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Review

The photochemical reflectance index (PRI) and the remote sensing of leaf, canopy and ecosystem radiation use efficiencies

A review and meta-analysis

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ABSTRACT

Traditional remote sensing techniques allow the assessment of green plant biomass, and therefore plant photosynthetic capacity. However, detecting how much of this capacity is actually realized is a more challenging goal. Is it possible to remotely assess actual carbon fluxes? Can this be done at leaf, canopy and ecosystem scales and at different temporal scales? Different approaches can be used to answer these questions. Among them, the Photochemical Reflectance Index (PRI) derived from narrow-band spectroradiometers is a spectral index increasingly being used as an indicator of photosynthetic efficiency. We examined and synthesized the scientific literature on the relationships between PRI and several ecophysiological variables across a range of plant functional types and ecosystems at the leaf, canopy and ecosystem levels and at the daily and seasonal time scales. Our analysis shows that although the strength of these relationships varied across vegetation types, levels of organization and temporal scales, in most reviewed articles PRI was a good predictor of photosynthetic efficiency or related variables with performances at least as good as the widely used NDVI as indicator of green biomass. There are possible confounding factors related to the intensity of the physiological processes linked to the PRI signals, to the structure of the canopies and to the illumination and viewing angles that warrant further studies, and it is expected that the utility of PRI will vary with the ecosystem in question due to contrasting environmental constraints, evolutionary strategies, and radiation use efficiency (RUE; the ratio between carbon uptake and light absorbed by vegetation) variability. Clearly, more research comparing ecosystem responses is warranted. Additionally, like any 2-band index that is affected by multiple factors, the interpretation of PRI can be readily confounded by multiple environmental variables, and further work is needed to understand and constrain these effects. Despite these limitations, this review shows an emerging consistency of the RUE–PRI relationship that suggests a surprising degree of functional convergence of biochemical, physiological and structural components affecting leaf, canopy and ecosystem carbon uptake efficiencies. PRI accounted for 42%, 59% and 62% of the variability of RUE at the leaf, canopy and ecosystem respective levels in unique exponential relationships for all the vegetation types studied. It seems thus that by complementing the estimations of the fraction of photosynthetically active radiation intercepted by the vegetation (FPAR), estimated with NDVI-like indices, PRI enables improved assessment of carbon fluxes in leaves, canopies and many of the ecosystems of the world from ground, airborne and satellite sensors.

Contents

Abbreviations: MODIS, MODerate resolution Imaging Spectroradiometer; RUE, radiation use efficiency; GPP, gross primary productivity; FPAR, fraction of the photosynthetic active radiation absorbed by the vegetation; APAR, absorbed photosynthetically active radiation by green vegetation; NDVI, normalized difference vegetation index; EVI, enhanced vegetation index; PRI, photochemical reflectance index; FWHM, full width of half maximum.

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1. Introduction

A key challenge in arriving at a sustainable world is to better understand biosphere–atmosphere carbon fluxes, which are extremely dynamic in time and space (Le Quere et al., 2009). Several questions remain open. What factors control photosynthetic and respiratory fluxes by terrestrial landscapes? How are these controls and source/sink patterns distributed in time and space? What is the capacity for terrestrial ecosystems to continue functioning as carbon sinks in the face of ongoing disturbance and climate change? Current tools for exploring these questions include eddy covariance and remote sensing. Eddy covariance is currently the only direct way to assess carbon flux of whole ecosystems with high temporal resolution. However, eddy covariance towers can effectively measure a single "point" over flat and uniform terrain, usually on the order of a few hundred squared meters (Baldocchi, 2008). Remote sensing has the ability to extend our knowledge of carbon flux in space. Combining remote sensing with eddy covariance in a modeling framework provides a powerful approach for addressing the carbon dynamics of terrestrial ecosystems.

The fraction of photosynthetically active radiation absorbed by the canopy (FPAR) can be estimated from remotely sensed vegetation indices. Vegetation indices, such us the Normalized Difference Vegetation Index (NDVI) or the Enhanced Vegetation Index (EVI) are normalized differences between the reflectance in the near infrared and the red regions of the spectrum, which are very often determined from satellite, or aircraft imagery. The FPAR provide a measure of potential and not of actual photosynthesis because of varying synchrony between green canopy development and photosynthetic fluxes across vegetation types (Field et al., 1995; Gamon et al., 1995; Myneni et al., 1995). They even can be empirical estimators of photosynthesis or primary productivity for certain ecosystems because they reflect both recent carbon gain and potential future carbon gain in the absence of constraints on photosynthesis (Field, 1991). However, for many ecosystems, considerable uncertainty still remains about how much of this capacity is realized in practice because the radiation use efficiency (RUE) varies significantly between plants, environmental conditions, and ecosystems due to varying environmental constraints (Field et al., 1994; Garbulsky et al., 2010). For example, in many evergreen-dominated ecosystems such as shrublands, Mediterranean or coniferous forests, seasonal or periodic stress events may shut down carbon uptake to near zero (Asensio et al., 2007; Ogaya and Peñuelas, 2003) through a process of photosynthetic downregulation, even though in the short term the vegetation continues to absorb light that might otherwise be used for photosynthesis. Consequently, NDVI can be a poor indicator of temporal variation in CO_2 fluxes, particularly for evergreen species subjected to periodic downregulation (Gamon et al., 1995; Running and Nemani, 1988). However, it is still a good estimator of the spatial variability of carbon uptake (Garbulsky and Paruelo, 2004).

The widely used radiation use efficiency model (Monteith, 1977) stated that gross (GPP) or net primary productivity (NPP) of a vegetation stand can be derived from the absorbed photosynthetically active radiation by green vegetation during the period of study (APARdt), the product of FPAR and photosynthetic active radiation (PAR), and from the efficiency (RUE) with which this absorbed radiation is converted into biomass:

$$\mathrm{GPP} = \int \mathrm{RUE} \times \mathrm{APARdt}$$

In various forms, these simple relationships have been the basis for many evaluations of photosynthesis and primary production from the canopy to the global scales (Field et al., 1995; Running et al., 2004). Many models have assumed a constant efficiency (Myneni et al., 1995) or derived this term from literature values by biome (Ruimy et al., 1994). Another approach is to downregulate the maximum efficiency by biome using climatic variables, like vapour pressure deficit (VPD) and temperature, as surrogates for photosynthetic stresses (Running et al., 2004). Because VPD and temperature alone are not always good surrogates of reduced efficiency, meteorologically based methods may not always explain efficiency variation. Many studies show that the efficiency greatly varies in time and space (Gamon et al., 1995; Garbulsky et al., 2010; Runyon et al., 1994) due to periodic environmental and physiological limitations. Factors contributing to this variability, include contrasting functional types (Gamon et al., 1997; Huemmrich et al., 2010), drought and temperature extremes (Landsberg and Waring, 1997; Sims et al., 2006a) and nutrient levels (Gamon et al., 1997; Ollinger et al., 2008).

In recent years, this RUE term of the model has been found to be accessible through spectral reflectance, thus opening the possibility of using remote sensing techniques to detect temporal and spatial variations in photosynthetic radiation use efficiency and therefore to improve the temporal and spatial characterization of carbon uptake by vegetation. Different approaches have arisen recently to remotely estimate RUE from a wide variety of wavelengths and sensor types. Among those approaches, the use of land surface temperature derived from thermal wavelengths was successfully tested for a set of 11 different sites distributed only in North America to estimate 16 day GPP, but it would be inadequate for the estimation of GPP in shorter time steps due to the inability to track short-term (e.g. diurnal) physiological variability (Sims et al., 2008). This study included many mesic sites, but did not include many arid or semiarid ecosystems where downregulation due to drought and temperature extremes would likely occur. Consequently, the ability of this approach to capture the full range of variability across biomes, particularly due to short-term stress, remains unclear. An alternate approach links the sun induced chlorophyll fluorescence, derived from an oxygen absorption band located at 760 nm, to the diurnal changes in RUE, but tests of this method have been limited (Damm et al., 2010). Consequently, the full capabilities of these promising approaches are not yet entirely clear.

The detection of the spatial and temporal variations in RUE could also be assessed through the remote sensing of plant pigments. This is a key tool to diagnose a range of plant physiological properties and processes (Blackburn, 2007; Peñuelas and Filella, 1998). In particular, different studies were conducted during the 1990s at the leaf and close canopy levels using close-range remote sensing from the ground or from low platforms to assess this efficiency parameter RUE based on concurrent xanthophyll pigment changes (Filella et al., 1996; Gamon et al., 1990; Gamon et al., 1992; Gamon et al., 1997; Gamon and Surfus, 1999; Peñuelas et al., 1995; Peñuelas et al., 1997a; Peñuelas et al., 1998; Peñuelas et al., 1994). The foundation of this remote sensing approach to estimate the RUE is the de-epoxidation state of the xanthophyll cycle which is linked to heat dissipation (Demmig-Adams and Adams, 1996). This is a decay process of excited chlorophyll that competes with and is complementary 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; Gamon et al., 1992; Peñuelas et al., 1995), a Photochemical Reflectance Index (PRI, typically calculated as $[R_{531}-R_{570}]/[R_{531}+R_{570}]$, where R indicates reflectance and numbers indicate wavelength nanometers at the center of the bands), was developed as a method to remotely assess photosynthetic efficiency using narrow-band reflectance (Gamon et al., 1992; Peñuelas et al., 1995). The mechanistic basis for these wavelength selections have been fully explored at the leaf scale (Gamon et al., 1993b), but are more poorly supported at canopy and larger scales, where a variety of alternate wavebands have been used, often based on statistical correlations (Gamon et al., 1992; Inoue et al., 2008) or determined by instrument limitations (Garbulsky et al., 2008b). The lack of a clear consensus in the literature on the "best" PRI wavelengths, has hindered cross-study comparisons. Consequently, it is not entirely clear if the best wavelengths for measuring this feature at the leaf scale (531 and 570 nm) are necessarily the best wavelengths at progressively larger scales, where multiple scattering and other confounding effects may alter the spectral response of the xanthophyll cycle feature, much in the way that pigment absorption peaks can vary depending upon their chemical and scattering medium. More work, therefore, may be needed to determine the ideal PRI algorithm for airborne or spaceborne platforms, and these studies have been hampered by the limited availability and high costs of suitable airborne and spaceborne instruments.

