

# Improving the ISBA(CC) land surface model simulation of water and carbon fluxes and stocks over the Amazon forest

E. Joetzjer, C. Delire, H. Douville, P. Ciais, B. Decharme, D. Carrer, H. Verbeeck, M. de Weirdt, D. Bonal

► **To cite this version:**

E. Joetzjer, C. Delire, H. Douville, P. Ciais, B. Decharme, et al.. Improving the ISBA(CC) land surface model simulation of water and carbon fluxes and stocks over the Amazon forest. Geoscientific Model Development, European Geosciences Union, 2015, 8 (6), pp.1709 - 1727. 10.5194/gmd-8-1709-2015 . hal-01557272

**HAL Id: hal-01557272**

**<https://hal.univ-lorraine.fr/hal-01557272>**

Submitted on 6 Jul 2017

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



# Improving the ISBA<sub>CC</sub> land surface model simulation of water and carbon fluxes and stocks over the Amazon forest

E. Joetzjer<sup>1</sup>, C. Delire<sup>1</sup>, H. Douville<sup>1</sup>, P. Ciais<sup>2</sup>, B. Decharme<sup>1</sup>, D. Carrer<sup>1</sup>, H. Verbeeck<sup>3</sup>, M. De Weirdt<sup>3</sup>, and D. Bonal<sup>4</sup>

<sup>1</sup>CNRM-GAME UMR3589, Groupe d'étude de l'atmosphère météorologique, 31000 Toulouse, France

<sup>2</sup>Laboratory of Climate Sciences and the Environment (LSCE), Joint Unit of CEA-CNRS, L'Orme des Merisiers, 91191 Gif-sur-Yvette, France

<sup>3</sup>CAVElab Computational and Applied Vegetation Ecology, Department of Applied Ecology and Environmental Biology, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, 9000 Ghent, Belgium

<sup>4</sup>INRA, UMR EEF, 54280 Champenoux, France

Correspondence to: E. Joetzjer (emilie.joetzjer@msu.montana.edu)

Received: 15 December 2014 – Published in Geosci. Model Dev. Discuss.: 11 February 2015

Revised: 7 May 2015 – Accepted: 15 May 2015 – Published: 10 June 2015

**Abstract.** We evaluate the ISBA<sub>CC</sub> (Interaction Soil Biosphere Atmosphere Carbon Cycle) land surface model (LSM) over the Amazon forest, and propose a revised parameterization of photosynthesis, including new soil water stress and autotrophic respiration ( $R_A$ ) functions. The revised version allows the model to better capture the energy, water and carbon fluxes when compared to five Amazonian flux towers. The performance of ISBA<sub>CC</sub> is slightly site dependent although similar to the widely evaluated LSM ORCHIDEE (Organizing Carbon and Hydrology In Dynamic Ecosystems – version 1187), which is based on different assumptions. Changes made to the autotrophic respiration functions, including a vertical profile of leaf respiration, lead to yearly simulated carbon use efficiency (CUE) and carbon stocks which is consistent with an ecophysiological meta-analysis conducted on three Amazonian sites. Despite these major improvements, ISBA<sub>CC</sub> struggles to capture the apparent seasonality of the carbon fluxes derived from the flux tower estimations. However, there is still no consensus on the seasonality of carbon fluxes over the Amazon, stressing a need for more observations as well as a better understanding of the main drivers of autotrophic respiration.

## 1 Introduction

The Amazon rainforest plays a crucial role in the regional energy, water and carbon cycles, thereby modulating the global climate system. The forest recycles about 25–35 % of the Amazonian precipitation through evapotranspiration (Eltahir and Bras, 1994) and stores about 10–15 % of the global aboveground biomass (e.g., Potter and Klooster, 1999; Malhi et al., 2006; Beer et al., 2010; Pan et al., 2011). Despite intense deforestation and land use change, this region has acted as a long-term carbon sink (Phillips et al., 2008; Gatti et al., 2010, 2014; Gloor et al., 2012; Espírito-Santo et al., 2014), meaning that the carbon uptake by photosynthesis exceeded on average the carbon released by autotrophic respiration ( $R_A$ ) and decomposition.

Recent observations showed that the Amazon sink has already been weakened by environmental perturbations such as deforestation (Lewis et al., 2009; Aragao et al., 2014; Pan et al., 2011) and extreme droughts (Marengo et al., 2011; Gatti et al., 2014). Any change from sink to source of carbon would have profound impacts, including enhancement of global warming through a positive carbon feedback loop (Foley et al., 2003; Cox et al., 2000; Huntingford et al., 2013). The response of the Amazon sink to the combined pressures of deforestation and climate change would be dramatic, especially as a majority of climate models project dryer and longer dry seasons at the end of the century (Fu et al., 2013; Joetzjer et al., 2013).

Given the strong coupling between climate and the carbon cycle and the emergence of holistic Earth system models (ESMs), modeling the Amazon rainforest is a significant project. However, carbon balance projections are still highly uncertain, especially in the tropics (Friedlingstein et al., 2006; Jones et al., 2013; Anav et al., 2013; Huntingford et al., 2013). Beyond the scenario of anthropogenic CO<sub>2</sub> emissions, key uncertainties are related to the carbon cycle response to a given scenario which depends on both model-dependent regional climate sensitivity (Berthelot et al., 2005; Ahlström et al., 2012) and model-dependent representation of carbon fluxes and stocks themselves (Dalmonech et al., 2014; Huntingford et al., 2013).

Most land surface models (LSMs) still struggle to capture the seasonal pattern of the net ecosystem carbon exchange (NEE) over the Amazon basin (Saleska et al., 2003; Baker et al., 2008; Verbeeck et al., 2011), which is defined as the difference between the carbon released by both heterotrophic respiration ( $R_H$ ) and  $R_A$  and taken up through photosynthesis by gross primary productivity (GPP). Recent model developments have focused on improving the seasonality of the simulated GPP, using an improved soil hydrology (Fisher et al., 2007; Baker et al., 2008; Grant et al., 2009), optimizing model's parameters (Verbeeck et al., 2011) or, and with more success, implementing new phenological processes (De Weirdt et al., 2012; Kim et al., 2012). Despite its major role in the carbon balance, less attention has been paid to ecosystem respiration ( $R_{ECO}$ ) (Atkin et al., 2014; Rowland et al., 2014). Ecosystem respiration is the sum of  $R_H$  and  $R_A$  and is the result of multiple contributions (roots, wood, leaves for  $R_A$  and litter, soil carbon for  $R_H$ ) that are all influenced by several environmental factors (temperature, soil water content (SWC), microbial dynamics). Ecosystem respiration plays a major role in explaining inter-annual variability of NEE at many forest ecosystems (Valentini et al., 2000; Saleska et al., 2003; Rowland et al., 2014).

In this paper, we evaluate the ISBA<sub>CC</sub> (Interaction Soil Biosphere Atmosphere Carbon Cycle) (Gibelin et al., 2008) LSM over the Amazon forest using in situ measurements and propose an alternative parameterization of both photosynthesis and  $R_A$ . Such a focus is justified not only because ISBA<sub>CC</sub> has never been really evaluated on tropical rainforests, but also because ISBA<sub>CC</sub> has been recently implemented in the CNRM (Centre National de Recherches Météorologiques) ESM to participate in the forthcoming phases of CMIP (Coupled Model Intercomparison Project) and C4MIP (Coupled Climate Carbon Cycle Model Intercomparison Project). In CMIP3, some early ESMs projected a possible Amazon dieback (represented as the depletion of ecosystem carbon pools) at the end of the 21st century (Cox et al., 2000, 2013; Huntingford et al., 2013). Such dramatic projections are, however, very uncertain, depending for instance on the projected change in precipitation and dry-season length (Good et al., 2013), on the response of forest water-use efficiency (Keenan et al., 2013), and therefore on the accuracy of the

water and carbon stocks and fluxes simulated at the land surface.

