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**Seasonal variation in  
ecosystem  
parameters derived  
from FLUXNET data**

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# Seasonal variation in ecosystem parameters derived from FLUXNET data

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## Abstract

The carbon dioxide sink is in a complex way related to weather and climate. In order to better understand the relationship and feedbacks, we present a methodology to simulate observed carbon dioxide flux data with a simple vegetation model (5PM) with weekly varying model parameters. The model parameters explain the interaction between vegetation and seasonal climate more general than the flux data. Two parameters ( $R_{\text{ref}}$  and  $E_0$ ) are related to ecosystem respiration and three parameters ( $J_m$ ,  $\alpha$  and  $\lambda$ ) to photosynthesis and transpiration. We quantified the weekly variability of ecosystem parameters as a function of vegetation type and climate region.

After statistical quality checks 121 FLUXNET sites were available for analysis of the weekly varying model parameters. The simulations of these sites have high correlation coefficients ( $r^2=0.6$  to  $0.8$ ) between the observed and simulated carbon and water fluxes. With weekly parameters we determined average seasonal cycles for the different combinations of vegetation type and climate regions (PFTs). The variation between PFTs is large, which provides an excellent dataset to study the differences in ecosystem characteristics. In general we observed that needleleaf forests and grasslands in warmer climates have relatively constant parameter values during the year. Broadleaf forests in all climate regions have large seasonal variation for each of the five parameters. In boreal regions parameter values are always lower than in temperate regions. A large seasonality of the model parameters indicates a strong relation between vegetation and climate. This suggests that climate change will have the largest impact on the terrestrial carbon fluxes in boreal regions and for deciduous forests, and less for grasslands and evergreen forests.

## 1 Introduction

The relationship between vegetation and climate is of fundamental importance in understanding and assessing potential feedbacks of vegetation on climate. The steady

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state relationship between vegetation and climate was expressed by Köppen (1918, 1936), who developed a classification of climatic regions based on patterns in native vegetation. Holdridge (1947) classified life zones as a function of temperature and precipitation. These classifications represent biomes, in which a number of different vegetation types may co-exist (e.g., savanna). When vegetation models were coupled to climate models, plant functional types (PFTs) were introduced to describe the specific properties of particular vegetation types with regard to the exchange of radiation, water and energy between the vegetation and the atmosphere (e.g., Dickinson et al., 1986; Sellers et al., 1986). Virtually all climate models use PFTs as the basis for their vegetation description.

PFTs were initially applied as a steady state in the climate models, studying the effects of deforestation (Eltahir and Bras, 1996; Hahmann and Dickinson, 1997; Costa and Foley, 1999). With the increasing interest in climate change research, vegetation models were coupled to carbon cycle models (e.g., Foley et al., 1998; Woodward et al., 1998; Friend and Cox, 1995), in which vegetation characteristics were allowed to change during simulations, in some models even across PFT boundaries. These latest developments put high requirements on the PFT formulations. This is illustrated by Kleidon et al. (2007), who found that strict separation of vegetation in PFTs may artificially cause multiple steady-states of the Earth's climate-vegetation system. The assumption that parameters in carbon exchange models are conveniently grouped into PFTs, just as parameters for energy exchange are, apparently violates smooth transitions between different ecosystem types.

A number of efforts have been made to relate terrestrial carbon fluxes, observed at flux stations as the net ecosystem exchange (*NEE*), to climate (e.g., Falge et al., 2002; Law et al., 2002; Reichstein et al., 2007). From these efforts it appears that *NEE* cannot be explained well by climate on the annual time scale (Baldocchi, 2008). After partitioning into respiration and photosynthesis temperature appears as the main driver of annual respiration, but in arid and tropical regions soil moisture also is an important variable (Irvine and Law, 2002). For photosynthesis the main drivers are the

water vapour deficit, temperature and leaf area index (van Dijk et al., 2005; Reichstein et al., 2007; Lindroth et al., 2008). An important factor controlling the annual *NEE* is the growing season length, with an almost linear increase of carbon uptake with an increasing growing season (Leuning et al., 2005). Looking more into the seasonal variation helps to improve the understanding of the relations between carbon fluxes and climate.

An alternative, slightly more complex way to search for relationships between carbon fluxes and climate, is to use a simple vegetation model, optimize the model parameters to best describe the observed fluxes, and then study patterns in the parameter values. Such a model should be simple, while at the same time contain parameters that describe fundamental properties of the ecosystem. We have developed such a simple vegetation model with only five parameters (5PM), two to describe ecosystem respiration and three to describe photosynthesis and transpiration and an associated optimization method described in this paper.

On the very short term, minutes to hours, vegetation responds to weather variation by controlling the opening of stomata in the leaves, in order to prevent excessive water loss while optimizing CO<sub>2</sub> uptake for photosynthesis. This represents regulation on the shortest time scale, which for practical reasons we call stomatal control. The model is capable of describing the diurnal cycles of carbon and water exchange between the ecosystem and the atmosphere and the response to diurnal changes in temperature and vapor pressure deficit (van der Tol et al., 2007). As such, there is no need to optimize the parameters on time scales shorter than daily and by using the 5PM model we effectively remove the diurnal time scale from the data set. Any variation in the optimized parameters thus represents changes in ecosystem characteristics on time scales longer than one day, for which we will investigate the variability as potentially related to environmental conditions.

On the short term of days to weeks, ecosystems may respond to variations in weather by semi-permanent physical adaptation, such as growing new leaves after a period of drought, or growing extra roots. This type of regulation changes the vegeta-

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tion characteristics and should be reflected in changes in parameter values at ecosystem level. We hypothesize that the parameter values, optimized on weekly time scales show seasonal cycles and respond to extreme conditions, thus quantifying the regulation capacity of the ecosystem. In the medium term, seasons to years, the effects of regulation are integrated to variations in allocation of assimilated carbon to roots, stems and branches, and leaves, while still inter-annual weather variations may cause regulation. On this time scale, the effects of regulation may lag behind the timing of the cause: a wet winter may recharge soil moisture storage, cause abundant leaf growth and enhanced photosynthesis in the following summer. On the long term of decades, ecosystems adapt to repeated occurrences of climate extremes and competition with other ecosystem types. Parameter values optimized on this time scale are expected to converge into groups (plant functional types) or onto a sliding scale of vegetation characteristics.

The objective of this paper is to quantify the short term variability of ecosystem parameters of different vegetation types and climate regions. Specific questions we want to address: (1) are the model parameters clearly different between PFTs and (2) do the model parameters vary in an understandable way and (3) does the variation in model parameters have implications for our understanding of the feedback between vegetation and climate? In Sect. 2.1 we describe the 5PM model, which simulates the respiration, photosynthesis and transpiration fluxes. The observations of the FLUXNET project are described in Sect. 2.2. The model is optimized with these observed fluxes and climate variables to derive the model parameters. Model quality, seasonal variation of model parameters and relations with climate variables are presented in Sect. 3 and discussed in Sect. 4.

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## 2 Methodology

### 2.1 Simulations

In this section we describe 5PM (5 Parameter Model), which simulates carbon and water exchange between the vegetation and the atmosphere. The model consists of two modules, one for ecosystem respiration (Sect. 2.1.1) and one for photosynthesis and transpiration (Sect. 2.1.2). The model requires input variables air temperature, vapour pressure deficit and global radiation.

#### 2.1.1 Ecosystem respiration

Ecosystem respiration ( $R_e$ ) consists of two components, soil (heterotrophic) respiration and plant (autotrophic) respiration. Heterotrophic respiration is the carbon release due to decomposition of organic matter in the soil. It is a function of availability of organic matter (amount, composition and aeration) and microbiological activity (microbial pool, temperature, and soil moisture availability). Autotrophic respiration consists of maintenance and growth respiration and it occurs below ground in the roots and above ground in the branches and leaves of the vegetation. It is a function of the amount and composition of below and above ground biomass, and temperature, biological activity and weather (history).

Due to the different sub-processes, ecosystem respiration is complex to model. However, there are a few simplifications that may be made. On short time scales (< years) soil organic matter and biomass can be considered constant and variations in  $R_e$  are caused by weather. On long time scales (>10 years),  $R_e$  is controlled by the pools of carbon in organic matter and biomass. The pools represent the balance between production and decomposition.

Since we focus on short term processes, we will consider the pools to be fixed and use a model that describes  $R_e$  as a function air temperature ( $T_a$ ) with the exponential

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function of Lloyd and Taylor (1994).

$$R_e = R_{\text{ref}} \times e^{E_0(1/(T_{\text{ref}}-T_0)-1/(T_a-T_0))} \quad (1)$$

The ecosystem respiration module uses two parameters,  $R_{\text{ref}}$  and  $E_0$ .  $R_{\text{ref}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) is the respiration rate at the reference temperature ( $T_{\text{ref}}$ , 283.15 K),  $E_0$  is the activation energy (K) and  $T_0$  is a constant of 227.13 K. In this way we lump autotrophic and heterotrophic respiration. We use air temperature and not soil temperature in Eq. (1), because it has been shown by van Dijk and Dolman (2004) and Stoy et al. (2006) that when using air temperature the observed and simulated frequency distributions of  $R_e$  match better, and parameter values are more consistent.

### 2.1.2 Photosynthesis and transpiration

Photosynthesis and transpiration are closely linked through stomatal conductance of plants. Stomatal conductance regulates both transpiration and photosynthesis. At the diurnal timescale Cowan (1977) assumed that plants optimize their stomatal conductance to maximize photosynthesis for a given amount of transpiration. In this optimality hypothesis the intrinsic water use efficiency ( $\lambda$ ) defines the ratio between water loss ( $E$ ) and carbon production ( $A$ ) as a function of stomatal conductance ( $g_s$ ).

$$\lambda = \frac{\delta E / \delta g_s}{\delta A / \delta g_s} \quad (2)$$

Ecosystem water and carbon fluxes are simulated as a function of  $J_m$ ,  $\alpha$  and  $\lambda$ . The full equations are given in Appendix A.  $J_m$  is the maximum potential electron transport rate and  $\alpha$  is the quantum yield or light use efficiency.  $J_m$  and  $\alpha$  describe the amount of absorbed photosynthetic active radiation, which with the internal  $\text{CO}_2$  concentration defines the photosynthesis rate. Because we found that simulated photosynthesis was limited by light for the largest part of time, and not  $\text{CO}_2$  concentration, we chose to present only  $J_m$  and not  $V_{c,m}$  in the results.

