2000–5000 (variable)	
IRIS	Infrared Imaging Spectroradiometer	ERIM		256	2000–15000	
ISM	Imaging Spectroscopic Mapper	DESPA		128	800–3200	
LIVTIRS 1	Livermore Imaging Fourier Transform Imaging Spectrometer	Lawrence Livermore			3000–5000 (variable)	
LIVTIRS 2	Livermore Imaging Fourier Transform Imaging Spectrometer	Lawrence Livermore			8000–12000 (variable)	
MAIS	Modular Airborne Imaging Spectrometer	Shanghai Institute of Technical Physics		71	440–11800 (20–800)	
MAS	MODIS Airborne Simulator	Daedalus Enterprise Inc.	NASA Ames and GSFC	50	529–14521 (20–800)	
MERIS	Medium Resolution Imaging Spectrometer	ESA		15	400–1050 (2.5–20)	
MIDIS	Multiband Identification and Discrimination Imaging Spectroradiometer	Surface Optics Corp., JPL		256	400–30000 (11–1000)	
MIVIS	Multispectral Infrared and Visible Imaging Spectrometer	Daedalus Enterprise Inc.	CNR, Rome	102	433–12700 (20–500)	
MODIS	Moderate Resolution Imaging Spectrometer	NASA	EOS	36	415–14240 (10–500)	
ROSIS	Reflective Optics System Imaging Spectrometer	DLR, GKSS, MBB	DLR	84/30	450–850 (4–12)	
SFSI	SWIR Full Spectrographic Imager	CCRS	CCRS	122	1200–2400 (10)	
SMIFTS	Spatially Modulated Imaging Fourier Transform Spectrometer	Hawaii Institute of Geophysics		75	1000–5200 (100–200)	
SSTI HIS (defunct)	Small Satellite Technology Initiative Hyperspectral Imager	TRW Inc.	NASA	384	400–2500 (5–6.38)	
TRWIS III	TRW Imaging Spectrometer	TRW Inc.		384	300–2500 (5–6.25)	
VIFIS	Variable Interference Filter Imaging Spectrometer	University of Dundee		60	440–890 (10–18)	
VIMS-V	Visible Infrared Mapping Spectrometer	ASI	NASA Cassini Mission	352	350–5100 (7–14)	
WIS	Wedge Imaging Spectrometer	Hughes St. Barbara Research Center		170	400–2500 (9.6–37.8)	