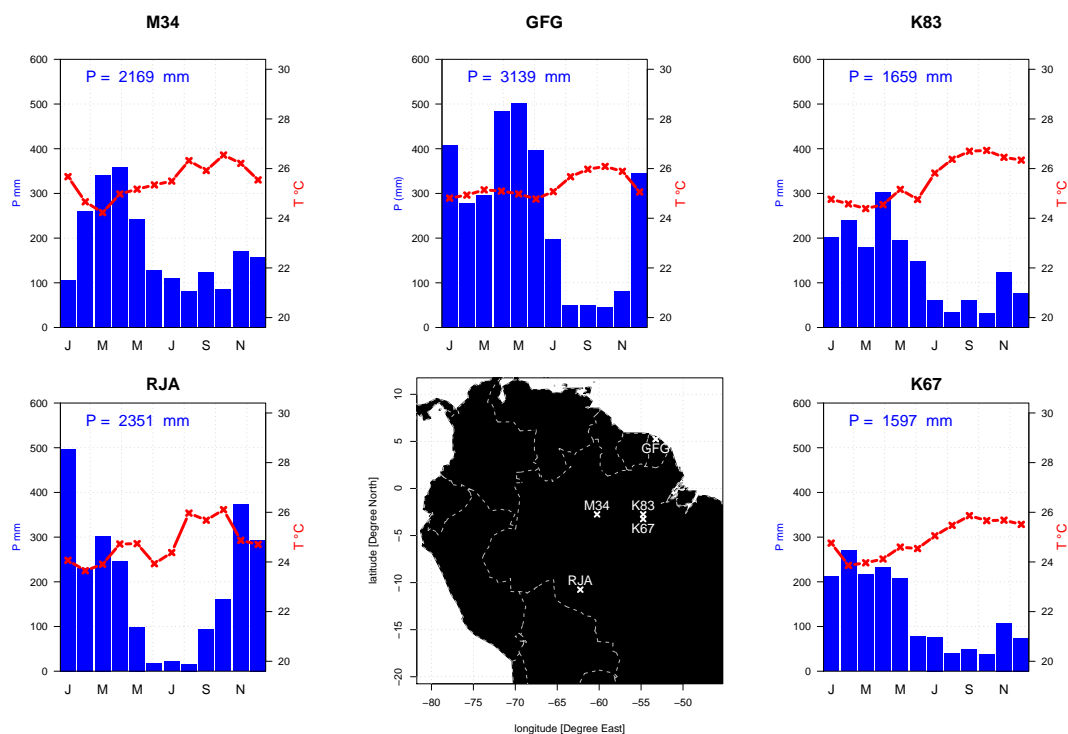
Here we conduct a step-by-step evaluation of the ISBA<sub>CC</sub> LSM against in situ observations collected at five instrumental sites over the Amazon forest. To illustrate rather than really quantify model uncertainties, we also compare ISBA<sub>CC</sub> to the ORCHIDEE (Organizing Carbon and Hydrology In Dynamic Ecosystems – version 1187) LSM (Krinner et al., 2005), which is based on different assumptions for the representation of photosynthesis, carbon allocation and growth. In Sect. 2, we first briefly describe both models and the available observations. In Sect. 3, we propose alternative parameterizations of photosynthesis and photosynthesis sensitivity to soil water stress and of  $R_A$  in ISBA<sub>CC</sub>. In Sect. 4, we compare the skill of the various ISBA<sub>CC</sub> parameterizations to capture the observed water and carbon fluxes and stocks. The main conclusions are summarized in Sect. 5.

## 2 Material and method

### 2.1 Observations

To evaluate carbon and water fluxes over the Amazon tropical forest, we use field measurements of five eddy flux towers in Amazonia. Four towers are located in Brazil and were established during the LBA (Large-scale Biosphere–Atmosphere) project (Da Rocha et al., 2009): Manaus km34 (M34), Santarem km67 (K67) and km83 (K83) and Reserva Jaru (JRU). The fifth tower is the Guyaflux tower (GFG) located at Paracou in French Guiana (Bonal et al., 2008). At JRU the forest is a semi-deciduous forest, whereas the other sites are representing typical tropical rainforests. Site location is shown in Fig. 1 together with the corresponding monthly mean climatologies of temperature and precipitation. Large seasonal variations in precipitation are found at GFG and JRU, the two wettest sites, in contrast with the other sites. Most data sets can be downloaded from the LBA website. For a detailed description of each site, please refer to the literature indicated in Table 1 or Costa et al. (2010) and Baker et al. (2013) for a comparative analysis of the Brazilian sites.

For each site, meteorological forcings, such as incoming solar and infrared radiations, precipitation ( $P$ ), temperature ( $T$ ) and specific humidity, are recorded every 30 min above the canopy. Observations also include turbulent sensible heat ( $H$ ) and latent heat (LE) fluxes and NEE measured using the eddy-covariance method (Shuttleworth et al., 1984; Aubinet et al., 2000; Baldocchi et al., 2001). Further information on data acquisition and pre-processing can be found in the references indicated in Table 1. Note that evaluation scores are computed here only against the more reliable daytime measurements (Aubinet et al., 2002). At K83, measurements of soil moisture were collected in two adjacent soil pits which



**Figure 1.** Mean annual cycle of precipitation (blue) and temperature (red) calculated over 3 years (see Table 1), and the location of the flux towers used in this study.

**Table 1.** Characteristics and references of flux towers used in this study.

Site	Code	Cover period	Texture (fraction)	Root depth	Soil depth	References
Manaus km34	M34	2003 → 2005	CLAY = 0.68; SAND = 0.20	8 m	12 m	Araujo et al. (2002)
Paracou	GFG	2007 → 2009	CLAY = 0.51; SAND = 0.33	8 m	12 m	Bonal et al. (2008)
Santarem km83	K83	2001 → 2003	CLAY = 0.80; SAND = 0.18	8 m	12 m	Goulden et al. (2004)
Santarem km67	K67	2002 → 2004	CLAY = 0.42; SAND = 0.52	8 m	12 m	Saleska et al. (2003)
Reserva Jarù	JRU	2000 → 2003	CLAY = 0.10; SAND = 0.80	4 m	4 m	Kruijt et al. (2004)

are 10 m deep (Bruno et al., 2006) and 2 m deep (da Rocha et al., 2004).

Gross primary productivity and carbon released by the whole  $R_{ECO}$  were retrieved from NEE data using the Reichstein et al. (2005) algorithm. However, it does not give any information either on the partitioning between  $R_A$  and  $R_H$  or on carbon allocation to canopy, wood and roots. Yet, these are essential processes to correctly represent the functioning of the Amazon ecosystem (Malhi et al., 2011). Malhi et al. (2009) gathered ecological measurements from K67, M34 and Caxiuana (1.72° S, 51.46° W; eastern Amazon) to evaluate yearly average carbon cycling and allocation. We here use this data set to evaluate the annual carbon fluxes (GPP,  $R_A$ , NEE), the carbon stocks and the carbon allocation between the different pools in ISBA<sub>CC</sub> (Sect. 4.4).

Finally, flux data are noisy. Hollinger et Richardson (2005) evaluated the relative uncertainty of  $H$ , LE and CO<sub>2</sub> fluxes

to be around 25 % on a temperate site. Energy balance closure in eddy-covariance data can also be problematic. At the five sites considered here, the overall energy balance ratio calculated as the sum of (LE +  $H$ ) divided by the sum of net radiation over the whole period (Wilson et al., 2002) varies between 0.69 at M34 and 1.008 at K67, with values of 0.79 at JRU, 0.87 at K83 and 0.96 at GFG. Energy balance would be achieved with a ratio of one. For the carbon fluxes, according to Desai et al. (2008), the flux partitioning method to retrieve GPP and  $R_{ECO}$  from NEE may add up to 10 % uncertainty. Despite these uncertainties, eddy flux measurements are for now the best way to investigate fluxes between the vegetation and the atmosphere especially when combined with ecological measurements like those gathered by Malhi et al. (2009).

## 2.2 Models and experimental design

ISBA<sub>CC</sub> (Noilhan and Planton, 1989; Noilhan and Mahfouf, 1996) and ORCHIDEE LSMs compute the exchange of water, energy and carbon between the land surface and the atmosphere. Both models deal with photosynthesis and allocate photosynthetic assimilates in several living biomass carbon pools defined by histological functional type. In both models each carbon pool is associated with a respiration function and a specific turnover rate. None of these two models take into account demography.

Carbon assimilation and allocation in the biomass pools differ greatly between the two models. In ORCHIDEE, carbon assimilation is based on the leaf-scale equation of Farquhar et al. (1980) for C<sub>3</sub> plants and is assumed to scale from leaf to canopy with APAR (Absorbed Photosynthetically Active Radiation) decreasing exponentially with leaf area index (LAI), according to the “big leaf” approximation. Stomatal conductance is proportional to the product of net CO<sub>2</sub> assimilation by atmospheric relative humidity divided by atmospheric CO<sub>2</sub> concentration in the canopy (Ball et al., 1987). Standard equations are given in Krinner et al. (2005) and Verbeeck et al. (2011) for tropical forest plant functional types (PFTs). In contrast, ISBA<sub>CC</sub> has a semi-empirical parameterization of net carbon assimilation and the mesophyll conductance ( $g_m$ ) following the model of photosynthesis proposed by Jacobs (1994), based on Goudriaan et al. (1985) and implemented by Calvet et al. (1998). In its standard version, ISBA<sub>CC</sub> uses Goudriaan’s (1986) solution of radiative transfer to calculate net photosynthesis in three canopy layers. The standard ISBA<sub>CC</sub> equations are given in Calvet et al. (1998, 2004) and Gibelin et al. (2008). In ORCHIDEE (v1187), the carbon allocation model accounts for eight biomass compartments (leaves, roots, fruits/harvested organs, reserves, aboveground sapwood, belowground sapwood, aboveground heartwood, belowground heartwood) for tree PFTs.