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## 2.2 Observations

With environmental variables and observations of the carbon and water fluxes, the parameters can be derived by inverting the model. We use a database of carbon and water fluxes measured with the eddy covariance technique. See Table B1 for a complete list and Table 1 for a summary of sites within PFTs used in this study. The data are available in the form of half-hourly averages. All data is processed in a harmonized manner within the FLUXNET project (Baldocchi et al., 2001; Baldocchi, 2008) and retrieved from the database in April 2008<sup>1</sup>. Data processing is described in Papale et al. (2006), Reichstein et al. (2005), Moffat et al. (2007) and Papale and Valentini (2003).

The observed latent heat flux ( $LE$ ) consists of transpiration from vegetation and evaporation from the soil. We use only dry periods with no precipitation, or no precipitation during the previous three hours. For these periods it is assumed that  $LE$  is equal to the transpiration of vegetation.

The observed carbon flux represents the net exchange of carbon between the ecosystem and the atmosphere and consists of different fluxes. The observed flux ( $F_c$ ) plus a storage term within the vegetation is assumed to be equal to  $NEE$ . Night-time  $NEE$  is assumed to be equal to ecosystem respiration ( $R_e$ ), because during the night there is no photosynthetic activity. Selection criteria for turbulent nighttime data are thresholds of global radiation ( $R_g$ ) and friction velocity ( $u_*$ ). The  $R_g$  threshold is set to  $0 \text{ W m}^{-2}$ . The  $u_*$  threshold determination is based on the procedure as described in Gu et al. (2005). The data is divided into subsets of three month periods. For each of the subsets (reference sample) the threshold is estimated by a Moving Point Test (MPT). First, outliers are removed when nighttime  $NEE$  is larger than three standard deviations of the reference sample. Secondly, the fluxes are ordered from low to high  $u_*$ . Thirdly, a moving sample ( $n=30$ , starting with lowest  $u_*$  values) of the data is compared with the reference sample with a statistical t-test, to determine if the sample has

<sup>1</sup>www.fluxdata.org, dataset DS2

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a different mean *NEE*. This step is repeated by moving the subset with one step to a higher value of  $u_*$  until the sample has an equal distribution as the subset. This point is the threshold  $u_*$ , below which the turbulence is too low to observe reliable nighttime fluxes. Instead of using the thresholds of the three month periods, we decided to use the highest threshold for each site, which is comparable to the conservative approach by Reichstein et al. (2005). In Table B1  $u_*$  thresholds of individual sites can be found.

## 2.3 Model parameter estimation

### 2.3.1 Model optimization

The respiration module is optimized first using the simplex search method (Lagarias et al., 1998). The least squares objective function, or normalized root mean square error ( $RMSE_n$ ), is minimized to search for the optimal respiration model parameters  $R_{ref}$  and  $E_0$ :

$$RMSE_n = \frac{\sqrt{(\sum(R_{e,sim} - R_{e,obs})^2)/N}}{\overline{R_{e,obs}}} \quad (3)$$

where  $R_{e,sim}$  is the simulated and  $R_{e,obs}$  the observed  $R_e$ ,  $\overline{R_{e,obs}}$  the average observed  $R_e$  and  $N$  the number of observations. The observed respiration is the nighttime *NEE*.

Secondly the photosynthesis and transpiration module is optimized. This is a multi criteria problem and therefore the objective function consists of two parts. The normalized root mean square errors ( $RMSE_n$ ) of photosynthesis and transpiration are added up, giving equal weight to both processes:

$$RMSE_n = \frac{\sqrt{(\sum(A_{sim} - A_{obs})^2)/N}}{\overline{A_{obs}}} + \frac{\sqrt{(\sum(E_{sim} - E_{obs})^2)/N}}{\overline{E_{obs}}} \quad (4)$$

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where  $A_{\text{sim}}$  is simulated photosynthesis,  $A_{\text{obs}}$  daytime  $GPP$ ,  $E_{\text{sim}}$  simulated transpiration and  $E_{\text{obs}}$  observed transpiration.  $GPP$  is calculated as the difference between observed  $NEE$  and simulated  $R_e$ . Three parameters are used in the optimization,  $J_m$ ,  $\alpha$  and  $\lambda$ . All other parameters are kept constant as in Table 2. When these three parameters are being derived together, a global minimum of the objective function could not be found. Therefore the optimization is done in two steps. First the values of  $J_m$  and  $\alpha$  are determined. Here  $\lambda$  is kept constant at an initial value. Secondly the value of  $\lambda$  is determined by minimizing the objective function, when  $J_m$  and  $\alpha$  are kept constant. These two steps are repeated until all three parameters converge to a constant value, which is very fast, because  $J_m$  and  $\alpha$  are only related to photosynthesis.

Weekly parameters are estimated with all observations within a week. Only for weeks with more than 30 half-hourly observations parameters are estimated. Gap-filled fluxes were not used, because we did not want to add uncertainties to the parameters due to gap-filling procedures.

### 2.3.2 Parameter uncertainty

Flux measurements have random and systematic sources of uncertainty. Systematic errors result from the equipment used and data processing procedures, such as inaccurate calibrations, high- and low-frequency flux losses. And random errors occur because of storage related problems during low turbulence conditions and advection and from the measurement instruments (Raupach et al., 2005; Richardson et al., 2008; Lasslop et al., 2008). Hollinger et al. (2004) use two closely located towers at Howland to estimate the random flux error, which is a substitute for various types of errors. From the differences between the half hourly fluxes at the two towers a standard deviation was calculated. This methodology can be applied to one tower as well, by replacing space by time (Hollinger and Richardson, 2005; Richardson et al., 2006). We estimated the flux data uncertainty of all sites by using this method of selecting paired observations representing the random flux error. We do not include the systematic error because there is no systematic general approach to derive this for all sites, although

this will underestimate the flux uncertainty (Lasslop et al., 2008).

The criteria used for selecting the paired observations are that they have to occur in 2 subsequent days, at the same time of the day, under nearly identical environmental conditions (PAR within  $75 \mu\text{mol m}^{-2} \text{s}^{-1}$ , air temperature within  $3^\circ\text{C}$  and vapour pressure deficit within  $0.2 \text{ kPa}$ ). The difference between the paired observed fluxes is the random error and from all paired observation a frequency distribution of the flux uncertainty and a standard deviation is calculated.

The flux uncertainty is used to generate 500 randomly modified data sets for each site separately. First paired observations are selected, which are used to define a polynomial relation between flux size and uncertainty. Secondly, each half hourly flux (average) is multiplied by this relation (standard deviation) and a random number from a normal distribution to generate 500 datasets. Thirdly, the model is optimized for all 500 datasets in a Monte Carlo simulation, which gives 500 parameters sets from which the parameter uncertainty is calculated.

## 3 Results

### 3.1 Model quality and parameter uncertainty

Three quality criteria are applied to select sites which will be used in the analysis. First simulated fluxes are compared with observations by a statistical t-test, which compares the distributions and means of two samples. Site years with a significance level of  $p > 0.05$  were removed. Secondly, site years with correlation coefficients ( $r^2$ ) below 0.2 were removed. Thirdly, site years with a parameter uncertainty above 10% were removed.

In Fig. 1 an example of the relation between flux size and uncertainty (dNEE and dLE) is given for a pine forest (NL-Loo). As in Richardson et al. (2006) uncertainty increases with flux size. With these flux uncertainties the model parameter uncertainties were determined. This was only done for long term parameters, which represent all data years of each individual site, because of the very long computing time needed.

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Only sites are selected with a parameter uncertainty below 10%.

In Fig. 2 the initial distribution of site year  $r^2$  values are compared with the values after removal of sites. The  $r^2$  values are comparisons of half-hourly observations with simulations for each year at each site. From the initial 223 sites with 834 site years there are now 121 sites with 377 site years left for further analysis. The distribution of  $r^2$  is presented for the main vegetation types in Fig. 3. Nighttime  $NEE$  is poorly simulated for the evergreen broadleaf forests. For the other vegetation types the respiration simulations are very good, with a median  $r^2$  of almost 0.9.  $NEE$  is simulated with almost similar quality for all vegetation types, with a median  $r^2$  of around 0.6. Simulations of  $LE$  are slightly better than of  $NEE$ , with the best simulations for grasslands with a median  $r^2$  of almost 0.8. The quality of the model is good enough to analyze the model parameters, only for the evergreen broadleaf forests we will need to be careful interpreting the model results.

## 3.2 Seasonal variation

In Fig. 4 to 8 we show the mean seasonal cycles of each of the five model parameters as a function of vegetation type and climate region (as in Table 1). For clarity reasons, we only show the three vegetation types and four climate regions containing the majority of the sites.  $R_{ref}$  (Fig. 4) has a clear seasonal cycle, particularly for the colder climate regions. For Mediterranean sites there is almost no such variation between seasons, or even a decrease of  $R_{ref}$  during the dry summer.  $E_0$  (Fig. 5) varies between 200 K and 350 K, but does not show a seasonal pattern. The seasonal patterns of the respiration model parameters suggests that  $E_0$  can be kept constant, and that  $R_{ref}$  is (partly) a function of seasonal varying climate variables.

The photosynthesis and transpiration model parameters  $J_m$ ,  $\alpha$  and  $1/\lambda$  (Fig. 6 to 8) have a clear seasonality that is closely related to vegetation phenology. For Mediterranean PFTs  $J_m$  has the most pronounced variation throughout the year. For Mediterranean broadleaf forests  $\alpha$  and  $1/\lambda$  have some seasonal variation, whereas for Mediterranean needleleaf forests and grasslands  $\alpha$  and  $1/\lambda$  are quite constant. For

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the colder climates  $J_m$  of broadleaf forests have shorter growing seasons, but the  $J_m$  summer maxima are similar for all climates. For needleleaf forests,  $J_m$  shows less variation with growing season than broadleaf forests, but  $J_m$  summer maxima are higher in warmer climates. For grasslands,  $J_m$  shows a large variation with both growing season length and summer maxima.