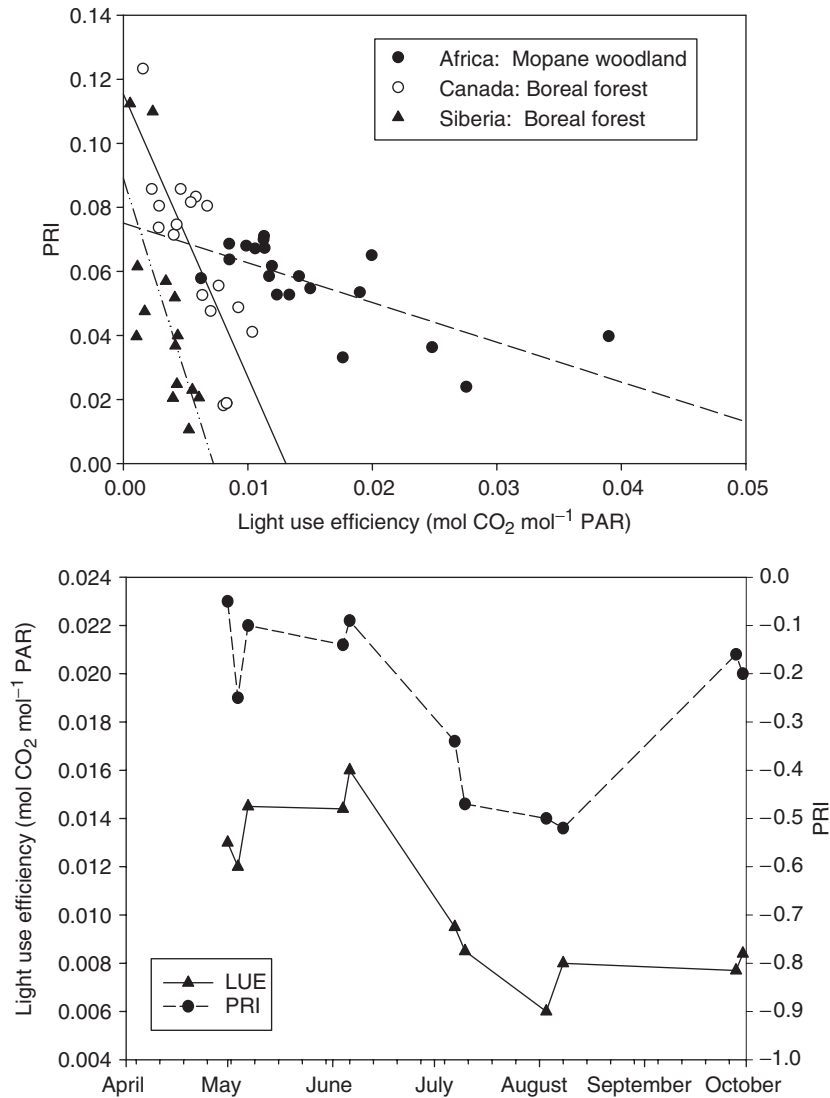


Fig. 1 (Upper panel) Relationship between photochemical reflectance index (PRI) and light use efficiency (LUE) calculated from CO₂ flux measured from eddy covariance towers for ecosystems in the boreal forests of Canada (Nichol *et al.*, 2000) and Siberia (Nichol *et al.*, 2002) and tropical woodland in Botswana (C. J. Nichol *et al.*, unpublished results). (Lower panel) the seasonal trend in moderate resolution imaging spectroradiometer (MODIS) photochemical reflectance index (PRI) and the observed light use efficiency (LUE) (mol CO₂ per mol absorbed photons) over a secondary growth deciduous broadleaf forest in Southern Indiana for the leaf-on season (Rahman *et al.*, 2004).

Strictly speaking, any 'efficiency' should be expressible as a percentage or fraction, and so the numerator and the denominator ought to have the same units (this rule is adhered to in physics and chemistry but not in biology). Thus, possible units for ϵ are mols of CO₂ captured per mol photons of light absorbed (LUE), or Joules captured in chemical bonds during photosynthesis per Joule of solar energy absorbed (RUE). Various deviations from this ideal are however used. Agronomists and foresters prefer to use biomass as the numerator without first converting biomass into energy units using the heat of combustion. Some authors use

not the energy absorbed as the denominator but the solar energy incident on the canopy. Especially confusing is the fact that solar energy is sometimes expressed as the global solar energy (i.e. the entire waveband) and at other times expressed as the solar energy in the photosynthetically active region of the waveband (usually assumed to be 400–700 nm). In photobiology, the efficiency of photosynthesis is called 'the quantum efficiency'; it usually relates to the gas exchange of leaves at low light, and is found from the initial slope of the photosynthesis–light response curve. From this brief overview, it is clear that similar