ISBA<sub>CC</sub> represents aboveground metabolic and structural biomass pools, above- and belowground woody biomass pools and belowground structural biomass pools adapted from Lemaire and Gastal (1997), implemented in ISBA<sub>CC</sub> by Calvet and Soussana (2001) and detailed in Sect. 3.3. The description of the litter and soil carbon content and the associated heterotrophic fluxes is similar between the two models and is based on the CENTURY model developed by Parton et al. (1988). We only use the first top meter of soil carbon from the data set of Malhi et al. (2009) to evaluate ISBA<sub>CC</sub> since CENTURY was designed to represent the carbon content in the first top meter. The litter is described by four pools defined by the lignin content and the location (metabolic and structural above- and belowground). The soil organic cycling module differentiates three carbon pools (active, slow, passive) according to their turnover times (from a few years for the active pool to 1200 years for the passive pool).

At each site, we ran ISBA<sub>CC</sub> and ORCHIDEE offline forced by in situ hourly meteorological measurements (gap

filled when necessary) made on top of each flux tower (available at <http://daac.ornl.gov/>, except for GFG which is available from the FLUXNET website following the “LaThuile” data sharing policy). We imposed the same evergreen tropical broadleaf tree PFT at the five sites and used the in situ soil texture, root and soil depth information for each site found in the literature and summarized in Table 1. Soil texture is used to compute the wilting point and field capacity, and the hydrological and thermal exchange coefficients following Decharme et al. (2011). The organic content in the upper soil layers, which also affects the hydrological and thermal exchange coefficients, is given by HWSO (Harmonized World Soil Database; Nachtergaele et al., 2012). Both models were run until the slowest storage pools had reached equilibrium by cycling the atmospheric forcing over the available 3 years including the observed CO<sub>2</sub> concentration. To simulate soil moisture content in the deep Amazonian soils we used the soil multilayer diffusion scheme implemented in ISBA by Decharme et al. (2011, 2013) and in ORCHIDEE by de Rosnay et al. (2000, 2002). Both models impose a vertical distribution of roots following a decreasing exponential function of depth.

## 3 Towards a new parameterization of the tropical forest in ISBA<sub>CC</sub>

ISBA<sub>CC</sub> has never been evaluated over the tropical rainforest biome (Gibelin et al., 2008), and, as shown below, in this control version (CTL), LE and  $R_A$  were seriously biased and needed to be corrected. Large biases in the simulated LE and respiration fluxes are indeed not acceptable when modeling a region where precipitation recycling is important and where changes in the carbon fluxes could have profound effects on the global climate. This section describes the original ISBA<sub>CC</sub> model (CTL) and the implemented modifications. The main parameters of ISBA<sub>CC</sub> are given in Table 2. We first describe the changes made on the photosynthesis parameterization and its sensitivity to soil moisture as summarized in Table 3. Second, we present the modified  $R_A$  functions (version PS+R) and the original ones (CTL) as summarized in Table 4.

### 3.1 ISBA<sub>CC</sub>: selection of the reference version

As pointed out by Carrer et al. (2013), ISBA<sub>CC</sub> overestimates gross primary productivity at global scale, and especially in the tropical forests where the original radiative transfer code (Calvet et al., 1998) resulted in too high available radiation. Carrer et al. (2013) proposed a new radiative transfer scheme, dividing the canopy in 10 layers and accounting for the effect of direct and diffuse light and for sunlit and shaded leaves. As illustrated in Fig. 2 for the K67 site, the original radiative transfer scheme greatly overestimates the GPP at hourly and seasonal timescales. The other sites have a similar behavior

**Table 2.** ISBA<sub>CC</sub>: nomenclature.

Symbols	Units	Description
$A_m$	$\text{kgCO}_2 \text{ m}^{-2} \text{ s}^{-1}$	Photosynthesis rate (light saturated)
$C_a$	ppmv	Atmospheric $\text{CO}_2$ concentration
$C_i$	ppmv	Leaf internal $\text{CO}_2$ concentration
$D_s$	$\text{g kg}^{-1}$	Saturation deficit at the leaf surface
$D_{\text{max}}$	$\text{g kg}^{-1}$	Maximum value of $D_s$
$f$	unitless	Coupling factor
$f_0$	unitless	Coupling factor at saturating air humidity ( $D_s = 0$ )
$f_0^*$	unitless	Coupling factor in well-watered conditions and at saturating air humidity ( $D_s = 0$ )
$f_{\text{min}}$	unitless	Coupling factor at maximum air humidity deficit ( $D_s = D_{\text{max}}$ )
$\Gamma$	ppmv	$\text{CO}_2$ concentration compensation point
$g_m$	$\text{mm s}^{-1}$	Mesophyll conductance defined as the light-saturated rate of photosynthesis (Jacobs, 1994)
$g_m^*$	$\text{mm s}^{-1}$	$g_m$ in well-watered conditions
$g_s$	$\text{mm s}^{-1}$	Stomatal conductance

**Table 3.** ISBA<sub>CC</sub> modifications: photosynthesis and transpiration PS version.

Parameter	CTL	PS
$A_{m,\text{max}}$	$2.2 \times 10^{-6}$	$0.36 \times 10^{-6}$
$g_m$	$g_m = g_m^*$ $g_m = g_m^* - (g_m^* - g_m^N) \cdot \frac{(1-\text{SWI})}{(1-\text{SWIc})}$ $g_m = g_m^N \cdot \frac{\text{SWI}}{\text{SWIc}}$	$g_m = g_m^*$ $\text{SWI} \geq 1$ $g_m = \text{SWI} \cdot g_m^*$ $\text{SWIc} < \text{SWI} < 1$ $g_m = \text{SWI} \cdot g_m^*$ $\text{SWI} \leq \text{SWIc}$
$f_0$	$f_0 = \frac{4.7 - \ln(g_m)}{7}$ $f_0 = \frac{2.8 - \ln(g_m)}{7}$	$f_0 = 0.74$ $\text{SWIc} < \text{SWI}$ $f_0 = 0.74$ $\text{SWI} \leq \text{SWIc}$
Symbol used		
$A_{m,\text{max}}$ ( $\text{kgCO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	Maximum photosynthesis rate for $\text{C}_3$ plants	
SWI	Soil wetness index ( $\text{SWI} = \frac{\Theta - \Theta_{\text{wilt}}}{\Theta_{\text{fc}} - \Theta_{\text{wilt}}}$ )	
$\Theta$	Soil water content ( $\text{m}^3 \text{ m}^{-3}$ )	
$\Theta_{\text{fc}}$	Field capacity ( $\text{m}^3 \text{ m}^{-3}$ )	
$\Theta_{\text{wilt}}$	Wilting point ( $\text{m}^3 \text{ m}^{-3}$ )	
$\text{SWIc}$	Critical extractable soil wetness index ( $\text{SWIc} = 0.3$ )	
$g_m^N$	Value of $g_m$ at $\text{SWI} = \text{SWIc}$ in $\text{mm s}^{-1}$	
$g_m^*$ ( $\text{mm s}^{-1}$ )	Value of $g_m$ in well-watered conditions ( $\text{SWI} \geq 1$ ) ( $g_m = 2 \text{ mm s}^{-1}$ for broadleaf tropical forest)	

(not shown). The new version of the radiative transfer allows ISBA<sub>CC</sub> to better capture the amount of GPP thanks to a more detailed and physical approach. To avoid unrealistic GPPs, we chose to test the version of ISBA<sub>CC</sub> with a radiative transfer scheme from Carrer et al. (2013) and call it our control version (CTL).