For all climate regions,  $\alpha$  of broadleaf forests shows the clearest seasonality, with similar summer maxima of 0.4 to 0.5. For evergreen needleleaf forests and grasslands  $\alpha$  is less variable, with only clear seasonality for the colder regions. The warmest region does not have the highest values for  $\alpha$ , as was the case for  $J_m$ . This might be an indication that drought or high temperatures limits primarily  $\alpha$ .

For both broadleaf and needleleaf forests, temperate climates have higher summer maxima of water use efficiency ( $1/\lambda$ ) than boreal and Mediterranean forests. For temperate continental forests, with warm summers, the efficiency is lower than in the temperate (maritime) forests. Grasslands are less water efficient than forests during the entire year.

Overall the five parameters show seasonal variation for most vegetation types and climate regions, which we will try to relate to climate seasonality in the next section. General patterns that we observed are the relative constant  $R_{\text{ref}}$ ,  $\alpha$  and  $1/\lambda$  during the year for needleleaf forests and grasslands in warmer climates. Largest seasonal variation for all five parameters is seen at broadleaf forests in all climate regions. In boreal regions values of  $R_{\text{ref}}$ ,  $J_m$ ,  $\alpha$  and  $1/\lambda$  are generally lower than in temperate regions for all vegetation types.

### 3.3 Statistical analysis

The seasonal patterns of the model parameters are very similar at first sight. To define how similar, a principal component analysis (PCA) is performed to determine the variance between model parameters. The parameters are replaced by components, of which the principal component gives a measure for the covariance between the parameters. For the PCA first the parameters are normalized. The correlation matrix is

calculated from which the eigenvalues are determined representing the explained variance of the components. Within the eigenvector of each component the loadings give the weight of the parameters within the component.

First a PCA is performed for all five parameters. When all weekly parameters for all sites are used it can be seen from Table 3 that the explained variation is 36.78% with the principal component. When the PCA is performed for sites within each vegetation type separately the explained variation is slightly higher, e.g., 44.71% for deciduous broadleaf forest and 41.14% for evergreen needleleaf forest. These values of 35 up to 45% of explained variation give the overlap in seasonal patterns and show that the model is not over parameterized. The differences in loadings between vegetation types show that the variation in parameters is not equal. For example the loadings for  $1/\lambda$  are lower for closed shrubland, grassland and woody savanna, which indicates that these have a different behaviour than the other vegetation types.

The seasonal variation for the three parameters in the photosynthesis and transpiration module is very similar (Fig. 6 to 8). Therefore a PCA is performed with these three parameters separately. In Table 4 can be seen that indeed the explained variance by the principal component for these three parameters is higher than for all five parameters combined. For parameters of one vegetation type the explained variance is 68.47% for deciduous broadleaf forest and 52.15% for evergreen needleleaf forest. This high explained variance and similar loadings shows that these three parameters follow more similar patterns between vegetation types.

To test which climate variables are related to the model parameters we performed a stepwise multiple regression with air temperature, precipitation, global radiation, vapour pressure deficit (*VPD*), and soil water content (*SWC*) (Table 5). The performance of the regression models is very poor, with correlation coefficients below 0.1 when using model parameters of all sites lumped together. When sites are grouped into vegetation classes the model performs somewhat better. Overall the temperature seems to be the climate variable that explains most of the parameter variation.

Only for the deciduous broadleaf forests is there statistical evidence that the photo-

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synthesis parameters can be explained linearly with climate variables, and temperature is the most important determinant. Most likely the poor result for the other vegetation types is a result of the fact that the relations between climate variables and model parameters are not linear. This supports the idea that a complex model is needed to explain the relation between climate and carbon and water fluxes.

#### 4 Discussion

We used a simple vegetation model (5PM) to study the variability of the parameters. A weekly parameter time step length was chosen, because this is the scale on which plants respond to weather variations by regulation through changes in vegetation characteristics. Several motivations for the choice for weekly model parameters can be given. First of all, by using much longer times steps we hinder the model to capture the seasonality of the carbon and water fluxes. Seasonal variation of model parameters is needed because the original models of Cowan (1977), Cowan and Farquhar (1977) and Farquhar et al. (1980) were developed to simulate the variation of leaf level photosynthesis and transpiration on a daily time scale. Upscaling is needed to apply the model on the ecosystem level and on longer time scales. In this study, the derivation of seasonally varying model parameters can be considered as such an upscaling exercise.

There is some debate as to which level LAI may predict model parameters. Lindroth et al. (2008) suggest that model parameters scale with LAI for northern European forests. However, Kolari et al. (2007) report that the photosynthetic efficiency of shoots, without influence of amount of needles, show seasonality, following the mean daily temperature with a delay. Wilson et al. (2001) shows similar results for deciduous trees. This supports that the parameters are valuable to study the processes on this scale. We did not use LAI as a model parameter, primarily because LAI measurements were insufficiently available for the majority of the sites. Distributing the FLUXNET sites into classes of PFT and climate zone probably removes the largest variability within groups. Omitting LAI as a model parameter may limit the predictive skills of the model when

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vegetation adapts by growing extra leaves. However the effects of LAI are represented within the model parameters, implicitly accounting for variation in LAI.

The importance of seasonality of model parameters for improvement of carbon flux simulations is already suggested in different studies. Wang et al. (2003) show seasonal photosynthesis parameters for both coniferous and deciduous temperate forests derived from eddy covariance data. Wang et al. (2007) show that seasonal variation is related to leaf phenology for three deciduous forests and one savanna site and also to soil water and temperature for a tree-grass savanna site. For evergreen needleleaf forests no seasonality was observed in parameter values in this study. Wilson et al. (2001) observed that at the leaf level there is also an almost similar seasonality for different tree species, which they related to leaf age. We observed similar seasonality for photosynthesis parameters,  $J_m$  and  $\alpha$  in Figs. 6 and 7, with maximum values during summer. For needleleaf forests we found not as much seasonality as for deciduous broadleaf forests.

The use of the intrinsic water use efficiency ( $\lambda$ ) to describe the relation between ecosystem carbon production and water use is not used in many studies. Our model results are similar as the model of Ball et al. (1987) and Leuning (1995), but our model has the advantage that fewer parameters need to be fitted.  $\lambda$  gives new insights in the adaptation of vegetation to weather seasonality (Schymanski et al., 2007). A general finding from our study is that  $1/\lambda$  is highest, or water use is most efficient, during the warmer summer months. This seems to be opposite as found by Schymanski et al. (2007), who stated that vegetation was less water use efficient during the dry season. van der Tol et al. (2007) also found high values of  $1/\lambda$  for Mediterranean deciduous forest sites with low water availability, supporting our results. From Fig. 8 we see that the subtropical-Mediterranean and boreal needleleaf forests have lower values for  $1/\lambda$  in summer than temperate needleleaf forests. But for broadleaf forests this is not observed. Because we did not find a clear relation with soil water content, as proposed by Cowan (1982), it is still unclear what the relation between  $1/\lambda$  and the climate variables is. It is clear that more research is needed to fully understand the

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variation of this parameter, as this optimality hypothesis is already developed in 1977, but only recently being applied for different regions.

It is tempting to linearly relate the seasonal variation of model parameters with plant phenology and weather variations, but it remains challenging to unravel the precise dependencies, as consequences often follow some time after the cause. We could not find well-defined relations between the parameters and climate variables. For example the parameter describing maximum electron transport ( $J_m$ ), used in the function to simulate photosynthesis, does not show a well defined relation with air temperature, global radiation, vapour pressure deficit and soil water content. We hypothesize that  $J_m$  is more sensitive to climate variables in spring and autumn than in the summer and we intend to study such seasonally varying dependencies in a follow-on paper.

We hypothesize that the absence of well-defined relations between model parameters and climate is because different climate variables influence the parameter values or vegetation characteristics during different stages of phenology. This is supported by results from Thum et al. (2008) where  $J_m$  and  $V_{cm}$  are described with an exponential temperature function for four boreal needleleaf forests. Up to four different fits were needed to describe this seasonal variation, which shows that temperature responses are variable through the year, and not one parameter can be related to climate variables with a single annual fit. This explains why we found very poor relations between weekly model parameters and climate in the multiple regression analysis. This also implies that it is not sensible to relate the annual mean  $J_m$  with annual mean climate.

## 5 Conclusions

For understanding the global variation in carbon and water balances and predicting the ecosystem sensitivities to climate it is important to identify the processes driving the differences. In this study a methodology is presented using FLUXNET data and vegetation model (5PM) to obtain seasonally varying model parameters. Two parameters ( $R_{ref}$  and  $E_0$ ) are related to ecosystem respiration and three parameters ( $J_m$ ,  $\lambda$  and  $\alpha$ ) to photosynthesis and transpiration. These model parameters are a resultant of the

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interaction between both climate and vegetation and therefore very valuable to study ecosystem sensitivities to climate.

The quality of the simulated half hourly carbon and water fluxes is good for 121 sites, with a correlation coefficient between 0.5 and 0.8 and a model parameter uncertainty below 10%. This shows that the 5PM model can be applied globally for sites in all vegetation and climate classes. Only for evergreen broadleaf forests the respiration simulations have a poor quality, which means that we need to be careful when interpreting these results.

The fact that neither carbon fluxes nor model parameters are linearly related to climate shows that more complex models, like 5PM, are needed to investigate the change of carbon fluxes related to climate.

The variation of weekly model parameters is large between PFTs, which allows to study the differences in ecosystem characteristics. General patterns that we observed are the relative constant  $R_{ref}$ ,  $\alpha$  and  $\lambda$  during the year for needleleaf forests and grasslands in warmer climates. Largest seasonal variation for all five parameters is seen at broadleaf forests in all climate regions. In boreal regions values of  $R_{ref}$ ,  $J_m$ ,  $\alpha$  and  $1/\lambda$  are always lower than in temperate regions for all vegetation types. When seasonality of the model parameters is large, there is a strong relation between vegetation and climate. This suggests that climate change will have the largest impact on the terrestrial carbon fluxes in boreal regions and for deciduous forests, and less for grasslands and evergreen forests.

