RESEARCH PAPER

Patterns and controls of the variability of radiation use efficiency and primary productivity across terrestrial ecosystems

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ABSTRACT

Aim The controls of gross radiation use efficiency (RUE), the ratio between gross primary productivity (GPP) and the radiation intercepted by terrestrial vegetation, and its spatial and temporal variation are not yet fully understood. Our objectives were to analyse and synthesize the spatial variability of GPP and the spatial and temporal variability of RUE and its climatic controls for a wide range of vegetation types.

Location A global range of sites from tundra to rain forest.

Methods We analysed a global dataset on photosynthetic uptake and climatic variables from 35 eddy covariance (EC) flux sites spanning between 100 and 2200 mm mean annual rainfall and between −13 and 26°C mean annual temperature. RUE was calculated from the data provided by EC flux sites and remote sensing (MODIS).

Results Rainfall and actual evapotranspiration (AET) positively influenced the spatial variation of annual GPP, whereas temperature only influenced the GPP of forests. Annual and maximum RUE were also positively controlled primarily by annual rainfall. The main control parameters of the growth season variation of gross RUE varied for each ecosystem type. Overall, the ratio between actual and potential evapotranspiration and a surrogate for the energy balance explained a greater proportion of the seasonal variation of RUE than the vapour pressure deficit (VPD), AET and precipitation. Temperature was important for determining the intra-annual variability of the RUE at the coldest energy-limited sites.

Main conclusions Our analysis supports the idea that the annual functioning of vegetation that is adapted to its local environment is more constrained by water availability than by temperature. The spatial variability of annual and maximum RUE can be largely explained by annual precipitation, more than by vegetation type. The intra-annual variation of RUE was mainly linked to the energy balance and water availability along the climatic gradient. Furthermore, we showed that intra-annual variation of gross RUE is only weakly influenced by VPD and temperature, contrary to what is frequently assumed. Our results provide a better understanding of the spatial and temporal controls of the RUE and thus could lead to a better estimation of ecosystem carbon fixation and better modelling.

Keywords
Carbon cycle, climatic controls, eddy covariance, gross primary productivity, radiation use efficiency, remote sensing, terrestrial vegetation.

INTRODUCTION

At present one of the most important endeavours of ecosystem ecologists is to estimate the photosynthetic carbon uptake by vegetation, its spatial and temporal variability and to understand what controls this variability (Schulze, 2006). Estimates of carbon uptake by terrestrial vegetation at different spatial and temporal scales are often based on the radiation use efficiency (RUE) model (Monteith, 1972). This model proposed that photosynthetic uptake of the vegetation depends on the amount of radiation absorbed by the vegetation and on the efficiency with which the vegetation transforms the absorbed radiation into plant biomass, namely the RUE) (Ruimy *et al.*, 1994):

$$GPP = PAR \times FPAR \times RUE \qquad (1)$$

where GPP is the gross primary productivity, PAR is the incident photosynthetically active radiation (400–700 nm), FPAR is the fraction of PAR absorbed by the vegetation, and RUE is the gross radiation use efficiency. The product of PAR and FPAR, namely APAR, is the PAR absorbed by the vegetation. The simplicity of the model makes it attractive and therefore useful for estimating the photosynthetic uptake of vegetation at different spatial and temporal scales. Remote sensing techniques to estimate the photosynthetic uptake of terrestrial vegetation are commonly based on this model because it is possible to estimate FPAR from remotely sensed data (Tucker & Sellers, 1986).

Eddy covariance (EC) methods are an important tool for estimating fluxes of CO_2, water and energy at the ecosystem scale, between terrestrial ecosystems and the atmosphere, and, nowadays, for a large number of locations world-wide (Baldocchi, 2008). Moreover, this methodology can be used to measure fluxes in most vegetation types, thus producing comparable datasets between contrasting sites, which constitutes a valuable dataset for validating remote sensing methods (Baldocchi, 2008).

Different studies have assessed the control of the annual carbon uptake by terrestrial vegetation and the components of the RUE model. Annual FPAR for a wide range of biomes from grasslands to rain forests is known to be positively controlled by rainfall (Garbulsky & Paruelo, 2004). The availability of water is also considered to be a main control on carbon uptake (Reichstein *et al.*, 2007). Above-ground net primary productivity (ANPP) is strongly influenced across biomes by actual evapotranspiration (AET; Rosenzweig, 1968; Lieth, 1975) and also by precipitation (Lieth, 1975; Huxman *et al.*, 2004). The controls on the spatial variability of GPP are currently being elucidated. Firstly, Valentini *et al.* (2000) showed that GPP does not depend on latitudinal changes for a wide range of European forests. Later works (Law *et al.*, 2002) showed that the mean annual temperature (MAT) and the site water balance explain much of the variation in GPP across different biomes. Globally, the GPP of forests increases with higher temperatures and precipitation (Luyssaert *et al.*, 2007a). Others suggest that water availability is the main control of GPP for southern European forests, while temperature is considered the most important control for northernmost forests (Reichstein *et al.*, 2007). Along

a wide diversity of Asian ecosystems, both precipitation and temperature are considered to be the main determinants of GPP (Kato & Tang, 2008).

The seasonal variability of carbon uptake, as related to FPAR and RUE, depends on the structural and physiological constraints on ecosystem functioning. The ability to estimate the seasonality of photosynthetic uptake of vegetation from leaf area or other surrogates such as FPAR depends on the coupling of the seasonality of absorbed radiation and the photosynthetic RUE to the environmental constraints on plant growth (Bondeau *et al.*, 1999). Strong seasonal and positive coupling of leaf area and photosynthesis occur in vegetation types such as tundra (Boelman *et al.*, 2005), temperate deciduous forests (Waring *et al.*, 1995) and annual crops, where leaf area, PAR and climatic limitations also covary throughout the growing season. Although strong correlation between seasonal changes in FPAR and carbon uptake can occur in some evergreen vegetation (Sims *et al.*, 2006), a lack of seasonal change in FPAR and a low correlation with carbon uptake occurs in many evergreen vegetation types such as rainforests or Mediterranean forests (Sims *et al.*, 2006; Garbulsky *et al.*, 2008).

In contrast to our knowledge of the relationship between carbon uptake and FPAR, RUE is a less well known parameter than the other components of the RUE model, particularly for different vegetation types and along different time-scales. It is certainly the most elusive of the model terms, since it is not possible to measure it directly as it depends on estimates of GPP and absorbed radiation (Gower *et al.*, 1999; Schwalm *et al.*, 2006). In general, vegetation type alone is assumed to be the main control of RUE at the annual scale, but there is a large scatter of RUE values within each vegetation type (Ruimy *et al.*, 1994; Gower *et al.*, 1999). Forest age or management practices, for example, have been described as controls of RUE values at annual scales (Landsberg *et al.*, 1997). Nutritional status, such as foliar nitrogen concentration, could be another driver of spatial and temporal variability in RUE (Mäkelä *et al.*, 2008; Ollinger *et al.*, 2008). However, this may operate mostly at local scales since there is a wide dispersion in the data on the relation between foliar nitrogen concentration and the maximum rate of photosynthesis among different vegetation types (Woodward & Smith, 1995). There is little evidence for relationships between the spatial variability of RUE for different vegetation types and climatic or biogeochemical controls (Turner *et al.*, 2003; Still *et al.*, 2004). Furthermore, a substantial number of those relationships were derived from models rather than using evidence from actual measurements.

