

# Spatial variability and controls over biomass stocks, carbon fluxes, and resource-use efficiencies across forest ecosystems

Marcos Fernández-Martínez · Sara Vicca · Ivan A. Janssens ·  
Sebastiaan Luyssaert · Matteo Campioli · Jordi Sardans ·  
Marc Estiarte · Josep Peñuelas

Received: 4 September 2013 / Revised: 18 December 2013 / Accepted: 20 December 2013 / Published online: 1 January 2014  
© Springer-Verlag Berlin Heidelberg 2013

## Abstract

**Key message** Stand age, water availability, and the length of the warm period are the most influencing controls of forest structure, functioning, and efficiency.

**Abstract** We aimed to discern the distribution and controls of plant biomass, carbon fluxes, and resource-use efficiencies of forest ecosystems ranging from boreal to tropical forests. We analysed a global forest database containing estimates of stand biomass and carbon fluxes (400 and 111 sites, respectively) from which we calculated resource-use efficiencies (biomass production, carbon sequestration, light, and water-use efficiencies). We used the WorldClim climatic database and remote-sensing data derived from the Moderate Resolution Imaging Spectroradiometer to analyse climatic controls of ecosystem

functioning. The influences of forest type, stand age, management, and nitrogen deposition were also explored. Tropical forests exhibited the largest gross carbon fluxes (photosynthesis and ecosystem respiration), but rather low net ecosystem production, which peaks in temperate forests. Stand age, water availability, and length of the warm period were the main factors controlling forest structure (biomass) and functionality (carbon fluxes and efficiencies). The interaction between temperature and precipitation was the main climatic driver of gross primary production and ecosystem respiration. The mean resource-use efficiency varied little among biomes. The spatial variability of biomass stocks and their distribution among ecosystem compartments were strongly correlated with the variability in carbon fluxes, and both were strongly controlled by climate (water availability, temperature) and stand characteristics (age, type of leaf). Gross primary production and ecosystem respiration were strongly correlated with mean annual temperature and precipitation only when precipitation and temperature were not limiting factors. Finally, our results suggest a global convergence in mean resource-use efficiencies.

Communicated by A. Geßler.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00468-013-0975-9) contains supplementary material, which is available to authorized users.

M. Fernández-Martínez (✉) · J. Sardans · M. Estiarte ·  
J. Peñuelas

CSIC, Global Ecology Unit, CREAF-CEAB-CSIC-Universitat  
Autònoma de Barcelona, Cerdanyola del Vallés,  
08193 Catalonia, Spain  
e-mail: m.fernandez@creaf.uab.cat

M. Fernández-Martínez · J. Sardans · M. Estiarte · J. Peñuelas  
CREAF, Cerdanyola del Vallès 08193, Catalonia, Spain

S. Vicca · I. A. Janssens · M. Campioli  
Research Group of Plant and Vegetation Ecology, Department of  
Biology, University of Antwerp, 2610 Wilrijk, Belgium

S. Luyssaert  
LSCE CEA-CNRS-UVSQ, Orme des Merisiers,  
91191 Gif-sur-Yvette, France

**Keywords** Carbon cycle · Budget · Partitioning ·  
Allocation · Climate · LUE · WUE · Nitrogen deposition

## Abbreviations

### Biomass and carbon-flux variables

LAI	L area index ( $\text{m}^2 \text{m}^{-2}$ )
SLA	Specific leaf area ( $\text{m}^2 \text{kg}^{-1}$ )
GPP	Gross primary production ( $\text{gC m}^{-2} \text{year}^{-1}$ )
Re	Ecosystem respiration ( $\text{gC m}^{-2} \text{year}^{-1}$ )
NEP	Net ecosystem production ( $\text{gC m}^{-2} \text{year}^{-1}$ )

TBP	Total biomass production ( $\text{gC m}^{-2} \text{ year}^{-1}$ )
ABP	Aboveground biomass production ( $\text{gC m}^{-2} \text{ year}^{-1}$ )
FNPP	Foliage net primary production ( $\text{gC m}^{-2} \text{ year}^{-1}$ )
WNPP	Wood net primary production ( $\text{gC m}^{-2} \text{ year}^{-1}$ )
BBP	Belowground biomass production ( $\text{gC m}^{-2} \text{ year}^{-1}$ )
ABP %	ABP to GPP ratio (%)
FNPP %	FNPP to GPP ratio (%)
WNPP %	WNPP to GPP ratio (%)
BBP %	BBP to GPP ratio (%)

### Efficiency variables

CUEe	Carbon use efficiency at the ecosystemic level (%)
BPE	Biomass production efficiency (%)
LUE	Light-use efficiency ( $\text{gC MJ}^{-1}$ )
LUE % <sub>APAR</sub>	Light-use efficiency relative to absorbed PAR (%)
LUE % <sub>PAR</sub>	Light-use efficiency relative to incident PAR (%)
PAR	Photosynthetically active radiation ( $\text{MJ m}^{-2}$ )
LUE % <sub>TRad</sub>	Light-use efficiency relative to total incident radiation (%)
WUE	Water-use efficiency ( $\text{gC L}^{-1}$ )

### Climatic variables

AET	Actual evapotranspiration ( $\text{mm year}^{-1}$ )
PET	Potential evapotranspiration ( $\text{mm year}^{-1}$ )
WD	Water deficit (%)
MAT	Mean annual temperature ( $^{\circ}\text{C}$ )
MAP	Mean annual precipitation ( $\text{mm year}^{-1}$ )

## Introduction

The increasing atmospheric  $\text{CO}_2$  concentration and its influence on global climate (IPCC 2007) highlight the necessity to better understand the mechanisms driving the global carbon cycle. Forest ecosystems sequester and store large amounts of carbon, both as living biomass and as dead organic matter (Dixon et al. 1994). Understanding how these ecosystems are structured and how they function is therefore of paramount importance for improving our knowledge of the global carbon cycle and for predicting future climate.

Previous studies (Margalef 1974; Dixon et al. 1994; Malhi et al. 1999; Gower et al. 2001; Litton et al. 2007; Luyssaert et al. 2007; Keith et al. 2009; Pan et al. 2011) have reported estimates of the stocks and distribution of

biomass among different ecosystemic compartments, carbon fluxes, or resource-use efficiencies for different regions and taxa, but most of the combined analyses of biomass distributions, carbon fluxes, and resource-use efficiencies were based on limited subsets of climate space. Continuous efforts of the research community have rapidly increased data availability, and following methodological harmonisation has provided these data to be compared more easily.

Despite extensive literature on controls of resource-use efficiencies (Garbulsky et al. 2010; Gu et al. 2002; Jenkins et al. 2007; Landsberg and Waring 1997; Wang et al. 2003 for light or radiation-use efficiency and Field et al. 1983; Huxman et al. 2004; Yu et al. 2008; Troch et al. 2009; Lu and Zhuang 2010; Peñuelas et al. 2011 for water- or precipitation-use efficiency), differences in resource-use efficiency among biomes or forest types are seldom explicitly reported (but see Goetz and Prince 1999 for LUE and Yu et al. 2008 for WUE), or the available data are insufficient for generalising the results to the entire biome or forest type under study. In this study, we will consider the resource-use efficiency for light (LUE), water (WUE), biomass production (BPE), and short-term carbon sequestration at the ecosystemic level (CUEe).

Studies of climatic control concerning forest production or functioning have frequently tested the influence of temperature, precipitation, drought indices, or radiation (Kato and Tang 2008; Law et al. 2002; Luyssaert et al. 2007; Magnani et al. 2007; Valentini et al. 2000), although some other variables such as thermal amplitude, seasonality of precipitation, and actual or potential evapotranspiration may be key determinants of forest functioning (Garbulsky et al. 2010). In addition, the relative contributions to ecosystem structure and functioning of climate and forest characteristics such as stand age (Goulden et al. 2011; Magnani et al. 2007; Vicca et al. 2012), management (Luyssaert et al. 2007; Vicca et al. 2012), or nitrogen deposition (De Vries et al. 2009; Luyssaert et al. 2010; Magnani et al. 2007) are still debated.

In this study, we have updated a global database (Luyssaert et al. 2007) of forest carbon pools and fluxes and have extended this database with 45 new forests and data up to 2010, remote-sensing observations of actual evapotranspiration (AET) and the absorbed fraction of photosynthetically active radiation (fPAR) to calculate water-use and light-use efficiencies (WUE, LUE). Our aim was to update the analysis done by (Luyssaert et al. 2007) and to extend it with: (1) an accurate and detailed description of the biomass stocks, annual carbon fluxes, and resource-use efficiencies of forest ecosystems in different biomes on a global scale based on field and remote-sensing data, and (2) a determination of the main drivers of the spatial variability in biomass stocks and in their distribution among ecosystem compartments, the annual carbon fluxes, and the resource-use efficiencies.

## Materials and methods

### Collection and selection of data

#### *Global forest database*

To characterise forest ecosystems, we used a publicly available database of global forests (Luyssaert et al. 2007). This database contains measurements, and in some cases their uncertainties, for several structural, functional, and bioclimatic characteristics and a compilation of simulated data such as, for example, nitrogen deposition for 558 forests around the world. To characterise forest ecosystems, we extracted from this database, for each forest, the following variables (whenever available): (1) maximum LAI, (2) stand biomass of living trees, comprising estimates of aboveground biomass (typically distinguishing between woody and foliar biomass) and of fine and coarse roots, (3) mean annual carbon fluxes, comprising estimates of GPP, Re, NEP (derived from eddy covariance towers), TBP, aboveground and belowground biomass production, and NPP of wood and leaves, and iv) APAR (absorbed photosynthetically active radiation) used to calculate LUE (GPP:APAR; see “MODIS time series”).