We started the introduction by describing the use of PFTs in climate models. The question is now how our results may be used to better quantify model parameters, as a function of climate. We found quit large differences between the PFTs, but this may be an artifact of looking at averages, and it cannot be ruled out that model parameters change gradually between PFTs. We intend to study this in a follow-on publication. The key question is what causes variations in model parameters.

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## Appendix A

### 5PM model description

5 Transpiration ( $LE$ ,  $W m^{-2}$ ) is a function of stomatal conductance ( $g_s$ ,  $m s^{-1}$ ) and the gradient of the  $H_2O$  concentration between vegetation and air:

$$LE = 1.6Dg_s \quad (A1)$$

where  $D$  is the molar vapor gradient between stomata and the air ( $mol m^{-3}$ ) and 1.6 the ratio of molecular diffusivity of  $H_2O$  to  $CO_2$ . Photosynthesis or  $CO_2$  assimilation ( $A$ ,  $\mu mol m^{-2} s^{-1}$ ) is a function of  $g_s$  as well:

$$10 A = g_s(C_a - C_i) \quad (A2)$$

where  $C_a$  is the  $CO_2$  concentration in the air and  $C_i$  the internal  $CO_2$  concentration (ppm). To obtain  $g_s$ , first photosynthesis ( $A$ ) is determined as in Farquhar et al. (1980). Photosynthesis is the minimum of carboxylation ( $W_c$ ), which is enzyme limited, and RuBP regeneration ( $W_j$ ), which is light limited.

$$15 A = (1 - \Gamma^*/C_i) \min\{W_c, W_j\} \quad (A3)$$

where  $\Gamma^*$  (bar) is the compensation point for  $CO_2$  in absence of dark respiration. Dark respiration is not included in this equation, because it is already simulated within the ecosystem respiration as described in the previous section.  $W_c$  and  $W_j$  are determined with the following equations (Farquhar et al., 1980; von Caemmerer and Farquhar, 20 1981; Harbinson et al., 1990):

$$W_c = \frac{V_{cm}C_i}{C_i + k'} \quad (A4)$$

$$W_j = \frac{JC_i}{4(C_i + 2\Gamma^*)} \quad (A5)$$

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$$k' = K_c(1 + O/K_o) \quad (\text{A6})$$

$$\Gamma^* = 0.5 \frac{V_{om} K_c}{V_{cm} K_o O} \quad (\text{A7})$$

$$J = \frac{\alpha I_{\text{PAR}} J_m}{\alpha I_{\text{PAR}} + 2.1 J_m} \quad (\text{A8})$$

where  $I_{\text{PAR}}$  is the photosynthetic active radiation ( $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ),  $J$  the electron yield,  $V_{cm}$  the maximum carboxylation capacity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $V_{om}$  the maximum rate of oxygenation of Rubisco ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $J_m$  the maximum potential electron transport rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $\alpha$  the quantum yield or light use efficiency ( $\text{mol mol}^{-1}$ ),  $K_c$  the kinetic coefficient for  $\text{CO}_2$  (bar),  $K_o$  the kinetic coefficient for  $\text{O}_2$  (bar) and  $O$  the  $\text{O}_2$  concentration (bar).  $K_c$  and  $K_o$  are corrected for temperature with an Arrhenius function.  $C_i$  is calculated as described in Arneeth et al. (2002), where the models of Cowan (1977) and Farquhar et al. (1980) are combined, by solving the following quadratic equation:

$$k_2 C_i^2 + k_1 C_i + k_0 = 0 \quad (\text{A9})$$

There are 2 sets of solutions for the  $k$  parameters, under enzyme limited conditions ( $W_c$ ) and light limited conditions ( $W_j$ ). In the enzyme limited case the values for the  $k$  parameters are calculated with the following equations:

$$k_2 = \lambda - \frac{1.6D}{k' + \Gamma^*} \quad (\text{A10})$$

$$k_1 = 1.6D - 2\lambda C_a + \frac{1.6D(\Gamma^* - k')}{k' + \Gamma^*} \quad (\text{A11})$$

$$k_0 = (\lambda C_a - 1.6D)C_a + \frac{1.6D\Gamma^* k'}{k' + \Gamma^*} \quad (\text{A12})$$

And in the light limited case by:

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$$k_2 = \lambda - \frac{1.6D}{3\Gamma^*} \quad (\text{A13})$$

$$k_1 = 1.6D - 2\lambda C_a + \frac{1.6D\Gamma^*}{3\Gamma^*} \quad (\text{A14})$$

$$k_0 = (\lambda C_a - 1.6D)C_a + \frac{1.6D2\Gamma^{*2}}{3\Gamma^*} \quad (\text{A15})$$

where  $C_a$  is the  $\text{CO}_2$  concentration in the air (bar),  $D$  the air saturation deficit (bar) and  $\lambda$  the intrinsic water use efficiency ( $\text{mol mol}^{-1}$ ).

## Appendix B

### FLUXNET sites

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**Table 1.** Number of FLUXNET sites used in this study in plant functional types as classes of vegetation and climate.

	Boreal	Dry	Subtropical Mediterranean	Temperate	Temperate Continental	Tropical	Total
Cropland			2	6	6		14
Closed shrubland			3				3
Deciduous broadleaf forest	1		5	3	4		13
Evergreen broadleaf forest		1	4	1		4	10
Evergreen needleleaf forest	17	1	5	10	5		39
Grassland	2	1	6	10	5		24
Mixed Forest	2			1	4		7
Open shrubland	1		1		1		3
Savanna			1				1
Wetland	1						1
Woody Savanna		2	4			1	7
<b>Total</b>	<b>24</b>	<b>5</b>	<b>31</b>	<b>31</b>	<b>25</b>	<b>5</b>	<b>121</b>

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**Table 2.** Parameters used in this study in the photosynthesis and transpiration module of the 5PM model.

Parameter	Description	Value
$V_{cm}$	Carboxylation capacity ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	variable
$J_m$	Electron transport rate, ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	variable
$\alpha$	Quantum yield ( $\text{mol mol}^{-1}$ )	variable
$\lambda$	Intrinsic water use efficiency ( $\text{mol mol}^{-1}$ )	variable
$O$	$\text{O}_2$ concentration (mbar)	209
$T_{\text{ref}}$	Reference temperature (K)	298
$K_C$	Kinetic coefficient for $\text{CO}_2$ at $T_{\text{ref}}$ ( $\mu\text{bar}$ )	460
$K_O$	Kinetic coefficient for $\text{O}_2$ at $T_{\text{ref}}$ (mbar)	330
$E_{kC}$	Activation energy for $\text{CO}_2$ ( $\text{J mol}^{-1}$ )	59 356
$E_{Jm}$	Activation energy for $J_m$ ( $\text{J mol}^{-1}$ )	45 000
$J_m/V_{cm}$	Ratio	2.5
$V_{om}/V_{cm}$	Ratio	0.21

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**Table 3.** Details of principal component analysis with explained variation (%) and loadings (–) of model parameters for classes of vegetation.

	Number of sites	Explained variation	Loadings				
			$R_{ref}$	$E_0$	$J_m$	$\alpha$	$1/\lambda$
All site	121	36.78	0.38	0.34	0.49	0.56	0.44
Cropland	14	38.20	0.27	0.06	0.58	0.58	0.50
Closed shrubland	3	45.03	0.57	–0.42	0.49	0.44	0.25
Deciduous broadleaf forest	13	44.71	0.22	0.27	0.55	0.53	0.54
Evergreen broadleaf forest	10	43.19	–0.41	0.63	0.40	0.33	0.41
Evergreen needleleaf forest	39	41.14	0.43	0.39	0.49	0.51	0.40
Grassland	24	40.59	0.59	0.12	0.56	0.54	0.18
Mixed Forest	7	48.14	0.51	0.17	0.48	0.52	0.45
Open shrubland	3	44.49	0.42	0.35	0.54	0.26	0.59
Woody Savanna	7	33.33	0.17	0.50	0.58	0.59	0.20

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**Table 4.** Details of principal component analysis with explained variation (%) and loadings (–) of photosynthesis and transpiration model parameters for classes of vegetation.

	Number of sites	Explained variation	Loadings		
			$J_m$	$\alpha$	$1/\lambda$
All site	121	50.45	0.58	0.58	0.57
Cropland	14	60.99	0.59	0.60	0.54
Closed shrubland	3	50.30	0.66	0.62	0.43
Deciduous broadleaf forest	13	68.47	0.60	0.55	0.59
Evergreen broadleaf forest	10	45.81	0.62	0.58	0.53
Evergreen needleleaf forest	39	52.15	0.59	0.58	0.55
Grassland	24	47.58	0.66	0.66	0.37
Mixed Forest	7	60.46	0.58	0.58	0.57
Open shrubland	3	56.73	0.64	0.39	0.66
Woody Savanna	7	45.05	0.68	0.64	0.36

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**Table 5.** Stepwise multiple regression of weekly model parameters with weekly average air temperature ( $T_a$ ), global radiation ( $R_g$ ), vapour pressure deficit ( $VPD$ ) and soil water content ( $SWC$ ).