At short time-scales (hours to days), environmental stresses (water, temperature) have been shown to modify RUE (Russell *et al.*, 1989). For annual crops, variability in RUE was negatively related to vapour pressure deficit (VPD, Kiniry *et al.*, 1998) and positively related to temperature (Andrade *et al.*, 1993). Variability in RUE was also positively related to temperature in forests (Landsberg & Waring, 1997). For other vegetation types such as shrublands, only a few studies have examined the temporal variation of gross RUE (Sims *et al.*, 2005; Turner *et al.*, 2005), and its biophysical controls are not yet well understood. Never-

theless, several terrestrial models that estimate the seasonality of primary productivity use RUE as an input (Haxeltine & Prentice, 1996; Ruimy *et al.*, 1999). The maximum or potential RUE is set as a constant and is subsequently downregulated by minimum temperature and different estimators of water stress in models that estimate GPP (Potter *et al.*, 1999; Running *et al.*, 2004; Yuan *et al.*, 2007; Mäkelä *et al.*, 2008). Different strategies to define the maximum RUE values and each of the coefficients that account for the stress effects are used to estimate the actual RUE. The maximum RUE is commonly set as a universal invariant across sites and biomes or it is defined for each vegetation type. This assumption of a global constant maximum RUE for different sites within a given biome is far from optimum and is the possible cause of the low performance of the photosynthetic uptake models (Heinsch *et al.*, 2006). The surrogates of water stress to estimate the actual RUE from the downregulation of the maximum RUE vary between models and, as far as we know, to date there has been no evaluation of the different strategies. The possibility of estimating FPAR from several remotely sensed vegetation indices [i.e. the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI)], adds another dimension to the problem.

The EC technique provides an excellent opportunity to test the relationships between carbon uptake and its environmental drivers. In addition, remote sensing data provide a way to gather intercepted radiation from around the globe. In this study we provide evidence about the gross RUE variability estimated from carbon flux data provided by EC flux sites and FPAR estimates from satellite observations in rain forests, deciduous and evergreen forests, grasslands, crops and tundra. The objectives of this study were to analyse and synthesize: (1) the spatial and temporal variability of GPP and RUE for a wide range of vegetation types and from two surrogates for FPAR; and (2) the climatic controls of RUE at global and local scales. We sought to answer whether the spatial variability of mean climatic variables (i.e. precipitation, temperature and AET) are quantitatively more important determinants of the gross RUE than the vegetation types. Furthermore, we hypothesized that the strength of the relationships between temporal variability of gross RUE throughout the growing season and the climatic variables are related to the mean climatic characteristics of the sites.

MATERIALS AND METHODS

We analysed EC data of carbon fluxes and FPAR MODIS (Moderate Resolution Imaging Spectroradiometer) Terra data. We synthesized data from 35 sites included in the networks Ameriflux (http://public.ornl.gov/ameriflux/), CarboEurope, CarboAfrica and TCOS-Siberia (http://gaia.agraria.unitus.it/database/carboeuropeip/). These sites represent different vegetation types distributed throughout Europe, Asia, Africa and America (Table 1, Fig. 1, see also Appendix S1 in Supporting Information) and cover a great proportion of the global climatic space defined by the range of MAT and mean annual precipitation (MAP). The selected sites comprised homogeneous stands of each vegetation type and were large enough to gather the

spectral reflectance of the stand with the satellite images. We discarded sites representing small stands and those adjacent to contrasting land covers (i.e. water bodies, urban) to minimize problems or errors related to tower footprint. Different periods between January 2001 and December 2007 were analysed including at least one complete growing season for each site (Table 1), making a total of 90 growing seasons.

GPP was estimated from the Net Ecosystem Exchange (NEE) fluxes measured at the EC towers with 30′ resolution using a standardized partitioning method for all the sites as described by Reichstein *et al.* (2005) and Papale *et al.* (2006). We discarded GPP values lower than 0.1 μmol m^{-2} s^{-1} for our analysis. An average for the 8-day composites of the half-hour values for GPP (gC m^{-2} day^{-1}; gC = grams of carbon) and incoming PAR (MJ m^{-2} day^{-1}), derived from the EC tower data, was calculated for days having MODIS FPAR data (MOD15A2). These images consist of an 8-day value at 1-km spatial resolution provided by the MODIS team (Myneni *et al.*, 2002). For all the MODIS data, quality flags were checked to discard low-quality images. The basic temporal resolution of the analysis is 8 days, which corresponds to that of the MOD15A2 images. Theoretically, this represents 46 images per year; however, we obtained fewer than this for each year and site owing to a lack of data or at times the bad quality of the MODIS or the EC data. We defined the 8-day gross RUE as:

$$\text{RUE}\,(\text{gC MJ APAR}^{-1}) = \text{GPP} \times \text{FPAR}^{-1} \times \text{PAR}^{-1}. \qquad (2)$$

The average annual RUE was calculated as:

$$\begin{aligned}\text{annual RUE }(\text{gC MJ APAR}^{-1}) &= \text{total annual GPP} \\ (\text{gC m}^{-2}\text{ year}^{-1}] &\times \text{APAR}^{-1}\,(\text{MJ m}^{-2}\text{ year}^{-1}).\end{aligned} \qquad (3)$$

To minimize the uncertainties derived from the known quality problems of MODIS FPAR data (e.g. underestimation of winter FPAR in boreal forest; Garrigues *et al.*, 2008) in the calculation of the annual RUE in the northernmost sites (i.e. tundra and boreal sites) we only included GPP and APAR data for the growing season. Since the EVI showed better performance than the MODIS FPAR as an estimator of FPAR for certain vegetation types (Zhang *et al.*, 2006), we also calculated the RUE derived from EVI (RUE EVI), considering EVI = FPAR (Garbulsky *et al.*, 2008). We calculated the EVI from the 8-day MODIS surface reflectance data [MOD09A1 band 1 (620–670 nm), band 2 (841–876 nm), band 3 (459–479 nm)] as EVI = 2.5 (band 2 − band 1)/(band 2 + band 1 − 7.5 band 3). Finally, we defined the maximum RUE (gC MJ APAR^{-1}) calculated from each FPAR estimator for each site as the maximum gross RUE attained by the vegetation for all the growing seasons analysed. We also calculated the annual GPP/PAR ratio as an overall estimator of the ecosystem efficiency with which the incident radiation is used.

