Seasonal variation of photosynthetic model parameters and leaf area index from global Fluxnet eddy covariance data

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[1] Global vegetation models require the photosynthetic parameters, maximum carboxylation capacity (V_{cm}), and quantum yield (α) to parameterize their plant functional types (PFTs). The purpose of this work is to determine how much the scaling of the parameters from leaf to ecosystem level through a seasonally varying leaf area index (LAI) explains the parameter variation within and between PFTs. Using Fluxnet data, we simulate a seasonally variable LAI_F for a large range of sites, comparable to the LAI_M derived from MODIS. There are discrepancies when LAI_F reach zero levels and LAI_M still provides a small positive value. We find that temperature is the most common constraint for LAI_F in 55% of the simulations, while global radiation and vapor pressure deficit are the key constraints for 18% and 27% of the simulations, respectively, while large differences in this forcing still exist when looking at specific PFTs. Despite these differences, the annual photosynthesis simulations are comparable when using LAI_F or LAI_M ($r^2 = 0.89$). We investigated further the seasonal variation of ecosystem-scale parameters derived with LAI_F. V_{cm} has the largest seasonal variation. This holds for all vegetation types and climates. The parameter α is less variable. By including ecosystem-scale parameter seasonality we can explain a considerable part of the ecosystem-scale parameter variation between PFTs. The remaining unexplained leaf-scale PFT variation still needs further work, including elucidating the precise role of leaf and soil level nitrogen.

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1. Introduction

[2] Global land surface schemes represent ecosystem characteristics by model parameters and state variables [e.g., *Sellers et al.*, 1997; *Foley et al.*, 1998; *Bonan et al.*, 2002; *Sitch et al.*, 2003; *Krinner et al.*, 2005]. A key issue for modelers is how to balance the detail required for process-

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Table 1. List of Most Important Parameters Derived for All Sites in Appendix A[a]

Parameter	Scale	Data	Definition
$V_{cm,F}$	Ecosystem, seasonal	Fluxnet	Ecosystem carboxylation capacity (μmol m^{-2} s^{-1})
$v_{cm,25F}$	Leaf, constant	Fluxnet	Leaf carboxylation capacity (μmol m^{-2} s^{-1})
$V_{cm,M}$	Ecosystem, seasonal	MODIS	Ecosystem carboxylation capacity (μmol m^{-2} s^{-1})
$v_{cm,25M}$	Leaf, constant	MODIS	Leaf carboxylation capacity (μmol m^{-2} s^{-1})
$V_{cm,B}$	Ecosystem, seasonal	Fluxnet	Bulk carboxylation capacity (μmol m^{-2} s^{-1})
$\alpha_{e,F}$	Ecosystem, seasonal	Fluxnet	Ecosystem quantum yield (mol mol^{-1})
α_F	Leaf, constant	Fluxnet	Leaf quantum yield (mol mol^{-1})
$\alpha_{e,M}$	Ecosystem, seasonal	MODIS	Ecosystem quantum yield (mol mol^{-1})
α_M	Leaf, constant	MODIS	Leaf quantum yield (mol mol^{-1})
$\alpha_{e,B}$	Ecosystem, seasonal	Fluxnet	Bulk quantum yield (mol mol^{-1})

[a]Parameters are derived with Fluxnet or MODIS data and kept constant over time or are seasonally variable.

oriented simulations against the need for generality and the availability of parameters at large spatial and temporal scales. Leaf and canopy processes are well-known, but the level of understanding at the global scale is still inadequate. The pragmatic solution is to apply small-scale knowledge at the larger spatial and temporal scales [*Jarvis*, 1995].