	Parameter	Intercept	$T_a$	$R_g$	$VPD$	$SWC$	$r^2$
All site	$R_{ref}$	3.07	0.02	0.01	-0.21	-0.005	0.09
	$E_0$	169.76	4.01				0.01
	$J_m$	-5.24	8.15			1.12	0.07
	$\alpha$	0.33	0.01		-0.02	-0.002	0.11
	$1/\lambda$	0.38	0.02			-0.003	0.02
Deciduous broadleaf forest	$R_{ref}$	3.63		0.01	-0.19	-0.03	0.07
	$E_0$						
	$J_m$	-15.79	11.71				0.45
	$\alpha$	0.30	0.02		-0.03	-0.004	0.28
	$1/\lambda$	0.05	0.05				0.22
Evergreen broadleaf forest	$R_{ref}$	1.96				0.03	0.06
	$E_0$	254.96				4.05	0.03
	$J_m$	118.80				4.31	0.08
	$\alpha$	0.32	-0.01			0.01	0.32
	$1/\lambda$						
Evergreen needleleaf forest	$R_{ref}$	3.91	0.06		-0.18	-0.01	0.03
	$E_0$	209.69	3.26			-1.27	0.01
	$J_m$	73.85	4.22			-0.73	0.04
	$\alpha$	0.39	0.01		-0.03	-0.002	0.13
	$1/\lambda$	0.42	0.03			-0.01	0.01
Grassland	$R_{ref}$	1.26	0.10	0.01	-0.31	0.02	0.25
	$E_0$	146.62	4.66		-5.12		0.01
	$J_m$	-76.14	12.53	0.45	-16.10	1.80	0.23
	$\alpha$	0.20	0.01		-0.02	0.001	0.15
	$1/\lambda$	0.63				-0.01	0.004

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**Table B1.** Site characteristics of the FLUXNET sites used in this study. The site name codes are composed by the country (first two letters) and site name (last three letters). Vegetation types are closed shrubland (CSH), cropland (CRO), deciduous broadleaf forest (DBF), evergreen broadleaf forest (EBF), evergreen needleleaf forest (ENF), grassland (GRA), mixed forest (MFO), open shrubland (OSH), savanna (SAV), wetland (WET) and woody savanna (WSA). Climate regions are arctic (AR), boreal (BO), dry (DR), subtropical-Mediterranean (SM), temperate (TE), temperate-continental (TC) and tropical (TR). The friction velocity thresholds ( $u_*$ ,  $\text{m s}^{-1}$ ) are used to select turbulent nighttime data. For each site the average ( $\pm$  standard deviation) of each parameter is given of all weekly values derived for a site.  $R_{ref}$  and  $J_m$  are presented in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $E_0$  in K,  $\alpha$  in  $\text{mol mol}^{-1}$  and  $1/\lambda$  in  $\mu\text{mol mol}^{-1}$ . References are given describing the sites, when no reference was available the site researcher is named.

Site	Vegetation	Climate	$u_*$	$R_{ref}$	$E_0$	$J_m$	$\alpha$	$1/\lambda$	Reference or PI
AT-Neu	GRA	TE	0.11	6.28±1.96	125.1±87.4	172.7±90.1	0.39±0.17	0.68±0.47	Wohlfahrt et al. (2005)
AU-How	WSA	TR	0.40	1.39±1.39	447.2±464.6	221.2±184.4	0.26±0.15	0.47±0.54	Beringer et al. (2007)
AU-Tum	EBF	TE	0.32	5.30±1.14	41.8±18.0	216.3±198.1	0.25±0.11	0.32±0.59	Leuning et al. (2005)
BE-Lon	CRO	TE	0.23	1.99±1.22	317.2±394.3	108.8±92.6	0.30±0.18	0.47±0.68	Moureaux et al. (2006)
BR-Ban	EBF	TR	0.13	1.23±1.48	608.3±420.8	408.3±181.0	0.38±0.13	1.19±1.31	Humberto da Rocha
BR-Ma2	EBF	TR	0.14	3.58±2.70	454.8±432.5	516.3±259.4	0.58±0.10	1.27±0.42	Kruijft et al. (2004)
BR-Sa1	EBF	TR	0.30	2.93±2.71	616.6±532.7	422.6±286.6	0.57±0.17	0.70±0.37	Rice et al. (2004)
BW-Ma1	WSA	DR	0.14	1.08±0.89	117.0±82.2	42.3±40.0	0.12±0.12	0.38±0.26	Veenendaal et al. (2004)
CA-Ca1	ENF	TE	0.27	5.91±4.17	294.3±259.7	137.9±64.5	0.65±0.18	1.42±1.51	Humphreys et al. (2006)
CA-Ca2	ENF	TE	0.08	4.52±2.56	154.7±153.1	47.2±38.8	0.25±0.12	0.41±0.43	Humphreys et al. (2006)
CA-Ca3	ENF	TE	0.16	3.89±1.30	231.8±241.5	113.2±141.6	0.34±0.14	0.58±0.93	Humphreys et al. (2006)
CA-Gro	MFO	TC	0.31	3.18±1.51	101.7±57.5	135.6±188.1	0.27±0.17	0.24±0.16	McCaughy et al. (2006)
CA-Let	GRA	TC	0.27	1.64±0.95	141.8±129.5	91.2±86.3	0.14±0.10	0.32±0.30	Flanagan et al. (2002)
CA-Man	ENF	BO	0.39	2.64±1.13	170.2±108.8	63.9±26.3	0.33±0.14	0.35±0.33	Dunn et al. (2007)
CA-Mer	OSH	TC	0.04	1.68±0.55	114.9±86.0	57.5±27.2	0.21±0.09	0.10±0.06	Lafleur et al. (2001)
CA-NS1	ENF	BO	0.38	2.51±2.93	176.1±128.8	72.4±36.1	0.25±0.11	0.59±1.04	Goulden et al. (2006)
CA-NS2	ENF	BO	0.44	1.64±0.52	207.0±148.4	73.4±42.5	0.23±0.10	0.54±0.36	Goulden et al. (2006)
CA-NS3	ENF	BO	0.27	3.18±1.41	108.9±96.3	55.5±25.8	0.25±0.14	0.31±0.21	Goulden et al. (2006)
CA-NS4	ENF	BO	0.24	1.59±0.66	196.8±104.3	35.7±24.8	0.15±0.07	0.39±0.42	Goulden et al. (2006)
CA-NS5	ENF	BO	0.23	2.73±1.12	166.9±129.7	64.3±39.0	0.27±0.14	0.30±0.24	Goulden et al. (2006)
CA-NS6	OSH	BO	0.36	2.26±0.88	170.5±145.2	40.3±32.3	0.18±0.11	0.20±0.17	Goulden et al. (2006)
CA-Oas	DBF	BO	0.42	3.89±1.28	123.4±93.4	112.2±86.6	0.33±0.16	0.51±0.40	Chen et al. (2006)
CA-Obs	ENF	BO	0.24	2.77±1.18	113.9±69.8	63.7±29.4	0.24±0.11	0.33±0.15	Jarvis et al. (1997)
CA-Ojp	ENF	BO	0.25	2.20±0.98	133.8±84.0	50.7±25.3	0.22±0.11	0.36±0.21	Chen et al. (2006)
CA-Qcu	ENF	BO	0.31	2.49±0.93	172.8±131.6	43.0±15.5	0.18±0.08	0.08±0.06	Giasson et al. (2006)
CA-SF1	ENF	BO	0.26	4.10±2.00	181.6±103.2	101.4±42.3	0.31±0.13	0.31±0.17	Amiro et al. (2006)
CA-SF2	ENF	BO	0.20	3.57±2.23	216.6±155.9	125.2±85.6	0.34±0.18	0.60±0.41	Amiro et al. (2006)
CA-SJ1	ENF	BO	0.31	1.09±0.41	244.9±155.5	38.0±20.3	0.10±0.04	0.15±0.14	Chen et al. (2006)

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Table B1. Continued.