Since PRI measures the relative reflectance on either side of the green reflectance "hump" (550 nm), it also compares the reflectance in the blue (chlorophyll and carotenoids absorption) region of the spectrum with the reflectance in the red (chlorophyll absorption only) region. Consequently, it can serve as an index of relative chlorophyll:carotenoid levels, often referred to as bulk pigment ratios or "pool sizes". Over longer time scales (weeks–months), changes in bulk pigment content and ratios due to leaf 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., 1997a; Sims and Gamon, 2002; Stylinski et al., 2002). Thus, PRI is also often related to chlorophyll/carotenoid ratios in leaves across a large number of species, ages and conditions (Filella et al., 2009; Stylinski et al., 2002). Therefore, to the extent that photosynthetic activity correlates with changing chlorophyll/carotenoid ratios in response to stress, ontogeny or senescence, PRI may provide an effective measure of relative photosynthetic rates. Together, these responses to de-epoxidation state of the xanthophyll cycle and to chlorophyll/carotenoid ratios ensure that PRI scales with photosynthetic efficiency across a wide range of conditions, species and functional types (Filella et al., 1996; Gamon et al., 1992; Gamon and Qiu, 1999; Peñuelas et al., 1995; Stylinski et al., 2002).

Nowadays, the PRI is increasingly being used as an index of photosynthetic performance in general and of RUE in particular in natural and seminatural vegetation (e.g. Asner et al., 2004; Mänd et al., 2010; Middleton et al., 2009; Peñuelas and Llusia, 2002) or in crops (e.g. Strachan et al., 2002; Zhou and Wang, 2003). The relationships between PRI and different ecophysiological related variables have been tested over a wide range of species, plant functional types, temporal steps and environmental conditions. However, different problems that preclude its generalization to ecosystem scales and its global and operational use as an estimator of RUE have recently been described (Barton and North, 2001; Grace et al., 2007). In brief, these problems are related to the interference to the PRI signal produced by other plant pigments not related to photosynthetic efficiency, to the structural differences of the canopies, to varying "background effects" (e.g. soil color, moisture, or shadows) to the different PRI formulations or signals derived from a variety of sensors and to illumination and viewing angles variations. This may help explain why different ecosystems or conditions can appear to have slightly different RUE–PRI responses.

In this study we reviewed the literature reporting the use of the PRI to assess physiological variables related to photosynthetic efficiency such as epoxidation state of xanthophylls (EPS), non photochemical quenching (NPQ), actual photochemical fluorescence yield, RUE derived from gas exchange, and net photosynthesis. Our aim was to analyse the use of PRI as an indicator of RUE at the leaf, stand and ecosystem scales for different vegetation types and time scales, to identify knowledge gaps and to present perspectives for future research. Our final additional aim was to evaluate and construct a general calibration of the relationship of RUE with PRI at the leaf, canopy and ecosystem levels.

2. Methods

We gathered the published articles that reported relationships between remote sensed PRI and any kind of plant physiological variables. This primarily included Science Citation Index articles reporting results at different spatial and temporal scales and from a wide range of plant species or vegetation types. This broad spectrum of studies necessarily included different sensor types, from hand held spectroradiometers to satellite sensors. For each article we registered the main features of the study and the coefficient of determination (R^2) as an indicator of the strength of each presented relationship. For those studies that presented data for PRI and physiological variables but did not present the statistical results of the relationship, we extracted the raw data from the plots, and calculated the statistical results of the relationships ourselves. We analyzed and drew the coefficients of determination of all the correlations using boxplots for each vegetation types (herbaceous, broadleaf, conifers, etc.), time scale (daily or seasonal, i.e. changes within seasons and across seasons), and organization level (leaf, canopy — from plant to stand — or ecosystem). In this review, the term "canopy" refers to either a single plant or a monospecific stand, whereas the term "ecosystem" refers to a mixed-species stand. We tested the differences in R^2 between vegetation types using a t test when there were enough cases studied per vegetation type.

Table 1

List of studies found in the literature that linked PRI with ecophysiological variables. Specrad = spectroradiometer. Acronyms for the ecophysiological variables are: RUE = radiation use efficiency; EPS = epoxidation state of the xantophylls; DEPS = de-epoxidation state of the xanthophylls; Fv/Fm = maximum photochemical efficiency of PSII; ΔF/Fm′ = effective quantum yield or actual photochemical efficiency or photochemical efficiency of Photosystem II (ΦPSII); Amax = maximum photosynthesis rate; Fs = steady state value of fluorescence; Jmax = electron transport under saturating light; NPQ = non photochemical quenching; and Chl/Car = ratio chlorophyll content/carotenoids content.

Article order by publication date	Year	Reference	Scale	Variance factor	Species/vegetation type	Vegetation type	Sensor	Figure #	Ecophysiological variables
3	1995	(Peñuelas et al., 1995)	Leaves	Hours	*Hedera canariensis*, *Phaseolus vulgaris*, *Rhus ovata*/*R. integrifolia*, *Heteromeles arbutifolia*, Succulents (*Agave americana*, *Opuntia ficus-indica* and *Cereus hexagonus*)	Broadleaf	Specrad	1d–4–10 1e	RUE ΔF/Fm′
31	2004	(Evain et al., 2004)	Leaves	Hours	*Vitis vinifera*	Broadleaf	Specrad	1a 1e	NPQ ΔF/Fm′
45	2006	(Weng et al., 2006b)	Leaves	Hours	Mango	Broadleaf	Specrad	1a 1e	NPQ Fv′/Fm′
52	2007	(Rascher et al., 2007)	Leaves	Hours	*Pterocarpus indicus*, *Ceiba pentandra*, *Pachira aquatica*, *Inga sapindoides*	Broadleaf	Specrad	1a 1e	NPQ ΔF/Fm′
64	2008	(Meroni et al., 2008a)	Leaves	Hours	*Populus deltoides* (ozone treatments)	Broadleaf	Specrad	1d–4–10	RUE
41	2006	(Nakaji et al., 2006)	Leaves	Hours	Japanese larch (*Larix kaempferi* Sarg.)	Conifers	Camera	2b 1d–4–10	Chl Car/Chl RUE
9	1999	(Methy et al., 1999)	Leaves	Hours	Alfalfa	Herbaceous/crop	Specrad	1e	ΔF/Fm′
10	1999	(Gamon and Surfus 1999)	Leaves	Hours	Sunflower	Herbaceous/crop	Specrad	1c	EPS (ΔPRI)
27	2004	(Guo and Trotter 2004)	Leaves	Hours/dif species	*Lycopersicon esculentum*, *Populus deltoides* x *P. Nigra*, Evergreen perennials (*Coprosma robusta*, *Pseudopanax arboreus*) + 3 evergreen perennials	Mixture	Specrad	1a 1b 1d–3c–4–10 1e–3b 1f	NPQ Car/Chl RUE ΔF/Fm′ Net CO_2 uptake
2	1994	(Peñuelas et al., 1994)	Leaves	Hours/seasonal	Sunflower	Herbaceous/crop	Specrad	1c 1d–3f–10 1f–3f	EPS RUE Net CO_2 uptake
5	1997	(Peñuelas et al., 1997b)	Leaves	Seasonal	*Quercus ilex*/*Phillyrea latifolia*	Broadleaf	Specrad	2a 2d–10 2e	NPQ RUE ΔF/Fm′
29	2004	(Peñuelas et al., 2004)	Leaves	Seasonal	*Phillyrea angustifolia*	Broadleaf	Specrad	2f	Net CO_2 uptake
63	2008	(Letts et al., 2008)	Leaves	Seasonal	*Populus angustifolia*	Broadleaf	Specrad	2e	ΔF/Fm′
74	2009	(Panigada et al., 2009)	Leaves	Seasonal	*Fagus sylvatica*	Broadleaf	Specrad	2a 2e	NPQ ΔF/Fm′
47	2006	(Weng et al., 2006c)	Leaves	Seasonal	Pinus (*P. taiwanensis*, *P. armandi* and *P. morrisonicola*), Evergreen trees (*Stranvaesia niitakayamensis*, *Rhododendron mori* and *Trochodendron aralioides*) and perennial grasses (*Yushania niitakayamensis*, *Miscanthus transmorrisonensis* and *M. floridulus*)	Conifers	Specrad	3e	Fv′/Fm′
76	2009	(Weng et al., 2009)	Leaves	Seasonal	*Pinus taiwanensis*	Conifers	Specrad	2e	Fv′/Fm′
82	2009	(Filella et al., 2009)	Leaves	Seasonal	*Pinus sylvestris - Quercus ilex*	Conifers	Specrad	2b 2c	DEPS Car/Chl
83	2009	(Busch et al., 2009)	Leaves	Seasonal	*Pinus banksiana*	Conifers	Specrad	2a 2c	NPQ EPS
24	2002	(Winkel et al., 2002)	Leaves	Seasonal	*Chenopodium quinoa*	Herbaceous/crop	Specrad	2d–4–10 2e	RUE ΔF/Fm′
26	2002	(Tambussi et al., 2002)	Leaves	Seasonal	Wheat	Herbaceous/crop	Specrad	2c	DEPS
35	2005	(Inamullah and Isoda 2005)	Leaves	Seasonal	Soya/cotton	Herbaceous/crop	Specrad	2a 2e	NPQ ΔF/Fm′
49	2006	(Chen et al., 2006)	Leaves	Seasonal	Rice	Herbaceous/crop	Specrad	2b	Car/Chl
78	2009	(Gerosa et al., 2009)	Leaves	Seasonal	*Phaseolus vulgaris*	Herbaceous/crop	Specrad	2e	ΔF/Fm′
42	2006	(Weng et al., 2006a)	Leaves	Seasonal	*Mangifera indica*, *Podocarpus nagi* and *Alnus formosana*	Mixture	Specrad	2e 2a	ΔF/Fm′ NPQ
54	2007	(Martin et al., 2007)	Leaves	Dif populations	*Metrosideros polymorpha*	Broadleaf	Specrad	3a 3b	Car/Chl ΔF/Fm′

Table 1 (*continued*)