We analysed the climatic controls of GPP and RUE at the inter-annual and intra-annual scales. For the annual analysis, we calculated the annual value for each of the variables: GPP, gross RUE and maximum gross RUE and the annual precipitation, annual temperature and annual actual evapotranspiration for

Table 1 Main vegetation type, period analysed and reference for the sites included in the analysis (see Appendix S1 for further details).

Site and period analysed	Vegetation category	Reference
Atqasuk (USA) 2006	Tundra	Oechel *et al.* (2000)
Cherski (Russia) 2003	Tundra	Merbold *et al.* (2009)
Santa Rita mesquite (USA) 2004–05	Shrubland	Scott *et al.* (2009)
Fort Peck (USA) 2001–03	Grassland	Meyers (2008)
Vaira (USA) 2001–02	Grassland	Baldocchi *et al.* (2004)
Lethbridge (Canada) 2002–03	Grassland	Flanagan *et al.* (2002)
Goodwin Creek (USA) 2003	Grassland	Meyers (2008)
Dripsey (Ireland) 2003	Grassland	Jaksic *et al.* (2006)
Tchizalamou (Congo) 2006–07	Grassland	Merbold *et al.* (2008)
Hakasia steppe (Russia) 2004	Grassland	Belelli Marchesini *et al.* (2007)
Tonzi (USA) 2002–03	Savanna	Baldocchi *et al.* (2004)
Maun (Botswana) 2000–01	Savanna	Veenendaal *et al.* (2004)
Demokeya (Sudan) 2007	Savanna	Ardö *et al.* (2008)
Bondville (USA) 2003–05	Annual crops	Hollinger *et al.* (2005)
Roccarespampani (Italy) 2002–03	Deciduous temperate forest	Rey *et al.* (2002)
Hesse (France) 2001–03	Deciduous temperate forest	Granier *et al.* (2002)
Hainich (Germany) 2002–03	Mixed temperate forest	Kutsch *et al.* (2008)
Sylvania (USA) 2003–05	Mixed temperate forest	Desai *et al.* (2005)
Bartlett Experimental Forest (USA) 2004–05	Mixed temperate forest	Jenkins *et al.* (2007)
Loobos (Netherlands) 2001–03/05	Evergreen temperate forest	Dolman *et al.* (2002)
Howland Forest main tower (USA) 2000–04	Evergreen temperate forest	Hollinger *et al.* (2004)
Griffin (Scotland) 2000–01	Evergreen temperate forest	Clement *et al.* (2003)
Wind River crane site (USA) 2000–04	Evergreen temperate forest	Chen *et al.* (2002)
Fyodorovskoye (Russia) 2002–03	Evergreen temperate forest	Milyukova *et al.* (2002)
UCI 1981 (Canada) 2002	Evergreen boreal forest	Goulden *et al.* (2006)
UCI 1964 burn site (Canada) 2002	Evergreen boreal forest	Goulden *et al.* (2006)
Sodankyla (Finland) 2001–03	Evergreen boreal forest	Aurela(2005)
Zotino (Russia) 2002	Evergreen boreal forest	Tchebakova *et al.* (2002)
Yatir (Israel) 2001–02	Evergreen mediterranean forest	Maseyk *et al.* (2008)
Castelporziano (Italy) 2001–05	Evergreen mediterranean forest	Garbulsky *et al.* (2008)
Puechabon (France) 2001–04	Evergreen mediterranean forest	Allard *et al.* (2008)
Mize (USA) 2001–03	Evergreen subtropical forest	Clark *et al.* (2004)
Austin Cary (USA) 2005	Evergreen subtropical forest	Powell *et al.* (2008)
Donaldson (USA) 2001 – 03	Evergreen subtropical forest	Powell *et al.* (2008)
Santarem km 67 primary forest (Brazil) 2002–03	Rainforest	Saleska *et al.* (2003)

the corresponding period and long-term MAP and MAT from a global climatic model (W. Cramer, pers. comm., Leemans & Cramer, 1991, http://www.pik-potsdam.de/members/cramer/climate/). ANCOVAs (R Development Core Team, 2008) were used to analyse the contribution of each climatic variable, the vegetation type and their interactions to the spatial variability of RUE.

For the analysis throughout the growing season, we evaluated the controls on the gross RUE by analysing the correlations between RUE and different environmental variables. We averaged the climatic and the flux variables to match the 8-day temporal resolution of the MODIS FPAR and EVI data. We included for this analysis the precipitation and temperature and different estimates of the annual water stress: vapour pressure deficit (VPD), evaporative fraction (EF), potential evapotranspiration (PET), actual evapotranspiration (AET) and the AET/PET ratio. The VPD was calculated from temperature and relative humidity measurements at the EC towers. EF is a

measure of the portion of the available energy used for evapotranspiration and was calculated as LE/(LE + H), where LE is the latent heat (the amount of energy released or absorbed by water during a change of state) and H is the sensible heat flux, both of which are measured at the EC towers. PET was estimated using the Jensen and Haise methodology (Vörösmarty *et al.*, 1998) using air temperature and incident radiation. AET was calculated from the EC LE flux measurements divided by the specific latent heat of vaporization of water. Akaike's information criterion (AIC) was used to select the best correlations between RUE and the environmental variables.