Site	Vegetation	Climate	$u_*$	$R_{ref}$	$E_0$	$J_m$	$\alpha$	$1/\lambda$	Reference or PI
CA-TP4	ENF	TC	0.46	2.85±1.39	248.7±325.8	96.1±64.1	0.34±0.16	1.52±6.29	Restrepo and Arain (2005)
CA-WP1	MFO	BO	0.09	1.99±0.96	135.3±139.4	87.4±60.6	0.15±0.09	0.21±0.15	Syed et al. (2006)
CH-Oe1	GRA	TE	0.09	4.52±1.71	250.8±214.0	188.3±104.8	0.41±0.15	0.41±0.34	Gilmanov et al. (2007)
CN-Du2	GRA	TC	0.11	1.57±1.14	174.6±91.8	51.6±32.9	0.11±0.07	0.09±0.05	Shiping Chen
CN-HaM	GRA	AR	0.14	3.33±1.41	123.4±82.8	91.6±56.9	0.16±0.09	0.15±0.08	Tomomichi Kato
CN-Ku1	EBF	DR	0.29	0.49±0.33	235.4±179.5	31.6±19.5	0.08±0.04	0.11±0.05	Shiping Chen
CN-Xi2	GRA	TC	0.18	1.03±0.61	186.9±144.5	28.3±13.8	0.07±0.07	0.14±0.09	Shiping Chen
DE-Bay	ENF	TE	0.34	4.52±1.37	164.2±123.4	132.6±48.4	0.36±0.11	0.54±0.42	Subke and Tenhunen (2004)
DE-Geb	CRO	TE	0.27	2.95±2.69	249.1±258.8	170.3±130.2	0.33±0.19	0.82±0.67	Anthoni et al. (2004)
DE-Gri	GRA	TE	0.12	2.72±0.96	192.8±82.8	92.3±56.6	0.30±0.12	0.97±0.76	Gilmanov et al. (2007)
DE-Hai	DBF	TE	0.61	3.33±1.63	215.9±211.2	140.7±113.7	0.31±0.18	0.78±0.83	Knohl et al. (2003)
DE-Kil	CRO	TE	0.24	3.96±1.50	186.8±142.9	169.4±174.2	0.24±0.14	0.52±0.47	Christian Bernhofer
DE-Meh	MFO	TE	0.07	3.30±1.66	195.5±123.8	114.4±129.5	0.21±0.11	0.47±0.44	Axel Don
DE-Tha	ENF	TE	0.39	3.17±1.37	203.3±245.4	126.2±77.9	0.49±0.17	1.00±0.77	Feigenwinter et al. (2004)
DE-Wet	ENF	TE	0.57	5.08±2.83	177.8±138.5	136.7±62.6	0.43±0.15	0.71±0.37	Anthoni et al. (2004)
DK-Lva	GRA	TE	0.22	3.36±1.54	242.9±159.5	117.0±88.8	0.45±0.22	0.70±0.90	Gilmanov et al. (2007)
DK-Sor	DBF	TE	0.64	5.14±3.17	247.7±206.9	114.4±92.1	0.47±0.22	0.51±0.57	Pilegaard et al. (2003)
ES-ES1	ENF	SM	0.44	1.98±0.79	245.3±235.6	102.8±47.5	0.27±0.11	0.37±0.24	Sanz et al. (2004)
ES-ES2	CRO	SM	0.08	1.10±0.77	443.2±388.7	219.2±153.9	0.28±0.18	0.47±0.36	Maria Jose Sanz
ES-LMa	SAV	SM	0.11	2.24±1.01	113.3±86.9	85.0±64.2	0.19±0.10	0.35±0.40	Maria Jose Sanz
ES-VDA	GRA	TE	0.11	2.15±0.39	152.4±89.4	59.7±15.1	0.15±0.05	0.10±0.06	Gilmanov et al. (2007)
FI-Hyy	ENF	BO	0.48	3.26±3.65	214.2±201.9	105.1±90.4	0.30±0.13	0.47±0.43	Suni et al. (2003)
FI-Kaa	WET	BO	0.28	1.43±0.46	158.7±70.0	35.2±14.2	0.19±0.07	0.06±0.04	Aurela et al. (2001)
FR-Gri	CRO	TE	0.35	4.53±8.55	297.4±261.5	128.7±131.5	0.29±0.15	0.30±0.26	Pierre Cellier
FR-LBr	ENF	TE	0.27	3.77±1.37	212.3±144.3	153.9±61.2	0.38±0.13	0.64±0.55	Berbigier et al. (2001)
FR-Lq2	GRA	TE	0.26	4.39±1.75	176.9±193.0	131.7±83.1	0.31±0.19	0.26±0.14	Gilmanov et al. (2007)
FR-Pue	EBF	SM	0.26	2.27±0.94	182.6±165.7	97.4±74.5	0.28±0.10	0.76±0.62	Rambal et al. (2003)
HU-Mat	GRA	TE	0.15	2.28±1.28	163.0±107.6	76.1±69.4	0.19±0.09	0.19±0.11	Zoltan Tuba
IE-Dri	GRA	TE	0.37	4.53±1.71	199.3±128.5	149.8±61.3	0.48±0.17	0.39±0.22	Gerard Kiely
IL-Yat	ENF	DR	0.36	1.21±0.88	276.7±301.2	63.1±54.3	0.22±0.10	0.52±0.39	Reichstein et al. (2005)
IS-Gun	DBF	TE	0.09	2.74±0.86	232.7±129.2	119.8±71.7	0.38±0.18	0.89±1.51	Sigurdsson et al. (2001)
IT-Amp	GRA	SM	0.09	3.16±1.88	129.5±106.7	74.4±48.7	0.30±0.13	0.29±0.20	Gilmanov et al. (2007)
IT-BCi	CRO	SM	0.16	2.22±1.37	312.9±169.8	406.0±570.4	0.35±0.18	0.83±0.81	Reichstein et al. (2003)
IT-Be2	CRO	TE	0.10	3.11±1.34	148.0±92.6	95.2±132.7	0.20±0.10	0.58±0.71	Alessandro Peressotti
IT-Col	DBF	SM	0.66	2.54±0.84	181.4±144.5	151.6±75.6	0.44±0.21	1.06±0.80	Valentini et al. (1996)
IT-Cpz	EBF	SM	0.24	2.40±1.08	296.2±330.8	177.9±238.5	0.36±0.16	0.98±1.03	Reichstein et al. (2002)
IT-MBo	GRA	TE	0.13	5.19±2.04	208.3±191.6	199.9±141.6	0.26±0.13	0.27±0.23	Rodeghiero and Cescatti (2005)
IT-Noe	CSH	SM	0.11	2.24±0.88	159.3±141.8	79.8±36.3	0.26±0.10	0.61±0.51	Rossi et al. (1998)
IT-Non	DBF	SM	0.12	3.00±0.99	131.3±93.3	153.4±96.9	0.31±0.12	1.15±0.87	Reichstein et al. (2003)
IT-Pia	OSH	SM	0.52	0.56±0.42	330.9±29.8	46.4±36.6	0.15±0.09	0.14±0.11	Reichstein et al. (2005)
IT-Ren	ENF	TE	0.38	3.67±3.02	316.4±277.2	116.2±77.0	0.32±0.17	0.24±0.18	Rebmann et al. (2005)
IT-Ro1	DBF	SM	0.28	2.65±1.12	250.2±203.2	109.5±79.5	0.25±0.11	0.52±0.39	Tedeschi et al. (2005)
JP-Tak	DBF	TC	0.41	2.71±1.38	281.0±265.1	103.1±110.7	0.30±0.18	0.56±0.54	Yamamoto et al. (1999)
JP-Tef	MFO	TC	0.40	4.49±1.67	159.3±102.6	107.3±59.1	0.32±0.14	0.53±0.36	Kentaro Takagi
JP-Tom	MFO	TC	0.31	4.57±2.00	176.4±137.6	156.3±117.0	0.54±0.29	0.38±0.29	Hirano et al. (2003)
NL-Ca1	GRA	TE	0.22	3.17±1.45	140.4±84.7	105.2±61.8	0.29±0.15	0.22±0.16	Gilmanov et al. (2007)
NL-Loo	ENF	TE	0.33	3.97±1.49	220.3±207.2	143.8±90.2	0.50±0.15	0.60±0.55	Dolman et al. (2002)

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Table B1. Continued.

Site	Vegetation	Climate	$u_*$	$R_{ref}$	$E_0$	$J_m$	$\alpha$	$1/\lambda$	Reference or PI
PT-Esp	EBF	SM	0.48	2.17±1.16	326.7±233.8	130.8±38.9	0.37±0.13	1.11±0.85	Gabriel Pita
PT-Mi1	EBF	SM	0.24	1.73±1.07	152.4±110.9	49.0±22.5	0.18±0.12	1.54±2.18	David et al. (2004)
PT-Mi2	GRA	SM	0.13	2.02±1.49	175.8±144.1	79.3±70.7	0.14±0.12	0.30±0.19	Gilmanov et al. (2007)
RU-Che	MFO	BO	0.25	1.83±0.56	175.3±175.0	50.1±26.8	0.15±0.07	0.27±0.21	Corradi et al. (2005)
RU-Fyo	ENF	TC	0.37	5.02±2.31	211.8±203.0	118.3±73.3	0.45±0.17	0.89±2.36	Andrej Varlagin
RU-Ha1	GRA	BO	0.25	1.73±0.56	181.2±127.7	48.4±18.9	0.19±0.06	0.19±0.15	Dario Papale
RU-Zot	ENF	BO	0.60	2.13±1.21	202.2±135.9	76.9±34.9	0.22±0.11	0.40±0.29	Tchebakova et al. (2002)
SE-Fla	ENF	BO	0.48	2.43±1.63	313.7±199.8	55.8±33.0	0.27±0.17	0.28±0.20	Lindroth et al. (1998)
SE-Nor	ENF	TC	0.58	4.96±2.43	290.0±274.6	100.4±55.4	0.41±0.20	1.43±3.25	Lindroth et al. (1998)
UK-ESa	CRO	TE	0.28	6.43±5.92	355.3±325.1	141.3±95.2	0.42±0.19	0.98±0.88	John Moncrieff
UK-Gri	ENF	TE	0.37	4.26±3.84	215.4±166.2	124.0±57.7	0.54±0.16	0.77±1.08	Valentini et al. (2000)
US-ARb	GRA	SM	0.44	2.53±1.47	187.1±200.7	222.6±198.1	0.18±0.12	0.42±0.36	Fischer et al. (2007)
US-ARc	GRA	SM	0.51	2.99±1.42	96.0±76.5	162.9±135.1	0.17±0.09	0.28±0.21	Fischer et al. (2007)
US-Aud	GRA	DR	0.16	0.65±0.46	300.7±229.8	58.0±66.6	0.10±0.08	0.30±0.32	Tilden Meyers
US-Bkg	GRA	TC	0.16	2.05±0.70	165.1±90.4	121.2±80.0	0.19±0.05	0.07±0.04	Gilmanov et al. (2005)
US-Blo	ENF	SM	0.25	2.55±1.48	297.1±259.1	158.1±101.9	0.23±0.09	0.42±0.33	Misson et al. (2005)
US-Bn1	ENF	BO	1.06	1.34±0.87	356.0±226.8	32.6±18.5	0.20±0.10	0.23±0.14	Liu et al. (2005)
US-Bo1	CRO	TC	0.41	2.10±1.51	354.8±306.7	277.8±379.6	0.27±0.18	0.53±0.72	Meyers (2001)
US-Bo2	CRO	TC	0.34	2.53±1.70	369.2±329.2	396.0±609.1	0.28±0.16	1.95±4.33	Meyers (2001)
US-FR2	WSA	SM	0.28	1.62±0.93	247.3±167.2	105.0±65.4	0.19±0.05	0.58±0.61	Heinsch et al. (2004)
US-Goo	GRA	SM	0.20	2.31±1.41	205.8±131.6	142.3±125.4	0.18±0.10	0.43±0.59	Tilden Meyers
US-Ha1	DBF	TC	0.76	3.63±2.01	212.2±195.2	197.1±294.2	0.35±0.22	0.69±1.19	Wofsy et al. (1993)
US-Ho1	ENF	TC	0.27	3.60±1.67	160.8±106.0	121.1±67.8	0.44±0.17	0.83±0.50	Hollinger et al. (2004)
US-IB1	CRO	TC	0.27	2.57±3.44	431.8±284.5	428.2±539.5	0.31±0.16	0.94±0.75	Sluis (2002)
US-IB2	GRA	TC	0.09	2.79±1.10	127.8±75.8	152.7±109.2	0.28±0.19	0.35±0.28	Sluis (2002)
US-KS2	CSH	SM	0.19	2.54±1.43	191.7±194.9	183.7±64.6	0.24±0.06	0.55±0.27	Powell et al. (2006)
US-MMS	DBF	SM	0.53	2.60±1.05	161.6±118.6	157.8±137.1	0.30±0.13	0.44±0.32	Schmid et al. (2000)
US-MOz	DBF	SM	0.51	2.81±1.59	208.9±208.0	149.2±138.6	0.25±0.15	0.51±0.40	Gu et al. (2006)
US-NC2	ENF	SM	0.24	2.67±1.11	302.1±215.1	147.8±91.7	0.60±0.19	0.55±0.16	Jiquan Chen
US-Ne1	CRO	TC	0.21	3.92±2.02	191.9±139.2	548.6±494.0	0.32±0.18	0.83±0.65	Verma et al. (2005)
US-Ne2	CRO	TC	0.17	4.04±1.98	172.1±117.4	482.6±441.9	0.33±0.17	0.80±0.65	Verma et al. (2005)
US-Ne3	CRO	TC	0.21	3.33±1.73	206.4±115.9	572.0±570.9	0.32±0.16	1.37±0.81	Verma et al. (2005)
US-NR1	ENF	BO	0.44	2.79±0.86	183.5±155.7	62.4±25.7	0.24±0.13	0.20±0.12	Monson et al. (2002)
US-PFa	MFO	TC	0.36	3.25±1.48	364.7±195.4	144.2±89.4	0.37±0.22	0.22±0.24	Davis et al. (2003)
US-SO2	WSA	SM	0.59	1.85±0.14	175.6±163.8	45.9±13.6	0.62±0.08	0.25±0.12	Hibbard et al. (2005)
US-SO3	WSA	SM	0.32	0.92±1.08	325.1±275.9	29.0±15.1	0.10±0.05	0.12±0.08	Hibbard et al. (2005)
US-SO4	CSH	SM	0.38	0.52±0.76	551.5±507.9	25.2±16.0	0.09±0.04	0.27±0.66	Walt Oechel
US-SP2	ENF	SM	0.39	3.80±1.27	146.9±128.5	171.6±90.9	0.34±0.16	0.62±0.50	Gholz and Clark (2002)
US-SP3	ENF	SM	0.29	2.51±1.24	242.8±237.7	193.6±84.8	0.33±0.14	0.66±0.47	Gholz and Clark (2002)
US-SRM	WSA	DR	0.25	0.45±0.39	273.1±129.1	19.9±30.2	0.14±0.19	0.18±0.13	Scott et al. (2006)
US-Ton	WSA	SM	0.21	1.87±1.31	138.3±135.5	104.3±218.7	0.14±0.07	0.81±0.78	Baldocchi et al. (2004)
US-UMB	DBF	TC	0.21	3.85±0.85	123.3±73.8	143.9±78.6	0.38±0.16	0.33±0.16	Gough et al. (2008)
US-Var	GRA	SM	0.08	2.53±1.70	159.3±116.2	103.2±105.8	0.22±0.17	0.58±2.96	Xu and Baldocchi (2004)
US-WCr	DBF	TC	0.63	3.88±2.69	267.6±185.0	143.1±139.5	0.32±0.23	0.38±0.39	Cook et al. (2004)
US-Wi4	ENF	TC	0.68	1.96±1.58	345.0±286.0	153.3±48.2	0.49±0.16	0.89±0.48	Noormets et al. (2007)
VU-Coc	EBF	TR	0.35	3.02±2.58	457.3±405.4	310.1±97.0	0.54±0.13	0.70±0.37	Roupsard et al. (2006)