Article order by publication date	Year	Reference	Scale	Variance factor	Species/vegetation type	Vegetation type	Sensor	Figure #	Ecophysiological variables
38	2005	(Raddi et al., 2005)	Leaves	Dif species	Mediterranean forests	Broadleaf	Specrad		NPQ
6	1997	(Gamon et al., 1997)	Leaves	Dif species	20 sps (annual, deciduous perennial, and evergreen perennial)/cotton	Mixture	Specrad	1e–3b 1d–3c–4–10	ΔF/Fm′ RUE
25	2002	(Sims and Gamon 2002)	Leaves	Dif species	53 different species	Mixture	Specrad	3a	Car/Chl
43	2006	(Guo and Trotter 2006)	Leaves	Dif species	13 different species ambient and elevated CO_2	Mixture	Specrad	3b 3c–10	ΔF/Fm′ RUE
14	2000	(Stylinski et al., 2000)	Leaves	Leaves	*Quercus pubescens*	Broadleaf	Specrad	3a	Jmax Car/Chl
15	2000	(Moran et al., 2000)	Leaves	N treatment × light	*Picea engelmannii*	Conifers	Specrad		Chl (A + B)
44	2006	(Inoue and Peñuelas 2006)	Leaves	N × water condition	Soybean	Herbaceous/ crop	Specrad	3c–4–10	RUE
70	2008	(Naumann et al., 2008a)	Leaves	Salt concentration	*Myrica cerifera*	Broadleaf	Specrad	3b	ΔF/Fm′
21	2002	(Richardson and Berlyn 2002)	Leaves	Spatial	*Betula papyrifera*	Broadleaf	Specrad	3c	RUE
48	2006	(Asner et al., 2006)	Leaves	Spatial	*Metrosideros polymorpha*	Broadleaf	Specrad		Chl–Car Car/Chl
81	2009	(Martin and Asner 2009)	Leaves	Spatial	*Metrosideros polymorpha*	Broadleaf	Specrad	3a	Car/Chl
17	2001	(Richardson et al., 2001)	Leaves	Spatial	Red spruce and balsam fir	Conifers	Specrad	3b	ΔF/Fm′
37	2005	(Whitehead et al., 2005)	Leaves	Spatial × sps	Three different species from six mixed forests	Mixture	Specrad		Amax
12	2000	(Methy 2000)	Leaves/ canopy	Hours	*Quercus ilex*	Broadleaf	Specrad	1e 2f	ΔF/Fm′ Net CO_2 uptake
1	1992	(Gamon et al., 1992)	Leaves/ canopy	Hours	Sunflower	Herbaceous/ crop	Specrad	1c	EPS RUE
20	2002	(Stylinski et al., 2002)	Leaves/ canopy	Seasonal	3 chaparral shrubs (*Quercus berberidifolia, Ceanothus greggii, Adenostoma fasciculamtum*)	Broadleaf	Specrad	3a	ΔF/Fm′ Net CO_2 uptake Car/Chl DEPS
33	2005	(Gamon et al., 2005)	Leaves/ plant	Hours	*Anacardium excelsum, Luehea seemanni*	Broadleaf	Specrad		ΔF/Fm′
39	2005	(Dobrowski et al., 2005)	Canopy	Hours	*Vitis vinifera*	Broadleaf	Specrad		Fs
11	2000	(Nichol et al., 2000)	Canopy	Seasonal	Broadleaf deciduous (Aspen–Fen), Conifers (old jack pine–old black spruce)	Broadleaf	Helicopter Specrad	5–7–10	RUE
36	2005	(Serrano and Peñuelas 2005)	Canopy	Seasonal	Mediterranean forest	Broadleaf	Specrad transmitance	5–10	Net CO_2 uptake RUE
40	2006	(Nichol et al., 2006)	Canopy	Seasonal	Mangrove (*Rhizophora* and *Avicennia*)	Broadleaf	Specrad		ΔF/Fm′ NPQ
50	2006	(Sims et al., 2006a)	Canopy	Seasonal	Chaparral shrubs	Broadleaf	Tram Specrad	5–10	RUE
69	2008	(Peguero-Pina et al., 2008)	Canopy	Seasonal	*Quercus coccifera*	Broadleaf	Specrad		ΔF/Fm′ Fs EPS NPQ
75	2009	(Naumann et al., 2009)	Canopy	Seasonal	*Myrica cerifera* and *Iva frutescens*	Broadleaf	Airborne spectro		ΔF/Fm′
79	2009	(Cheng et al., 2009)	Canopy	Seasonal	Douglas fir forest	Conifers	Specrad	5–10	RUE
8	1998	(Carter 1998)	Canopy	Seasonal	*Pinus taeda-P. elliotti*	Conifers	Specrad		Amax
18	2002	(Nichol et al., 2002)	Canopy	Seasonal	Boreal forest Siberia	Conifers	Specrad	5–7–10	RUE
34	2005	(Louis et al., 2005)	Canopy	Seasonal	Scots Pine	Conifers	Specrad		Net CO_2 uptake
51	2007	(Nakaji et al., 2007)	Canopy	Seasonal	*Larix kaempferi*	Conifers	Specrad	5–10	RUE
57	2008	(Hall et al., 2008)	Canopy	Seasonal	Douglas fir	Conifers	Specrad	5–7–10	RUE
58	2008	(Hilker et al., 2008)	Canopy	Seasonal	Douglas fir	Conifers	Specrad	5–7–10	RUE
66	2008	(Nakaji et al., 2008)	Canopy	Seasonal	Three sites: *Larix kaempferi, Chamaecyparis obtuse* and *Larix gmelinii x L. kaempferi* + *Sasa senanensis* and *S. kurilensis*	Conifers	Specrad	5–7–10	RUE

(*continued on next page*)

Table 1 (*continued*)

Article order by publication date	Year	Reference	Scale	Variance factor	Species/vegetation type	Vegetation type	Sensor	Figure #	Ecophysiological variables
72	2009	(Middleton et al., 2009)	Canopy	Seasonal	Douglas fir	Conifers	Specrad	5–10	RUE
80	2009	(Hilker et al., 2009b)	Canopy	Seasonal	Douglas fir forest	Conifers	Specrad	5–10	RUE
84	2009	(Ac et al., 2009)	Canopy	Hours	Montane grassland	Grassland	Specrad		$\Delta F/Fm'$ Chl (A + B)
65	2008	(Meroni et al., 2008b)	Canopy	Seasonal	*Trifolium repens*	Herbaceous/crop	Specrad		Fs Net CO$_2$ uptake
4	1996	(Filella et al., 1996)	Canopy	Hours	Barley	Herbaceous/crop	Specrad	10	RUE
77	2009	(Wu et al., 2009)	Canopy	Nutrients	Wheat	Herbaceous/crop	Specrad	6–10	RUE
13	2000	(Peñuelas and Inoue 2000)	Canopy	Seasonal	*Brassica napus*	Herbaceous/crop	Specrad		Net CO$_2$ uptake
22	2002	(Strachan et al., 2002)	Canopy	Seasonal	Maize (99 and 155 kg N/ha)	Herbaceous/crop	Specrad	5–7–10	RUE
56	2008	(Inoue et al., 2008)	Canopy	Seasonal	Rice	Herbaceous/crop	Specrad	5–10	RUE
67	2008	(Strachan et al., 2008)	Canopy	Seasonal	Maize	Herbaceous/crop	Specrad/CASI		GPP
19	2002	(Trotter et al., 2002)	Canopy	Dif species	8 sps	Mixture	Specrad	6–10	RUE
62	2008	(Harris 2008)	Canopy	Seasonal	5 *Sphagnum* species (*S. tenellum*, *S. capifolium*, *S. pulchrum*, *S. subnitens*, *S. papillosum*)	Non higher plants (mosses)	Specrad	5–10	ΦPSII
30	2004	(Filella et al., 2004)	Plant/canopy	Seasonal	Mediterranean shrubland (*Erica multiflora* and *Globularia alypum*)	Broadleaf	Specrad	5–10	Net CO$_2$ uptake RUE
68	2008	(Suárez et al., 2008)	Canopy	Spatial	*Olea europea*	Broadleaf	AHS airborne		Water content
71	2008	(Naumann et al., 2008b)	Canopy	Spatial	*Myrica cerifera*	Broadleaf	Airborne Specrad		$\Delta F/Fm'$
16	2001	(Rahman et al., 2001)	Canopy	Spatial	4 sites × 2 dates (3 conifers + 1fen) Canada	Conifers	AVIRIS		CO$_2$ uptake
61	2008	(Black and Guo 2008)	Canopy	Spatial	Grassland	Grassland	Specrad		Net CO$_2$ uptake
7	1997	(Peñuelas et al., 1997a)	Canopy	Spatial	Aquatic emergent macrophytes	Herbaceous	Specrad	6–10	RUE
46	2006	(Yamano et al., 2006)	Canopy	Water stress effects	Soil crusts	Non higher plants (mosses)	Specrad		Fv/Fm
23	2002	(Lovelock and Robinson 2002)	Canopy	Water stress effects	Mosses	Mosses	Specrad		Fv/Fm
53	2007	(Van Gaalen et al., 2007)	Canopy	Water stress effects	*Sphagnum*	Mosses	Specrad		NPQ water content
73	2009	(Goerner et al., 2009)	Ecosystem	Seasonal	Mediterranean Forests	Broadleaf	MODIS	8–10	RUE
28	2004	(Rahman et al., 2004)	Ecosystem	Seasonal	Broadleaf deciduous forest (Sugar maple (*Acer saccharum*), tulip poplar (*Liriodendron tulipifera*), sassafras (*Sassafras albidium*), white oak (*Quercus alba*), black oak (*Quercus nigra*))	Broadleaf	MODIS	8–9a–10	RUE
32	2005	(Drolet et al., 2005)	Ecosystem	Seasonal	*Populus tremuloides*	Broadleaf	MODIS	8–9b–10	RUE
55	2008b	(Garbulsky et al., 2008b)	Ecosystem	Seasonal	Mediterranean Forest	Broadleaf	MODIS	8–9a–10	RUE
60	2008a	(Garbulsky et al., 2008a)	Ecosystem	Seasonal	Mediterranean Forests	Broadleaf	MODIS	8–10	RUE
59	2008	(Drolet et al., 2008)	Ecosystem	Seasonal	Boreal coniferous forest	Conifers	MODIS	8–9c–10	RUE

We also finally analyzed the overall relationship between RUE and PRI reported in different articles, by plotting in the same x–y graph the points for all the comparable studies together. For this analysis, we selected those articles which presented the plots with all the measured values using the same definition of PRI and similar protocols for the measurements of the variables for the different scales. We evaluated the differences among the slopes and the intercepts of the relationships between RUE and PRI for different vegetation types through analysis of covariance (ANCOVA).

3. Results

We found more than 80 articles published between 1992 and 2009 that reported results on the PRI and its relationship with one or more

Table 2
Summary of the most common ecophysiological variables linked to PRI, acronyms and methods used in the literature for their estimation.

Acronym	Full name	Determination methods
	Net CO_2 uptake	Gas exchange at the leaf or stand (eddy covariance) level
RUE	Radiation use efficiency	Gas exchange
EPS or DEPS	Epoxidation or de-epoxidation state of the xanthophylls	Chromatography high performance liquid chromatography (HPLC)
ΔF/Fm′ or ΦPSII	Effective quantum yield or actual photochemical efficiency or photochemical efficiency of Photosystem II	Chlorophyll fluorescence
NPQ	Non photochemical quenching	Chlorophyll fluorescence
Car/Chl	Carotenoids/chlorophyll contents	Spectrophotometry HPLC

variables related to photosynthesis performance (Table 1). More than a third part of these studies were published during 2008–09, emphasizing the increasing interest of the scientific community on this subject. These studies were performed at the leaf, the canopy and the ecosystem level and some of them presented more than one relationship, e.g. for different species or different sites. The highest number of relationships reported was for relationships with the effective quantum yield or actual photochemical efficiency (ΔF/Fm′), but the PRI was also linked to several different variables for different spatial and temporal scales: RUE, net CO_2 uptake, NPQ, EPS (or DEPS), the ratio chlorophyll/carotenoids (Table 2). Other less frequent ecophysiological variables reported in the literature were chlorophyll (A + B) content, maximum photosynthesis rate (Amax), steady state value of fluorescence (Fs), and water content.