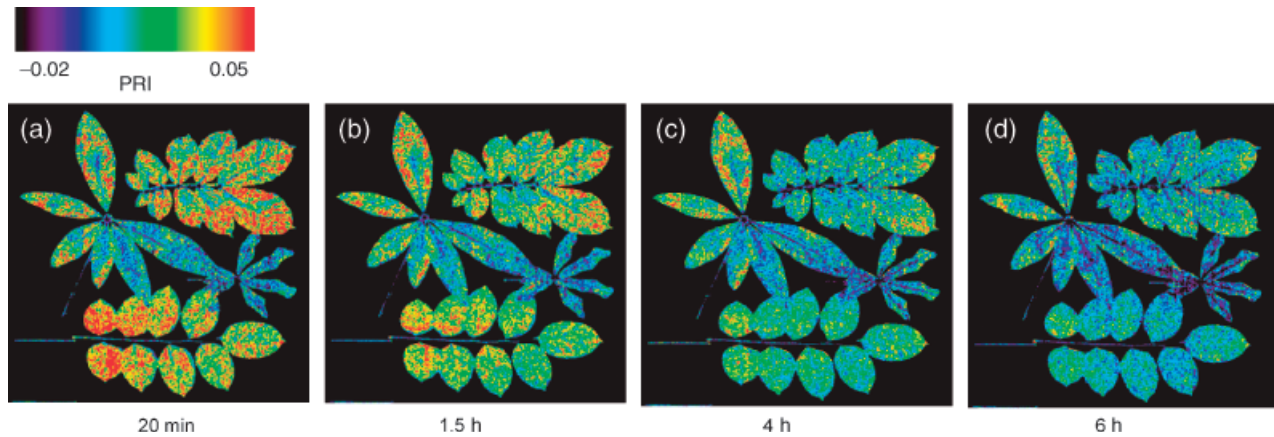


Fig. 2 Changes in photochemical reflectance index (PRI) of leaves of four tropical trees during drying. Leaf reflectance was measured after excising the leaves and allowing evaporation for 20 min, 1.5, 4, and 6 h. The species were *Pterocarpus indicus*, *Ceiba pentandra*, *Pachira aquatica* and *Inga cf. sapindoides*. From Rascher *et al.* (2006).

terms are used to describe contrasting scales and even somewhat different processes. Of paramount importance of course is that each author should state which definition they have chosen, so that interpretation is possible.

PRI has been found to be strongly correlated with ϵ at the leaf scale (Peñuelas *et al.*, 1995b, 1997; Gamon *et al.*, 1997), small canopy scale (Gamon *et al.*, 1992; Filella *et al.*, 1996; Stylinski *et al.*, 2002; Trotter *et al.*, 2002; Nichol *et al.*, 2006) and recently at the ecosystem scale (Fig. 1) (Nichol *et al.*, 2000, 2002; Rahman *et al.*, 2004). It has also been shown that PRI provides an optical measure of ϵ across species and nutrient levels (Peñuelas *et al.*, 1994; Gamon *et al.*, 1995; Moran *et al.*, 2000; Nichol *et al.*, 2000; Strachan *et al.*, 2002; Trotter *et al.*, 2002; Guo & Trotter, 2004). Visualization of PRI over the surface of leaves provides a clear indication of how spatial variations in photosynthetic efficiency may vary over time (Fig. 2). Now, there is considerable interest in using PRI at the large spatial scale (~ 10 m² to 10 km²) calculated from spectral reflectance measured on remote sensing platforms to assess ϵ and model global ecosystem dynamics (Field *et al.*, 1995; Goetz & Prince, 1999; Nichol *et al.*, 2000; Peñuelas & Inoue, 2000; Barton & North, 2001; Rahman *et al.*, 2001; Strachan *et al.*, 2002; Stylinski *et al.*, 2002).

Despite a number of studies demonstrating convincing relationships between PRI and ϵ , the coefficients of determination (r^2) for this relationship vary quite significantly, from 0.38 to 0.94 (Trotter *et al.*, 2002; Guo & Trotter, 2004; Rahman *et al.*, 2004), and there are differences between the slope of the relationship between the two variables (Fig. 1). In general, correlations at the field scale are less convincing than correlations at the leaf scale. Here, we look at factors, which may account for

real or apparent differences between the results of different studies at the field and landscape scale.

- (i) There are possibilities of interference by other pigments. PRI detection uses wavebands on either side of a chlorophyll absorption peak, at 531 nm, which could be affected by chlorophyll absorbance, and at 570 nm, which could be affected by a combination of chlorophyll and carotenoid absorbance (Peñuelas *et al.*, 1995a,b; Sims & Gamon, 2002; Stylinski *et al.*, 2002). As the radiance from the changes in the xanthophyll pigments contributes about 2% of the total reflectance, it is clearly important that the waveband is suitably narrow to minimize the possibility of such interference.
- (ii) There may be differences between spectral responses of the sensors being used to measure PRI, as there has so far been no standardization between laboratories, and there is enough variation in the wavebands of 'suitable' interference filters that have been used in the construction of sensors to introduce error. In addition, the PRI should be calculated from atmospherically corrected data (i.e. at-surface reflectance) to avoid variations due simply to differences in atmospheric composition. The work of Rahman *et al.* (2004) for example, used only top-of-atmosphere radiance data
- (iii) There are differences between studies in the viewing and illumination configurations. In particular, in some types of vegetation (savannas, scrublands) there is much visible soil and relatively little leaf, so any PRI response is small and hard to see against the bright background (Barton & North, 2001). We also note that as a normalized ratio, PRI will suffer from many of the issues associated with NDVI