RESULTS

For all sites, there was an appreciable range of long-term MAP (121 mm < MAP < 2252 mm) and MAT (−10.9 °C < MAT < 26.3 °C). The mean annual GPP ranged from 122 gC m^{-2} year^{-1} in the tundra site to 3125 gC m^{-2} year^{-1} in the rain forest site.
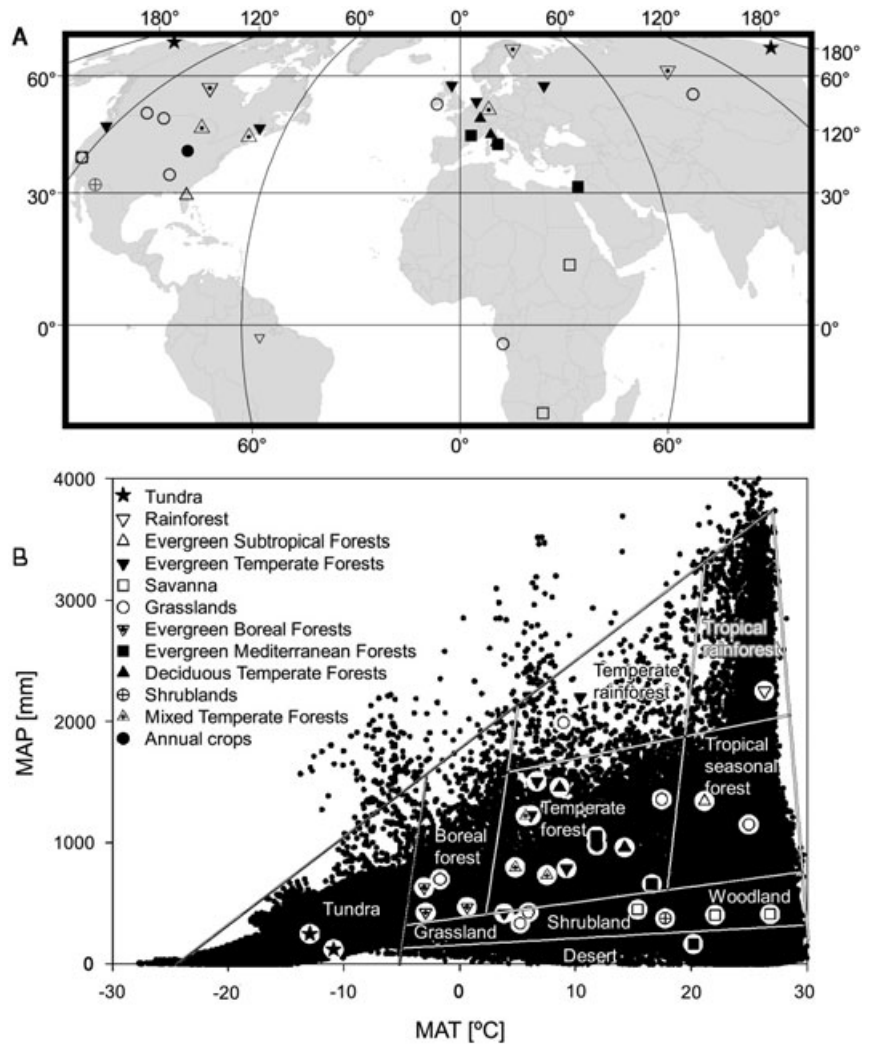
Figure 1 (a) Map of the location of the sites studied (Mollweide projection, central meridian 0°) and (b) their distribution along the climatic space defined by long-term mean annual temperature (MAT) and mean annual precipitation (MAP). The vegetation type symbols represent each site and black points represent 0.5° × 0.5° land pixels from a global climatic database (W. Cramer, pers. comm.; Leemans & Cramer, 1991). Limits between vegetation types are schematic.
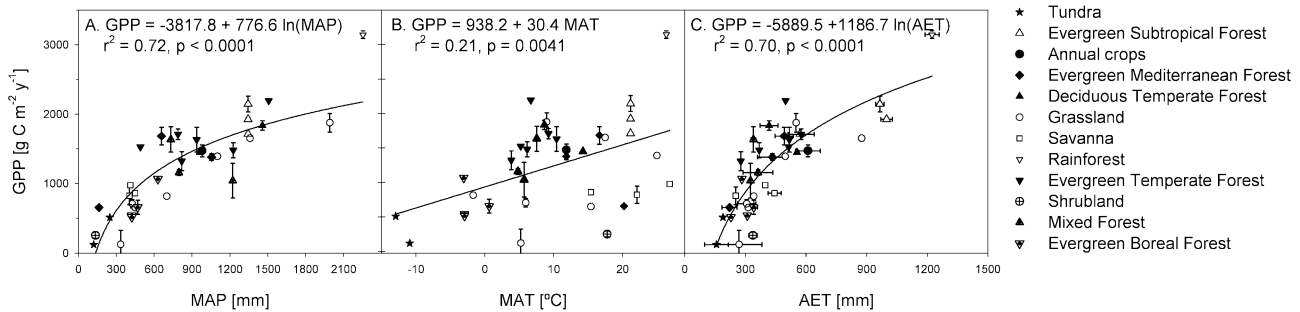

Figure 2 Relationships between gross primary productivity (GPP) and the climate variables. Precipitation (MAP) and temperature (MAT) are long-term annual means from Leemans & Cramer (1991) and actual evapotranspiration derived from eddy covariance towers (AET) is the mean for the studied period. Error bars show the standard errors of GPP and climatic variables for the included growing season for each site.

GPP was positively correlated with MAP, which accounted for 72% of its variance in a logarithmic relationship (Fig. 2a); in contrast, the actual precipitation for the corresponding analysed period accounted only for 56% ($P < 0.001$) of the variance. GPP for all the biomes showed a positive relationship with MAT, with a lower coefficient of determination of 21% (Fig. 2b). In a multiple regression, MAP, MAT and their interaction accounted for 76% of the variability in GPP (GPP = $-2615.9 - 79.3$MAT $+ 552.4$ ln(MAP) $+ 14.8$ ln(MAP)MAT). In contrast, MAT accounted for a great proportion of the spatial variability of GPP
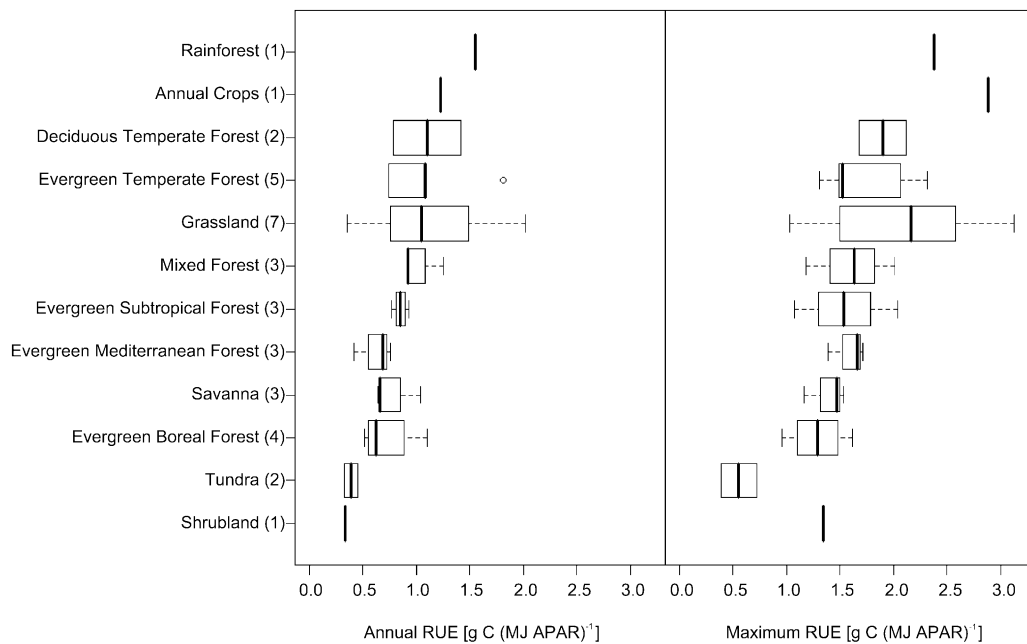
Figure 3 Average gross annual and maximum gross radiation use efficiency (RUE) for the different vegetation types. The numbers of sites included for each vegetation type are shown in brackets. APAR is the product of photosynthetically active radiation (PAR) and the fraction of photosynthetically active radiation absorbed by the vegetation (FPAR). Boxes represent 50% of the data, and the whiskers represent the minimum and maximum values.

when analysing only the subset of the forests sites (GPP = 915.6 + 60.3 MAT; $r^2 = 0.76$; $P < 0.0001$; $n = 18$). When also including the three afforested sites, MAT accounted only for 45% of the variability (GPP = 993 + 49.2 MAT; $r^2 = 0.46$; $P < 0.0001$; $n = 21$). The relationship between GPP and MAT was also strong when analysing the subset of the northernmost forests (> 45° N) with the lowest incoming radiation (GPP = 925.9 + 90.5 MAT; $r^2 = 0.68$; $P < 0.0001$; $n = 14$). AET also accounted for a high proportion of the variability of GPP for all the sites ($r^2 = 0.70$, Fig. 2c).