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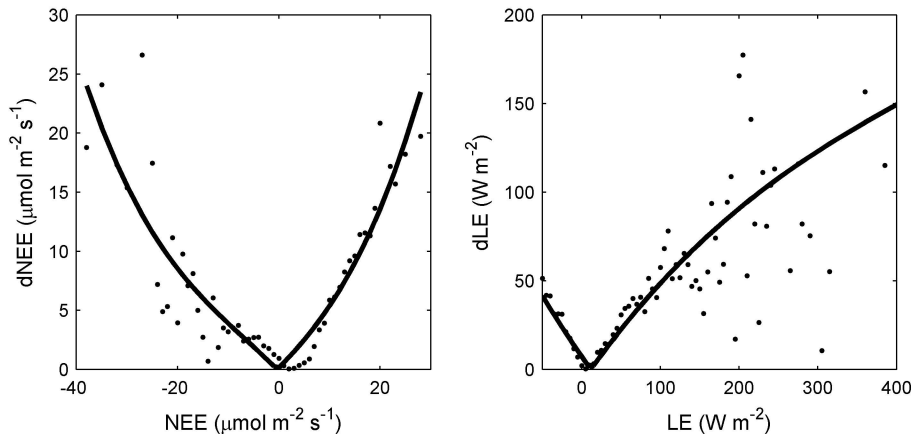
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**Fig. 1.** Flux uncertainty ( $dNEE$  and  $dLE$ ) derived from paired observation for  $NEE$  and  $LE$  at the NL-Loo site. The points are the binned average values, and in the line is the polynomial fit.

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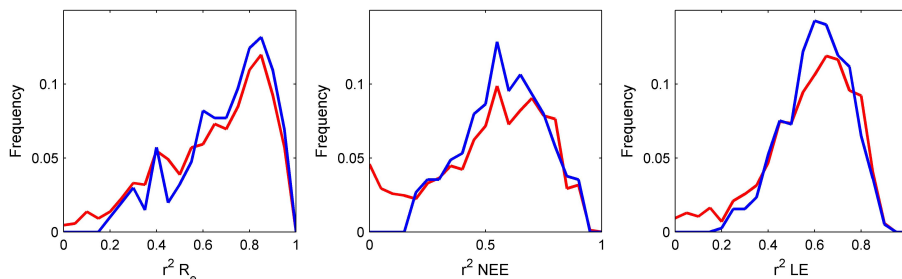
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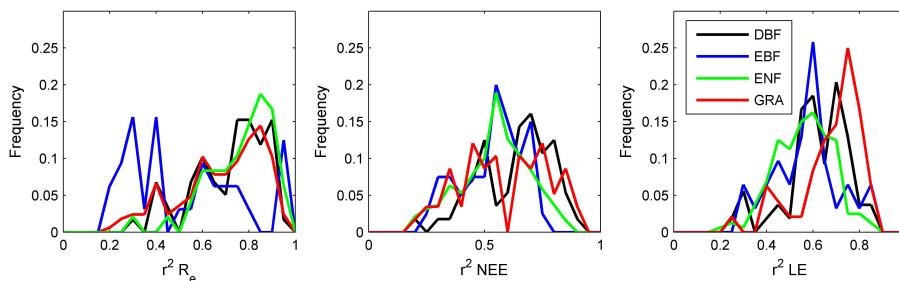


**Fig. 2.** Frequency distributions of site year correlation coefficients ( $r^2$ ) of half hourly observed and simulated  $R_p$ ,  $NEE$  and  $LE$ . Initial distribution in red and distribution after removal of sites as explained in the text in blue.

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**Fig. 3.** Frequency distributions of site year correlation coefficients ( $r^2$ ) of half hourly observed and simulated  $R_e$ ,  $NEE$  and  $LE$ . The different colors represent the following vegetation types: deciduous broadleaf forest (DBF), evergreen broadleaf forest (EBF), evergreen needleleaf forest (ENF) and grassland (GRA).

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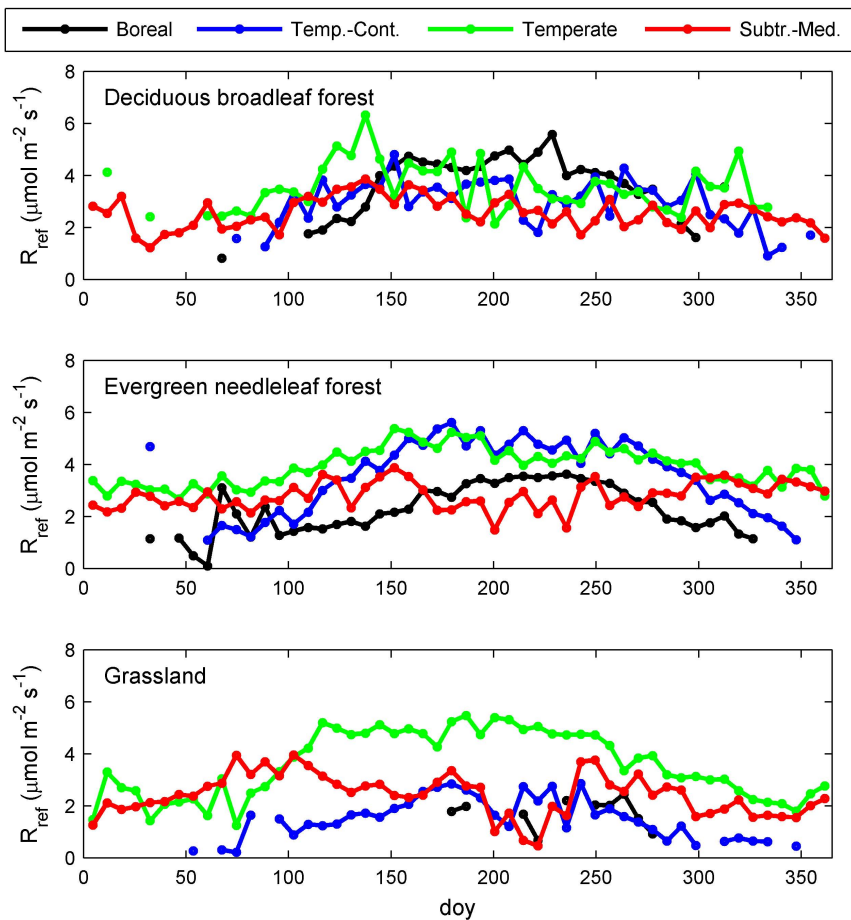


Fig. 4. Seasonal variation of  $R_{ref}$  for different vegetation types and climate regions.