### 3.2 Water and carbon coupling and drought sensitivity: description of the original and modified parameterization (PS version)

The original ISBA<sub>CC</sub> photosynthesis model relies on a “mesophyll conductance” ( $g_m$ ), defined by Jacobs (1994) as the initial slope of the  $\text{CO}_2$  response curve at high light intensity

and limiting  $\text{CO}_2$  concentrations.

$$g_m = \frac{A_m}{C_i - \Gamma}, \tag{1}$$

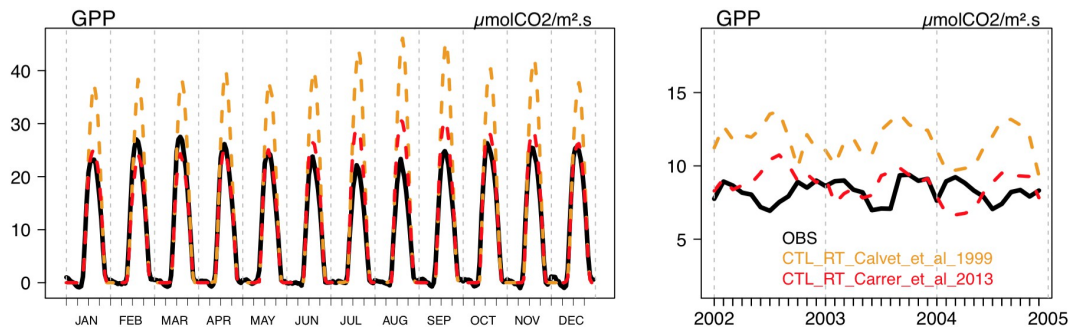
where  $C_i$  is the leaf-internal  $\text{CO}_2$  concentration,  $\Gamma$  the  $\text{CO}_2$  compensation point and  $A_m$  the photosynthesis rate at saturating light and low  $C_i$ .

The model also supposes a constant ratio of  $C_i$  to atmospheric  $\text{CO}_2$  concentration ( $C_a$ ) when atmospheric humidity is constant.

$$f = \frac{C_i - \Gamma}{C_a - \Gamma} \tag{2}$$

**Table 4.** ISBA<sub>CC</sub>: modifications autotrophic respiration ( $R_A$ ) functions PS+R version.

Parameter	CTL	PS+R
$\frac{1}{SLA}$	$\simeq 68.5 \text{ gDM m}^{-2}$	$= 120 \text{ gDM m}^{-2}$
$R_{1\text{leaves}}$	$\frac{A_m}{9}$	$\frac{A_m}{9} \cdot \exp(-k_n \cdot LAI) \cdot \frac{1}{LAI}; k_n = 0.2$
$R_2$	$B_2 \cdot \eta \cdot Q_{10}^{\frac{T_s-25}{10}}; \eta = 0.01 \text{ g g}^{-1} \text{ day}^{-1}$ and $Q_{10} = 2$	$B_2 \cdot \beta \cdot f(T_s); \beta = 1.25$
$R_4$	$B_4 \cdot R_0(1 + 0.16T_p); R_0 = 1.9 \times 10^{-4} \text{ g g}^{-1} \text{ day}^{-1}$	$B_4 \cdot \beta \cdot f(T_p); \beta = 1.25$
$R_5$	0	$B_5 \cdot \lambda_{\text{sap}} \beta_{\text{wood}} \cdot f(T_s); \beta_{\text{wood}} = 0.0125$
		$f(T) = \exp\left\{E_0 \left(\frac{1}{15-T_0} - \frac{1}{T-T_0}\right)\right\}; T_0 = 25 \text{ }^\circ\text{C}$
Symbol used		
$T_s$	Surface temperature	
$T_p$	Soil temperature	
$\lambda_{\text{sap}}$	Fraction of sap wood	

**Figure 2.** Observed and simulated GPP with the CTL version of ISBA<sub>CC</sub> comparing the two radiative transfers at K67. The left panel shows the diurnal cycle for each month averaged over 3 years (2002–2004); the right panel shows the monthly mean time series for 2001–2003.

In drier atmospheric conditions, the ratio decreases according to

$$f = f_0 \left(1 - \frac{D_s}{D_{\max}}\right) + f_{\min} \left(\frac{D_s}{D_{\max}}\right), \quad (3)$$

where  $D_s$  is the atmospheric humidity deficit,  $D_{\max}$  the deficit resulting in complete stomatal closure,  $f_{\min}$  the value of  $f$  at  $D_{\max}$  and  $f_0$  the value of  $f$  at saturating humidity ( $D_s = 0$ ).  $f_{\min}$ ,  $f_0$  and  $D_{\max}$  are model parameters depending on plant type and based on available observations. Following Eq. (2),  $C_i$  also decreases with drying air (increase in  $D_s$ ):

$$C_i = f \cdot C_a + \Gamma(1 - f). \quad (4)$$

Assimilation is then calculated from light (Eqs. (A7)–(A9) in Calvet et al., 1998), air humidity,  $C_a$ , the ratio of  $C_i/C_a$  and, finally, the stomatal conductance ( $g_s$ ) is deduced from the assimilation rate.

Jacobs (1994) photosynthesis model was designed to simulate the assimilation rate and the stomatal conductance of grapevines in semi-arid conditions. While ISBA<sub>CC</sub> is used

for large-scale studies using a PFT approach, there were few attempts to adapt the ecophysiological parameters to each functional group, especially for evergreen tropical broadleaf trees. We used published measurements from about 20 different tree species (Domingues et al., 2005, 2007) from Tapajos National forest to derive  $A_{m,\max}$ , the maximum photosynthesis rate at high light intensity and  $f_0$  (see Eq. 3). The original values and the values of these two parameters are given in Table 3.

The soil water stress function (WSF) empirically describes the effect of soil moisture on transpiration and photosynthesis. In the case of ISBA<sub>CC</sub>, SWC weighted by the roots profile, affects transpiration and photosynthesis through changes in  $g_m$  and, in the CTL version,  $f_0$ . The WSF implemented in ISBA<sub>CC</sub> by Calvet (2000) was first designed for herbaceous species and adapted for trees (Calvet et al., 2004). As described in Table 3 the parameterization for trees supposes a relationship between  $f_0$  and soil wetness index (SWI) and was derived from measurements taken on saplings from *Pinus pinaster* and *Quercus petraea*. It had never been tested on mature trees and tropical species and does not perform

well when tested in the Amazon as shown below. Therefore, we propose an alternative parameterization assuming a constant  $f_0$  coherent with in situ observations (Domingues et al., 2007) and validated against the two artificial drought experiments completed in the eastern Amazon (Joetzjer et al., 2014, and references within). Later in this paper, we call version PS ISBA<sub>CC</sub> with these different values of  $A_{m,max}$ ,  $f_0$  and the modified WSF.

### 3.3 Autotrophic respiration and specific leaf area description of the original and modified parameterization (PS+R version)

An analysis of the yearly carbon use efficiency (CUE) defined by the fraction of GPP invested into the net primary productivity (NPP/GPP) (Rowland et al., 2014) shows that ISBA<sub>CC</sub> overestimates  $R_A$  from leaves, roots and wood, leading to a loss of more than 90 % of the carbon assimilated on an annual basis (corresponding to a CUE < 0.1). This result is not realistic. Over the Amazon, the CUE is roughly estimated to be around 0.3 (Chambers et al., 2004; Malhi et al., 2009, 2011; Metcalfe et al., 2010). Therefore, a new parameterization of each respiration term is proposed and described below.

ISBA<sub>CC</sub> simulates six biomass pools, originally described in Gibelin et al. (2008) as:

- $B_1$ , leaf biomass;
- $B_2$ , an active structural biomass pool which represents the stem in the case of grass and crop, and can be assimilated to new twigs for trees;
- $B_3$ , a small biomass pool used for numerical stability purposes, and accounts for a negligible amount of the carbon actually stored;
- $B_4$ , a belowground structural biomass pool representing the roots's sapwood and the fine roots;
- $B_5$ , an aboveground woody biomass pool representing the aboveground wood (trunk and branches);
- $B_6$ , a belowground woody biomass pool representing the roots's heartwood.

The evolution of each biomass pool  $B$  ( $\text{kg m}^{-2}$ ) is given by

$$\frac{\Delta B}{\Delta t} = A_B - D_B - R_B, \quad (5)$$

where  $\Delta t$  is 1 day,  $A_B$  ( $\text{kg m}^{-2} \text{ day}^{-1}$ ) is the increase in biomass coming from photosynthetic assimilation or allocation from another reservoir,  $D_B$  ( $\text{kg m}^{-2} \text{ day}^{-1}$ ) represents turnover or carbon reallocation to another pool and  $R_B$  ( $\text{kg m}^{-2} \text{ day}^{-1}$ ) is a decrease term due to respiration.