[3] The process of photosynthesis is central to any land surface scheme that aims to model the global carbon balance. For example, the photosynthesis model of *Farquhar et al.* [1980] is used in many global models [e.g., *Sellers et al.*, 1997; *Knorr*, 2000; *Arora*, 2002; *Sitch et al.*, 2003; *Krinner et al.*, 2005]. Yet, although this model was developed for individual leaves at a temporal scale of several hours, it is applied at larger spatial scales by using leaf area index (*LAI*) to upscale the leaf-scale maximum carboxylation capacity ($v_{cm,25}$) and quantum yield (α) or the leaf-scale photosynthesis flux. Upscaling assumes a particular radiation distribution within a canopy, in big leaf [*Sellers et al.*, 1992], multilayer [*Baldocchi and Harley*, 1995], sun/shade [*de Pury and Farquhar*, 1997], and three-dimensional models [*Dauzat et al.*, 2001]. This is combined with assumptions about the distribution of leaf nitrogen and photosynthetically active radiation (*PAR*) over the canopy profile [*Reich et al.*, 1997].

[4] Photosynthetic parameters are normally estimated at the leaf scale but can be determined at the ecosystem scale through the inverse application of ecosystem models using eddy-covariance (EC) flux observations. At the leaf scale there is evidence that parameters are seasonally variable and change with leaf age, temperature, water availability, and nitrogen content [e.g. *Wilson et al.*, 2001; *Medlyn et al.*, 2002; *Xu and Baldocchi*, 2003; *Mäkelä et al.*, 2004; *Misson et al.*, 2006; *Kolari et al.*, 2007; *Misson et al.*, 2010]. At the ecosystem-scale, seasonal variability of V_{cm} and α_e (Table 1) derived from EC observations has been observed for a range of sites [*Reichstein et al.*, 2003a; *Wang et al.*, 2003; *Owen et al.*, 2007; *Wang et al.*, 2007; *Mo et al.*, 2008; *Thum et al.*, 2008], but between-site differences could be related to the mean summer *LAI* [*Lindroth et al.*, 2008].

[5] Photosynthetic parameters in global models are usually defined by plant functional types (PFTs) [*Box*, 1996; *Bonan et al.*, 2002; *Sitch et al.*, 2003; *Krinner et al.*, 2005]. The variation of leaf-scale $v_{cm,25}$ between and within PFTs is derived by *Kattge et al.* [2009] and related to leaf nitrogen content in natural vegetation. This relationship varies by vegetation type, but the relationship with nitrogen-use

efficiency is independent of vegetation type. *Williams et al.* [2009] state that the Fluxnet data could be used to challenge and enrich the PFT approach at the ecosystem scale. A comparison of annual photosynthetic model parameters derived from 101 sites in the global Fluxnet data indicated that the ecosystem parameters are more variable than assumed within the PFTs and that a PFT-based classification does not reflect the reality of short-term photosynthesis and transpiration flux variation [*Groenendijk et al.*, 2011]. Furthermore, *Alton* [2011] reported that model parameters overlap between PFTs and that modeled carbon fluxes are especially sensitive to the classification of model parameters. These three examples raise issues regarding the classification and distribution of model parameters. This study aims to answer the question: what is the influence of seasonal variability on the ecosystem parameter variation within a PFT? Our hypothesis is that meteorological data can be used to constrain seasonal ecosystem-scale parameter variation.

[6] The overall objective of this study is thus to improve the understanding of the temporal and spatial variation of the photosynthetic model parameters, with an emphasis on their relationship with *LAI* and meteorological variables. The study aims to expand upon previous work [*Groenendijk et al.*, 2011] by further refining photosynthetic parameters derived from tower flux observations. Specific objectives are: (1) determine if *LAI* scaling of the parameters results in a better understanding of the parameter variation within and between PFTs; (2) quantify sensitivity of photosynthetic parameters to *LAI* variations; (3) determine if the Fluxnet EC and meteorological data can be used to derive a seasonal *LAI*; and (4) if this is comparable to *LAI* derived from MODIS, which can be used over larger areas.