3.1. Leaf level

3.1.1. Diurnal changes

We found twelve articles that linked the PRI with ΔF/Fm′, NPQ, DEPS (or EPS), ratio chlorophyll/carotenoids and RUE at the leaf scale over short (diurnal) time scales. The largest numbers of relationships was found for ΔF/Fm′ (n = 17) and RUE (n = 16). The median coefficients of determination for the relationships between PRI and RUE varied between 0.60 and 0.85 and for ΔF/Fm′varied between 0.62 and 0.82 depending on the vegetation type (Fig. 1d, e). Except for chlorophyll/carotenoid levels, which were limited to a single study for herbaceous vegetation (Fig. 1b), there were no remarkable differences within the variables among vegetation types. Non-significant

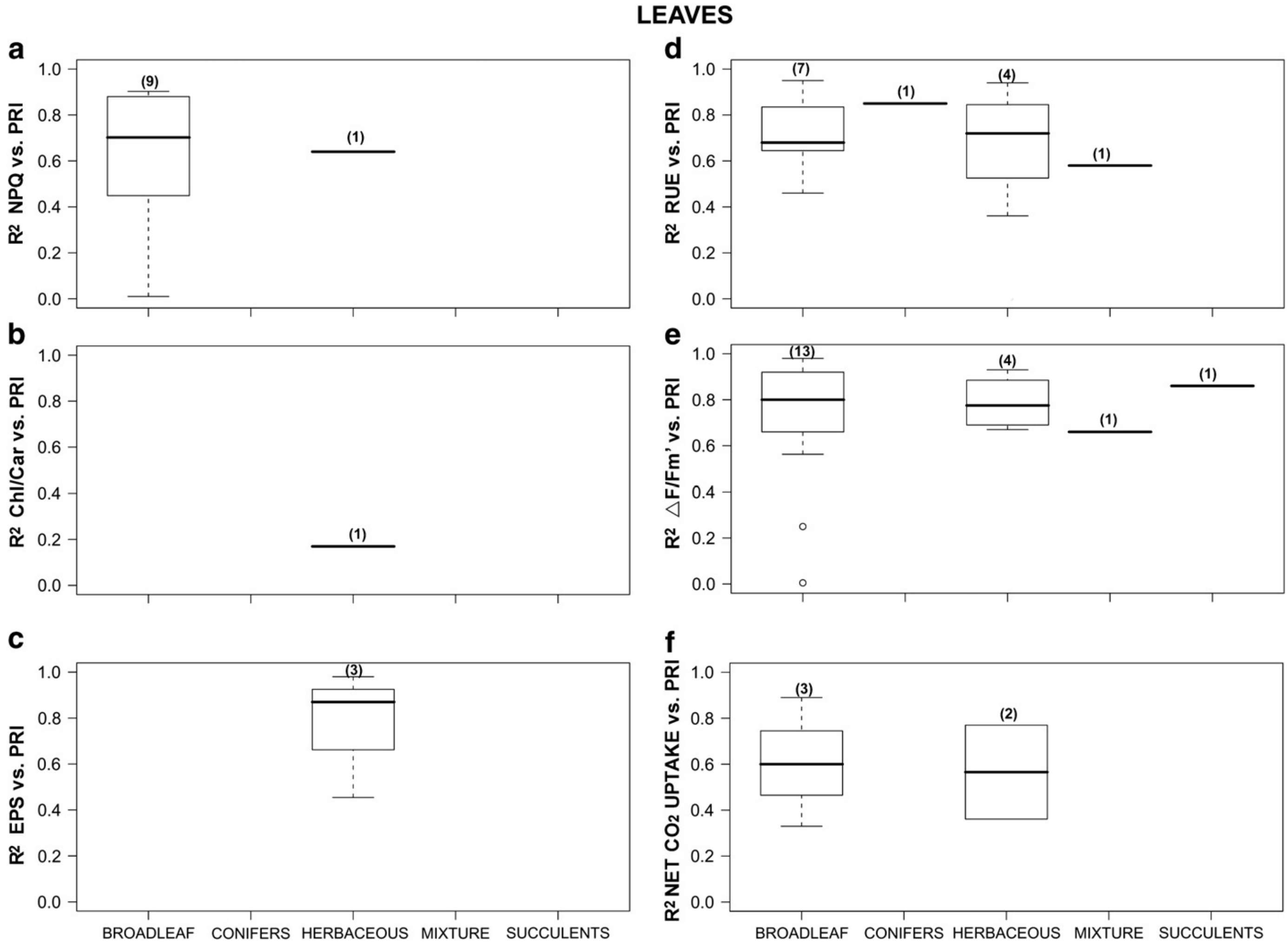

Fig. 1. Boxplots for the coefficients of determination for the relationships between the physiological variables: a) non phothochemical quenching (NPQ), b) chlorophyll/carotenoid (Chl/Car), c) epoxidation state of xantophylls (EPS), d) radiation use efficiency (RUE), e) actual photochemical efficiency (ΔF/Fm′) and f) Net CO_2 uptake, and PRI at the leaf scale and at the short daily time scale. Central lines represent the medians, boxes represent 50% of the data, the whiskers represent the minimum and maximum values and the circles the outliers. The numbers of reported relationships found in the literature are shown in brackets.

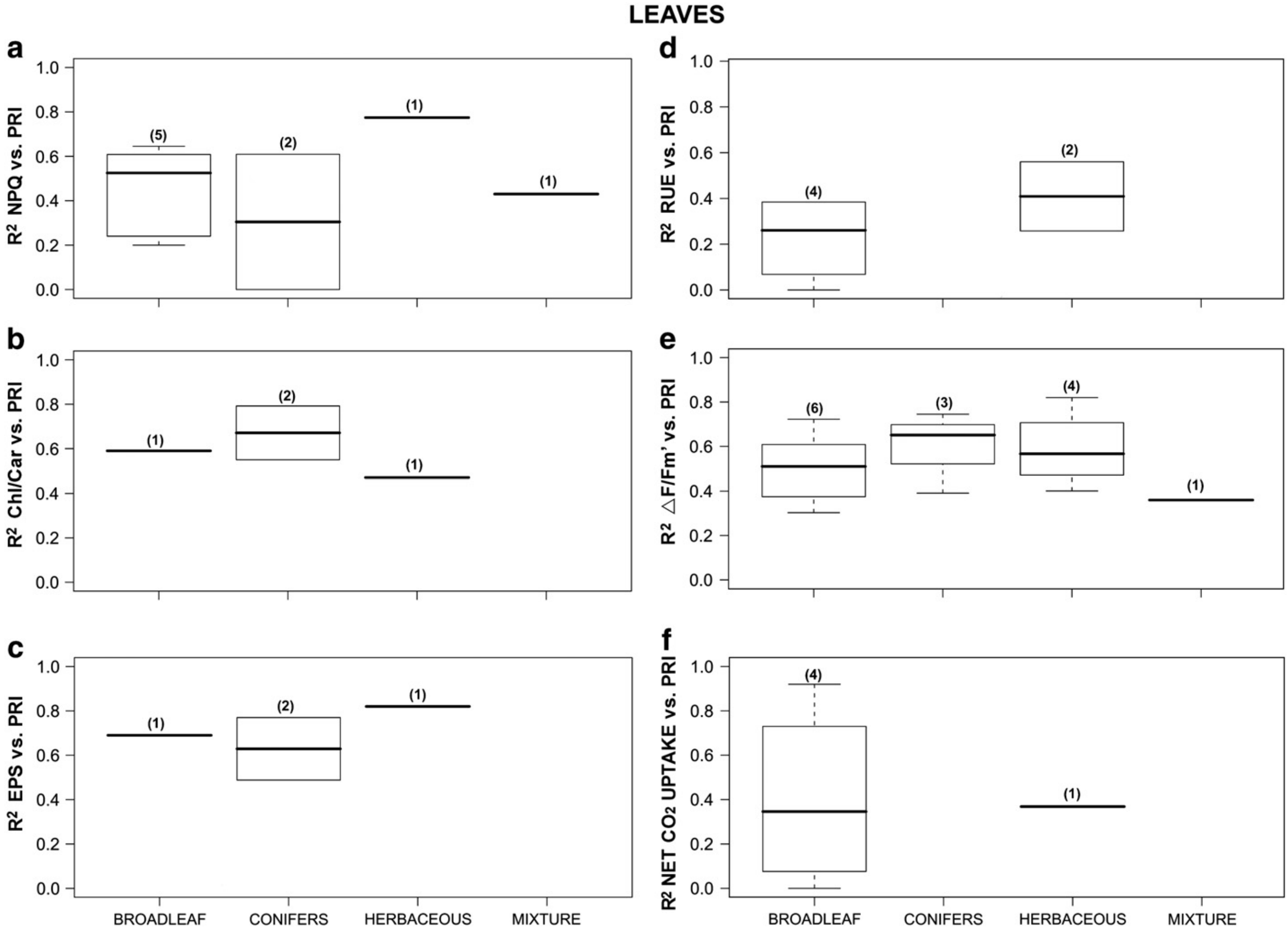

Fig. 2. Boxplots of the coefficients of determination (R^2) for the relationships between the ecophysiological variables and PRI at the leaf scale and at the seasonal time scale. Central lines represent the medians, boxes represent 50% of the data, and the whiskers represent the minimum and maximum values. The numbers of reported relationships found in the literature are shown in brackets.

relationships for herbaceous plants were reported for the relationship with ΔF/Fm′ and also with NPQ (Fig. 1).