The average gross annual RUE varied between vegetation types from 0.4 gC MJ^{-1} in the tundra to 1.5 gC MJ^{-1} in the rainforest site (Fig. 3) and the maximum RUE between 0.55 in the tundra and 2.8 gC MJ^{-1} in the annual crops site. Mean and maximum RUE was most variable in grassland. Gross annual RUE varied across vegetation types from 0.34 gC MJ^{-1} in the shrubland to 2.01 gC MJ^{-1} for a grassland site. Gross RUE calculated from EVI presented similar patterns with higher values for both the annual mean and for the maximum RUE (see Appendix S2 in Supporting Information). Annual RUE EVI was highly correlated with the RUE FPAR across sites ($r = 0.82$, $n = 35$); the correlation was weaker between the maximum RUE EVI and FPAR ($r = 0.52$, $n = 35$).

MAP accounted for the greatest proportion of the variability of mean RUE FPAR (Table 2). Actual precipitation accounted for a greater proportion of the variability of maximum RUE than long-term MAP. The annual gross RUE was not correlated with temperature and AET accounted for a small part of the spatial variability in RUE (Fig. 4a). The vegetation type and its interaction with the climatic variables did not significantly

account for the variability of RUE (Table 2). The relationships between RUE and precipitation did not differ between forests and non-forest sites when considering long-term climate averages or the climate variables for the specific analysed period. RUE was not influenced by temperature, either by interaction of the vegetation type with the climatic variables or by interaction between precipitation and temperature. The dynamics of gross RUE showed a wide range of seasonal patterns between sites. Annual precipitation was the best explanatory variable for maximum RUE (Table 2), which increased along the precipitation gradient (Fig. 4b). Temperature, instead, did not account for any of the variability of maximum RUE. AET explained a smaller portion of the variability than the precipitation (Fig. 4b). Precipitation was also the most important variable to explain the variability of RUE EVI (see Appendix S3); however, precipitation accounted for a lower proportion of the variability of RUE EVI compared with RUE FPAR. Moreover, vegetation type was an important variable to explain the variability of mean and maximum RUE EVI.

The relationships between annual and maximum RUE and the climatic variables were similar to the relationships found using the GPP/PAR ratio, instead of GPP/APAR (data not shown). We also analysed the GPP/PAR ratio as a measure of RUE that provides the overall ecosystem efficiency, instead of the efficiency with which the absorbed radiation is used by the vegetation. The annual mean FPAR accounted for approximately half of the spatial variability of the annual GPP/PAR (results not shown). From the three variables included in the radiation use efficiency model, the FPAR accounted for 62% of the GPP spatial variability. RUE accounted for 53% and the

Table 2 Analysis of covariance for mean annual radiation use efficiency (RUE) and maximum RUE across vegetation type (forest, $n = 21$; non-forest, $n = 14$) and climatic variables and their interactions: long-term mean annual precipitation (MAP) and long-term mean annual temperature (MAT), and precipitation (precip) and temperature (temp) for the analysed periods.

Response:	Mean RUE					Maximum RUE				
	d.f.	Sum of squares	F value	P value	%SS	d.f.	Sum of squares	F value	P value	%SS
Forest	1	0.000	0.002	0.961	0.0	1	0.000	0.000	0.976	0.0
ln(precip)	1	3.215	25.150	< 0.0001	46.1	1	7.909	47.986	< 0.0001	59.7
temp	1	0.060	0.470	0.499	0.9	1	0.019	0.117	0.734	0.1
Forest × ln(precip)	1	0.009	0.068	0.796	0.1	1	0.095	0.581	0.452	0.7
Forest × temp	1	0.017	0.136	0.715	0.2	1	0.572	3.472	0.073	4.3
ln(precip) × temp	1	0.100	0.784	0.383	1.4	1	0.025	0.156	0.695	0.2
Residuals	28	3.579				28	4.615			
Total		6.981					13.238			
Forest	1	0.000	0.003	0.956	0.0	1	0.000	0.000	0.980	0.0
ln(MAP)	1	3.841	37.825	< 0.0001	55.0	1	5.091	20.995	< 0.0001	38.5
MAT	1	0.004	0.043	0.836	0.1	1	0.530	2.186	0.150	4.0
Forest × ln(MAP)	1	0.288	2.832	0.103	4.1	1	0.578	2.383	0.134	4.4
Forest × MAT	1	0.001	0.005	0.943	0.0	1	0.092	0.380	0.542	0.7
ln(MAP) × MAT	1	0.003	0.026	0.872	0.0	1	0.155	0.639	0.431	1.2
Residuals	28	2.844				28	6.790			
Total		6.981					13.238			

incident PAR did not correlate with GPP (Fig. 5). APAR by itself accounted for 45% of the spatial variability of GPP.

Throughout the growing season, RUE FPAR and RUE EVI had a range of responses to the variability of the environmental factors depending on the site. The coefficients of correlation varied from −0.8 to 0.9 and non-significant correlations, and the slopes of the relationships also varied. Examples of the relationships between RUE FPAR and the environmental variables for contrasting vegetation types can be seen in Fig. 6. The general patterns of the relationships were similar when analysing RUE FPAR or RUE EVI (see Appendix S4). Strong and positive relationships, varying with the environmental variable ($0.77 \leq r \leq 0.95$), were found for the correlations between RUE FPAR and RUE EVI when comparing all the sites.

During the 8-day periods RUE correlated poorly or not at all with precipitation, presumably because of the large buffering provided by antecedent soil water content. There was contrast between the negative effects of within-season temperature and VPD variation on RUE in the warmer sites (i.e. rain forest, savannas, Mediterranean forest and probably subtropical forest) and the positive effects in the cooler ecosystems. Depending on the site, VPD and AET accounted positively or negatively for part of the variation in RUE. MAT accounted for the variability of the temporal relationship between RUE and temperature. In the colder ecosystems, RUE increased with temperature, AET and AET/PET. In the savanna RUE decreased with temperature and increased with AET and AET/PET. In the Mediterranean forest, RUE also decreased with temperature and AET, but increased with AET/PET. EF accounted for the variability of RUE FPAR for the largest number of sites (28 sites) compared with other variables and with the highest coefficient of correlation for 22 of them (see Table S1). AET accounted for the vari-

ability of RUE EVI at the greatest number of sites (28 sites), but EF also accounted for a large number of sites (27).

Overall, EF was the single variable that best explained the variability of RUE FPAR and RUE EVI for all the sites and periods ($P < 0.0001$). However, more complex models, including more than one variable, presented lower AIC values.