2. Methods

2.1. Overview

[7] We use a big leaf model that can be applied at all Fluxnet sites without additional site-specific information on canopy architecture. Ecosystem-scale parameters (V_{cm} and α_e) are derived from an integrated light exponential profile, leaf-scale parameters ($v_{cm,25}$ and α) and *LAI* [*Field*, 1983; *Sellers et al.*, 1992]. Parameter definitions are presented in Table 1. The leaf-scale model parameters $v_{cm,25}$ and α are assumed constant in time and scaled with *LAI* to obtain seasonally variable ecosystem-scale parameters V_{cm} and α_e. This assumption separates spatial and temporal parameter
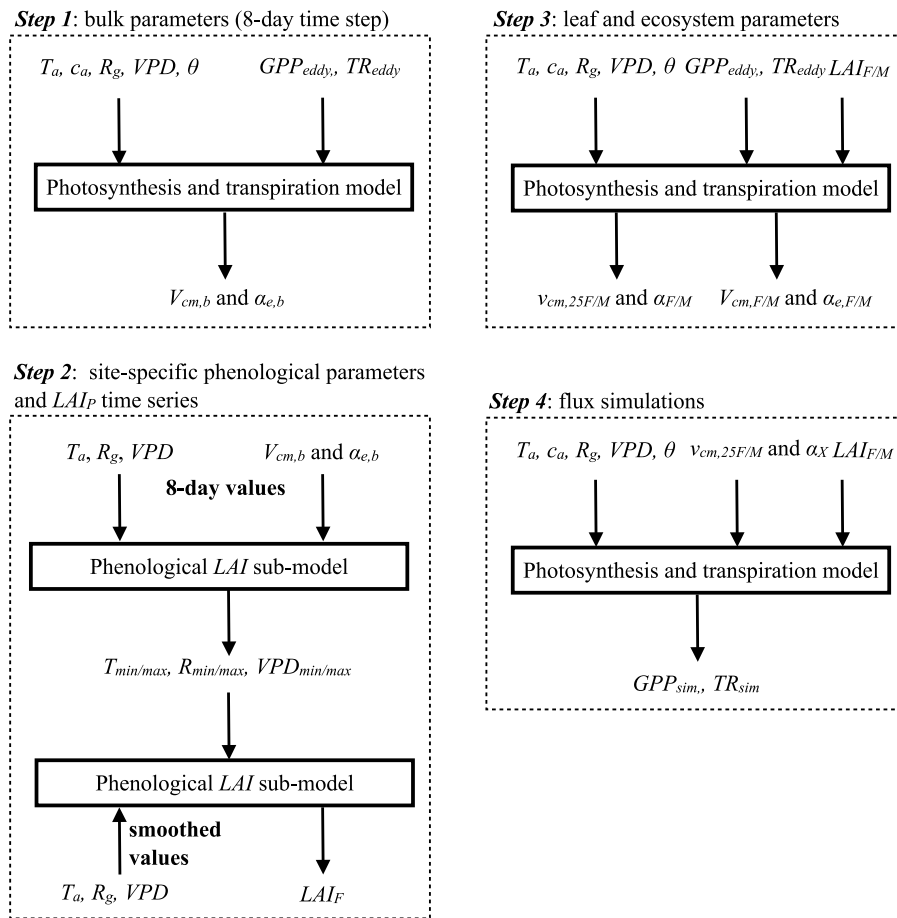
Figure 1. Data flow diagram used to derive leaf-scale ($v_{cm,25F/M}$ and $\alpha_{F/M}$) and ecosystem-scale parameters ($V_{cm,F/M}$ and $\alpha_{e,F/M}$) from observed meteorological data (T_a, C_a, R_g, VPD, θ) and flux data (GPP_{eddy}, TR_{eddy}). In steps 3 and 4 either LAI_F (Fluxnet) or LAI_M (MODIS) is used.

contributions to the overall variation. To account for seasonal changes in LAI and meteorology, a phenological submodel [*Jolly et al.*, 2005; *Stöckli et al.*, 2008] is used as an alternative to MODIS retrievals of LAI [*Distributed Active Archive Center (DAAC)*, 2009]. This modeling strategy is chosen to produce insights in the climatic constraints on LAI and the influence of LAI on the variation of ecosystem-scale physiological parameters. In addition, it allows examination of the potential for simulating LAI using only meteorological tower observations that are measured at the same spatial scale as the eddy covariance fluxes. The range of parameters (Table 1) provides flexibility identifying relationships at different scales.