We also extracted several variables to use as predictors of the stand characteristics: (1) nitrogen deposition derived from interpolated gridded maps based on ground observations (Holland et al. 2005) and model simulations (Galloway et al. 2004), (2) stand age, (3) leaf habit (evergreen or deciduous) and type (needleleaved or broadleaved), (4) management (managed, unmanaged, disturbed), and (5) biome (boreal, temperate, Mediterranean, and tropical). The methodologies used to estimate all the variables within the database were reported by (Luyssaert et al. 2007). We selected these predictor variables since they have been previously suggested to influence carbon balance and functioning in terrestrial ecosystems (De Vries et al. 2009; Luyssaert et al. 2007; Janssens et al. 2010; Magnani et al. 2007; Peñuelas et al. 2012; Vicca et al. 2012).

#### *Geographical scale and forest types*

All continents and biomes were represented in our database and analyses, but the available forests were distributed mostly around Europe and North America (Fig. S1 and Fig. S2 in Supporting Information), containing forests belonging to four different biomes (boreal [ $N = 102$ ], temperate [ $N = 252$ ], Mediterranean [ $N = 11$ ], and tropical [ $N = 35$ ] from which 10 were semiarid forests and 25 were humid). Boreal and especially temperate forests were well represented in our database, but tropical and especially Mediterranean forests were underrepresented. The southern hemisphere was also poorly represented. The database

contained evergreen, deciduous, needleleaved, broadleaved, and mixed (broadleaved–needleleaved) forests. Both leaf type and habit were well represented, but mixed forests were clearly in a minority.

#### *WorldClim database*

We used the WorldClim database (Hijmans et al. 2005) because (1) it has a high spatial resolution (30 arc seconds  $\sim 1$  km at the equator), (2) it contains robust monthly climatic data derived from long time series (from 1950 to 2000), and (3) although only data for temperature and precipitation are available, the dataset provides several bioclimatic variables such as annual thermal amplitude or seasonality of temperature and precipitation.

#### *MODIS time series*

We downloaded the evapotranspiration time series (MOD16A2) from MODIS (Moderate Resolution Imaging Spectroradiometer) for the period between January 1, 2000 and December 27, 2009 to obtain climatic surrogates of potential and actual evapotranspiration (PET and AET, respectively, Mu et al. 2007) to use them as climatic predictors and to calculate WUE (GPP divided by AET). The resolution of the data was  $9 \text{ km}^2$  around the central coordinates of the forest. We selected such a coarse resolution because of the poor resolution of the coordinates provided by the database.

To calculate LUE relative to total PAR (GPP:PAR), we downloaded the fPAR (absorbed fraction of PAR) time series (MOD15A2) from MODIS (Fritsch et al. 2012) for the period between February 18, 2000 and December 27, 2011 with a resolution of  $9 \text{ km}^2$  around the central coordinates of the forest. Once we calculated the average fPAR for each forest during the entire time series, we calculated total PAR using the following equation:  $\text{APAR} = \text{fPAR} \times \text{PAR}$ , using APAR from the global forest database (see above).

### Data analyses

#### *Studied forest variables*

To describe the characteristics and analyse the functioning of forest ecosystems, we separated the variables under study into three groups: (1) stand biomass, (2) annual carbon flux, and (3) resource-use efficiency. The biomass variables were total, aboveground, belowground (coarse + fine roots), woody (trunk + branches), and foliar biomass. We also included the maximum LAI, a surrogate of SLA ( $\text{maximum LAI} \cdot \text{foliar biomass}^{-1}$ ), and the percentage of foliar, woody, and belowground biomass

relative to total biomass. The variables of carbon flux were GPP, TBP, aboveground, belowground, woody and foliar biomass production ( $\sim$  NPP), Re, NEP, and the percentage of GPP partitioned into aboveground (ABP %), belowground (BBP %), woody (WNPP %), and foliar NPP (FNPP %).

Finally, the variables of resource-use efficiency were (1) carbon-use efficiency at the ecosystemic level (CUEe), defined as the percentage of NEP to GPP, (2) biomass production efficiency (TBP:GPP, see Vicca et al. 2012) in percentage (BPE), (3) light-use efficiency (LUE), as the ratio of GPP to APAR and, and (4) water-use efficiency (WUE), as the ratio of GPP to AET. We additionally calculated LUE expressed as the percentage of the energy converted into organic matter (glucose) relative to the amount received as APAR, PAR, and total incident radiation, considering that: (1) 1 g of glucose equals 4.1 kcal (Margalef 1974), (2) APAR equals  $\text{PAR} \times \text{fPAR}$ , and (3) PAR represents 45 % of the total incident radiation.

### Climatic predictors

We extracted mean monthly and annual values for temperature (MAT) and precipitation (MAP) from the WorldClim database. We also extracted two key bioclimatic variables: annual thermal amplitude (mean maximum minus mean minimum temperature for the year, which provides information not only about the latitude of the forest but also about its continentality and elevation) and seasonality of precipitation (measured as the coefficient of variation of precipitation among months), which provides information about seasonal differences in the amount of precipitation.

We calculated the percentage of water deficit (WD) as an indicator of the intensity of water stress that the forests must tolerate. We calculated it from MODIS data as a percentage  $[\text{WD} = (1 - (\text{AET}/\text{PET})) \times 100]$  rather than as an absolute value (Stephenson 1998) due to the large climatic gradient included in our data that might lead to different sensitivities of the biological variables to absolute values of water deficit in forests from different biomes (e.g. a change of  $50 \text{ mm year}^{-1}$  in a boreal forest with a  $\text{MAP} = 300 \text{ mm year}^{-1}$  may have a greater influence than in a tropical forest with  $\text{MAP} = 2,500 \text{ mm year}^{-1}$ ). We also calculated the length of the warm period, considered as the number of months whose mean temperature was above  $5^\circ\text{C}$ . We then extracted mean temperature, precipitation, potential and actual evapotranspiration, and water deficit during the warm period.

Summarising, we used 13 climatic predictor variables: PET, AET, WD, MAT, MAP (these five calculated both on an annual basis and for the warm period only), length of the warm period, annual thermal amplitude, and seasonality of

precipitation. Correlations among the climatic variables are shown in Table S1, Supporting information.

### Statistical analyses

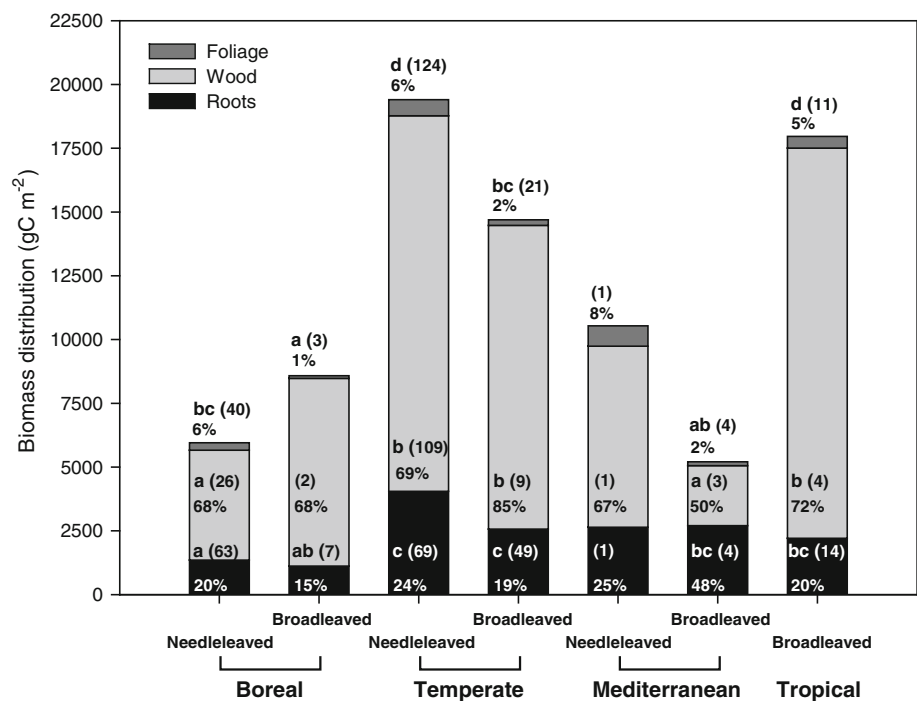
To describe forest ecosystems, we first computed the averages of biomass, carbon flux, and efficiency variables grouping forests according to biome and leaf type. As data were usually not normally distributed, we opted to perform bootstrapped ( $n = 1,000$ ) weighted means and to use the bias-corrected and accelerated 95 % confidence intervals (Efron 1987) to test for differences between groups. We weighted cases according to the inverse of the uncertainty, except for biomass variables for which uncertainty was not reported in the database. We subsequently explored the possible relationships among different variables of biomass and flux via Pearson correlation analysis. We correlated the same dependent variable up to 10 times, so we controlled the rate of false discovery with Bonferroni corrections.

We performed stepwise forward regression models to correlate the variables of biomass, carbon flux, and resource-use efficiency with climate, management, leaf habit and type, stand age, and nitrogen deposition. Predictor covariates were entered twice in the models, without transformation and transformed into the natural logarithm, to check for possible nonlinearities. We excluded the variables from the models when presenting high collinearity (Variance Inflation Factor [VIF]  $> 5$ ).