#### 3.3.1 Leaf respiration

Originally, leaf dark respiration integrated over the canopy was parameterized, following Van Heemst (1986) as

$$R_{\text{leaf}} = \frac{A_m}{9} \cdot \text{LAI}, \quad (6)$$

where LAI is the leaf area index and  $A_m$  the photosynthetic rate at high light intensities (Table 1).  $A_m$  being constant throughout the canopy, respiration is identical from the top to the bottom leaves, while assimilation decreases from top to bottom according to the absorbed fraction of PAR calculated by the radiative transfer scheme (Carré et al., 2013). However, observations show that leaf respiration is positively correlated to area-based leaf nitrogen content ( $N_{\text{AREA}}$ ) (Meir et al., 2001, 2008; Reich et al., 2006), and  $N_{\text{AREA}}$  is driven by light availability according to the theory of optimal nutrient allocation availability (Field and Mooney, 1986). Indeed,  $N_{\text{AREA}}$  is highly correlated to photosynthesis capacity as most of the leaf nitrogen is dedicated to the synthesis of photosynthetic proteins. So, a constant value for dark respiration throughout the canopy as supposed in ISBA<sub>CC</sub> is not reasonable, particularly for high canopies. Therefore, we imposed a vertical profile of respiration based on an exponential profile of leaf nitrogen (Sect. 2.5 in Bonan et al., 2011, 2012).

$$R_{\text{leaf}} = \frac{A_m}{9} \exp(-k_n \cdot \text{LAI}), \quad (7)$$

where  $k_n$  is the within-canopy profile of photosynthetic capacity set to 0.2 according to Mercado et al. (2009) and Bonan et al. (2011). This parametrization greatly reduces the leaf dark respiration of the canopy compared to the original one.

#### 3.3.2 Twigs, stem and trunk

In the original version of ISBA<sub>CC</sub> (Gibelin et al., 2008), the woody biomass ( $B_5$ ) does not respire. If heartwood does not respire, sapwood made of living cells (including phloema cells) does. We adopted the simple parameterization of sapwood respiration from IBIS (Integrated BIOSphere Simulator) (Kucharik et al., 2000). We first calculate an estimated sapwood fraction ( $\lambda_{\text{sap}}$ ) from an assumed sap velocity, the maximum transpiration rate and the tree height following Kucharik et al. (2000). Then, the respiration of the 5th reservoir,  $R_5$  is computed as

$$R_5 = B_5 \cdot \lambda_{\text{sap}} \cdot \beta_{\text{wood}} \cdot f(T) \quad \text{with} \quad \beta_{\text{wood}} = 0.0125 \text{ yr}^{-1}, \quad (8)$$

where  $\beta_{\text{wood}}$  is a maintenance respiration coefficient defined at 15 °C and  $f(T)$  is given by the Arrhenius temperature function modified by Lloyd et Taylor (1994).

$$f(T) = \exp \left[ E_0 \left( \frac{1}{15 - T_0} \right) - \frac{1}{T - T_0} \right], \quad (9)$$



where  $T$  is the temperature of the given carbon pool in °C (here, the surface temperature because ISBA<sub>CC</sub> does not simulate a vegetation temperature),  $E_0$  a temperature sensitivity factor (equal to 3500) and  $T_0$  a temperature reference set at 25 °C.

For the  $B_2$  biomass reservoir (twigs), the function proposed in ISBA<sub>CC</sub> is

$$R_2 = B_2 \cdot \eta \cdot Q_{10}^{\frac{T_s - 25}{10}}, \quad (10)$$

where  $Q_{10} = 2$ ,  $\eta = 0.01$  ( $\text{g g}^{-1} \text{day}^{-1}$ ) and  $T_s$  (°C) is the temperature of the surface. We did not find any measurement for respiration of twigs and did not find any other model representing this reservoir. We assumed that respiration per unit biomass of this reservoir had to be lower than respiration of leaves, and similar or slightly larger than sapwood. A comparison with respiration functions from other models showed that Eq. (10) is about the same magnitude as respiration functions for leaves from ORCHIDEE, the Lund–Potsdam–Jena (LPJ) (Sitch et al., 2003) and IBIS (Foley et al., 1996) for temperatures up to 30 °C, but increases strongly at higher temperatures. It is also an order of magnitude larger than respiration of sapwood from these models, which does not seem realistic. To be coherent with  $B_5$ , we adopted the Kucharik et al. (2000) formulation. Therefore,

$$R_2 = B_2 \cdot \beta \cdot f(T) \quad \text{with} \quad \beta = 1.25 \text{ yr}^{-1}. \quad (11)$$

### 3.3.3 Root respiration

Originally, root respiration followed the linear respiration given in Ruimy et al. (1996):

$$R_4 = B_4 \cdot R_0 (1 + 0.16 T_p) \quad \text{with} \quad R_0 = 1.9 \times 10^4 \text{ g g}^{-1} \text{ day}^{-1}. \quad (12)$$

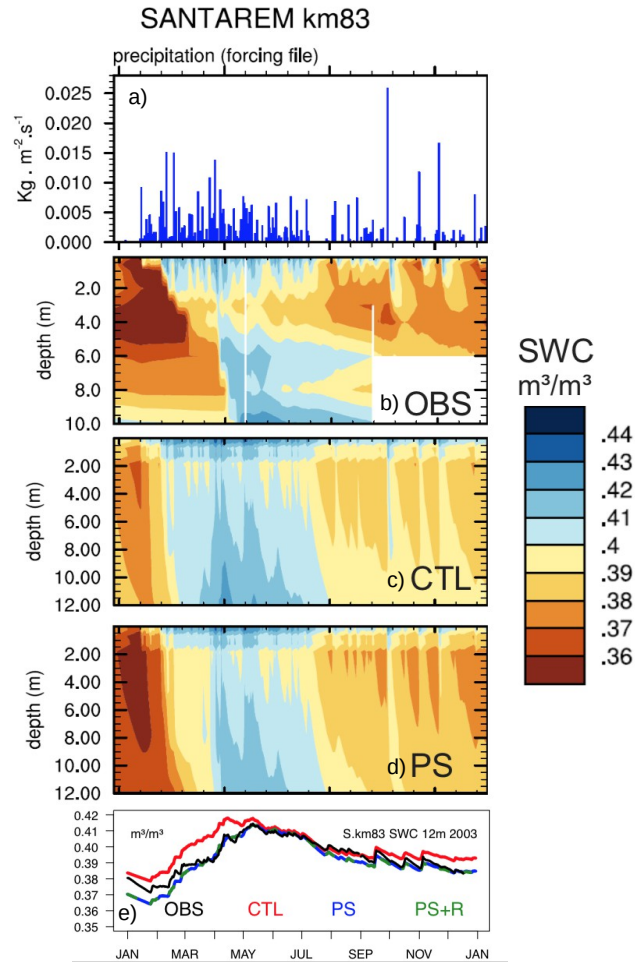
To be consistent with sapwood respiration,  $R_4$  is now computed as

$$R_4 = B_4 \cdot \beta \cdot f(T) \quad \text{with} \quad \beta = 1.25 \text{ yr}^{-1}. \quad (13)$$

### 3.3.4 Specific leaf area

ISBA<sub>CC</sub> calculates interactively the leaf biomass and the LAI using a simple growth model (Calvet et al., 1998). Leaf biomass results directly from the carbon balance of the leaf: increasing with the carbon assimilated by photosynthesis and depleted by respiration, turnover and allocation to the other reservoirs (Calvet and Soussana, 2001). LAI is simply calculated as leaf biomass times the specific leaf area (SLA). Hence, there is no explicit phenology model in ISBA<sub>CC</sub>. Phenology is simply the result of the leaf carbon balance.

In the CTL version the SLA depends on the leaf nitrogen concentration, a fixed parameter depending on the plant type



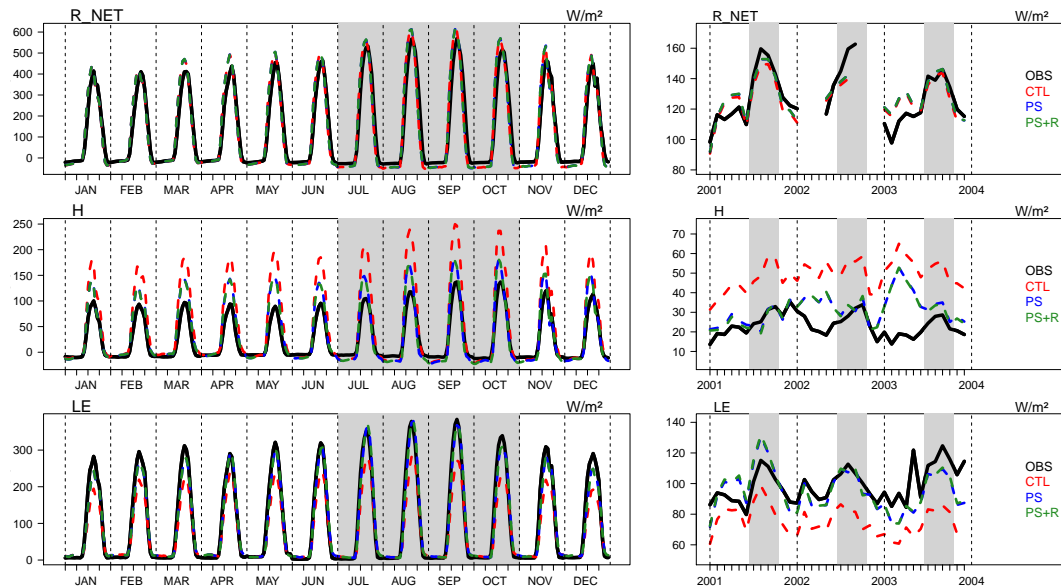
**Figure 3.** Daily precipitation (a): observed (b) and simulated (c and d) soil moisture at K83 during 2003. The total soil water content over the whole 12 m column is shown on plot (e). We linearly rescaled the soil moisture content of the 10 m pit (Bruno et al., 2006) to the values of the 2 m one (da Rocha et al., 2004) by multiplying the 10 m SWC by the ratio of field capacities between the 2 m and the 10 m pit).