[8] We take a four step approach to using global Fluxnet and MODIS observations to quantify the influence of seasonal variation of photosynthetic model parameters on the parameter variation between sites and PFTs. Seasonal LAI is derived from Fluxnet observations (section 2.2) with the models described in sections 2.3 and 2.4. In this second step, seasonally variable bulk parameters $V_{cm,B}$ and $\alpha_{e,B}$ are used from the first step, where LAI scaling is implicitly included. This allows us to derive a seasonal signal from the parameters. Third, LAI derived from both the Fluxnet data (LAI_F) and MODIS data (LAI_M) is used to obtain two sets of leaf-scale photosynthetic parameters ($v_{cm,25F}$, α_F and

$v_{cm,25M}$, α_M). Finally, in the fourth step, the leaf-scale parameters and LAI_F or LAI_M are used to simulate the photosynthesis and transpiration fluxes.

2.2. Observations

[9] The Fluxnet database contains ecosystem fluxes of carbon, water, and energy measured with the eddy-covariance technique [*Aubinet et al.*, 2000]. All data are processed in a harmonized manner following *Baldocchi et al.* [2001], *Papale and Valentini* [2003], *Reichstein et al.* [2005], *Papale et al.* [2006], *Moffat et al.* [2007], and *Baldocchi* [2008]. The following variables are required to apply the photosynthesis and transpiration model and derive the photosynthetic parameters (Figure 1): net ecosystem exchange (*NEE*), latent heat flux (*LE*), air temperature (T_a), global radiation (R_g), vapor pressure deficit (*VPD*), soil water content (θ), and maximum leaf area index (LAI_{max}). Here θ is observed in the topsoil at an average depth of 5–15 cm. These point observations are not representative for the full tower footprint, but the temporal dynamics of wetting and drying are. We have excluded sites with data gaps of more than 50% during the growing season, missing input variables, or having less than 2 years of data. On the basis of these criteria the sites in Appendix A were selected from the Fluxnet database (www.fluxdata.org) of April 2008.

[10] Within the Fluxnet database, the observed *NEE* is partitioned into gross primary production (GPP_{eddy}) and ecosystem respiration (R_e). R_e is determined from the temperature dependence of nighttime ecosystem fluxes using the methodology of *Reichstein et al.* [2005] and subtracted from *NEE* to estimate GPP_{eddy}. GPP_{eddy} is compared with simulated photosynthesis (GPP_{sim}, see next section), but because GPP_{eddy} is derived from observed *NEE* and simulated R_e there are uncertainties associated with this method that may affect model results [*Lasslop et al.*, 2008; *Vickers et al.*, 2009; *Lasslop et al.*, 2010]. Simulated latent heat fluxes are compared with observations to estimate model parameters, but the observed flux is the sum of transpiration and soil evaporation. We assume that during periods with no precipitation total evaporation equals transpiration (TR_{obs}), which includes both the overstorey and understorey. These periods were selected by excluding data for days with precipitation and 3 days thereafter. All models (see Figure 1) are optimized with non-gap-filled observed data only.

[11] LAI_M is derived from the MODIS database [*DAAC*, 2009] for a 7×7 km area centered on each site. The database contains 8-day composite values of LAI_M with no clouds and no presence of snow and ice (1×1 km resolution). The average of observations over the 7×7 km areas is calculated, and the 8-day composites are linearly interpolated and smoothed with a moving average of 24 days to determine half-hourly values.

2.3. Photosynthesis and Transpiration Model

[12] The model used in this study is based on the equations of *Cowan* [1977], *Farquhar et al.* [1980], and *Arneth et al.* [2002] and is fully described in the appendix of *Groenendijk et al.* [2011]. Photosynthesis (GPP_{sim}) is given as the minimum of carboxylation (W_c) and Ribulose-1,5-bisphosphate (RuBP) regeneration (W_f) minus dark respiration (R_d).