DISCUSSION

GPP was primarily related to MAP in our analysis. In accordance with global patterns in ANPP (Huxman *et al.*, 2004) and net primary productivity (NPP, Garbulsky & Paruelo, 2004) GPP is also influenced at a global scale by MAP. We also found that actual evapotranspiration explains a great part of the spatial variability of GPP, in agreement with other previous works (Rosenzweig, 1968; Lieth, 1975). Long-term average climatic conditions, represented by MAP, and not the actual rainfall for the analysed period (< 6 years), showed better correlation with GPP. This result is probably evidence for the low capacity of each vegetation type to increase or decrease GPP with changes in water availability at the annual scale, because of the limitations imposed by the structure of the vegetation (e.g. rooting depth, density of meristems).

Previous studies showed a diversity of biotic and abiotic controls of GPP (Valentini *et al.*, 2000; Law *et al.*, 2002; Luyssaert *et al.*, 2007a; Magnani *et al.*, 2007; Reichstein *et al.*, 2007; Kato & Tang, 2008). Much of the divergence in those results is probably due to the difference in the environmental distribution of the datasets, the successional or disturbance stage of the vegetation and management practices. The correlation between precipitation and temperature of the sites selected in some of the datasets in the published analyses probably led to an overestimation of
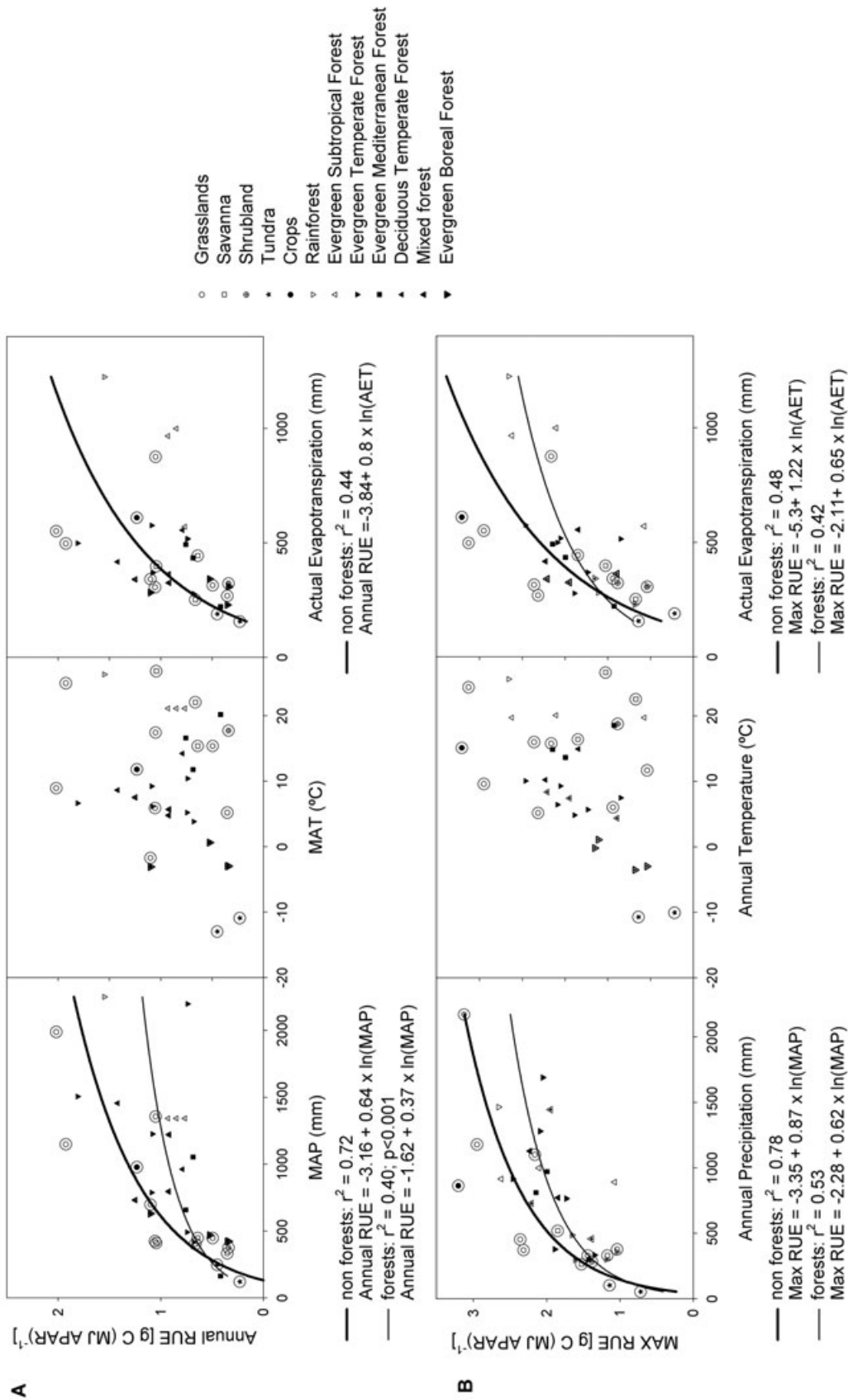
Figure 4 (a) Relationship between annual radiation use efficiency (RUE) and the long-term mean climate variables for forests and non-forest sites. (b) Relationship between the maximum seasonal RUE and the annual climate variables for forests and non-forest sites. Precipitation and temperature data for each site are the mean annual for the periods studied. Circled symbols represent the non-forest sites and thick lines are the regressions for non-forest sites and tiny lines are the regressions for forest sites. Presented relationships are significant $P < 0.01$. MAP, mean annual precipitation; MAT, mean annual temperature; AET, actual evapotranspiration.
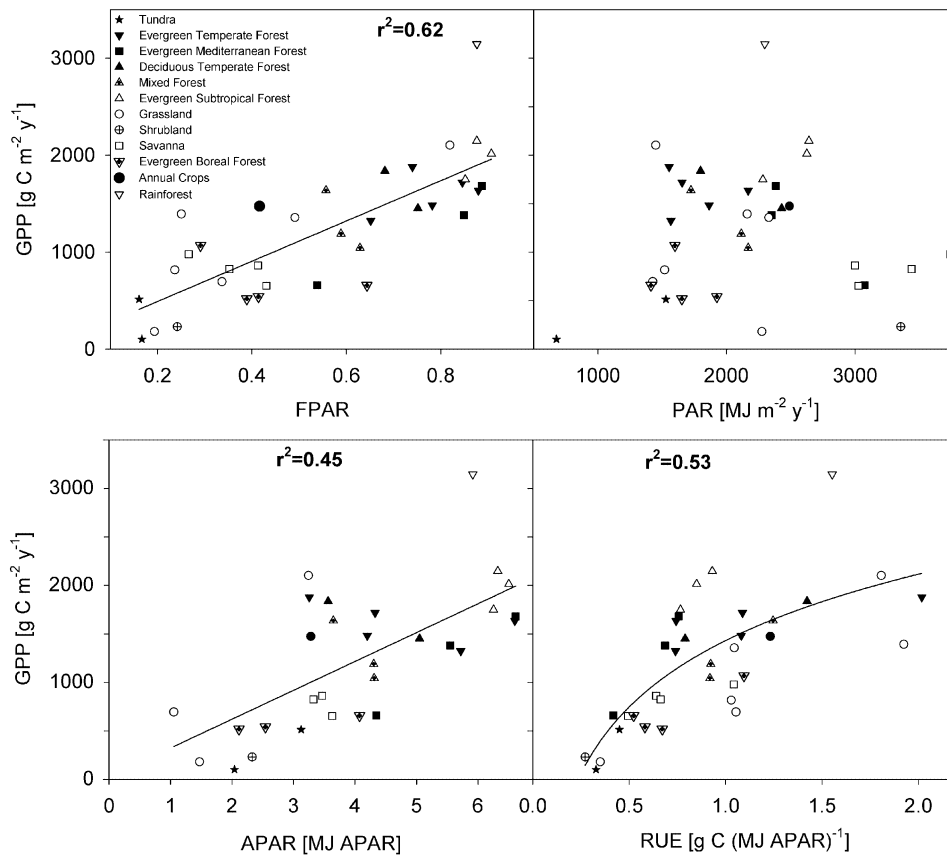
Figure 5 Relationship between average annual gross primary productivity (GPP) and the three components of the radiation use efficiency model: the average annual fraction of photosynthetically active radiation (PAR) absorbed by the vegetation (FPAR), PAR and gross radiation use efficiency (RUE). APAR is the product of photosynthetically active radiation (PAR) and the friction of photosynthetically active radiation absorbed by the vegetation (FPAR).