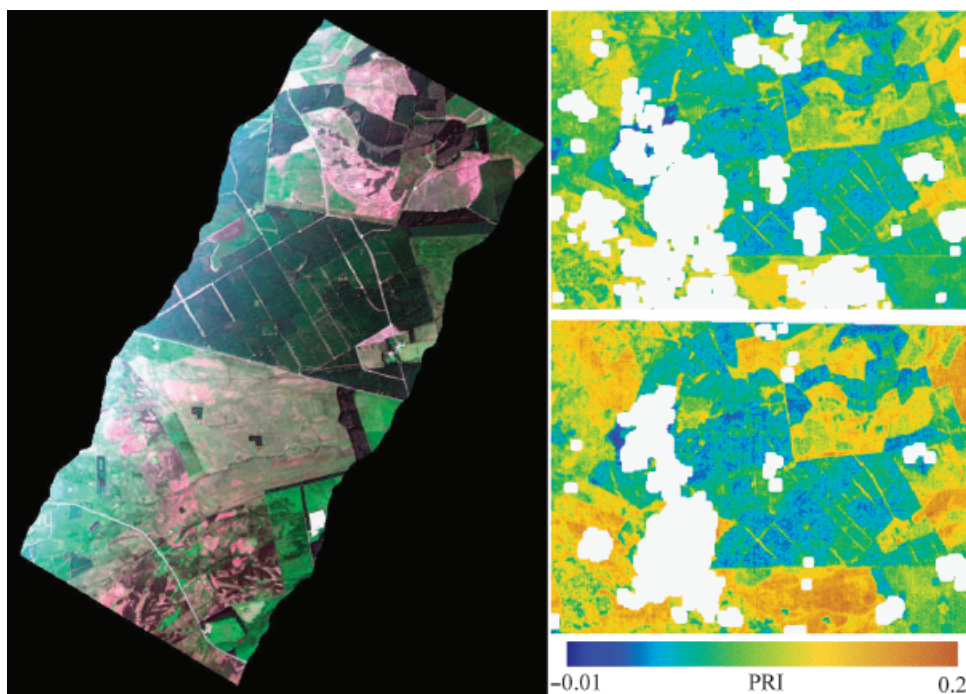


Fig. 3 Variations in photochemical reflectance index (PRI) over a forest plantation of *Picea sitchensis* at Harwood forest in northern England. The left-hand image is a radiance image obtained from an compact airborne spectrographic imager (CASI) on 13 July 2003. This is a 'true' colour composite radiance image of the 450, 552, and 670 nm wavebands. It shows clearly the layout of the forest blocks, which are in contrast to the surrounded rough moorland and agricultural land. The right hand panels show the photochemical reflectance index (PRI) images of the same site, derived from satellite data (the CHRIS-PROBA instrument on 22 May 2004). There is some cloud cover (white regions) but parts of the forest, moorland and agricultural land can be seen. The right upper image was acquired at 36° view angle and the right lower image at nadir. PRI values range from -0.01 (dark blue) to 0.2 (red) in each case. Variation can be seen in the PRI response in the dark, forested area as well as the contrast with surrounding agricultural and heathland areas. The difference in signal between the two view angles demonstrates the variation of PRI with view angle.

noted above. Rahman *et al.* (2004) suggest that PRI data would be most useful in heavily vegetated areas subjected to periodic stress.

- (iv) Although all vascular plants contain carotenoids, species may vary considerably in the configuration of their photoprotective mechanism and, therefore, their PRI behaviours. We already know that some species do not follow the 'conventional' pattern (Rascher *et al.*, 2006) and it would be surprising indeed if evolution had produced uniformity, considering the range of light environments to which different species are adapted.
- (v) There are marked differences in the structure of the canopies under investigation. Canopy structure is an important factor in determining the overall reflectance as it encapsulates the transition from individual scattering elements with known (hemispherical) reflectance and transmittance properties to a far more complex arrangement where multiple interactions between the scatterers and the lower boundary (soil and understory vegetation) combine to form the resulting (measured) signal at the top

of the canopy. The scatterers themselves (leaves, stems, branches) vary in developmental stage and orientation, both of which have the potential to influence the PRI (Barton & North, 2001; Disney *et al.*, 2005). Thus, when variations in PRI are seen from space, it is not immediately clear how far the apparent differences may be a consequence of variations in viewing angle and canopy structure (Fig. 3).