Because controls of GPP, Re, and NEP are of paramount importance in the carbon balance of ecosystems, we closely examined the relationships of these three variables of carbon flux with MAT and MAP. We thus classified forests according to MAT and MAP, defining thresholds based on the median of the distribution of our data. Forests with  $\text{MAP} \geq 827 \text{ mm year}^{-1}$  were considered *wet* forests, and forests with  $\text{MAP} < 827 \text{ mm year}^{-1}$  were classified as *dry*. Similarly, forests with  $\text{MAT} \geq 8^\circ\text{C}$  were considered *warm* forests, whereas forests with  $\text{MAT} < 8^\circ\text{C}$  were classified as *cold*. Hence, forests were classified according to two-factor variables, each with two levels (wet/dry, warm/cold). This classification allowed us to test whether the relationships of the different variables of carbon flux with MAT depended on the *wetness* and whether the relationships between carbon fluxes and MAP depended on the *warmness*. To this end, we constructed multivariate generalised linear models (MGLM), including the interaction between *wetness* or *warmness* and MAT or MAP. Significant interactions would indicate changes in the relationships between carbon fluxes and climate according to *wetness* or *warmness*.

Finally, to analyse the direct, the indirect, and the total effects of climate and nitrogen deposition on GPP, Re, and NEP, we performed a path analysis using AET, MAT, and

**Fig. 1** Biomass distribution among compartments in different forest types and biomes. It is also shown the percentage of biomass that each compartment represents in relation to the total biomass. Letters indicate significant differences among groups at the 0.05 level (see Table S3 in Supporting information for average values and confidence intervals) followed by the number of replicates (between brackets). Missing letters indicate that the comparison was not possible due to the lack of replicates



nitrogen deposition as exogenous variables and GPP, Re, and NEP as endogenous variables. The saturated model comprised all possible paths between exogenous and endogenous variables, a path from GPP to Re and a path from GPP and Re to NEP. We achieved the minimum adequate model by deleting, from the saturated model, those paths that were not found significant.

## Results

Global variation in biomass, carbon fluxes, and efficiency

### Characterisation of biomass stocks

According to the bootstrapped 95 % confidence intervals (which indicate significant differences when they do not overlap), the distribution of biomass among compartments revealed large differences among biomes (Fig. 1 and Table S2, Supporting information) despite comprising forests of similar age, around 80 years old (Factorial ANOVA test: age ~ biome × leaf type,  $P = 0.95$ ). Tropical and temperate forests presented the largest amounts of wood, aboveground biomass, and total stand biomass, with values above 10,000 gC m<sup>-2</sup>, while Mediterranean broadleaved forests exhibited the lowest values (Fig. 1 and Table S2, Supporting information). Belowground biomass was lowest for boreal forests. A statistically significant difference was detected only for boreal versus temperate forests, although

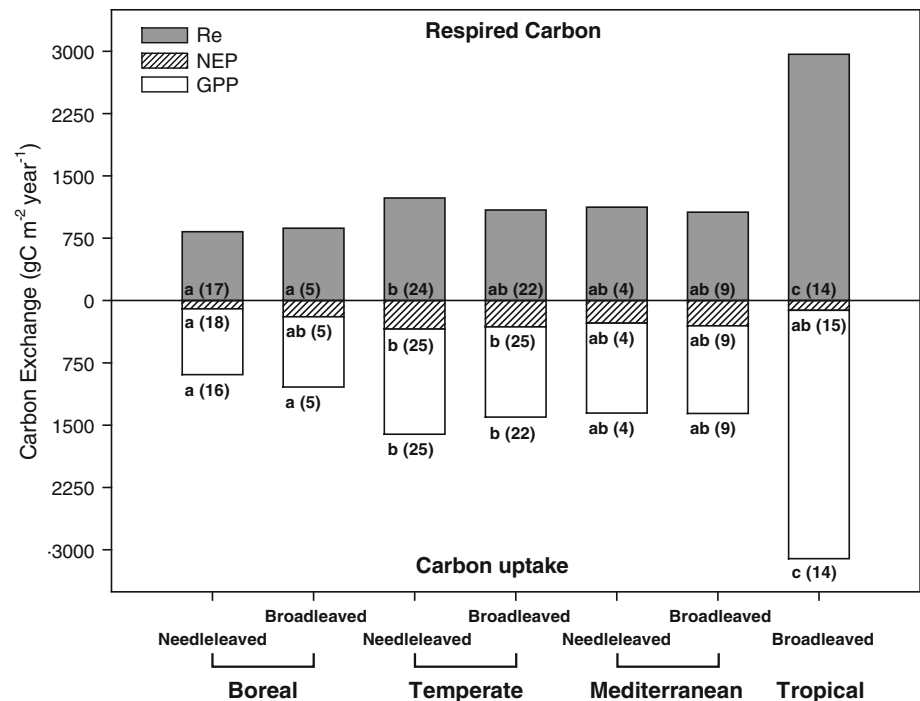
tropical forests also revealed a clear (and borderline significant) tendency of higher belowground biomass as compared to boreal forests (Fig. 1 and Table S2, Supporting information).

The distribution of the biomass stocks among different plant organs also differed among biomes. In both the boreal and temperate zone, needleleaved forests presented higher percentages of foliar biomass than broadleaved forests (above 5.5 % and below 2.5 %, respectively, Table S2, Supporting information). However, the percentage of biomass represented by wood, about 70 % in most cases, did not differ between biomes or type of leaf. Finally, almost half of the biomass in Mediterranean broadleaved forests occurred belowground, whereas root biomass did not exceed 25 % in all other forest types (Fig. 1 and Table S2, Supporting information).

The largest foliar biomass was found in temperate needleleaved and tropical broadleaved forests. The type of leaf was a crucial determinant of foliar biomass, because needleleaved forests had about 2.8 times more foliar biomass than did broadleaved forests across boreal and temperate biomes. Maximum LAI, however, did not significantly differ between leaf types within a single biome. The maximum values were found in temperate forests (LAI > 5), whereas the lowest were reported in Mediterranean broadleaved forests (LAI < 2.7, Table S2, Supporting information). In broadleaved forests, the specific leaf area (SLA = LAI · foliar biomass<sup>-1</sup>), decreased with decreasing latitude, ranging from about 36 in boreal forests to 14 m<sup>2</sup> kg<sup>-1</sup> in the tropics. Needleleaved boreal



**Fig. 2** Mean values of carbon exchange between forest ecosystems and the atmosphere for different biomes. Letters indicate significant differences among groups at the 0.05 level (see Table S3 in Supporting information for average values and confidence intervals) followed by the number of replicates between brackets



forests showed the lowest SLA ( $12.6 \pm 1.2 \text{ m}^2 \text{ kg}^{-1}$ , mean  $\pm$  SE) and statistically differed from both boreal and temperate broadleaved forests (Table S2, Supporting information).

#### Distribution of carbon fluxes

All carbon fluxes and their partitioning variables revealed significant differences among biomes but not between needleleaved and broadleaved forests (Figs. 2, 3 and Table S3, Supporting information). Tropical forests presented the highest rates for all fluxes, except for NEP (Figs. 2, 3a); the highest amount of NEP was observed at mid-latitudes (temperate and Mediterranean forests). Remarkably, tropical forests had rates of FNPP as high as the rates of TBP in boreal forests (Fig. 3a).

Boreal needleleaved forests partitioned about 6 % of their carbon uptake (i.e. GPP) into the foliage compartment (FNPP), whereas temperate and tropical broadleaved forests partitioned almost 12 % of GPP to foliage. Wood NPP ranged between 10 % (boreal needleleaved and tropical broadleaved forests) and 16 % (temperate broadleaved) of GPP, while roots received between 8 % (tropical broadleaved) and 18 % (temperate broadleaved) of total GPP (Fig. 3b).

#### Resource-use efficiency of biomes

CUEe followed the same pattern as NEP, being highest for temperate and lowest for tropical forests (Fig. 2, Table S4,

Supporting information). On average, about 20 % of GPP was sequestered (NEP) in temperate forest ecosystems, whereas only  $3.3 \pm 2.8$  % of the GPP of tropical broadleaved forests was actually stored. In contrast, BPE did not significantly differ among biomes, ranging from  $38 \pm 3.6$  to  $54 \pm 4.7$  % (Table S4, Supporting information).