the actual importance of temperature as a main control of GPP. Therefore, to decouple the role of temperature and precipitation, we included in our analysis sites with high temperature and low precipitation, and others with low temperature and high precipitation, thus reducing the correlation between MAP and MAT (Fig. 1; $n = 35$; $r^2 = 0.11$; $P = 0.014$). Our results show that water availability is more important than temperature and vegetation type for ecosystem processes along broad biogeographic patterns. Temperature is also an important driver of the GPP when analysing forest biomes and with increasing importance in the coldest and energy-limited forests, as suggested by previous studies (Valentini *et al.*, 2000; Law *et al.*, 2002; Luyssaert *et al.*, 2007a; Magnani *et al.*, 2007; Reichstein *et al.*, 2007). Obviously, our results are sensitive to the partitioning method used to derive GPP from the NEE measured at the EC sites. However, previous works using the same methodology showed that environmental variability is similar when using NEE at midday or midnight (Luyssaert *et al.*, 2007b; Reichstein *et al.*, 2007).

Our results suggest that spatial variability of both the average and maximum gross annual RUE is controlled firstly by precipitation, and secondly by the vegetation type. In general, ecosystems dominated by trees had lower RUE values than the vegetation types dominated by grasses or herbs. For both veg-

etation types, the annual RUE was primarily related to MAP and the maximum RUE to the yearly precipitation. These results are the first evidence showing that RUE is controlled by climatic factors at global scales. Therefore, our results are important because, although it is well known that climate and global change could affect FPAR (Nemani *et al.*, 2003; Paruelo *et al.*, 2004; Ciais *et al.*, 2005), there is not much evidence about the impact of these changes on the RUE of different vegetation functional types. Previous studies showed the spatial variability of RUE only for ANPP or NPP (Landsberg *et al.*, 1997; Goetz & Prince, 1999; Gower *et al.*, 1999), mainly because of the limitations in estimating RUE for below-ground processes. They suggested that less productive sites, in terms of their NPP, presented lower RUE values (Field *et al.*, 1995; Paruelo *et al.*, 1997), but the relationship with environmental factors was not tested. The variability of annual gross RUE across different biomes in this study was within the range of values observed in previous studies for different ecosystems (Lagergren *et al.*, 2005; Sims *et al.*, 2005; Turner *et al.*, 2005; Schwalm *et al.*, 2006; Li *et al.*, 2008; Mäkelä *et al.*, 2008). In contrast to total annual FPAR, which is positively related to MAP and is not related to temperature (Garbulsky & Paruelo, 2004), the spatial variability of RUE is commonly assigned to vegetation type (Ruimy *et al.*, 1994;
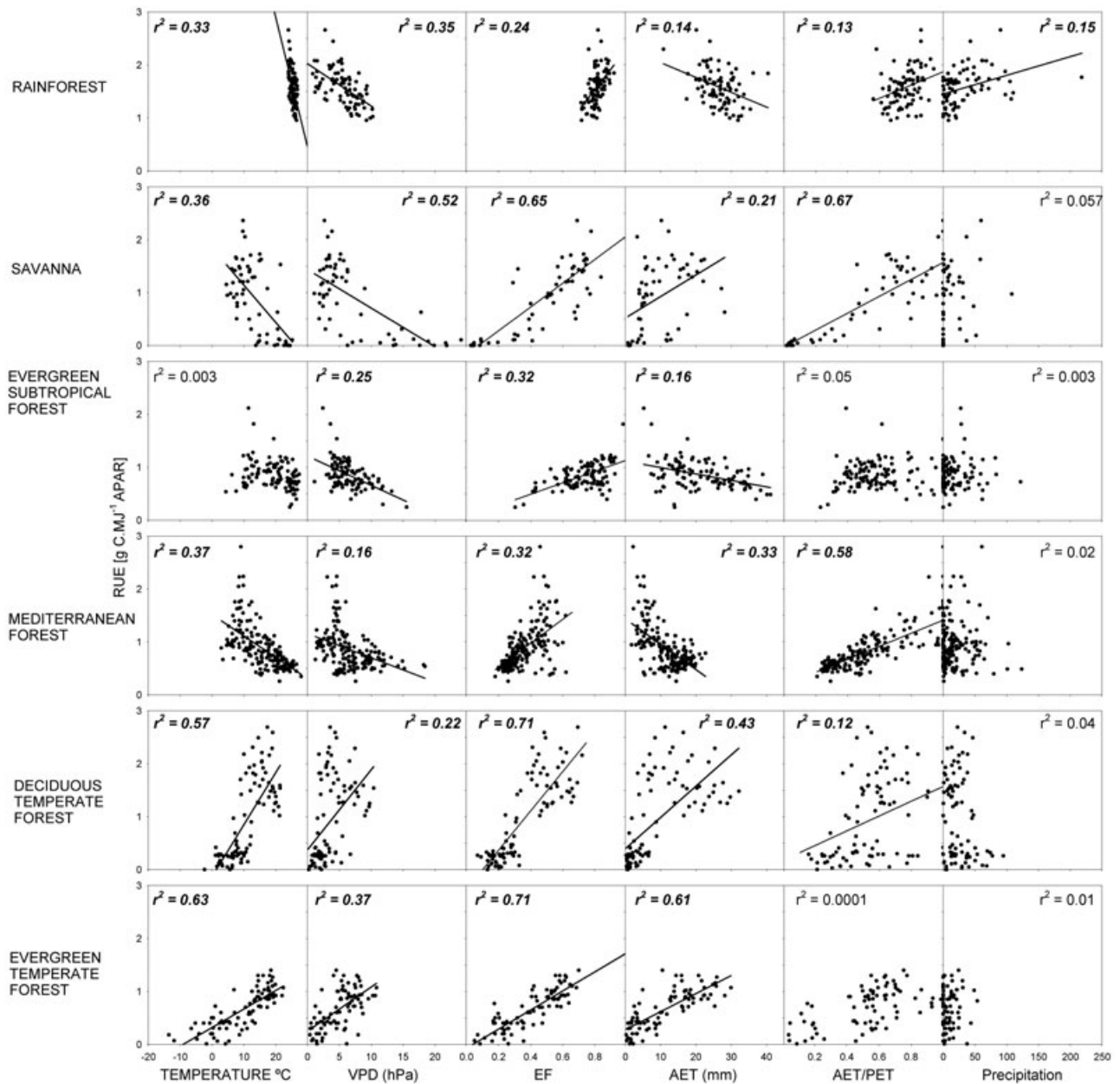
Figure 6 Relationships for 8-day periods between gross radiation use efficiency calculated using the fraction of photosynthetically active radiation absorbed by vegetation (RUE FPAR) and mean temperature, mean vapour pressure deficit (VPD), mean evaporative fraction (EF), sums of actual evapotranspiration (AET), mean ratio of actual evapotranspiration to potential evaporation (AET/PET) and precipitation sums for six contrasting ecosystems. The coefficients of determination (r^2) for significant linear relationships ($P < 0.001$), are highlighted in bold.