3.1.2. Seasonal changes

We found seventeen articles that reported relationships between PRI and ecophysiological variables at the leaf scale over seasonal time scales. Again, the larger number of relationships was found for variables related to quantum yield (ΔF/Fm′ or Fv/Fm) with PRI ($n = 14$) and only 6 were found for RUE (Fig. 2d, e). PRI accounted for 30 to 80% of the variability of ΔF/Fm′ or Fv/Fm (Fig. 2e). PRI accounted for from 77% of the variability of NPQ in herbaceous leaves and a median of 30% for conifers. A few non-significant relationships were also found between PRI and RUE, NPQ and CO_2 uptake. For broadleaf, conifers and herbaceous species PRI accounted for between 50 and 80% of the temporal variability of Chl/Car and EPS (Fig. 2b, c). The R^2 for the relationships between Net CO_2 uptake and PRI was highly variable for broadleaf vegetation, the vegetation type with multiple studies available (Fig. 2f). Three other studies, data not included in

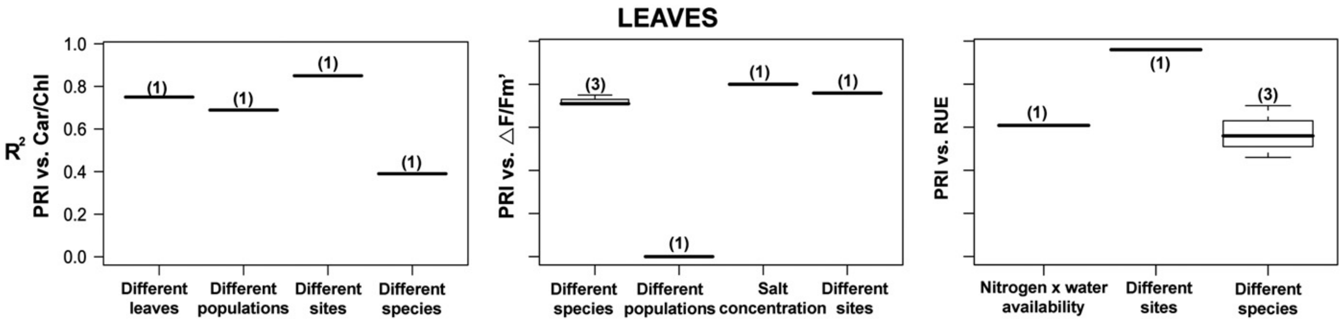

Fig. 3. Boxplots of the coefficients of determination of the relationships between physiological variables and PRI at the leaf scale and across different species, sites, leaves, N and water availabilities and salt concentrations. Central lines represent the medians, boxes represent 50% of the data, and the whiskers represent the minimum and maximum values. The numbers of reported relationships found in the literature are shown in brackets.

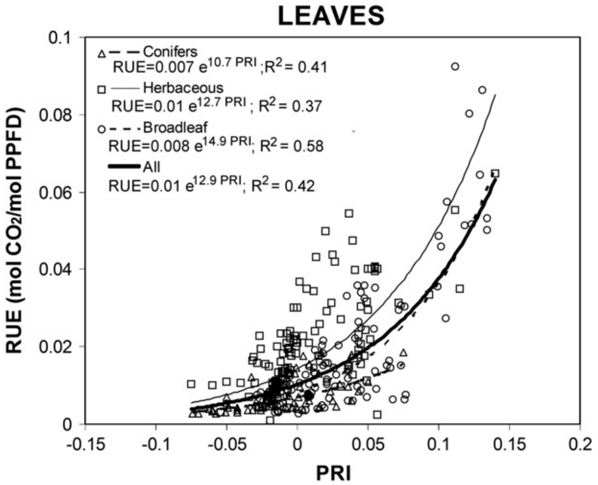

Fig. 4. Relationships between leaf scale photosynthetic RUE (RUE = Net photosynthetic rate/incident PPFD) and PRI for broadleaf (Guo and Trotter 2004; Meroni et al., 2008a; Peñuelas et al., 1995), conifers (Nakaji et al., 2006) and herbaceous (Gamon et al., 1997; Guo and Trotter 2004; Inoue and Peñuelas 2006; Peñuelas et al., 1995; Winkel et al., 2002; Wu et al., 2009) plants derived from published results spanning different temporal scales and factors of variances. See Table 1 for details.

Fig. 2, presented significant relationships with other variables such as total chlorophyll content and PRI (Nakaji et al., 2006; Weng et al., 2009) or also between ΔF/Fm′ and the difference between the PRI measured at predawn and noon (ΔPRI) (Weng et al., 2006a).

3.1.3. Other factors of change

We also found several studies that presented relationships between PRI and ecophysiological variables at the leaf level when different variance factors (e.g. different species, different populations of a same species or different sites) or different treatments types (e.g. levels of nitrogen × water availability or salt concentration) were measured in different vegetation types. All but one of these relationships were significant (Fig. 3). Other ecophysiological variables were less frequently tested against PRI. Total chlorophyll content was significantly correlated with PRI ($R^2 = 0.74$) when analyzing conifer leaves in a nitrogen availability experiment (Moran et al., 2000). NPQ was also correlated with PRI ($R^2 = 0.72$) in leaves of Mediterranean species (Raddi et al., 2005).

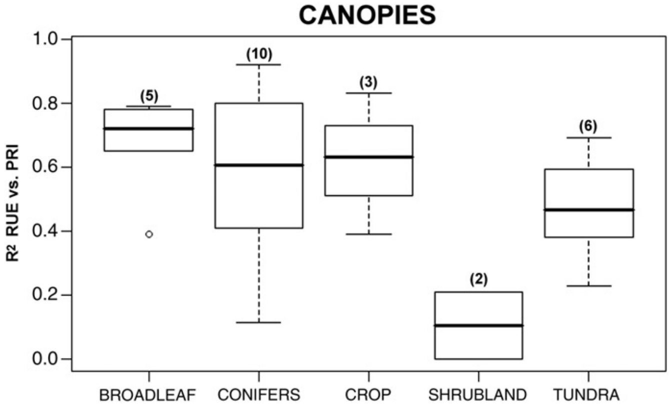

Fig. 5. Boxplots of the coefficient of determination for the relationships between RUE and PRI at the canopy scale and at the seasonal time scale. These analyses include mostly studies made on stands of individuals. The R^2 for shrublands is different to the other vegetation types (t-test, $p<0.05$). Central lines represent the medians, boxes represent 50% of the data, whiskers represent the minimum and maximum values and the circles the outliers. The numbers of reported relationships found in the literature are shown in brackets.

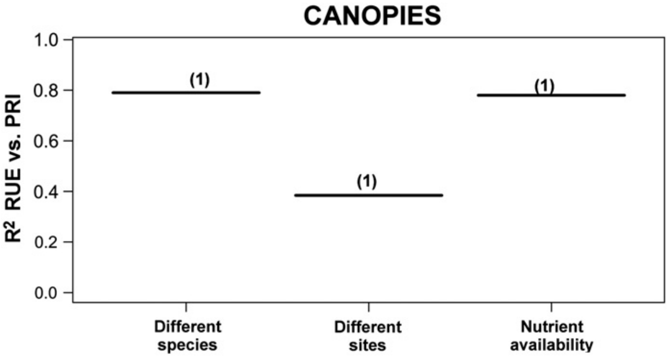

Fig. 6. Boxplots of the coefficients of determination of the relationships between RUE and PRI at the canopy scale across different species, nutrient availabilities and sites. These studies are based on reflectance data from hand held spectrometers on stands of wheat with different nutrient availabilities (Wu et al., 2009), different sites of aquatic vegetation (Peñuelas et al., 1997a) and eight different species (Trotter et al., 2002). Central lines represent the medians. The numbers of reported relationships found in the literature are shown in brackets.

3.1.4. General relationship at the leaf level

We analyzed the relationships between leaf level photosynthetic RUE and PRI to evaluate if the results reported by different authors are generalizable to different plant types. We reviewed the information reported by different articles that presented relationships between photosynthetic RUE and PRI for determined species (Gamon et al., 1997; Guo and Trotter, 2004; Inoue and Peñuelas, 2006; Meroni et al., 2008a; Nakaji et al., 2006; Peñuelas et al., 1995; Winkel et al., 2002; Wu et al., 2009). The most common protocol is to use the reflectance of the vegetation of a band centered at 531 nm and a reference band centered at 570 nm. We discarded for this analysis those articles that use other bands to calculated PRI to avoid results not directly comparable. We transformed the PRI values to have all them calculated as $PRI = (R531 - R570)/(R531 + R570)$. These studies calculated the efficiency as net photosynthetic exchange/incident photosynthetic photon flux density. The relationships between log RUE and PRI were significant for conifer ($R^2 = 0.41$), broadleaf

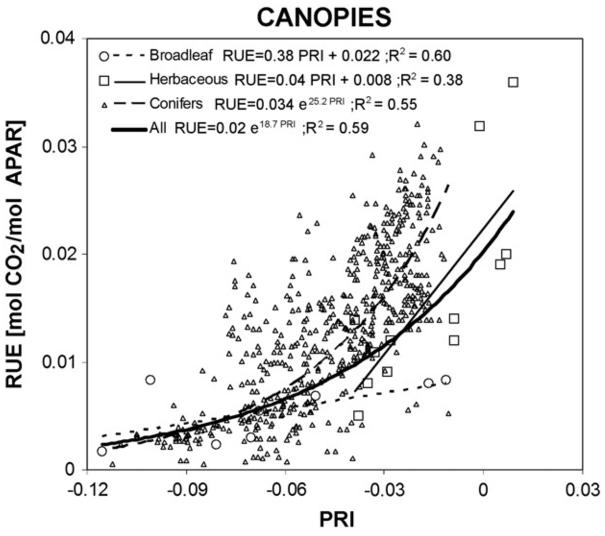

Fig. 7. Relationships between eddy covariance derived photosynthetic RUE and PRI for broadleaf (Nichol et al., 2000), conifers (Hall et al., 2008; Hilker et al., 2009b; Nakaji et al., 2008; Nichol et al., 2000; Nichol et al., 2002) and herbaceous vegetation (Strachan et al., 2002) types at the canopy level derived from published results. See Table 1 for details. In all the studies RUE = GPP/APAR, but in Nichol et al., (2000, 2002) was calculated as RUE = GPP/incident PAR. The relationship for all the datasets is based on all the data for broadleaf and herbaceous canopies and a random sample of the conifer canopies to equilibrate the number of data of each vegetation type ($p<0.001$; $n=37$).

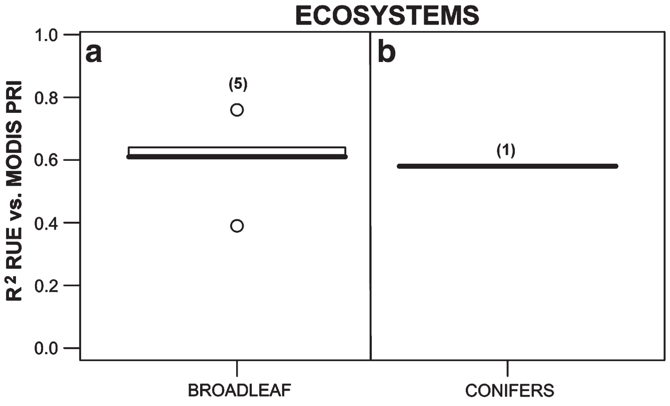

Fig. 8. Boxplots of the coefficient of determination for the relationships between RUE and MODIS PRI at the ecosystem scale a) at the seasonal time scale for broadleaf forests and b) at the seasonal time and spatial scale for different boreal coniferous forests. Central lines represent the medians, boxes represent 50% of the data, and the circles are outliers. The numbers of reported relationships found in the literature are shown in brackets.

($R^2 = 0.58$) and herbaceous ($R^2 = 0.37$) species. The slopes between vegetation types did not differ but the intercept for herbaceous species differed from the other two vegetation types. PRI accounted for 42% of the variability of RUE in a unique exponential relationship for all the vegetation types (Fig. 4; $R^2 = 0.42$, $n = 295$, $p < 0.0001$).