(Gibelin et al., 2006). We replaced the original SLA calculated by Gibelin et al. (2006) with the observed value from Domingues et al. (2007).

Later in this paper, we discuss version PS+R (ISBA<sub>CC</sub> version including the Table 3 parameters and functions) and the changed  $R_A$  and SLA summarized Table 4.

## 4 Results and discussion

We now evaluate and compare three versions of ISBA<sub>CC</sub>: CTL, PS and PS+R described in Sect. 3.1, 3.2 and 3.3, respectively. We illustrate the uncertainties linked to the choice of model by showing the fluxes simulated by the well-evaluated ORCHIDEE (v.1187) LSM over the same sites.



**Figure 4.** Observed and simulated net radiation ( $R_{Net}$ ), sensible heat ( $H$ ) and latent heat (LE) at K83. Left panels show the diurnal cycle for each month averaged over 3 years (2001–2003); and right panels, monthly mean time series for 2001–2003. Gray shaded areas indicate dry seasons (defined as periods with precipitation less than  $100 \text{ mm month}^{-1}$ ).

Note that we mostly show results from K83 because deep soil moisture measurements are available.

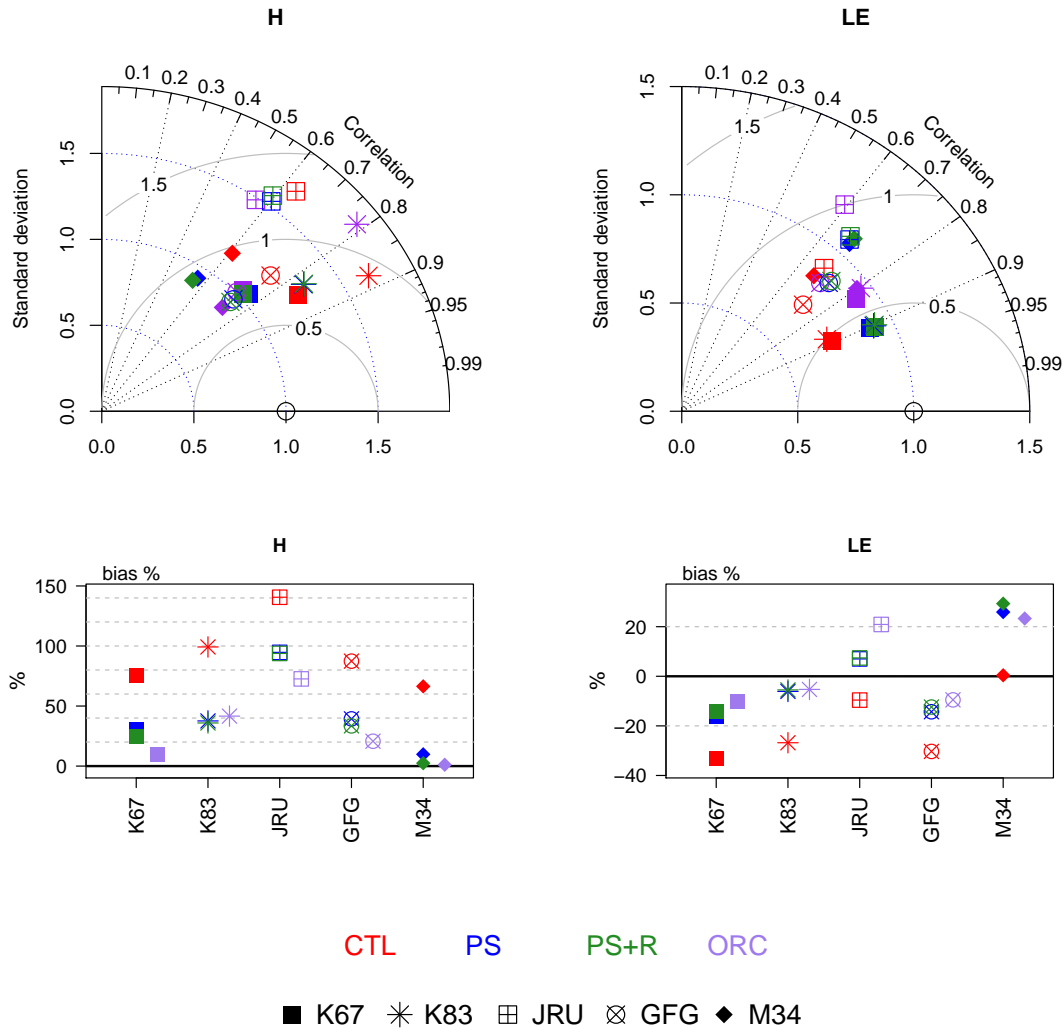
#### 4.1 Soil moisture

Looking at the top 10 m daily SWC simulated in 2003 at K83 (Fig. 3, bottom panel), the slight wet bias found in the original ISBA<sub>CC</sub> model (CTL) is reduced when using either the modified PS or PS+R versions. As shown in Sect. 4.2, this is due to the increased LE in the PS and PS+R versions. Note that the ISBA<sub>CC</sub> soil moisture content was also successfully evaluated at K67 and at Caxiuana (Joetzjer et al., 2014; Fig. 3, top panels). Moving to the vertical profile of soil moisture (Fig. 3, mid-panels), and whatever the model version, the vertical profile of organic matter prescribed in ISBA<sub>CC</sub> (Decharme et al., 2006) allows the model to simulate a relatively wet top 1 m horizon as observed (Fig. 3, mid-panels). However, it is not sufficient to capture accurately the observed soil moisture dynamics. From February to April the soil moisture increases slowly from the surface to 6 m, while ISBA<sub>CC</sub> simulates a much more rapid re-wetting, and after a heavy rain (e.g., October) water infiltrates too quickly. This might be due not only to uncertainties in water uptake by roots (prescribed according to Jackson et al., 1996) but also to the vertically uniform soil texture prescribed in ISBA<sub>CC</sub> due to the lack of in situ observations. In reality, the clay content is usually increasing with depth, which reduces the hydraulic conductivity at lower levels.

#### 4.2 Energy budget

Focusing again on K83, while net radiation ( $R_{NET}$ ) is well captured by the three ISBA<sub>CC</sub> simulations, the CTL experiment overestimates the  $H$  flux and underestimates the LE flux (Fig. 4). As expected, the partitioning of the energy budget is better represented with the simulation using  $A_{m,max}$  and  $f_0$  parameters derived from the in situ observations (PS version, Table 3). The increase in LE simulated by PS compared to the CTL explains the reduction of the wet bias in SWC simulated by the CTL run (Fig. 3). Not surprisingly, the modification of the  $R_A$  functions has little effect (run PS+R, Table 4) on the simulated energy budget and does not impact the temporal variability of  $R_n$ ,  $H$  and LE which are reasonably well simulated at both diurnal and seasonal timescales.

Figure 5 shows a summary of the annual mean scores of  $H$  and LE computed for the three versions of ISBA<sub>CC</sub> and for ORCHIDEE at the five flux towers using Taylor diagrams and a comparison of biases relative to the model mean climatology. Taylor plots are polar coordinate displays of the linear correlation coefficient and centered root mean square error (RMSE; pattern error without considering bias) between the simulated and observed fields, and the ratio of their standard deviations (Taylor, 2001). Correlations mainly reflect the diurnal cycle and are reasonable (above 0.6). The PS (and PS+R) parameterizations barely impact correlations and slightly improve the RMSE compared to the CTL. However, the standard deviation is improved for all sites compared to the CTL runs. The CTL runs show a systematic overestimation of  $H$  (positive bias; Fig. 5, bottom panel) that is strongly reduced in both PS and PS+R versions. Conversely,



**Figure 5.** Taylor diagrams (top) and bias (%) (bottom) calculated among hourly values removing night values (short-wave down  $\leq 5 \text{ W m}^{-2}$ ) for  $H$  and  $LE$  at the five flux towers and for each available period (see Table 1). In the Taylor diagrams, correlation extends radially from the origin. The blue lines indicate identical ratios of standard deviation of the simulated flux to the observed flux. The gray lines represent identical root mean square errors (RMSE) of the centered fluxes.