Until all five of these problems are tackled we cannot hope to obtain a universal PRI- ϵ relationship among ecosystems.

Sensing solar induced fluorescence

During photosynthesis, part of the energy captured by chlorophyll is dissipated as fluorescence (defined as the re-emission of light energy at a longer wavelength than the excitation energy) within the waveband 650–800 nm with peaks at 690 and 740 nm (Fig. 4). Chlorophyll fluorescence, combined with NPQ is an expression of

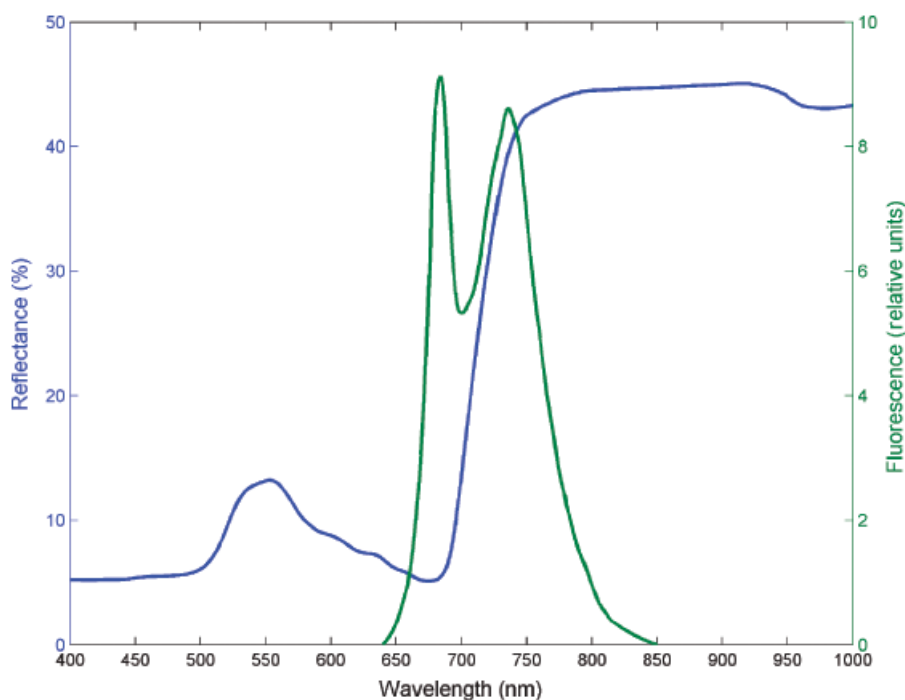


Fig. 4 Characteristic fluorescence emission spectrum with double-peaks at ~ 685 nm and ~ 740 nm. Superimposed is a characteristic reflectance spectrum. These spectra were generated with the FluorMOD software, a leaf and canopy reflectance model including fluorescence, developed by Zarco-Tejada *et al.* (2004) (<http://www.ias.csic.es/fluormod/>).

the balance between light harvesting (absorption), and light utilization in the photosynthetic process (Krause & Weis, 1991; Walker, 1992; Maxwell & Johnson, 2000). The 690 nm fluorescence signal from leaves and crops is therefore widely used by physiologists and agronomists as a field-based or laboratory-based diagnostic tool for detection of stress. In principle fluorescence is very closely related to the efficiency of light utilization as it represents 'wasted' energy. It is usual to make inferences from the changes in fluorescence over several minutes following illumination (see Bolhar-Nordenkamp *et al.*, 1989). However, in the more natural state of continuous illumination by sunlight, photosynthetic organisms fluoresce continuously thus adding a weak signal to the spectral reflectance (the so-called solar-induced steady-state fluorescence, F_s , or 'passive fluorescence'). The fluorescence signal is less than 3% of the reflected energy (and $<2\%$ in most cases), but in principle it can be separated from the reflectance signal. For example, if a suitable canopy model is available, known pigment concentrations can be incorporated into the model to produce a hypothetical reflectance signal which can then be compared with the measured reflectance signal to look for fluorescence (Zarco-Tejada *et al.*, 2000a, b). While recent research has shown that F_s can be detected using passive techniques, and related to CO_2 assimilation (e.g. Freedman *et al.*, 2002; Moya *et al.*,

2004; Louis *et al.*, 2005), much work remains to be done understanding the F_s signal before it can be unambiguously related to photosynthetic processes.