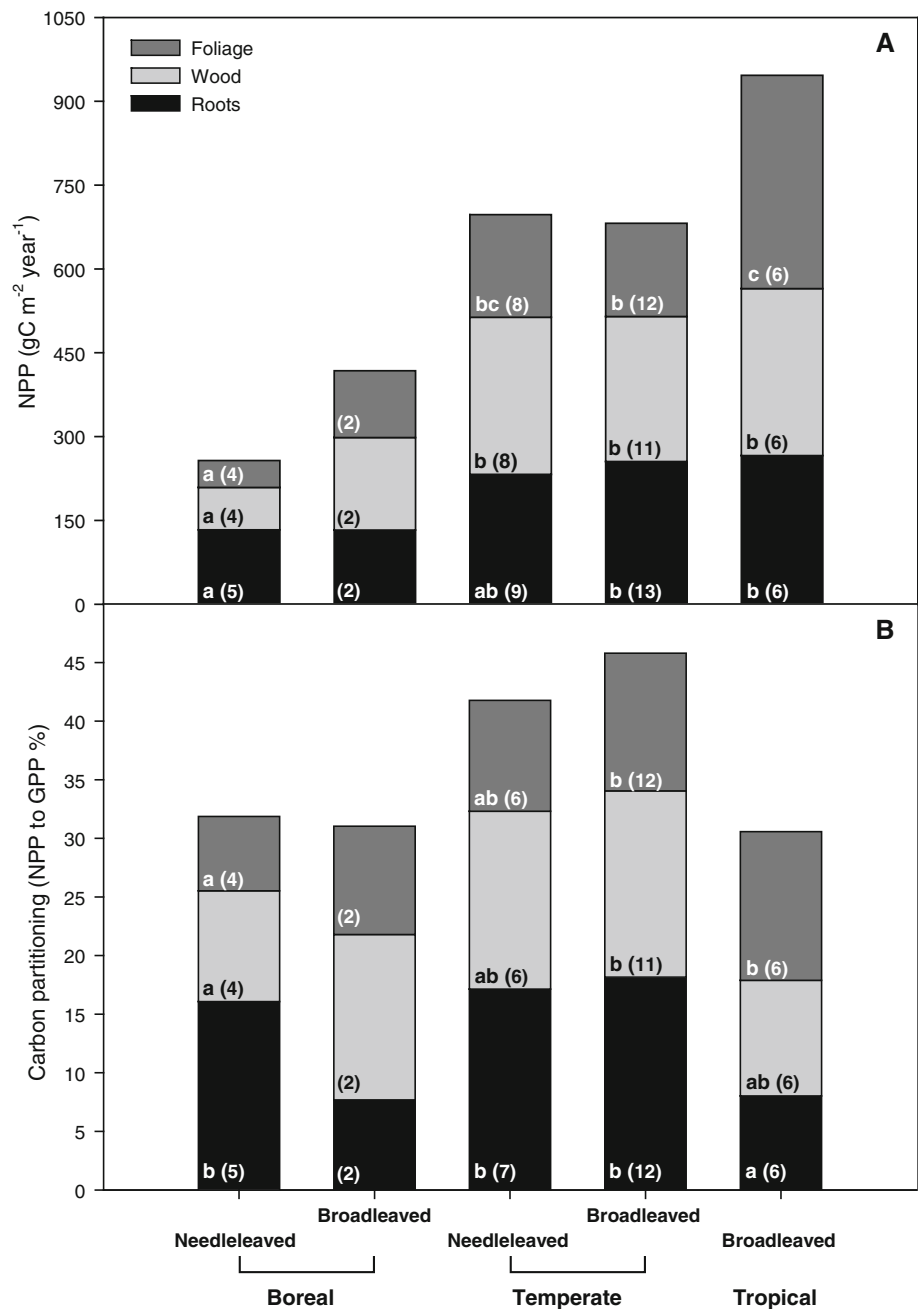
LUE ranged from  $2.0 \pm 0.2$  (in temperate and Mediterranean broadleaved forests) to  $2.6 \pm 0.1 \text{ gC MJ}^{-1}$  (in temperate needleleaved forests), with the former being significantly lower than the latter. When transforming this efficiency into the percentage of energy used, we found that forest ecosystems used between  $8.5 \pm 0.7$  % and  $11.1 \pm 0.6$  % of the absorbed light energy, between  $5.5 \pm 0.6$  % and  $7.6 \pm 0.5$  % of the total incident PAR, and between  $2.5 \pm 0.3$  % and  $3.4 \pm 0.2$  % of the total incident radiation (Table S4, Supporting information). Statistically, WUE did not differ among forest types due to high variability. On average, WUE ranged from  $2.1 \pm 0.2$  to  $3.1 \pm 0.6 \text{ gC mm}^{-1}$  in Mediterranean broadleaved and needleleaved forests, respectively.

Correlations with biomass stocks, carbon fluxes, and efficiencies

#### Biomass stocks and its distribution among ecosystem compartments

Table 1 shows an overview of the results of the stepwise regression models for biomass stocks, carbon flux, and efficiency (see Table S5 in Supporting information for a

**Fig. 3** **a** Net primary production (NPP) distribution (FNPP, WNPP, BBP) and **b** partitioning of gross primary production (GPP) among compartments (FNPP %, WNPP %, BBP %) in different forest types and biomes. In graphs **a** and **b**, the total heights of the bars represent TBP and BPE, respectively (only forests with foliar, wood, and root measurements available). Letters indicate significant differences among groups at the 0.05 level (see Table S3 in Supporting information for average values and confidence intervals) followed by the number of replicates between brackets. Missing letters indicate that the comparison was not possible due to the lack of replicates



more detailed description). Stand age, MAP, and the length of the warm period were the most correlated predictors with the spatial variability and distribution of the different compartments of biomass.

LAI and foliar biomass were positively correlated with indicators for water availability. Both were, respectively, 1.3 and 3 times higher in needleleaved than in broadleaved forests. Also, stand age and nitrogen revealed a significantly positive relation with LAI, whereas temperature during the warm period had a negative influence. Despite presenting a negative trend from boreal broadleaved to tropical broadleaved forests (Table S2, Supporting

information), SLA was not significantly correlated with any of the predictor variables used in this study.

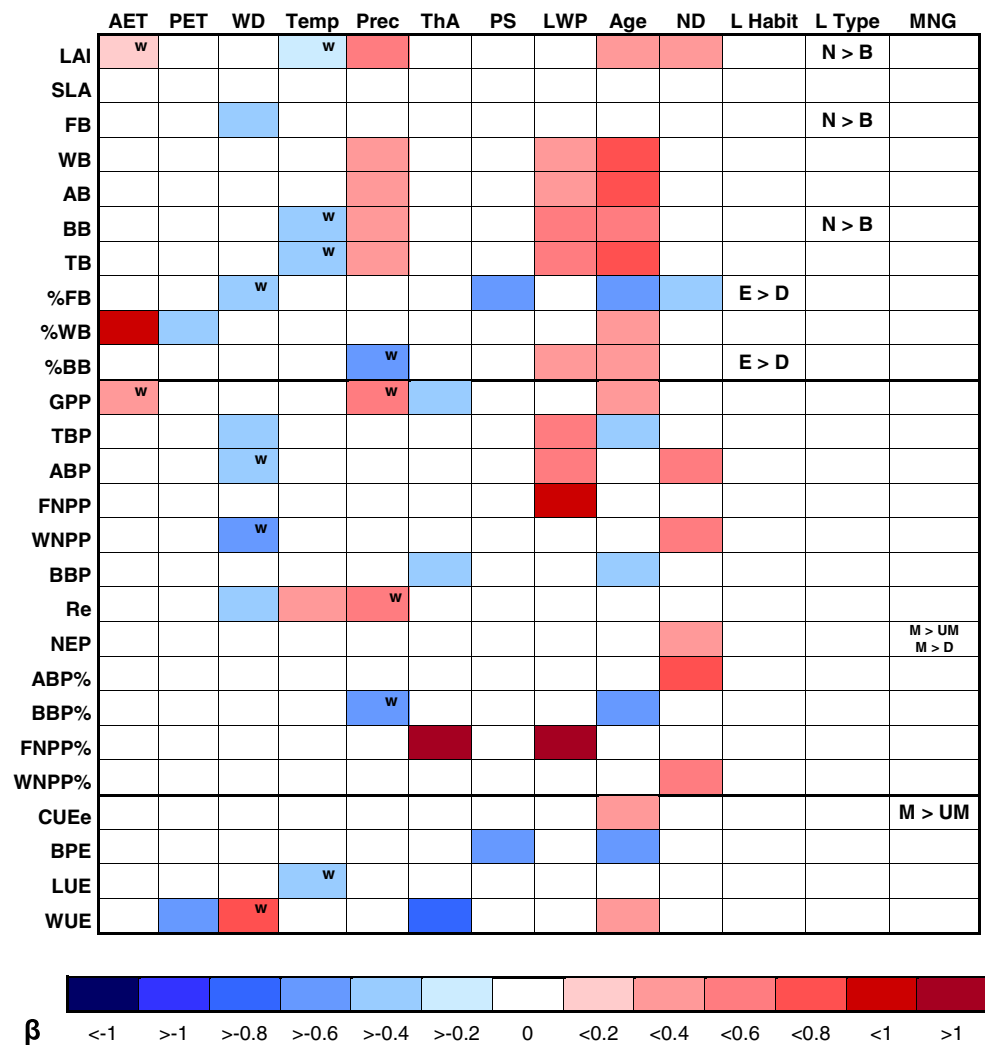
Woody, aboveground, belowground, and total biomasses increased with the logarithm of stand age. Precipitation and the length of the warm period were also positively correlated with these variables of biomass, whereas mean temperature of the warm period negatively influenced total and belowground biomass; the latter was also about 1.5 times higher in needleleaved than in broadleaved forests (Table 1).

Younger evergreen forests showed higher proportion of leaf biomass than other forest types, particularly when

**Table 1** The influence of climatic variables, stand age, leaf habit, leaf type, and management (MNG) on the biomass, flux, and efficiency variables of the forests

Squares indicate  $\beta$  weights of the stepwise regression models using a colour gradient where red indicates positive, blue indicates negative, and white indicates no correlation. In the table, “w” indicates that the relationship was with the variable calculated for the warm period. Otherwise, the relationship was with the annual variable

*AET* and *PET* actual and potential evapotranspiration, *WD* water deficit, *Temp* mean temperature, *Prec* total precipitation sum, *ThA* annual thermal amplitude, *PS* precipitation seasonality, *LWP* length of the warm period, *ND* nitrogen deposition. Annual and warm-period variables of *AET*, *PET*, *WD*, *Temp*, and *Prec* are represented in single columns to compact the table. Factor codes: leaf habit (*E* evergreen, *D* deciduous); leaf type (*N* needleleaved, *B* broadleaved); management (*M* managed, *UM* unmanaged, *D* disturbed)



seasonality of precipitation, nitrogen deposition, and water deficits were low (Table 1). The percentage of woody biomass increased with *AET* and the age of the forest. Interestingly, the percentage of belowground biomass was negatively correlated with precipitation of the warm period, the opposite of the other variables of biomass. In addition, longer warm periods, higher age, and the evergreen leaf habit increased the percentage of biomass assigned to roots.