$$GPP_{sim} = \beta\left[\left(1 - \Gamma^*/C_i\right)\min\{W_c, W_j\} - R_d\right] \quad (1)$$

where β is a factor to reduce photosynthesis during dry periods, Γ^* is the compensation point for CO_2 in the absence of dark respiration (ppm), and C_i the mole fraction of CO_2 (ppm) and $R_d = 0.07 V_{cm}$. W_c is a function of the parameter V_{cm}, and W_f is a function of the parameters J_m and α:

$$W_c = \frac{V_{cm}C_i}{C_i + k'} \quad (2)$$

$$W_j = \frac{JC_i}{4\left(C_i + 2\Gamma^*\right)} \quad (3)$$

$$k' = K_c(1 + O/K_o) \quad (4)$$

$$\Gamma^* = 0.5\frac{V_{om}}{V_{cm}}\frac{K_c}{K_oO} \quad (5)$$

$$J = \frac{\alpha I_{PAR}J_m}{\alpha I_{PAR} + 2.1J_m} \quad (6)$$

where I_{PAR} is the absorbed photosynthetically active radiation (μmol photons m^{-2} s^{-1}), J is the electron yield, V_{cm} is the rate of carboxylation mediated by the enzyme Rubisco (μmol m^{-2} s^{-1}), V_{cm} is the rate of oxygenation of Rubisco (μmol m^{-2} s^{-1}), J_m is the maximum potential electron transport rate (μmol m^{-2} s^{-1}), α is the quantum yield (mol mol^{-1}), K_c is the kinetic coefficient for CO_2 (bar), K_o is the kinetic coefficient for O_2 (bar), and O is the partial pressure for O_2 (bar). The ratio V_{cm}/V_{cm} is assumed to be a constant value of 0.21. The quantum yield is an adjustable parameter and contains a constant intrinsic quantum yield and a *PAR* absorption parameter, which is variable as a result of the optical characteristics of leaves, branches, and canopies. This model is developed for C_3 vegetation and therefore can introduce uncertainty to model parameters and fluxes derived for sites where a part of the vegetation is C_4. The number of sites containing C_4 vegetation is very small.

[13] Assuming an infinite boundary layer conductance, transpiration (TR_{sim}) is a function of stomatal conductance (g_s), which can be calculated from GPP_{sim}, C_a and C_i:

$$g_s = \frac{GPP_{sim}}{C_a - C_i} \quad (7)$$

$$TR_{sim} = 1.6Dg_s \quad (8)$$

where D is the molar vapor gradient between leaf intercellular space and ambient air and 1.6 is the ratio of molecular diffusivity of H_2O to CO_2. The internal pressure of CO_2 (C_i) is determined as described by *Arneth et al.* [2002], who linked the models of *Cowan* [1977] and *Farquhar et al.* [1980] using the parameter λ (the ratio between *TR* and *GPP* as a function of g_s (mol mol^{-1})).

[14] Ecosystem gross primary production (GPP_{sim}) and transpiration (TR_{sim}) are calculated from half-hourly meteorological data, leaf area index (LAI), and model parameters describing the ecosystem characteristics. The main leaf-scale parameters in this model are $v_{cm,25}$ (μmol m^{-2} s^{-1}), the rate of carboxylation mediated by the enzyme Rubisco at 25 °C and α (mol mol^{-1}), the quantum yield. The parameter $v_{cm,25}$ is converted to v_{cm} with a short-term temperature response [*Knorr and Kattge*, 2005; *Thum et al.*, 2008]. $j_{m,25}$ is related to $v_{cm,25}$ by a constant ratio [*Wullschleger*, 1993; *Leuning*, 2002]. In the work of *Groenendijk et al.* [2011] we derived $j_{m,25} = 3v_{cm,25}$ for the Fluxnet sites. Thus we introduce an additional constraint to the present model.

[15] The photosynthesis model of *Farquhar et al.* [1980] was originally developed for the leaf scale. To use this model at the ecosystem scale, the parameters or fluxes need to be upscaled. The assumption generally used is that the profile of leaf-nitrogen content per unit of leaf area through the depth of the canopy follows the time-mean profile of radiation intensity [*Sellers et al.*, 1992; *Reich et al.*, 1997; *Arora*, 2002]. Because the leaf photosynthetic properties are proportional to nitrogen content, they also acclimate to the radiation profile, which we used to derive the ecosystem-scale properties by multiplication with the integrated exponential function of *LAI* [*Kull and Jarvis*, 1995; *Cox et al.*, 1998; *Wolf et al.*, 2006]. The leaf parameters v_{cm} and α