Gower *et al.*, 1999) with very few studies linking the RUE with biophysical variables. Annual RUE has been reported to have a positive relationship with mean temperature for a temperature range between −4 and 10°C and for diverse biomes (Schwalm *et al.*, 2006). Our results showed a similar pattern for that temperature range, but with larger data dispersion for warmer areas.

Our results also demonstrated that the maximum gross RUE is regulated by global climatic patterns determined by precipitation (Fig. 4b). These results are particularly important, for example, with regard to the MODIS methodology (MOD17) for

estimating GPP (Heinsch *et al.*, 2006). We showed that the maximum RUE varies greatly, not only with vegetation type but also with the precipitation. Moreover, we found that the maximum RUE values for annual crops are higher than for any type of forest, which contradicts the maximum RUE assumptions of the MOD17 methodology. These assumptions were also previously questioned by Turner *et al.* (2003).

The diversity in the annual dynamics of gross RUE is the main factor controlling the differences in the relationships between annual and maximum RUE and precipitation. Sites with similar

annual RUE do not necessarily present the same maximum RUE (Fig. 4a,b) because of the differences in the seasonality of GPP and APAR produced by a wide range of environmental constraints. GPP, and therefore RUE, are much more variable in shrubland than in tundra, probably because of the high GPP rates during a short period of reduced water availability in a hot and dry climate, compared with lower GPP rates but a longer growing season in the tundra.

Different algorithms for estimating GPP consider maximum RUE by biome and use the temperature and an estimator of water availability to downregulate this maximum RUE (Running *et al.*, 2004; Yuan *et al.*, 2007). Thus, it is critical to make the correct assessment of the maximum RUE and to determine which are the best variables to use to downregulate that maximum RUE. Relationships of actual RUE with temperature and VPD showed high dispersion, suggesting that considerable noise can be generated with the downregulation of maximum RUE (Fig. 6). In any case the relationships between RUE and temperature and VPD are different for all the sites analysed. Thus, the use of another variable to estimate the water status of the vegetation (e.g. AET/PET, EF) is probably more meaningful for arriving at the best estimate of RUE. It is clear from our analysis that the ability to estimate the seasonality of gross RUE using the variables examined varies with gradients of the environmental factors. These relationships exhibited a high data dispersion and EF is the single best estimator for all the sites. It is important to highlight that whereas temperature influenced the temporal variability of RUE, the spatial variability of temperature did not appear as a main determinant of annual or maximum RUE. These results corroborate the temperature limitation of the RUE only in the coldest sites. For hot humid ecosystems, e.g. rainforest and evergreen subtropical forests, our results suggest that none of the variables analysed are confident surrogates for the actual RUE. In such cases, it would be necessary to analyse other environmental variables as controls of the seasonal variation of gross RUE, such as the ratio of diffuse radiation to the total incident radiation (Law *et al.*, 2002; Knohl & Baldocchi, 2008). Other remote sensing information not included in this analysis, such as the photochemical reflectance index (PRI; Garbulsky *et al.*, 2008) or surface temperature (Sims *et al.*, 2007), are promising new avenues for producing better remote sensed estimations of RUE and therefore of GPP.

In conclusion, the analysis of carbon uptake estimated by EC fluxes in terrestrial ecosystems over a wide range of latitudes, environments and vegetation types supports the idea that functioning of vegetation that is adapted to its local environment is more constrained by water availability than by temperature. The spatial variability of GPP can be largely explained by precipitation or by AET. Annual gross RUE and maximum gross RUE are positively related to long-term MAP along a wide environmental gradient. These results show that the RUE is globally controlled by climatic constraints and that the ecosystem type plays a secondary role as a control of RUE. Temperature only appears to determine a maximum limit. To date, this is the first study to relate gross RUE estimations based on ground and satellite measurements to global climatic controls.

It represents an important step forward in gross RUE estimation by providing information on a fundamental factor for estimating GPP. Variation of RUE throughout the year, although greatly dispersed, was linked to water availability and temperature depending on the climatic constrains of the ecosystems. Our results showed that EF and AET are the most confident estimators of RUE for all the ecosystems. However, overall, EF was a better estimator of RUE than other surrogates, the VPD and temperature.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Location, main vegetation type, references and standardized climatic features of the sites included in the analysis.

Appendix S2 Average gross annual and maximum gross radiation use efficiency (RUE) estimated from the enhanced vegetation index (EVI), as a surrogate for FPAR, for the different vegetation types.

Appendix S3 Analysis of covariance for mean annual radiation use efficiency (RUE) and maximum RUE estimated from the enhanced vegetation index (EVI) across vegetation type and climatic variables and their interactions.

Appendix S4 Coefficients of correlation for the 8-day period relationships between radiation use efficiency calculated from the fraction of photosynthetically active radiation absorbed by the vegetation (RUE FPAR) and RUE calculated from the enhanced vegetation index (RUE EVI) and seven environmental variables.

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BIOSKETCHES

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M.F.G., J.P. and I.F. conceived the ideas; M.F.G. gathered the databases and analysed the data; M.F.G., J.P. and I.F. led the writing and M.F.G., J.P., I.F, D.P., J.A., M.L.G., G.K., A.D.R., E.R. and E.M.V. contributed to discussion of the ideas and preparation of the paper.

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