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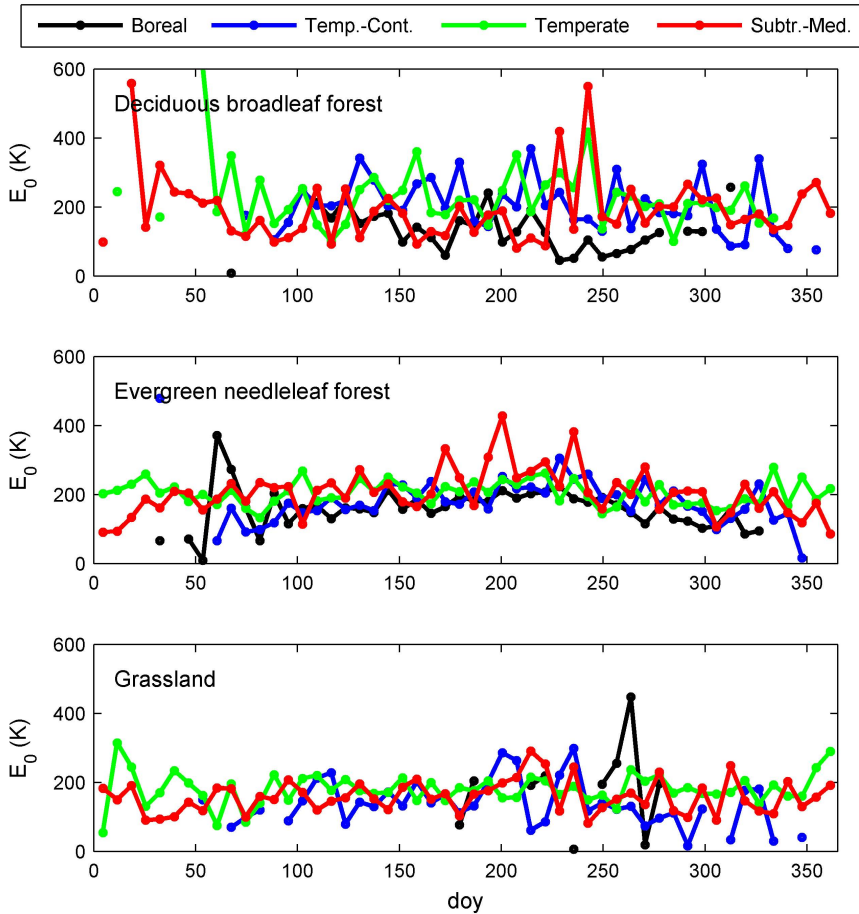


Fig. 5. Seasonal variation of  $E_0$  for different vegetation types and climate regions.

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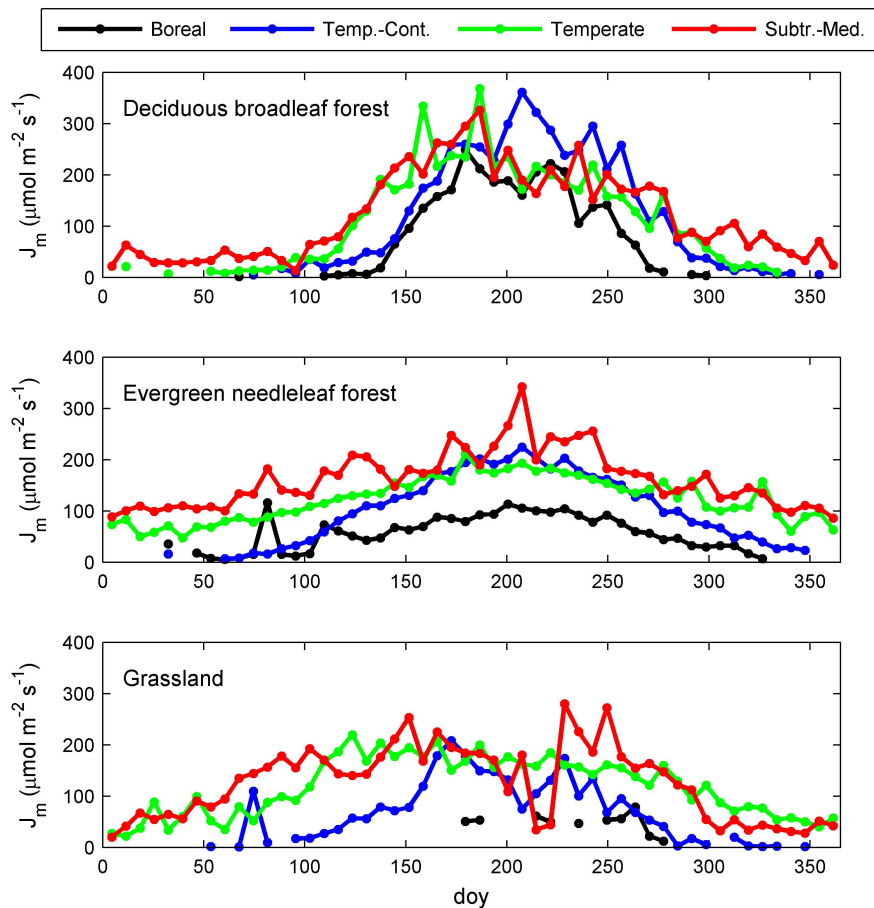


Fig. 6. Seasonal variation of  $J_m$  for different vegetation types and climate regions.

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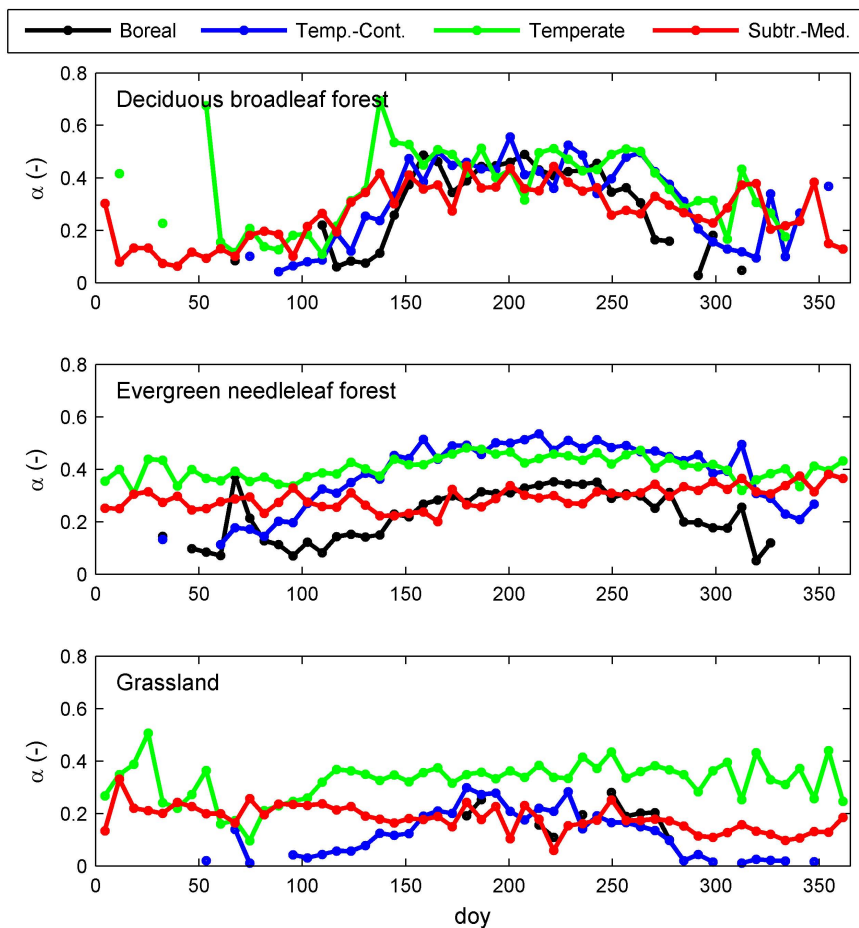


Fig. 7. Seasonal variation of  $\alpha$  for different vegetation types and climate regions.

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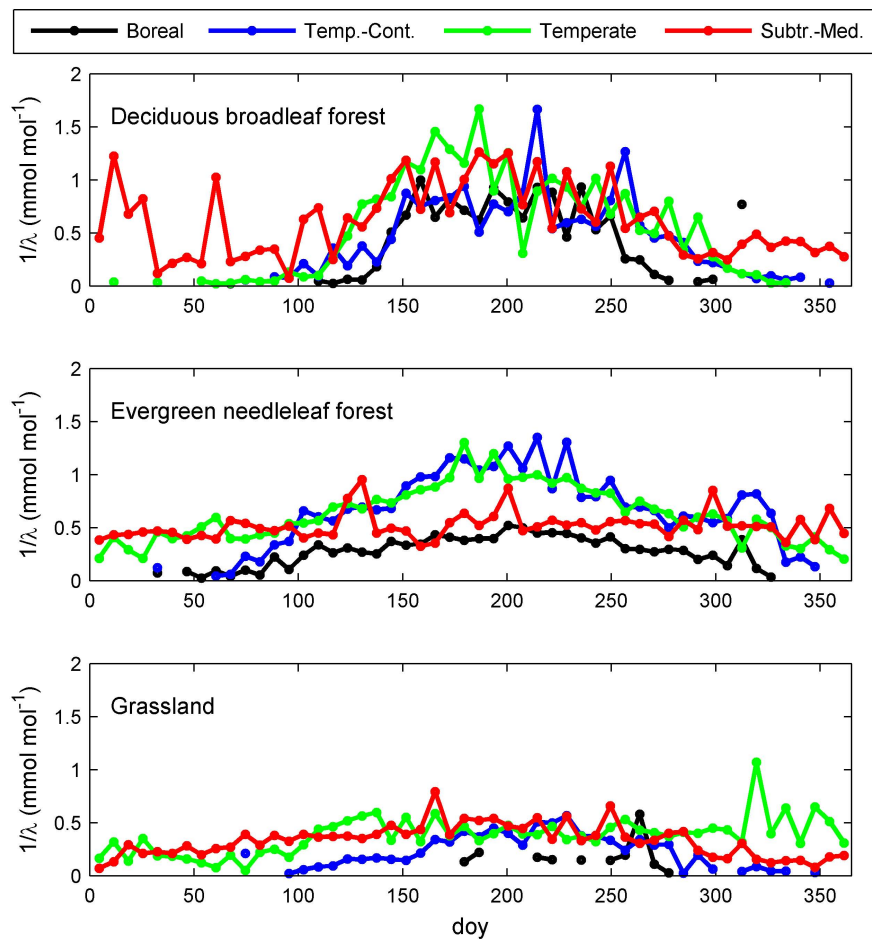


Fig. 8. Seasonal variation of  $1/\lambda$  for different vegetation types and climate regions.

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