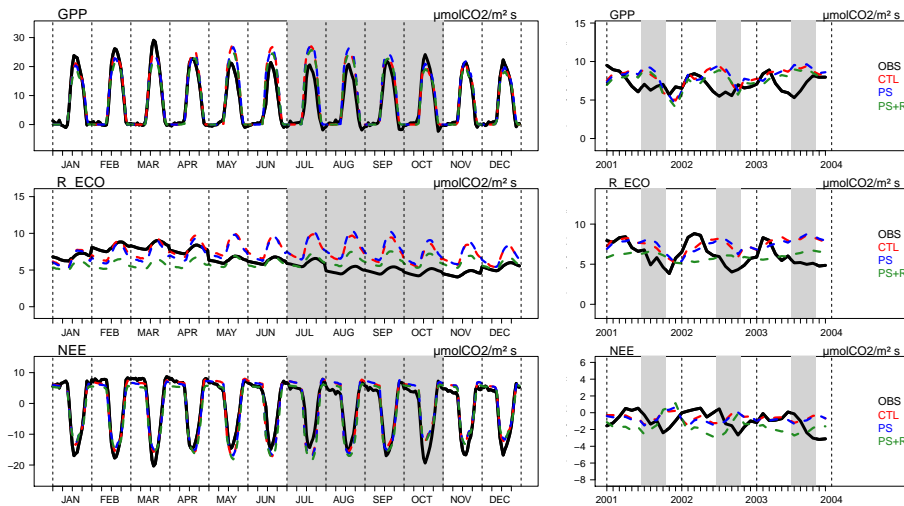
$LE$  is greatly underestimated (by about 30 %) by the CTL, whatever the season (not shown), at four among the five sites and this bias is reduced in the revised versions. At M34, although CTL overestimates  $H$ , it simulates reasonably well  $LE$ . The PS model version reduces the bias in  $H$  but overestimates  $LE$ . This result is coherent with the fairly low level of energy closure at this site (see Sect. 2.1) and suggests that the observed Bowen ratio should be considered with caution at M34.

The PS version improves the simulation of  $H$  and  $LE$  compared to the CTL version, whatever the season. Interestingly, changes in the parameterization of respiration (PS+R) barely alter the results compared to PS. The scores of ORCHIDEE are very close to those computed with the improved version of ISBA<sub>CC</sub> with large positive biases for  $H$  at JRU and  $LE$  at M34 (Fig. 5). The fact that the results are more site de-

pendent than model dependent suggests a problem in the prescribed atmospheric forcings or in the eddy-covariance measurements for these sites, as suggested by the level of energy closure on these sites. Considering the ISBA<sub>CC</sub> and ORCHIDEE models are based on different parameterizations of photosynthesis, respiration and growth, the likelihood of the models being both wrong at the same location is rather small, except for processes unaccounted for by both models like particular phenology adapted to the local conditions.

### 4.3 Carbon fluxes

Moving back to the K83 site, but looking at the carbon fluxes (Fig. 6), the ISBA<sub>CC</sub> model reasonably captures the annual amount of carbon taken up by photosynthesis (GPP), released by respiration ( $R_{\text{ECO}}$ ) and the net flux defined in the



**Figure 6.** Observed and simulated GPP,  $R_{ECO}$  and NEE at k83. Left panels show the diurnal cycle for each month averaged over 3 years (2001–2003); and right panels, monthly mean time series for 2001–2003. Gray shaded areas indicate dry seasons (defined as periods with precipitation less than  $100 \text{ mm month}^{-1}$ ).

model as the difference between  $R_{ECO}$  and GPP (NEE). The annual magnitude of GPP is correctly simulated by the CTL version thanks to the radiative transfer scheme proposed by Carrer et al. (2013) (Fig. 2). While the  $A_{m,max}$  chosen in the PS simulation is around 6 times smaller than initially (Table 3), the increase in  $f_0$  enhances the assimilation rate, leading to little change in GPP between CTL and PS. Therefore, there is a trade-off in the model between  $f_0$  and  $A_{m,max}$ , that can be expected from the photosynthesis module. A lower maximum assimilation rate ( $A_{m,max}$ ) tends to reduce the carbon assimilation (see Eq. (A7) in Calvet and Sousana, 2001). On the other hand, with a higher  $f_0$ , intracellular  $\text{CO}_2$  is higher (see Eq. 4), which favors carbon assimilation. PS barely impacts simulated  $R_{ECO}$  and therefore NEE compared to CTL. While the revised SLA and respiration functions lead to slightly decreased GPP (PS+R), the decrease in  $R_{ECO}$  is even stronger and leads to an increased net rate of carbon uptake (more negative NEE).

The annual cycle of GPP,  $R_{ECO}$  and NEE, although relatively small in these tropical regions (Fig. 6, right column), is poorly simulated by the model. The model tends to increase GPP at the beginning of the dry season when radiation increases and soil moisture is not yet limiting. As such, the model behaves as expected, radiation being the most limiting factor during the wet season, and the observed annual cycle results probably from processes that are not accounted for by the model, such as leaf phenology. Not surprisingly given the model formulation, but in contrast to the observations, the modeled seasonal cycle of GPP coincides with the seasonal cycle of LE in all ISBA<sub>CC</sub> simulations.

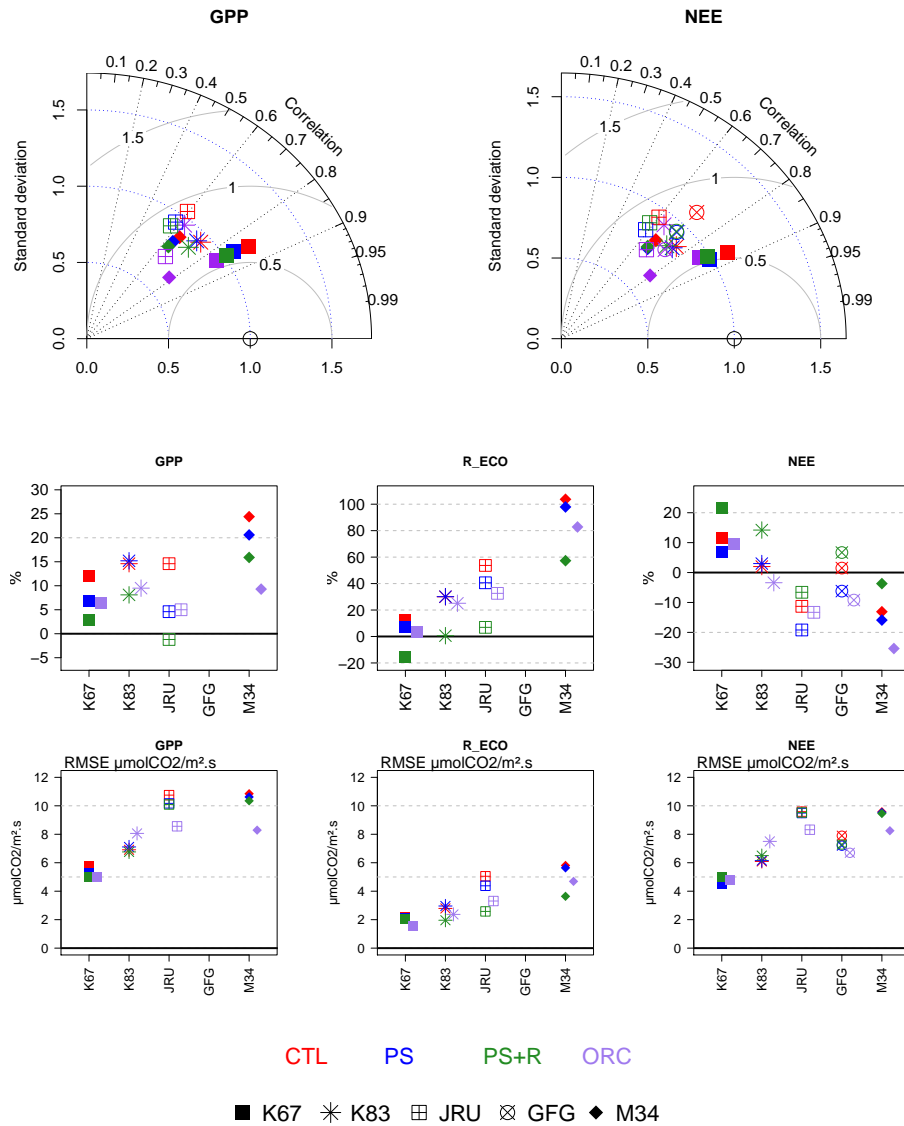
The statistical skill scores computed for the five flux towers are again summarized in Taylor diagrams (Fig. 7, top). The GPP relative standard deviation (RSD) computed with

PS is improved at K67 but is slightly lowered at M34, while there are no substantial changes at K83 and JRU compared to CTL; this is also valid for the NEE. At GFG, the RSD of NEE is also improved. PS+R exhibits scores quite similar to the PS run. The systematic positive bias in GPP (about 10 to 25 %) and in  $R_{ECO}$  (about 10 to 100 %) found in the CTL run is reduced in PS, and even more in PS+R (Fig. 7, bottom). Although model modifications reduce the bias in NEE at JRU and M34, they increase it at K67, K83 and GFG. This is not surprising since NEE is a small flux resulting from the difference between two large fluxes. Looking at the absolute RMSE, errors are reasonable (between 5 and  $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) compared to observation uncertainties, and the ORCHIDEE results once again suggest that scores are more site-dependent than model-dependent.