#### Correlations with carbon fluxes

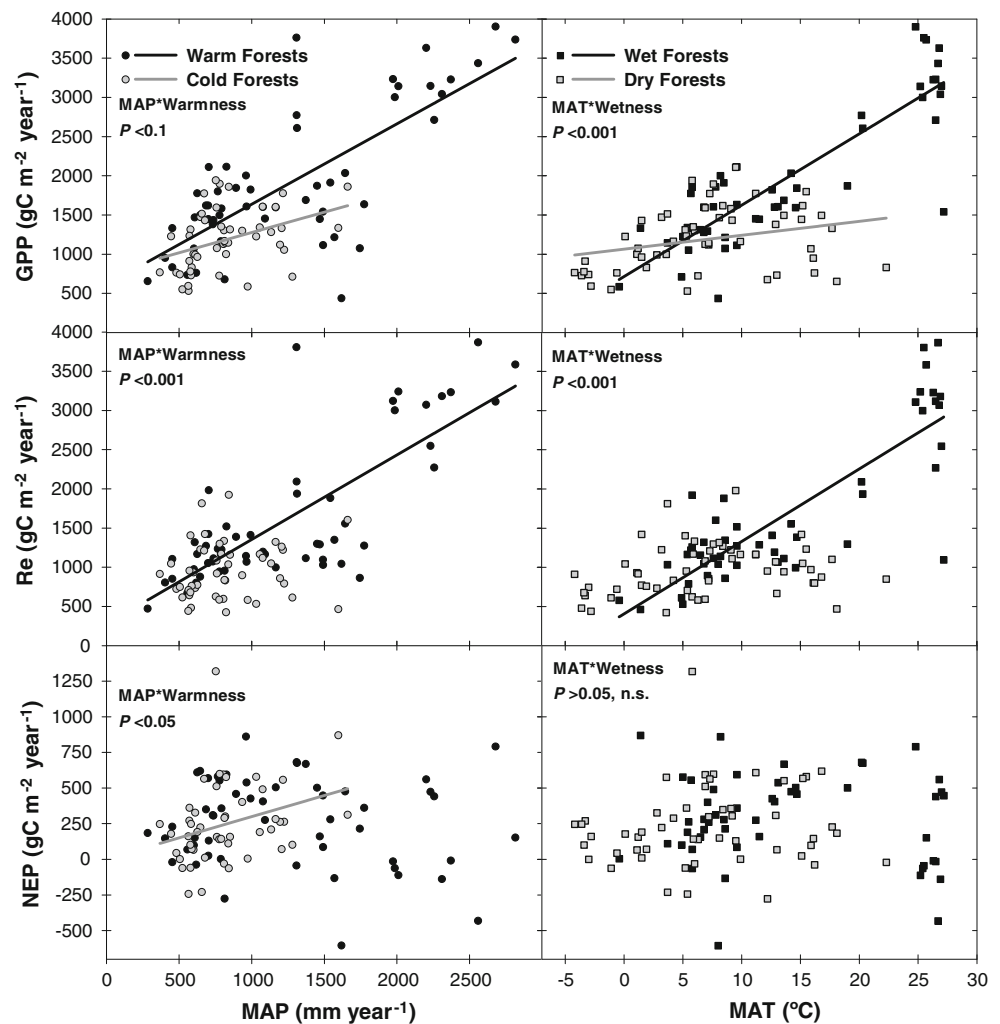
On a global scale, most of the fluxes (except *NEP*) were strongly influenced by climate variables (Table 1 and Table S5b, Supporting information). *GPP* was positively correlated with water availability (precipitation and *AET*) during the warm period and also by stand age but was negatively correlated with annual thermal amplitude. *Re* was correlated by the variables of water availability and

*MAT* (Table 1), with warm and wet forests presenting the highest rates of respiration. *NEP*, on the other hand, did not directly respond to climatic variables but was significantly correlated with nitrogen deposition and management. We tested whether this effect was not more prominent in North America and Europe than in the rest of the world, but the models indicated that the relationship did not vary among continents. The rates of *NEP* were about twice as high in managed as compared to unmanaged forests and 2.6 times higher in managed than in disturbed forests.

Comparison of warm versus cold forests and wet versus dry forests (Fig. 4), however, revealed that the relationships of *GPP*, *Re*, and *NEP* with *MAP* depended on warmth, whereas the relationships of *GPP*, *Re*, and *NEP* with *MAT* depended on wetness (*MAP*  $\times$  warmth:  $P < 0.0001$ ; *MAT*  $\times$  wetness:  $P < 0.001$ ; Fig. 4), and these relationships differed for each carbon flux. Warm forests revealed a significantly positive relation for both



**Fig. 4** Scatter plots showing how mean annual precipitation (MAP) and mean annual temperature (MAT) are correlated with GPP, Re, and NEP, depending on the climatic characteristics of the stands (Wet: MAP > 827 mm year<sup>-1</sup>; Warm: MAT > 8 °C). Only significant slopes ( $P < 0.05$ ) have been drawn. The levels of significance of the interaction MAP × MAT are also indicated

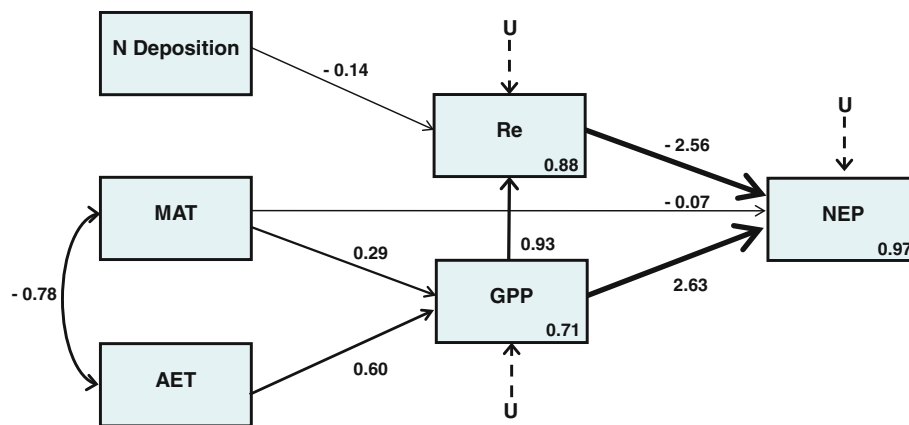


GPP and Re with MAP, both presenting a slope close to unity, while NEP was not correlated at all. Cold forests, instead, showed a lower slope for GPP versus MAP (single linear regression: 0.52;  $P < 0.01$ ), Re was not significantly correlated to MAP (0.17;  $P = 0.34$ ), and NEP revealed a significantly positive relationship with MAP (0.30;  $P = 0.03$ ). Similarly, wet forests showed a significant positive relationship of GPP and Re with MAT, whereas NEP was not significantly related to MAT. Dry forests showed a positive relation between GPP and MAT albeit with a lower slope than the wet forests, whereas Re showed no significant relationship with MAT (Fig. 4). However, NEP was not significantly related to MAT. Even when excluding the tropical forests (which strongly influenced our regressions, see Fig. 4) from these analyses, similar patterns were observed (MAP × warmness:  $P < 0.05$ ; MAT × wetness:  $P < 0.05$ , respectively) and remained significant despite presenting less evident changes in the slopes. With the exclusion of tropical forests, however, GPP presented a higher slope with MAP in cold forests

than in warm forests, and NEP presented a significant relationship with MAT in wet forests whereas NEP was no longer related with MAP in cold forests.

The path analysis relating AET, MAT, and nitrogen deposition with GPP, Re, and NEP (Fig. 5; Table 2) showed that AET and MAT only affected Re indirectly through their positive relationship with GPP. Also, nitrogen deposition presented a negative correlation with Re which, in turn, resulted in a positive and significant correlation with NEP (Table 2) just as the stepwise regression analysis revealed (Table 1). The relationship between GPP and Re was very tight (Fig. 5) and the calculated total effects for NEP revealed a greater sensitivity to Re (standardized coefficient for Re =  $-2.55 \pm 0.05$ ) than to GPP ( $0.26 \pm 0.11$ ) (Table 2).