It may be possible to detect and measure plant fluorescence by examination of the faint radiance in the well known dark lines (Fraunhofer lines) observed within the solar spectrum, caused by absorption in the sun's outer atmosphere. There are several hundred of these, produced by absorption of energy by the cooler gases near the solar surface. Almost all of the lines are very narrow (0.04–0.4 nm), but only one of them (656.3 nm) is within the region of the spectrum where most of the chlorophyll fluorescence occurs (650–800 nm). There are other dark lines in the solar radiation received at the earth's surface, produced by the absorption of energy by oxygen in the terrestrial atmosphere, one being at 760 nm. Using an instrument mounted above the canopy, Moya *et al.* (2004) demonstrated a good relationship between 'passive' fluorescence measured at 760 nm, and the fluorescence parameters measured on leaves using traditional physiological methods (pulse-modulated chlorophyll fluorescence with a PAM2000 portable fluorimeter). Of course, to operate such a sensor from satellite would require additional work to correct the signal for the absorption of the outgoing radiation by oxygen. Preliminary airborne and spaceborne experiments (e.g. ESA's 2003 and 2005

AIRFLEX campaigns) suggest that a fluorescence signal can be detected but very stringent atmospheric correction will be required to use it effectively, particularly concerning characterization of aerosol optical thickness and terrain altitude (Davidson *et al.*, 2003; Guanter, 2007). There are some indications that the signal can be picked up by airborne sensors (Borstad *et al.*, 1985; Maier, 2002; Zarco-Tejada *et al.*, 2000b). This work suggests that there is potential for using remote sensing measurements of radiance as a proxy for direct estimation of F_s . The advantage is that current orbiting hyperspectral sensors (e.g. Hyperion, MERIS) might be used (Guanter, 2007).

It is timely to note that at time of writing, the European Space Agency (ESA) has placed an initiative (led by Marc-Ph Stoll) called FLEX (a scientifically driven space mission to provide demonstration/validation of the instrumentation and technique for the measurement of natural vegetation fluorescence in the Fraunhofer lines), to go forward to a 'feasibility study' under pre Phase A development. If successful, this will present the first ESA satellite designed for the sensing of solar induced fluorescence from space.

Initial investigations of the 685 nm fluorescence signal from phytoplankton using the MODIS and MERIS signals have been promising (Gower & Borstad, 2004; Gower *et al.*, 2004). The method, typically used for detecting phytoplankton fluorescence, is to measure fluorescence line height (FLH). FLH is somewhat analogous to PRI in that it is a measure of the fluorescence signal over a narrow waveband in the fluorescent region relative to a baseline drawn through two other reference bands. For the MERIS ocean fluorescence product for example the target band wavelength is 680.5 nm while the reference bands are 664 and 708 nm (Gower *et al.*, 1999). This concept leads us directly to the prospect of using existing satellite data for fluorescence measurements over terrestrial vegetation at a large scale. It should be borne in mind, however, that it is potentially far more difficult to perform highly accurate atmospheric correction over land than water, given the higher brightness of the land, its higher spatial heterogeneity and aerosol content. The next section reviews the available instrumentation for hyperspectral remote sensing.

Instrumentation for hyperspectral remote sensing

Sensing PRI requires an instrument with a spectral resolution of the order of 3–10 nm, while detection of fluorescence through radiance in the Fraunhofer lines requires a resolution of <1 nm. Table 1 indicates the number of currently operational hyperspectral instruments, airborne and spaceborne, in the public and

private domain. There are already a large number of these in orbit on military platforms such as the Warfighter and MightySat-2. It may be possible to use MODIS products over the land surface, although application of such data would require custom atmospheric corrections to be applied which may be quite challenging.