3.2. Canopy level

3.2.1. Diurnal changes

We found only a few studies that reported results on the relationships at the canopy (individual plant to stand) level between ecophysiological variables and PRI on the daily course. PRI accounted for 89% of the diurnal changes in photosynthetic efficiency at a sunflower canopy (Gamon et al., 1992). Other studies showed that in a grapevine canopy (Dobrowski et al., 2005), the PRI was significantly correlated to Fs ($R^2 = 0.32$) and in a grassland (Ac et al., 2009) PRI was significantly correlated to the total content of Chl ($R^2 = 0.63$), the Fv/Fm ($R^2 = 0.55$), the Fs ($R^2 = 0.50$) and the ΔF/Fm′ ($R^2 = 0.47$). PRI was also related to diurnal changes in steady state fluorescence and in water stress-related variables, such as stomatal conductance and stem water potential over an olive orchard (Suárez et al., 2008).

3.2.2. Seasonal changes

There is a large quantity of studies on the relationships between ecophysiological variables and PRI illustrating seasonal patterns. These studies include analysis from a part of a growing season to multiple seasons. Most of these studies showed the link between RUE and PRI and presented median R^2 values between 0.4 and 0.75 for broadleaf, conifers, crops and tundra vegetation types. The R^2 for these four vegetation types were not significantly different (t-test, $p < 0.05$). The R^2 for shrublands was instead only *ca.* 0.1 which was significantly different to the other vegetation types (Fig. 5).

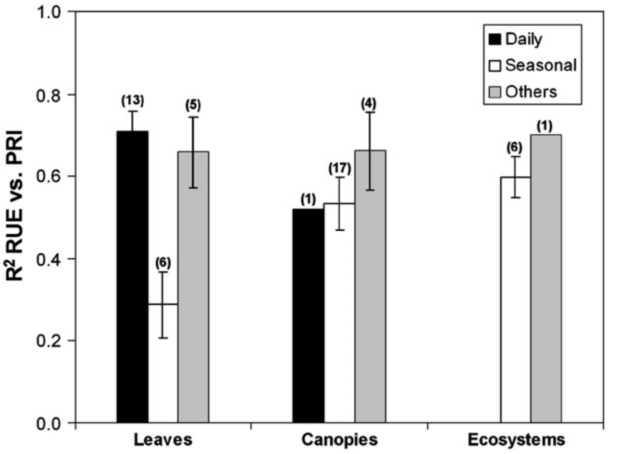

Fig. 10. Comparison of the strength of the relationships between RUE and PRI across temporal and spatial scales. Each bar represents the average coefficients of determination for each source of temporal variation (daily or seasonal) or other source of variation (e.g. species or nutrients availability) and spatial scales (leaf, canopy or ecosystem). Dispersion bars represent the standard errors and the numbers of reported relationships are shown in brackets.

3.2.3. Other factors of change

At the canopy level and at the seasonal time scale, different types of experiments have reported four significant relationships between canopy RUE and PRI (Fig. 6). PRI was also linked to ecophysiological variables in mosses (Harris, 2008; Lovelock and Robinson, 2002; Van Gaalen et al., 2007) and soil crusts (Yamano et al., 2006). Those studies showed that PRI links to Fv/Fm ($R^2 = 0.42 - 0.67$), to EPS ($R^2 = 0.29$), to NPQ ($R^2 = 0.80$) and to water content ($R^2 = 0.82$). Moreover, other studies analyzing other ecophysiological variables showed that PRI accounted for 46% of the spatial variability of CO_2 uptake for a semiarid grassland and also accounted for 77% of the variability for a coniferous forest across sites and dates (Black and Guo, 2008; Rahman et al., 2001).

3.2.4. General relationship at the canopy level

We analyzed the data provided by those studies that used eddy covariance to estimate RUE together with PRI at the canopy level

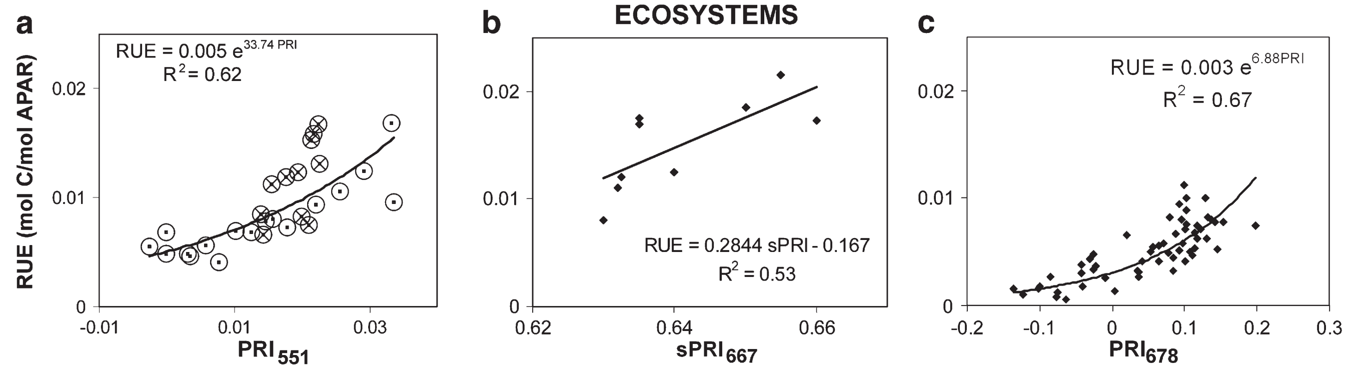

Fig. 9. Seasonal relationship between RUE calculated from eddy covariance derived GPP and absorbed PAR (RUE = GPP/APAR) and different formulations of PRI from MODIS data. a) PRI calculated from reflectance in bands 11 and 12 for a Mediterranean forest (Garbulsky et al., 2008b) and a temperate deciduous forest (Rahman et al., 2004). Regression line (circles, n = 30) corresponds to a random subset of the points in the Mediterranean forests (dots) and all the points for the temperate decidous forest (crosses) b) Atmospherically corrected sPRI = (1 + PRI)/2 calculated from bands 11 and 13 in a boreal deciduous forest (Drolet et al., 2005). c) Atmospherically corrected PRI calculated using band 14 (678 nm) as reference for eight boreal coniferous forests (Drolet et al., 2008). Recalculated and redrawn based on published data.

derived from spectroradiometers mounted on different types of platforms. PRI significantly accounted for the variability of RUE for each of the vegetation types (Fig. 7), but the slope and intercept of the relationships log RUE–PRI for conifers significantly differed from the other two vegetation types. When considering all the studies together, the RUE was exponentially related to PRI (Fig. 7), with PRI accounting for 59% of the overall variability of the RUE for all the vegetation types (Fig. 7; $R^2 = 0.42$, $n = 295$, $p < 0.0001$).

3.3. Ecosystem level

In recent years there have been assessments of whole-ecosystem carbon uptake conducted with simultaneous measurements of reflectance and gas exchange. These ecosystem studies demonstrate significant links between whole-ecosystem fluxes and MODIS PRI. It is worth remembering that MODIS PRI is based, by necessity, on different wavebands than most field studies due to the limited bands available from MODIS. These methods employ a combination of MODIS derived FPAR estimations with eddy covariance at the ecosystem scale in a variety of natural forests including temperate decidous 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; Garbulsky et al., 2008b; Goerner et al., 2009) (Fig. 8). The RUE-PRI analysis at the seasonal scales for different boreal forest showed non significant relationships for several sites (Drolet et al., 2008).

If PRI is an accurate estimator of RUE, then ecosystem CO_2 uptake could be expressed as

$$CO_2 \text{ uptake} = f(\text{PRI} \times \text{FPAR}) \times \text{PAR}$$

One of the steps needed to arrive at such a generalization of the use of the PRI is to have a general RUE–MODIS PRI relationship that could be used to assess RUE variation for different ecosystem types. We found six studies that present MODIS PRI data as well as concurrent RUE from eddy covariance data and FPAR. In order to build a unique relationship between RUE and MODIS PRI, we selected studies that used the same protocol. The 531 nm band used to calculate the PRI is located in a region of the spectra where the transmission through the atmosphere is very high (Kaufman, 1989). Therefore, the signal of the PRI is less affected by atmospheric interferences than other spectral indices like the NDVI, whose bands are located in regions of the spectra much more disturbed by the atmosphere. In fact, it has been demonstrated that the calculation of MODIS PRI without applying atmospheric corrections is an accurate estimator of RUE in different ecosystem types (Drolet et al., 2005; Garbulsky et al., 2008b). From the six studies we finally found only two that presented data on PRI using MODIS bands 11 (526–536 nm) and 12 (546–556 nm) with (Rahman et al., 2004) and without atmospheric correction (Garbulsky et al., 2008b), and transformed both studies to PRI and RUE in mol CO_2/mol photons. Two other studies analyzed data using other bands as references in the formulation of PRI (Drolet et al., 2005; Drolet et al., 2008) could not be used for these analysis because their results are not comparable: they either used band 1 or band 13 as reference bands (Fig. 9b, c). This analysis of studies from two different types of forest showed that the seasonal variability of RUE and MODIS PRI is linked by one unique relationship with PRI accounting for 62% of the variance of RUE (Fig. 9a).

3.4. RUE–PRI relationships across scales

The relationships between RUE and PRI were generally strong across spatial and temporal scales (Fig. 10). The average coefficients of determination presented the highest values for the daily analysis at the leaf level (Fig. 10). The seasonal analysis at the leaf level presented instead the lowest average values. At the canopy level, daily and seasonal relationships presented similar high coefficients of determination, although we only found one study that presented a daily analysis at the canopy level. The coefficients of determination for the relationships at the leaf and canopy levels for other factors of variation were similar. At the ecosystem level we only found results for seasonal analysis and the average coefficient of determination was higher than the results for the leaf level and similar to the canopy level.

4. Discussion

4.1. PRI assessment of RUE

PRI accounted for a great part of the variability of the ecophysiological variables linked to radiation use efficiency in most vegetation types analyzed in the literature. These results show thus that the PRI is a good spectral index estimator of RUE for leaf, canopy and most ecosystems, and at different temporal scales, from hourly to seasonal. There were only few studies that reflected non-significant relationships between RUE-related ecophysiological variables and PRI. Overall, 86% of the relationships included in this study were significant or accounted for more than 30% of the variability of the ecophysiological variables. The scarce non-significant relationships were particularly frequent when PRI was linked to Net CO_2 uptake or to Amax, not to RUE itself or to its proxy physiological variables (e.g. $\Delta F/Fm'$). We tested the agreement of the RUE–PRI relationships at the foliar (Fig. 4), canopy (Fig. 7) and ecosystem (Fig. 9) levels for different vegetation types derived from different studies in unique general relationships. In those general relationships PRI tends to saturate at increasing RUE and is less sensitive when RUE approaches zero but may be very useful in remote sensing assessment of RUE since they accounted for between 42 and 67% of the total variance of RUE at all spatial scales from leaves to ecosystems.