High TBPs were correlated with low water deficit and long warm periods but decreased with increasing stand age (Table 1). Forests with long warm periods produced more foliage and aboveground biomass as compared to forests with shorter warm periods. Also, aboveground biomass and



**Fig. 5** Resulting diagrams of the path analysis relating climate (AET and MAT) and nitrogen deposition as exogenous variables with carbon-flux variables (GPP, Re and NEP) as endogenous variables. The “U” represents the non-explained variance of the endogenous variables, the *arrows* show the standardized coefficients of the path

(direct effects), and the *boxes* of the endogenous variables show the variability explained ( $R^2$ ). All paths shown are significant and models were simplified to achieve the minimum adequate model according to AICc

**Table 2** Total effects (mean  $\pm$  SE) resulting from the path analysis shown in Fig. 5

Total effects	N dep	AET	MAT	GPP	Re
GPP		<b>1.60 <math>\pm</math> 0.23</b>	<b>27.44 <math>\pm</math> 8.08</b>		
Re	<b>-19.06 <math>\pm</math> 4.58</b>	<b>1.46 <math>\pm</math> 0.22</b>	<b>25.01 <math>\pm</math> 7.42</b>	<b>0.91 <math>\pm</math> 0.03</b>	
NEP	<b>18.44 <math>\pm</math> 4.44</b>	0.16 $\pm$ 0.31	0.22 $\pm$ 10.74	<b>0.09 <math>\pm</math> 0.04</b>	<b>-0.96 <math>\pm</math> 0.02</b>
Standardized total effects					
GPP		<b>0.60 <math>\pm</math> 0.09</b>	<b>0.29 <math>\pm</math> 0.09</b>		
Re	<b>-0.14 <math>\pm</math> 0.05</b>	<b>0.55 <math>\pm</math> 0.08</b>	<b>0.27 <math>\pm</math> 0.08</b>	<b>0.93 <math>\pm</math> 0.03</b>	
NEP	<b>0.37 <math>\pm</math> 0.14</b>	0.16 $\pm$ 0.31	0.01 $\pm$ 0.30	<b>0.26 <math>\pm</math> 0.11</b>	<b>-2.55 <math>\pm</math> 0.05</b>

Bold coefficients were significant at the 0.05 level

wood biomass production were higher in forests presenting low water deficit and high nitrogen deposition as compared to forests with high water deficit and low nitrogen deposition (Table 1).

Similarly, forests receiving higher nitrogen deposition assigned higher percentage of carbon to wood and above-ground biomass (Table 1). The percentage of carbon assigned to roots, on the other hand, was negatively correlated with precipitation during the warm period (as with the percentage of belowground biomass, mentioned in Sect. 3.2.1) and by stand age. Finally, the percentage assigned to foliar NPP was positively correlated with annual thermal amplitude and the length of the warm period.

Forests with higher LAI and aboveground biomasses also had higher rates of GPP (LAI:  $R^2 = 0.14$ ,  $P = 0.001$ ; aboveground biomass:  $R^2 = 0.26$ ;  $P < 0.001$ ). Also, Re was positively correlated with aboveground biomass ( $R^2 = 0.23$ ;  $P < 0.001$ ), and biomass production was positively correlated with woody biomass ( $R^2 = 0.62$ ;  $P = 0.004$ ). Other relationships emerged but were not

significant after correction by Bonferroni procedures ( $\alpha = 0.005$ ).

#### Correlations with forest resource-use efficiency

Stepwise regressions showed that CUEe and WUE were positively correlated with stand age, while BPE was negatively correlated with stand age (Table 1, Table S5c, Supporting information). In addition, CUEe was affected by management in the same way as NEP (i.e. CUEe was higher in managed than in unmanaged forests), and the seasonality of precipitation was negatively correlated with BPE. LUE and WUE responded differently to temperature: lower values of WUE were detected in forests with high annual thermal amplitudes (which could also indicate a negative effect of temperature: see Table S1, Supporting information), whereas LUE decreased with the temperature of the warm period (although very little variance was explained by the model; Table 1 and Table S5c, Supporting information). Also, WUE was negatively correlated with PET.

## Discussion

The relationships found in our global analyses mostly agreed with previous meta-analyses or established eco-physiological principles. However, our analyses also uncovered novel global trends that deserve thoughtful discussion. We must also point out that, unfortunately, fertility could not be directly assessed in this paper and, therefore, some relationships reported here might change according to the nutrient status of the forests.

Forest functioning, characteristics, and endogenous drivers

### *Biomass stocks and carbon fluxes*

We have confirmed that the largest stocks of biomass are found in temperate and tropical forests (Fig. 1) (Keith et al. 2009). These forests also have the highest rates of biomass production and carbon uptake (Figs. 2, 3a). In contrast, boreal and especially Mediterranean forests have the lowest stand biomasses. Because boreal forests are strongly limited by temperature and Mediterranean forests by water availability (Kramer et al. 2000), the low biomass stocks of these forests may be a consequence of their slow growth or conservative strategies imposed by strong constraints to growth (Ackerly and Stuart 2009). Our results agree with this hypothesis: indicators of water availability (MAP, AET, WD) and length of the warm period were the most influential climatic variables on forest structure and functioning (Table 1).

Logically, stand age was paramount in controlling woody, aboveground, and belowground biomasses, but its influence on foliage was negligible, suggesting the existence of a threshold to foliar biomass reached at young ages (Ryan et al. 1997; Chen et al. 2007, Table 1, Table S5a, Supporting information). This positive relationship of age with woody and root biomasses and the lack of a relationship with foliar biomass are surely the causes of the evident negative effect age has on the percentage of foliar biomass. Despite the positive relationship of age with root biomass, root NPP presented a negative response to ageing. This result may indicate that the older the forest, the lower the resources required investing in roots, because the necessity to achieve a robust root system (strong anchor structure and large provisioning area) might be fulfilled by the progressive accumulation of root biomass. Furthermore, changes in the ratio of fine-to-coarse roots to the belowground stock might change the belowground productivity as fine roots have different turnover rates than coarse roots.

The growth of some tropical forests is limited by solar radiation (Nemani et al. 2003). According to the functional

equilibrium hypothesis (Poorter et al. 2012), the limitation of light may account for the high percentage, amount, and production of foliar biomass in tropical broadleaved forests (Figs. 1, 2a, Table S2 and Table S3 in Supporting information). Poorter et al. (2012), however, suggested that this limitation of light should also lead to high values of SLA more than to high values of the percentage of foliar biomass at the plant level, but this is exactly opposite to our results at the ecosystem level (Table S2, Supporting information). This issue requires further examination as other evolutionary issues, such as herbivory, could be involved in SLA variation. On the other hand, needleleaved forests showed rather low values of SLA and higher amounts and percentages of foliar biomass, although GPP did not differ between leaf types within biomes. This observation agrees with the idea that needles photosynthesize less efficiently than broadleaves (Lusk et al. 2003).

The distribution of biomass among compartments is quite similar among forest biomes, with the exception of the Mediterranean forests, where roots represent ca. 50 % of the total biomass (Pausas 1999). This exception is the result of evolutionary adaptations to withstand summer droughts or repeated fires by the accumulation of non-structural carbohydrates in the lignotuber (Ackerly and Stuart 2009). Our results support this hypothesis; we found that the percentage of belowground biomass decreased with increasing amounts of precipitation during the warm period (Table 1 and Table S5a, Supporting information). Belowground biomass (or fraction), however, did not correlate with belowground biomass production (or carbon partitioning to roots), which may indicate that this higher amount of root biomass is more likely the result of a progressive accumulation than of higher carbon partitioning into roots. Because estimates of single-site root biomass stocks and production are very uncertain (as reported by Robinson (2004), for example), studies like ours that synthesise data represent a useful approach for acquiring reliable measures of belowground biomass (assuming that single-site uncertainty is random). However, forest biomes with few available data (see Fig. 1) may still require caution and further evaluation.

The positive relationship between GPP and stand age indicates that assimilation in forests is not only driven by climatic characteristics, as some models assume, and calls for a renewed attention from the forest carbon modelling community to the relationships between age and canopy or foliar characteristics. Despite the higher GPP of tropical forests than temperate forests, NEP is higher in temperate than in tropical forests. In fact, our data indicate that although tropical forests are most likely to be sinks of carbon (Stephens et al. 2007; Lewis et al. 2009), the average NEP in our study is not statistically significantly different from zero (Table S3, Supporting information).

(Pan et al. 2011). Accordingly, tropical forests showed the lowest CUEe and BPE ratios of all forests (Figs. 2, 3b), indicating that they are the least efficient in the use of GPP, possibly because of the high temperatures and water availabilities that enhance both autotrophic and heterotrophic respiration more than the rates of GPP (Fig. 4, Chambers et al. 2004; Kato and Tang 2008) and/or because of the low nutrient availability that could enhance the production of root exudates or other unaccounted for components of NPP (Goulden et al. 2011; Vicca et al. 2012). On the other hand, our results indicated that spatial variability in NEP was more sensitive to changes in Re than in GPP (Table 2) which agrees with results from previous studies (Valentini et al. 2000).

The decrease of BPE with age was one of the foundations used by Goulden et al. (2011) to suggest that in boreal forests decreasing nutrient availability with increasing age could enhance carbon partitioning into the fine-root fraction. Our results support this negative relationship of stand age with BPE, but stand age also presented a negative relationship with the fraction of GPP partitioned to root (fine + coarse) biomass and a positive relationship with the amount and percentage of belowground biomass (Table 1). These results do not necessarily contradict the hypothesis presented by Goulden et al. (2011), because our data did not differentiate from the fine-root to the coarse-root fraction. An overall decrease in the production of belowground biomass could also be possible if an increase in the fine-root fraction is compensated for by a decrease in the production of coarse-root biomass. Also, Goulden et al. (2011) reported a negative effect of age on the ratio of NEP to TBP, indicating that old stands approach a steady state. We obtained a similar pattern for CUEe (as the ratio of NEP to GPP), as efficiency of carbon sequestration increased with age and tended to reach a steady state with positive values of CUEe (because of a logarithmic relationship; Table 1 and Table S5c, Supporting information). However, the predicted confidence intervals of CUEe did not differ from zero.

#### *Light and water-use efficiency*

The similar values of LUE and WUE found across biomes (Table S4, Supporting information) suggest a convergence in the average of these resource-use efficiencies of forest ecosystems on a global scale (Goetz and Prince 1999; Huxman et al. 2004). On the other hand, the considerable variability observed within biomes and the lack of LUE data for tropical forests in particular, may obscure existing trends.