Nevertheless, three recent studies have related a satellite PRI signal to flux tower estimates of LUE. Middleton *et al.* (2004) and Rahman *et al.* (2004) used single orbit acquisitions from MODIS to estimate PRI for an Aspen stand in boreal Canada and a secondary deciduous forest in the United States. Near-nadir and backscatter directional observations (which minimize possible interference from shadow) over a flux site were used to calculate PRI and compared with LUE estimates from a flux tower. The relationship between MODIS-PRI and LUE for the Canadian site (both with and without atmospheric correction) was $r^2 = 0.75$ and 0.76 , respectively and for the deciduous site was stronger at $r^2 = 0.88$. These are particularly encouraging results both producing a linear relationship between MODIS-PRI and LUE in contrasting vegetation types. Drolet *et al.* (2005) followed this up with a thorough study utilizing MODIS scenes over an aspen site in Canada. In their study they highlighted the variability in the PRI and LUE during the MODIS overpasses and strong statistical correlations between PRI and LUE calculated from a micrometeorological flux tower. This study is the most comprehensive application of PRI to landscape scale fluxes (at time of writing) yet there are still a plethora of unanswered questions concerning the use of satellite data to this end. Future work should undoubtedly be focused in this direction as the possibility of describing 75% or more of the ecosystem variability in LUE as measured by flux towers is a very important development.

Future efforts will undoubtedly be focused on extending these findings in the temporal domain while taking into consideration other factors like view-angle, observation geometries, atmospheric correction and the extension to other sites. Satellite-based hyperspectral sensors will undoubtedly allow more in-depth investigations of LUE using such physiologically based indices as such a sensor could potentially discriminate between changes in xanthophylls, carotenoids, chlorophyll, and canopy structure. Canopy models are required to achieve the upscaling from leaf to canopy properties. Recent work has shown that the conventional radiative transfer approach to this problem can be modified through the consideration of idealized, energy conservation cases using totally absorbing or reflecting lower boundary layer (black soil/white soil cases) (Panferov *et al.*, 2001; Knyazikhin *et al.*, 2005). These modifications

allow the derivation of spectrally invariant canopy structural terms expressing the impact of canopy structure on canopy reflectance, being parametrized by the canopy 'recollision probability', a fundamental term describing the probability with which a photon will interact again with the vegetation after an initial scattering event (Smolander & Stenberg, 2005; Huang *et al.*, 2007). This permits separation of the measured signal into those components influenced by structural properties alone and those influenced by radiometric properties alone and may prove a fruitful route for practical models investigating leaf properties on activities.

Earth observation of photosynthesis and other terms of the carbon cycle

Most models of canopy photosynthesis or gross primary productivity (GPP) estimate photosynthetic rate using the biochemical model first proposed by Farquhar *et al.* (1980), coupled with one of several methods to compute stomatal conductance (Buckley, 2005). In many circumstances such models work very well, and after appropriate parameterization may be fitted to flux data obtained from a variety of biomes (Cramer *et al.*, 2001). There are, however, other instances where they fit less well (mostly unpublished, but see Saleska *et al.*, 2003), and perhaps there are more of these cases that remain unpublished. There is a trend towards the incorporation of carbon cycle models into global circulation models (GCMs), and a clear need to develop a modelling approach which can be linked to remote sensing, to achieve a system of data assimilation whereby models can be dynamically adjusted when their behaviour deviates from reality. All models calculate photosynthetic rate or GPP, and, as we have seen above, there is some prospect of directly measuring photosynthesis from detection of the light use efficiency. There are, however, other components of the carbon cycle, which do not reveal themselves as a spectral signal.

The determination of GPP is merely the first step towards closure of the carbon cycle. The overall flux at the ecosystem scale has familiar constituents, the photosynthetic rate, P ; respiration rate by green plants, R_p ; and respiration rates by heterotrophs, R_h :

$$\text{GPP} = P$$

$$\text{NPP} = P - R_p$$

$$\text{NEP} = P - R_p - R_h$$

$$\text{NBP} = P - R_p - R_h - D$$

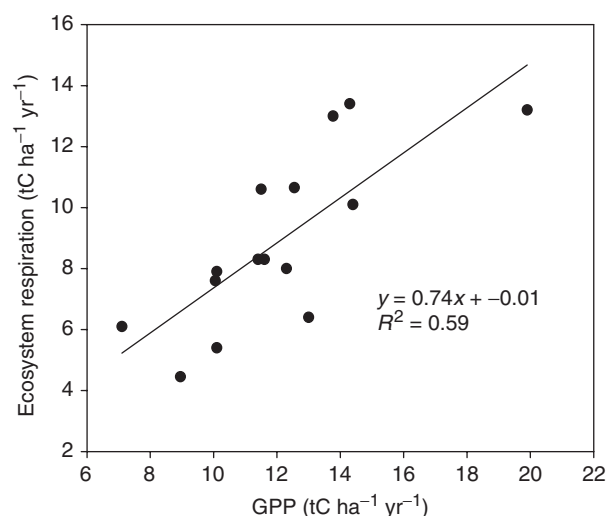


Fig. 5 The relationship between gross primary productivity (GPP) and total ecosystem respiration for middle-aged temperate forests in Europe. Plotted from observed fluxes given in Table 1 of Valentini *et al.* (2000).