Our analysis showed that PRI derived from top-canopy leaves and PRI derived from the whole canopy have been found to be closely linked, at least for relatively closed canopies (Filella et al., 1996; Gamon et al., 1992; Gamon and Qiu, 1999; Stylinski et al., 2002). Even more, the average strength of the relationships between RUE and PRI at the seasonal scale is even higher for the canopy level analyses than for the leaf-level analyses (Fig. 10). The low R^2 value for leaves across seasons, combined with the relatively high correlation between PRI and chlorophyll/carotenoids for leaves (Fig. 2b), can partly be explained by the strong influence of chlorophyll/carotenoid ratios on PRI, particularly as leaves undergo developmental and physiological changes associated with expansion and aging. In some cases, these large pigment changes may confound the RUE–PRI relationship,

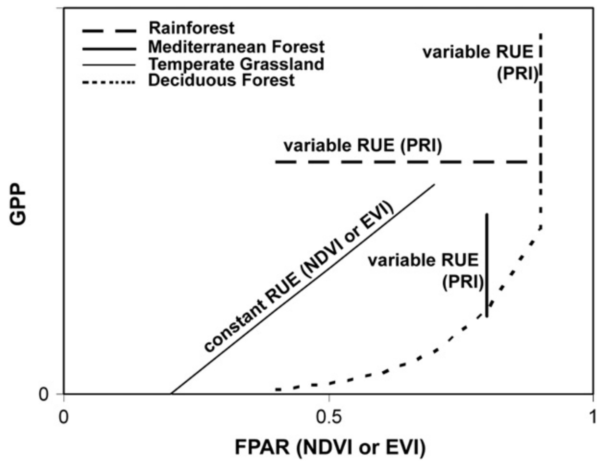

Fig. 11. Hypothesized seasonal relationships of GPP to FPAR in ecosystems with contrasting phenologies and GPP dynamics. The suggested best spectral index to estimate RUE is depicted between brackets for each ecosystem type.

possibly accounting for the poor R^2 values for leaves across seasons (see Fig. 10). The high strength of the RUE–PRI seasonal relationship at the canopy level therefore suggests that the optical properties of upper canopy regions can reveal the overall photosynthetic state of the canopy, opening the possibility of assessment of photosynthetic activity at larger scales, i.e. at ecosystem and regional levels. However, at the scale of whole vegetation stands and ecosystems, PRI can also be affected by canopy and stand structure (Barton and North, 2001; Hall et al., 2008; Hilker et al., 2008), and it is possible that canopy structural changes (e.g. changing LAI, leaf orientation, or percent vegetation cover) could also be driving seasonal changes in PRI. To confirm the capability of PRI as an ecosystem photosynthetic indicator, appropriate ecosystem scale methods to sample carbon flux and hyperspectral reflectance simultaneously have been recently, and are still being, developed (e.g. Gamon et al., 2006). Key challenges will be accounting for percent vegetation cover, sun angle and view angle, and background (e.g. soil, shadow, or standing water) effects, all of which are known to complicate PRI interpretation. Structural features, such as the percent of woody or dead canopy material, or the presence of visible soil or other non-green landscape components, can confound the PRI signal as shown for shrublands (Fig. 5, Filella et al., 2004; Sims et al., 2006a). The exact effects of these complexities on the reflectance signature have yet to be fully understood, but several studies showed that PRI can still function as a seasonal photosynthetic indicator at the ecosystem level in closed canopies (Fig. 5) including coniferous forests (Middleton et al., 2009; Nakaji et al., 2007; Nakaji et al., 2008; Nichol et al., 2000; Nichol et al., 2002; Rahman et al., 2001), broadleaf forests (Naumann et al., 2009; Nichol et al., 2000; Peguero-Pina et al., 2008; Serrano and Peñuelas, 2005) and crops (Inoue et al., 2008; Strachan et al., 2002). It is interesting to highlight that because of this connection to photosynthetic light regulation, PRI provides a remote assessment of instantaneous photosynthetic radiation use efficiency (Gamon et al., 1992; Gamon et al., 1997; Peñuelas et al., 1995) not only in higher plants but also in mosses (Harris, 2008; Lovelock and Robinson, 2002; Van Gaalen et al., 2007). Measurements made on crop canopies have confirmed that by including PRI it is also possible to improve the estimations of GPP (Gitelson et al., 2006; Strachan et al., 2008).

The estimation of radiation use efficiency from remote sensing is a much more recent application than estimations of FPAR. The links between spectral indices such as the NDVI with LAI–FPAR have been studied for much longer time than those of RUE with PRI, and yet, even recent studies do not totally agree over the accuracy of the remote estimations of FPAR, and the confidence of these estimations are not always high (Cohen et al., 2006; Fensholt et al., 2004; Gobron et al., 2006). Even in experiments in highly seasonal ecosystems, the correlation between FPAR and NDVI (Huemmrich et al., 2010) is not much higher ($R^2 = 0.7$) than the correlations between RUE and MODIS PRI reviewed in this study. These observations suggest that the use of the PRI, with a much shorter history, to estimate ecophysiological variables of terrestrial vegetation has a great potential to be converted to a good surrogate of RUE, which could, in turn, contribute to improved estimates of photosynthetic carbon gain in the context of current RUE models.

A remarkable finding of this study is that consistent results between PRI and ecosystem carbon uptake efficiency (Figs. 7–9) emerge even though there are a multitude of possible biochemical, ecological, and physical confounding factors operating at several levels of aggregation. At the leaf level, biochemical processes including photorespiration, PSI cyclic electron transport and nitrate reduction can compete with CO_2 fixation for reductant generated by photosynthetic electron transport (Niyogi 1999) and cause PSII efficiency (PRI) and CO_2 assimilation to diverge. There are even other pigment cycles, like those included in the lutein epoxide cycle especially in tropical trees (Esteban et al., 2009; Matsubara et al., 2008) that could also produce noise in the PRI signal. Despite these potential complications, the results summarized here suggest that the overall photosynthetic system is often sufficiently regulated to maintain consistent relationships between PSII processes and CO_2 fixation (Gamon et al., 1997; Stylinski et al., 2002). Seasonally varying pigment levels or ratios also strongly affect PRI (e.g. Stylinski et al., 2002), but, in some cases, this may actually help explain why PRI often works as well as it does, since varying chlorophyll/carotenoid ratios can covary with xanthophyll pigment levels, and this may enhance the ability of PRI to predict RUE. On the other hand, to the extent that pigment ratios are not closely related to RUE, changing pigment ratios would be a confounding variable, as mentioned above. At the ecosystem level, soil and plant respiration might produce significant scatter in the relationship between PRI and carbon uptake because while PRI tracks gross photosynthesis (i.e. direct carbon uptake not including respiratory loss), conventional flux sampling methods provide the net CO_2 flux (i.e. combined photosynthetic carbon gain and respiratory loss) from the sampling area (Moncrieff et al., 1996). Therefore, ecosystem respiration must be estimated, through the extrapolation of night-time values of ecosystem respiration into the daytime (Reichstein et al., 2005), and across latitudinal gradients respiration variation may largely dominate ecosystem carbon balance (Valentini et al., 2000). Soil respiration either may determine a relatively small part of the gas flux for many ecosystems, or it may be scaled to total biomass and thus stand photosynthesis in others (Gamon et al., 2006).Finally, there are also the confounding physical effects of canopy and stand structure (e.g. LAI changes), leaf movement, sun and viewing angles, soil background, and shadows that can significantly influence the PRI signal (Barton and North, 2001; Gamon et al., 1995). In particular, recent studies are revealing the extent to which PRI reflectance is affected by sun–target–sensor geometry, and stand structure (Asner, 1998; Barton and North, 2001; Drolet et al., 2005; Hall et al., 2008; Hilker et al., 2008).

Despite these many potentially confounding factors, the emerging consistency of the PRI–flux relationship suggests a surprising degree of "functional convergence" of biochemical, physiological, and structural components affecting ecosystem carbon fluxes (Field, 1991; Stylinski et al., 2002). In other words, ecosystems possess emergent properties that allow us to effectively explore their seemingly complex photosynthetic behavior using surprisingly simple optical sampling methods. Understanding the basis for this convergence, unearthing the "ecophysiological rules" governing these responses, remains a primary goal of current research in these topics.

The coexistence of MODIS TERRA and AQUA data since 2002 offers many novel ways to explore the PRI signal as an ecosystem scale RUE indicator. The availability of the sensors on board of the two satellites with revisiting time split by two hours increases the viewing and sun angle possibilities. Therefore the use of data provided by both satellites contributes to improve the coverage of backscatter images. These important sources of data have not yet been greatly exploited simultaneously for vegetation studies. We suggest that the analysis of this data could largely improve the assessment of RUE using the available data since 2002. A severe restriction to this has been the fact that the MODIS PRI bands were originally developed for ocean color and have not been routinely processed for land regions. Reprocessing of MODIS data to yield global PRI time series could greatly assist our ability to understand the utility of spaceborne PRI to improve our assessment of ecosystem carbon uptake.

4.2. PRI and RUE standardization

Our results show that, at the present state, there are reasonably consistent general RUE–PRI relationships (Figs. 7–9). Nevertheless, the methodological differences involved in the studies relating PRI with ecophysiological variables, the differences found in the regressions between different vegetation types and the lack of several comparable studies at the ecosystem level (Fig. 9) still hinder the use of a general RUE–PRI relationship without a proper calibration in each case. A primary difference among different studies is in the formulation of the PRI. We found that several formulations are being used to calculate PRI, including different target wavelengths (530 nm, 531 nm or 539 nm), different reference bands, and a contrasting order of the subtraction with the reference band. The use of different wavelengths could have significant impact on PRI's predictive ability (Inoue et al., 2008). There are probably also scale issues associated with the band selection. PRI using the 570 nm band was useful at a single leaf scale, for which it was originally defined (Gamon et al., 1993b; Peñuelas et al., 1995), but may be less useful at a canopy scale where PRI using the 550 nm band may have a higher predictive ability (Inoue et al., 2008). The use of the sPRI (1 + PRI)/2 added even further difficulties in comparing between studies. In the case of PRI derived from MODIS satellite data, bands 10 (488 nm), 12 (551 nm), 13 (667 nm) and 14 (678 nm) have been used as reference bands, rendering the different studies incomparable.