Binkley et al. (2004) stated that, at the ecosystemic level, an increase in efficiency modulated by an increase in a resource use could be due to an increased “*return on investment*” (e.g. a canopy with good hydric conditions would photosynthesise more carbon than another suffering

stomatal closure for the same investment in canopy). Old forests had higher WUEs, possibly due to (1) the positive relationship of stand age with LAI and GPP (given that we calculated  $WUE = GPP \cdot AET^{-1}$ ; Table 1, Magnani et al. 2007) and (2) an increase in the resources (e.g. water, nutrients) provided by the root system to the canopy as a result of increasing root biomass with age (Table 1) (Binkley et al. 2004; Ackerly and Stuart 2009). In agreement with Binkley’s hypothesis, we found a significant relationship between LAI and GPP similar to that reported by other authors (Gower et al. 2001; Law et al. 2002; Kato and Tang 2008).

#### *Exogenous drivers of forest functioning and characteristics*

##### *The role of climate*

Our analyses confirm that water availability and the length of the warm period ( $\sim$ temperature) are paramount for controlling forest structure and functioning (Luyssaert et al. 2007; Keith et al. 2009). Only SLA, NEP, ABP %, WNPP %, and CUEe (5 of 26 variables studied) were not related to climate variables. Carbon pools and fluxes were generally higher in warm and wet forests (Table 1).

We have refined the analysis of Luyssaert et al. (2007), distinguishing dry from wet and cold from warm forests, and adding insights into the relationship between NEP and climate. Our results suggest that the interaction between MAT and MAP is of paramount importance for understanding the effect of climate on NEP (Fig. 4). The relationships of GPP and Re with MAP in warm forests are very similar and prevent a relationship between NEP and MAP, because most of the carbon assimilation is counterbalanced by the ecosystem respiration. In cold forests, however, the effect of MAP on GPP is stronger than the effect of MAP on Re, and consequently NEP is positively influenced by MAP. These relationships suggest that, on a global scale, Re responds differently than GPP to the interaction between MAT and MAP, which is reflected by the correlation between NEP and MAP only in cold forests, where part of the production (GPP) is not respired due to limitations of temperature.

On the other hand, when looking for indirect relationships between climate and carbon fluxes, we found that Re does not present direct relationships neither with MAT nor with AET. Instead, the relation of Re with climate goes through the direct relationship with production (GPP, Fig. 5) as suggested by previous studies (Janssens et al. 2001). We found NEP to be directly correlated with MAT, but the correlation, although significant, was almost meaningless and was not significant when accounting for the total effects (Table 2).

The positive influence of water deficit during the warm period on WUE (Table 1) (Huxman et al. 2004; Yu et al. 2008; Troch et al. 2009) suggests an adaptive trait to maximise the efficiency of water use in those forests growing under water-limited conditions (Aranda et al. 2007; Ackerly and Stuart 2009). Our results also indicated that forests with lower thermal amplitudes can use water more efficiently, in terms of gross carbon fixation, than those exposed to wider oscillations in temperature. This relationship may be explained by several hypotheses: (1) in evergreen forests, extremely cold episodes can provoke massive degradation of chloroplast, which can take up to 8 weeks to recover (Malhi et al. 1999), (2) in warm forests presenting high thermal amplitude, elevated rates of evapotranspiration caused by extremely warm temperatures at the leaf and canopy levels can lead to higher photorespiration and thus lower GPP (Malhi et al. 1999), or (3) because warmer forests tend to have lower thermal amplitudes (Table S1, Supporting information), the longer periods of photosynthetic activity in warmer forests may enhance carbon uptake, whereas AET may remain constant on a yearly basis (if AET is limited by precipitation), thereby yielding higher WUEs. In addition, lower thermal amplitudes also reduce the risk of damage from extremely cold or warm events.

On the other hand, WUE was negatively related to PET. In dry forests, higher PET creates larger water-potential gradients between the stomata and the atmosphere, higher rates of evapotranspiration per unit of carbon gained (lower WUE), and hence stomatal closure by leaf water depletion, leading to increased foliar temperature which, in addition, increases photorespiration (Malhi et al. 1999; Yu et al. 2008). Also, high levels of PET lead to high rates of evapotranspiration in forests without water restrictions (e.g. humid tropical forests), which could also reduce WUE. Similarly, forests with warmer growing seasons may have lower values of LUE (Table 1) due to enhanced photorespiration produced at higher temperatures or due to a higher probability of stomatal closure caused by the high evaporative demand, thereby reducing photosynthesis per unit of APAR.

#### *The role of management*

Previous studies (Shan et al. 2002 and references therein) have suggested that management can alter the patterns of carbon allocation through an increase in the available resources due to a relaxation of competition. Shan et al. (2002) reported increases in early volume growth and in the ratio of shoots to roots after elimination of the understory. Despite the potential effect that management can have in forest ecosystems, our analyses confer little importance to it. We have not detected changes in the patterns of carbon

allocation, rates of production, or biomass stocks as a result of management (Table 1). This maybe partially due to the fact that we used a global dataset of forests for which each variable had a wide range of variation. Thus, changes in these variables may depend more on the characteristics of the climate than on management. In the present study, only NEP and CUEe were directly related to management. Reducing biomass stocks and lowering competition for light, water, and nutrients seem a key for increasing NEP and CUEe, although management had no significant effect on carbon uptake or ecosystem respiration.

#### *The role of nitrogen deposition*

Nitrogen deposition also had a relevant influence on the functioning of forest ecosystems, as previously reported by other authors (see De Vries et al. 2009; Janssens et al. 2010; Luyssaert et al. 2010; Magnani et al. 2007). For example, the increased biomass production and carbon allocation to wood with increased nitrogen deposition (Table 1) agree with the paradigm that partitioning to aboveground production increases with increasing belowground resources (Litton et al. 2007). Also, higher nitrogen availability allows to maintain higher nitrogen concentrations and consequently higher photosynthetic capacity per unit of leaf area (Field et al. 1983). We also found nitrogen deposition to positively influence LAI and NEP (Table 1). This influence may be related to an increase in the availability of nitrogen for plants, rendering nitrogen a less limiting factor to growth. Also, the negative influence of nitrogen deposition over the percentage of foliar biomass (Table 1) may indicate a shift towards more productive leaves when nitrogen is available. Regarding the effect on NEP, our path analysis revealed that the effect in NEP is, in fact, mediated by the effect of nitrogen deposition in Re (Fig. 5; Table 2). In this sense, nitrogen deposition has also been suggested to reduce heterotrophic respiration (Janssens et al. 2010) by means of: (1) changes in the saprotrophic community towards one more efficient in the use of carbon, which requires higher nitrogen availability, and (2) abiotic mechanisms of soil organic matter stabilisation, producing nitrogenous compounds that reduce the decomposability of soil organic matter. The maximum value of nitrogen deposition found in our forests was  $27.3 \text{ kg ha}^{-1} \text{ year}^{-1}$ ; higher amounts of nitrogen deposition may have opposite consequences in forest ecosystems (e.g. very high nitrogen deposition could cause negative impacts on carbon sequestration, De Vries et al. 2009).

Hence, this study provides an updated description of the structure, functioning, production, and resource-use efficiency of forests located in the main forest biomes of our planet. We also indicate the main controls of these



properties, highlighting the paramount role of water availability, temperature, and stand age. The results show a global positive synergic effect of MAP and MAT on forest production, growth, and carbon accumulation. Although climate has globally affected BPE, LUE, and WUE, mean efficiencies differed very little among biomes, suggesting a global convergence of resource-use efficiencies across ecosystems.

**Acknowledgments** This research was supported by the Spanish Government projects CGC2010-17172 and Consolider Ingenio Montes (CSD2008-00040), by the Catalan Government Project SGR 2009-458 and by the Catalan Government FI-2013 grant. S. Vicca and M. Campioli are postdoctoral fellows of the Research Foundation—Flanders (FWO). S. Luyssaert was funded through ERC starting grant 242564 and received additional funding through FWO Vlaanderen. We appreciated the financial support of the GHG Europe project.