NBP is the net biome productivity, appropriate at larger spatial and temporal scales (10–several 10^6 km² and decades or centuries), and includes D the disturbance flux which relates to the rate of change in land use and can be estimated from broad band remote sensing.

To obtain net primary productivity (NPP) by subtracting autotrophic respiration from GPP there are theoretical and empirical relationships described by many authors (Roy *et al.*, 2001). The relationship between GPP and NPP varies somewhat according to ecosystem, and there is still a degree of uncertainty because NPP is generally difficult-to-measure by either gravimetric or gas flux methods. In studies of forest ecosystems in United States and Australasia it was found that NPP/GPP was more or less constant at 0.47 (Waring *et al.*, 1998). Heterotrophic respiration is however complex, as the process of decomposition is dependent on a myriad of heterotrophic organisms, and the rate of CO₂ evolution is a function of temperature, moisture and the supply of organic matter. While simple representations of soil respiration as a function of temperature work quite well in many cases (Lloyd & Taylor, 1994; Falloon & Smith, 2002), they usually fail to accommodate the effect of extremes of soil moisture and the supply of organic matter as substrate. When viewed across sites, the oft-quoted relationship between ecosystem and temperature tends to break down, probably because the process of respiration depends ultimately on the supply of assimilates from photosynthesis (Davidson *et al.*, 2006). It is not surprising therefore to find that analyses of flux data suggest a linear relationship between GPP and the total ecosystem respiration,

with almost three-quarters of the production 'lost' as respiration (Fig. 5). Although it is possible to measure atmospheric CO₂ concentration from space (as in the planned Orbiting Carbon Observatory, OCO), it is more likely that in the foreseeable future, our models of productivity will be informed by these empirical relationships based on flux measurements at ground stations.

What remains to be done

In operation, the data acquired by hyperspectral sensing should be coupled to an ecosystem model, in such a way that the remotely sensed data can be used to train the model, especially to take into account the changing phenology and climatic conditions. The global network of flux towers (FLUXNET) enables comparison between real-world fluxes and modelled fluxes, and further model training at larger spatial scales will be possible from atmospheric measurements from tall towers and aircraft. To develop this system, so that remote sensing and flux data are integrated into an observational system (Running *et al.*, 1999), the following is required:

- (i) Standardization of the spectral definition and measurement protocol of the PRI, so that data are collected by different research groups are comparable.
- (ii) Installation of PRI sensors on flux towers to continuously monitor the relationship between the PRI and carbon flux. This started as a result of an initiative by John Gamon (<http://specnet.info>), called SpecNet, which has been designed to address scale-appropriate optical sampling in conjunction with flux measurements with a view to better understanding physiologically based indices as one of its objectives.
- (iii) Refine atmospheric corrections such that current hyperspectral satellite-borne sensors are capable of sensing PRI and NDVI without interference from aerosols. The temporal and spatial variability of aerosols over the land surface is large, it could be that the precision of a correction is what limits the accuracy of the final measurement of photosynthesis.
- (iv) Parameterization of vegetation structure so that leaf scale properties may be related to the properties of the ecosystem as a whole, taking into account the structure of the canopy.
- (v) Selection of one or more appropriate global ecosystem models (Cramer *et al.*, 2001; Running *et al.*, 2004) which are capable of simulation of photosynthetic and respiratory fluxes on an hourly basis.
- (vi) Development of data transmission to enable communication of remotely sensed spectral radiance data from satellites, and flux and meteorological data from a selection of flux towers.
- (vii) Development of appropriate data assimilation methodology, so that the model is capable of learning from the observations (Williams *et al.*, 2005).

Acknowledgements

The authors wish to acknowledge funding from the Natural Environment Research Council (NERC) through the Centre of Terrestrial Carbon Dynamics and the European Union programme Carboeurope-IP. We thank an anonymous reviewer for many useful comments made on the original manuscript.

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