On the other hand, the calculation of RUE involved a large set of differences among protocols, e.g. different approaches for carbon uptake estimations, use of total irradiance vs. PAR, or total vs. absorbed PAR, and use of different units (MJ or mol), among others. The eddy covariance technique, which is nowadays the most widespread way to measure carbon fluxes at the ecosystem scale, is not free from problems to reach reliable estimates of GPP (e.g. Serrano-Ortiz et al., 2010). For example, at this moment we cannot rule out interferences of abiotic or heterotrophic CO_2 fluxes at the ecosystem scale that can surely mask the true RUE–PRI relationship.

A greater availability of ground spectral measurements and technical improvements would help to make the PRI a more accurate estimator of RUE and therefore a more powerful tool. On one side, a ground PRI measurement network coupled to the eddy covariance towers (FLUXNET or others) could provide data for a definite assessment of the utility of the PRI to estimate RUE. This network should be built on the design of a homogeneous sensor for all the sites with the spectral information to calculate a ground-based PRI and other vegetation indices, with a field of view similar to the footprint of the tower. An effort in that direction has been advocated by the SpecNet community for several years (Gamon et al., 2006), and is currently being conducted at many flux tower sites. In addition, to overcome the problems related to the eddy covariance technique stated before (e.g. abiotic fluxes, separation of photosynthetic and respiratory fluxes) it would be highly desirable to make concurrent measurements of leaf-level photosynthetic rate and of soil respiration. To determine the photosynthetic contribution to the RUE–PRI relationship, and to clarify the influence of various pigment pools on the PRI, optical measurements coupled with pigment measurements of top-canopy leaves should also be made whenever possible. Finally, long-term studies should also evaluate how structural changes (e.g. due to canopy growth or changing leaf display) might be contributing to the measured PRI signals. Consistent pigment and structural measurements are rarely made in long-term studies, yet they remain essential to fully understand the mechanistic basis of the often high RUE–PRI correlation.

On the satellite side, the continued improvement of the spectral resolution provided by the sensors on board satellite platforms will help to obtain better estimations of PRI. The increase of the spectral (<10 nm) and the spatial (<1 km) resolution of the MODIS current products by fusion techniques with images with higher resolutions (Feng et al., 2006; Pohl and Van Genderen, 1998) or the increase of the backscatter view through techniques like the multiple viewing angle of the Chris–Proba satellite (Verrelst et al., 2008) are among the most immediate improvements. The nominal bandwidth of MODIS bands seems broader than the original bands used for the formulation of PRI at the leaf level. However, the FWHM (full width of half maximum) of the MODIS bands are probably not much different from the FWHM of many field sensors that have been used in defining PRI at leaf to stand scales. For example the Spectron (Spectron Engineering, Denver, CO, USA) and UniSpec (PP Systems, Amesbury MA, USA) sensors both have FWHM values of about 10 nm, even though their nominal bandwidth is 2–3 nm (Castro-Esau et al., 2006; Gamon et al., 1993a). So even though the nominal bandwidth is wider, the actual bandwidth is more similar across sensors than it might seem. A full exploration of this topic would require wider availability of airborne and spaceborne hyperspectral sensors (imaging spectrometers), which have been largely unavailable to the broader ecological research community, with the exception of “demonstration” missions (e.g AVIRIS or Hyperion). In the case of the spatial resolution, since most of the eddy covariance towers presently working do not represent an area larger than 1 km^2, and since the footprint varies constantly with windspeed and direction, it is a challenge to produce a satellite-based PRI with a sufficient spatial resolution to match the eddy covariance sampling region. This goal can be achieved by new sensors but also by fusion or simultaneous use of different sources provided by the actual sensors in orbit in order to obtain more information than can be derived from each of the single sensor data alone. In all cases, we advocate a standardization of both RUE (and proxy physiological variables) and PRI measurements and units that allow the comparison of results and the study of possible general relationships. Similarly, careful attention to sun–target–sensor geometry and characterization of stand structure will be needed to fully understand RUE–PRI relationships across ecosystems from contrasting biomes.

4.3. Ecosystem-specific PRI performances

Even if we standardize RUE and PRI measurements and calculation, there are still great differences between terrestrial ecosystems in the degree to which any one environmental factor controls photosynthetic rates and therefore on the capability of each vegetation index to estimate structural or functional variables. Therefore, using the available evidence, we find a wide variation in the degree to which FPAR and RUE individually track the dynamics of temporal and spatial patterns of carbon fluxes. Thus the ability to predict fluxes from these indices for different biomes should be quite variable and will depend upon dominant factors affecting photosynthetic carbon flux (Fig. 11). For some terrestrial ecosystems, FPAR, estimated from vegetation indexes such as NDVI or EVI, or APAR are good surrogates of GPP (e.g. temperate grasslands). For others, there is indeed a positive correlation between FPAR or APAR and GPP, but a high part of the variance of GPP is yet to be explained (Sims et al., 2006b). For those ecosystems, primarily evergreen-dominated ones, PRI provides a useful index of seasonal carbon fluxes because of its connection with RUE, whereas FPAR would presumably be less useful in this context since FPAR or NDVI of evergreen plants changes little over seasonal time scales (Gamon et al., 1995; Garbulsky et al., 2008b) (Fig. 11). On the contrary, PRI may not be effective in detecting ecosystem flux in ecosystems where FPAR closely follows the seasonal dynamic of CO_2 exchange. This seems to be the case in deciduous ecosystems where photosynthetic fluxes closely track seasonal greening and senescence of the landscape (Sims et al., 2006b) or in the Artic tundra, where net CO_2 uptake is often light limited, or in annual croplands and grasslands where seasonal patterns of temperature or moisture constrain production and carbon flux. In those ecosystems, FPAR scales well with photosynthetic rates and NDVI or EVI are closely tied to seasonal carbon dynamics and thus provide a dominant indicator of ecosystem CO_2 uptake assessment (Sims et al., 2006b). In some other ecosystems, such as shrublands, PRI presented problems for ecosystem gas exchange assessment (Fig. 5), in part due to sun angle effects on discontinuous canopies. In desert areas, or in general in areas with high percentage of bare soil, such as some shrublands, shadows and non photosynthetic or dead material can contribute strongly to the reflectance spectrum, rendering PRI less adequate for the estimation of RUE (Filella et al., 2004; Sims et al., 2006a). Thus, in sparsely vegetated regions, adjustment for percent cover may be needed to yield a useful PRI signal. In tropical areas, the atmospheric interference (e.g. cloudiness and aerosols) are often too high to obtain a good PRI signal and moreover, some field studies on tropical species have indicated that PRI does not scale well with ecophysiological variables, possibly due to the lutein epoxide cycle related reflectance (Martin et al., 2007; Rascher et al., 2007). Other tropical field studies have reported clear correlations between PRI and ecophysiological variables, but these relationships vary between species having different strategies for coping with light stress (Gamon et al., 2005).

The available data, although still scarce for most regions of the world, are beginning to show that the usefulness of PRI relative to the FPAR estimations depends on the particular combination of environmental conditions, radiation use efficiencies, and structural characteristics of the different ecosystems in question. Therefore, an effective application of remote sensing to carbon flux requires an ecological understanding of the environmental controls on carbon flux for these different ecosystems, including the contribution of biotic and abiotic factors to the overall PRI signal. Fortunately, a number of methods exist to help address these topics, including radiative transfer models (Jacquemoud et al., 2009), spectral mixture analysis (Numata et al., 2007), and BRDF (bidirectional reflectance distribution function) methods (Hilker et al., 2009a), and greater integration of these techniques with ecophysiological methods are needed to fully understand the best way to apply the PRI signal.

5. Concluding remarks

The available evidence shows that the PRI is a reliable estimator of ecophysiological variables closely related to the photosynthetic efficiency at the leaf and canopy levels over a wide range of species, plant functional types and temporal scales. However, there are also some exceptions and differences in the protocols of the studies that generate doubts about the generalization to satellite observable scales. The use of uniform protocols is needed to generate comparable data and at the end a possible general calibration of the relation PRI–RUE. Further studies are also needed to disentangle the several drivers of the PRI signal, and to resolve the potentially confounding factors so that we can improve the assessment of CO_2 fluxes in many different biomes using hyperspectral or narrow-band remote sensing. While flux towers still represent the current standard for ecosystem carbon flux, we must learn to properly calibrate these fluxes against the new remote sensing products if we are to develop reliable remote sampling methods for ecosystem carbon flux. This remains a significant challenge because flux towers sample in time, whereas remotely sensed imagery samples in space (Rahman et al., 2001). To conduct this calibration, we should blend these sampling domains by applying remote sensing aircraft and satellite measurements at the same temporal and spatial scales as flux tower footprint measurements, which is rarely done. Increased acquisition of coordinated 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. Once we have properly calibrated the surrogates for FPAR and PRI for different ecosystems, we will be able to apply remote sensing to extrapolate in time and space from tower sites. Although there are currently few spaceborne remote sensing instruments of high spectral resolution (note that Hyperion and Chris/Proba are exceptions, but these are demonstration instruments with limited accessibility), this type of data can now be collected from a range of novel helicopter and aircraft instruments (Malenovsky et al., 2009) and from the planned new satellite data. Meanwhile, the 530 nm waveband provided by the satellite-borne MODIS sensor, is starting to be used as a possible RUE indicator at the ecosystem scale across different vegetation types with significant success (Drolet et al., 2005; Drolet et al., 2008; Garbulsky et al., 2008a; Garbulsky et al., 2008b; Goerner et al., 2009; Rahman et al., 2004).

A goal of current studies should be to develop a robust, empirically tested model for ecosystem fluxes driven by a richer degree of remotely sensed information than in the past. This may provide an alternative to complex models that require extensive parameterization and a huge quantity of ground climate data (Running et al., 2004). In this simpler approach, a remote measure of FPAR would be complemented with PRI (a dynamic efficiency factor) to assess the carbon fluxes of the different ecosystems from remote sensing airborne sensors. Since the flux images obtained in this way provide instantaneous maps of gross CO_2 fluxes (Fuentes et al., 2006; Rahman et al., 2001), they have to be extended to daily values. These daily flux estimates could then be integrated throughout the year to derive spatially distributed NPP values for different biomes. This could be achieved with a weekly or biweekly measurement of NDVI and PRI from an aerial or satellite-based sensor, combined with estimated daily variations in PRI from calibration sites on the ground. The existing global network of eddy covariance towers (Baldocchi, 2008) provides an ideal ground data source for such calibration (Garbulsky et al., 2010).

The advances presented here have established the possibility of combining hyperspectral remote sensing and flux tower data to estimate spatially distributed carbon uptake over large areas, thus, up scaling point tower measurements to the regional scale (Drolet et al., 2008; Hilker et al., 2008). However, any application of the PRI at this regional scale requires very careful attention to a number of potentially confounding factors, many of which are discussed above. An important parallel effort will be to better partition net ecosystem carbon fluxes into their respiratory and photosynthetic components. Particularly if we further understand the ecological rules controlling ecosystem respiration and photosynthesis across multiple ecosystems, we should be able to use these new tools to build a better understanding of global carbon fluxes.

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