**Conflict of interest** The authors declare that they have no conflict of interest.

## References

- Ackerly DD, Stuart SA (2009) Physiological ecology: plants. In: Levin S (ed) Princeton guide to ecology. Princeton University Press, Princeton, pp 20–26
- Aranda I, Pardo M, Puértolas J et al (2007) Water-use efficiency in cork oak (*Quercus suber*) is modified by the interaction of water and light availabilities. *Tree Physiol* 27:671–677
- Binkley D, Stape JL, Ryan MG (2004) Thinking about efficiency of resource use in forests. *For Ecol Manage* 193:5–16. doi:10.1016/j.foreco.2004.01.019
- Chambers JQ, Tribuzy ES, Toledo LC et al (2004) Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency. *Ecol Appl* 14:72–88. doi:10.1890/01-6012
- Chen JM, Thomas SC, Yin Y et al (2007) Combining remote sensing imagery and forest age inventory for biomass mapping. *J Environ Manage* 85:616–623
- De Vries W, Solberg S, Dobbervin M et al (2009) The impact of nitrogen deposition on carbon sequestration by European forests and heathlands. *For Ecol Manage* 258:1814–1823. doi:10.1016/j.foreco.2009.02.034
- Dixon RK, Solomon M, Brown S, et al (1994) Carbon pools and flux of global forest ecosystems. *Science* (80) 263:185–90. doi:10.1126/science.263.5144.185
- Efron B (1987) Better bootstrap confidence intervals. *J Am Stat Assoc* 82:171–185
- Field C, Merino J, Mooney Ha (1983) Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. *Oecologia* 60:384–389. doi:10.1007/BF00376856
- Fritsch S, Machwitz M, Ehammer A et al (2012) Validation of the collection 5 MODIS FPAR product in a heterogeneous agricultural landscape in arid Uzbekistan using multitemporal Rapid-Eye imagery. *Int J Remote Sens* 33:6818–6837. doi:10.1080/01431161.2012.692834
- Galloway JN, Dentener FJ, Capone DG et al (2004) Nitrogen cycles: past, present, and future. *Biogeochemistry* 70:153–226. doi:10.1007/s10533-004-0370-0
- Garbulsky MF, Peñuelas J, Papale D et al (2010) Patterns and controls of the variability of radiation use efficiency and primary productivity across terrestrial ecosystems. *Glob Ecol Biogeogr* 19:253–267. doi:10.1111/j.1466-8238.2009.00504.x
- Goetz SJ, Prince SD (1999) Modelling terrestrial carbon exchange and storage: evidence and implications of functional convergence in light-use efficiency. *Adv Ecol Res* 28:57–92
- Goulden ML, Mcmillan MS, Winston GC et al (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Glob Chang Biol* 17:855–871. doi:10.1111/j.1365-2486.2010.02274.x
- Gower STG, Rankina OK, Olson RJO et al (2001) Net primary production and carbon allocation patterns. *Ecol Appl* 11:1395–1411
- Gu L, Baldocchi D, Verma SB et al (2002) Advantages of diffuse radiation for terrestrial ecosystem productivity. *J Geophys Res* 107:1–23
- Hijmans RJ, Cameron SE, Parra JL et al (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978. doi:10.1002/joc.1276
- Holland EA, Braswell BH, Sulzman J, Lamarque J-F (2005) Nitrogen deposition onto the united states and western Europe: synthesis of observations and models. *Ecol Appl* 15:38–57. doi:10.1890/03-5162
- Huxman TE, Smith MMD, Fay PAP et al (2004) Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654. doi:10.1038/nature02597.1
- IPCC (2007) Climate Change 2007—The Physical Science Basis: Working Group I Contribution to the Fourth Assessment Report of the IPCC (Climate Change 2007). Cambridge Univ Press Cambridge United Kingdom New York NY USA 996
- Janssens Ia, Lankreijer H, Matteucci G et al (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Glob Chang Biol* 7:269–278. doi:10.1046/j.1365-2486.2001.00412.x
- Janssens Ia, Dieleman W, Luyssaert S et al (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nat Geosci* 3:315–322. doi:10.1038/ngeo844
- Jenkins JP, Richardson AD, Braswell BH et al (2007) Refining light-use efficiency calculations for a deciduous forest canopy using simultaneous tower-based carbon flux and radiometric measurements. *Agric For Meteorol* 143:64–79. doi:10.1016/j.agrformet.2006.11.008
- Kato T, Tang Y (2008) Spatial variability and major controlling factors of CO<sub>2</sub> sink strength in Asian terrestrial ecosystems: evidence from eddy covariance data. *Glob Chang Biol* 14:2333–2348. doi:10.1111/j.1365-2486.2008.01646.x
- Keith H, Mackey BG, Lindenmayer DB (2009) Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. *Proc Natl Acad Sci* 106:11635–11640
- Kramer K, Leinonen I, Loustau D (2000) The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *Int J Biometeorol* 44:67–75
- Landsberg JJ, Waring RH (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For Ecol Manage* 95:209–228. doi:10.1016/S0378-1127(97)00026-1
- Law BE, Falge E, Gu L et al (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agric For Meteorol* 113:97–120
- Lewis SL, Lopez-Gonzalez G, Sonké B et al (2009) Increasing carbon storage in intact African tropical forests. *Nature* 457:1003–1006. doi:10.1038/nature07771
- Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. *Glob Chang Biol* 13:2089–2109. doi:10.1111/j.1365-2486.2007.01420.x
- Lu X, Zhuang Q (2010) Evaluating evapotranspiration and water-use efficiency of terrestrial ecosystems in the conterminous United

- States using MODIS and AmeriFlux data. *Remote Sens Environ* 114:1924–1939. doi:[10.1016/j.rse.2010.04.001](https://doi.org/10.1016/j.rse.2010.04.001)
- Lusk CH, Wright I, Reich PB (2003) Photosynthetic differences contribute to competitive advantage of evergreen angiosperm trees over evergreen conifers in productive habitats. *New Phytol* 160:329–336. doi:[10.1046/j.1469-8137.2003.00879.x](https://doi.org/10.1046/j.1469-8137.2003.00879.x)
- Luyssaert S, Inglima I, Jung M et al (2007) CO<sub>2</sub> balance of boreal, temperate, and tropical forests derived from a global database. *Glob Chang Biol* 13:2509–2537. doi:[10.1111/j.1365-2486.2007.01439.x](https://doi.org/10.1111/j.1365-2486.2007.01439.x)
- Luyssaert S, Ciais P, Piao SL et al (2010) The European carbon balance. Part 3: forests. *Glob Chang Biol* 16:1429–1450. doi:[10.1111/j.1365-2486.2009.02056.x](https://doi.org/10.1111/j.1365-2486.2009.02056.x)
- Magnani F, Mencuccini M, Borghetti M et al (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature* 447:848–850. doi:[10.1038/nature05847](https://doi.org/10.1038/nature05847)
- Malhi Y, Baldocchi DD, Jarvis PG (1999) The carbon balance of tropical, temperate and boreal forests. *Plant Cell Environ* 22:715–740. doi:[10.1046/j.1365-3040.1999.00453.x](https://doi.org/10.1046/j.1365-3040.1999.00453.x)
- Margalef R (1974) *Ecología trófica*. In: Margalef R (ed) *Ecología*, Ediciones. Barcelona, pp 435–472
- Mu Q, Heinsch FA, Zhao M, Running SW (2007) Development of a global evapotranspiration algorithm based on MODIS and global meteorology data. *Remote Sens Environ* 111:519–536
- Nemani RR, Keeling CD, Hashimoto H, et al. (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300(80):1560–3. doi:[10.1126/science.1082750](https://doi.org/10.1126/science.1082750)
- Pan Y, Birdsey RA, Fang J, et al (2011) A large and persistent carbon sink in the world's forests. *Science* 333(80):988–93. doi:[10.1126/science.1201609](https://doi.org/10.1126/science.1201609)
- Pausas JG (1999) Mediterranean vegetation dynamics: modelling problems and functional types. *Plant Ecol* 140:27–39
- Peñuelas J, Canadell JG, Ogaya R (2011) Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Glob Ecol Biogeogr* 20:597–608. doi:[10.1111/j.1466-8238.2010.00608.x](https://doi.org/10.1111/j.1466-8238.2010.00608.x)
- Peñuelas J, Sardans J, Rivas-ubach A, Janssens Ia (2012) The human-induced imbalance between C, N and P in Earth's life system. *Glob Chang Biol* 18:3–6. doi:[10.1111/j.1365-2486.2011.02568.x](https://doi.org/10.1111/j.1365-2486.2011.02568.x)
- Poorter H, Niklas KJ, Reich PB et al (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30–50. doi:[10.1111/j.1469-8137.2011.03952.x](https://doi.org/10.1111/j.1469-8137.2011.03952.x)
- Robinson D (2004) Scaling the depths: below-ground allocation in plants, forests and biomes. *Funct Ecol* 18(2):290–295
- Ryan MG, Binkley D, Fownes JH (1997) Age-related decline in forest productivity: pattern and process. *Adv Ecol Res* 27:213–262
- Shan J, Morris LA, Hendrick RL (2002) The effects of management on soil and plant carbon sequestration in slash pine plantations. *J Appl Ecol* 38:932–941. doi:[10.1046/j.1365-2664.2001.00648.x](https://doi.org/10.1046/j.1365-2664.2001.00648.x)
- Stephens BB, Gurney KR, Tans PP, et al (2007) Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO<sub>2</sub>. *Science* 316(80):1732–5. doi:[10.1126/science.1137004](https://doi.org/10.1126/science.1137004)
- Stephenson NL (1998) Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J Biogeogr* 25:855–870
- Troch PA, Martinez GF, Pauwels VRN et al (2009) Climate and vegetation water use efficiency at catchment scales. *Hydrol Process* 24:2409–2414. doi:[10.1002/hyp](https://doi.org/10.1002/hyp)
- Valentini R, Matteucci G, Dolman AJ et al (2000) Respiration as the main determinant of carbon balance in European forests. *Nature* 404:861–865. doi:[10.1038/35009084](https://doi.org/10.1038/35009084)
- Vicca S, Luyssaert S, Peñuelas J et al (2012) Fertile forests produce biomass more efficiently. *Ecol Lett* 15:520–526. doi:[10.1111/j.1461-0248.2012.01775.x](https://doi.org/10.1111/j.1461-0248.2012.01775.x)
- Wang K-Y, Kellomaki S, Li C, Zha T (2003) Light and water-use efficiencies of pine shoots exposed to elevated carbon dioxide and temperature. *Ann Bot* 92:53–64. doi:[10.1093/aob/mcg110](https://doi.org/10.1093/aob/mcg110)
- Yu G, Song X, Wang Q et al (2008) Water-use efficiency of forest ecosystems in eastern China and its relations to climatic variables. *New Phytol* 177:927–937. doi:[10.1111/j.1469-8137.2007.02316.x](https://doi.org/10.1111/j.1469-8137.2007.02316.x)