It is important to note that flux towers measure directly only NEE. The  $R_{ECO}$  is reconstructed from nighttime (i.e., when there is no photosynthesis) measurements which are however questionable (e.g., Reichstein et al., 2005). Daytime  $R_{ECO}$  is likely to differ from nighttime  $R_{ECO}$  because of the temperature diurnal cycle. Also, the lower wind speed at night and thus lower friction velocity ( $u^*$ ) limits the efficiency of the eddy-covariance technique (Aubinet et al., 2002; Saleska et al., 2003). As GPP is reconstructed from NEE and  $R_{ECO}$ , more bias can be expected for this flux and conclusions on GPP should be also considered with caution.

#### 4.4 Carbon stocks and carbon use efficiency

The data compilation of Malhi et al. (2009) at Caxiuanã, K67 and M34 provides valuable insights to evaluate the model ability to simulate the annual carbon storage per carbon pools (Fig. 8). While there are few differences between the CTL and PS+R simulations in terms of GPP and  $R_{ECO}$ , the carbon

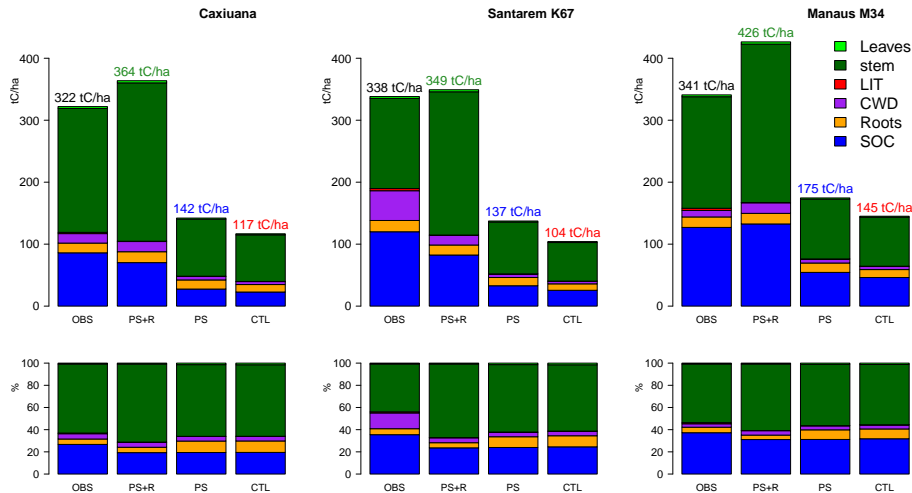


**Figure 7.** Taylor diagrams (top) for GPP and NEE and bias for GPP  $R_{ECO}$  and NEE (%) (bottom) calculated among hourly values removing night values (short-wave down  $\leq 5 \text{ W m}^{-2}$ ) at the five flux towers and for each available period (see Table 1). Note that at GFG only NEE time series was available. In the Taylor diagrams, correlation extends radially from the origin. The blue lines indicate identical ratios of standard deviation of the simulated flux to the observed flux. The gray lines represent identical root mean square errors (RMSE) of the centered fluxes.

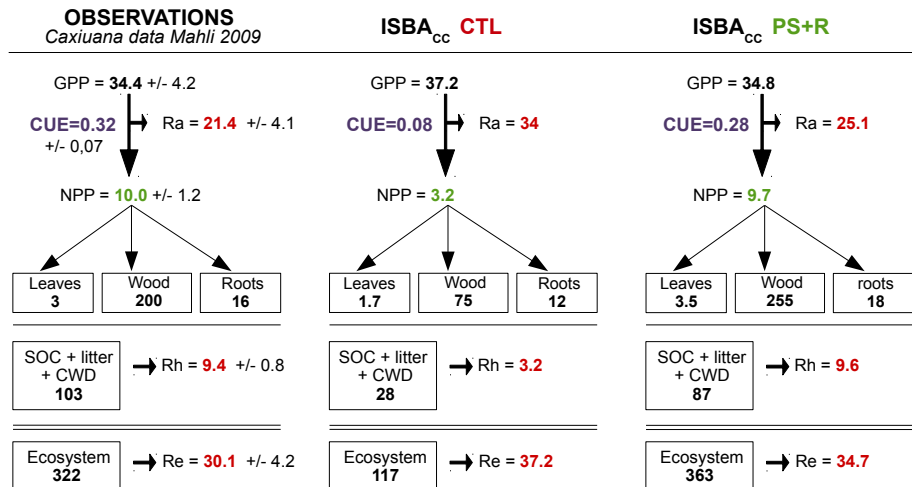
stocks greatly differ (Fig. 8). Over these three sites, observations indicate a total carbon stock of around  $330 \text{ t C ha}^{-1}$  with an error estimate of about  $30 \text{ t C ha}^{-1}$ . The original model (CTL) greatly underestimates the stock by a factor of 3. While modifications of the photosynthesis components (PS) slightly increases carbon stocks, the underestimation of the carbon storage persists. Changes in respiration functions (PS+R) lead to a more reasonable total amount of carbon stock.

Flux tower data provide high frequency information on the carbon flux between the ecosystem and the atmosphere, but do not allow us to distinguish between vegetation and soil

fluxes. The meta-analysis from Malhi et al. (2009) however allows us to evaluate the annual fluxes between the different carbon pools at Caxiuanã (Fig. 9). Compared to observations, the CTL run highly overestimates  $R_A$  and consequently underestimates the NPP. Therefore, the CUE, computed as the ratio  $\text{NPP}/\text{GPP}$ , is too low. 92 % of the carbon assimilated is directly respired, leaving only 8 % of the GPP to be allocated to the plant biomass pools. This result motivated the changes in  $R_A$  functions presented in Table 4. These changes (simulation PS+R, Table 4) lead to a more realistic CUE (around 0.3; e.g., Malhi et al., 2009; Rowland et al., 2014.), therefore enhancing the carbon storage in the leaf, wood and root



**Figure 8.** Observed (Mahli et al., 2009) and simulated (CTL, PS and PS+R) annual carbon pools (leaves (BL), stem ( $B_2 + B_5$ ), litter (LIT), coarse and woody debris (CWD), roots ( $B_4 + B_6$ ) and soil organic content (SOC)) at Caxiuana, K67 and M34. Top panels show the absolute carbon stock in  $\text{tC ha}^{-1}$  and below panels the relative carbon stock (%).



**Figure 9.** Annual carbon pools (in  $\text{tC ha}^{-1}$ ) and fluxes (in  $\text{tC ha}^{-1} \text{ yr}^{-1}$ ) from a synthesis of observations at Caxiuana (Malhi et al., 2009) compared to ISBA<sub>CC</sub> (CTL and PS+R simulations). Adapted from Randerson et al. (2009).

pools, and the litterfall. The litter and the soil organic matter are increased, and, as a result,  $R_H$ , largely underestimated by the original model (CTL), is now correctly simulated. Note that the CTL version has a reasonable estimation of  $R_{ECO}$  because the overestimation of  $R_A$  is partly counterbalanced by an underestimation of  $R_H$  through an underestimation of the heterotrophic carbon stock (Fig. 9).

In spite of reasonable  $R_A$  at each site, the ISBA<sub>CC</sub> model tends to overestimate the amount of carbon stored in the stems (Fig. 8). This pattern can very likely be explained by a too low mortality rate. At K67, the high amount of CWD (Saleska et al., 2003) and the low amount of aboveground biomass observed compared to the other sites suggest a recent higher than normal tree mortality. This could be trig-

gered by drought associated with the strong El Niño events of the 1990s (Rice et al., 2004; Pyle et al., 2008) that these simulations forced by 3 years meteorological forcing cannot represent.

#### 4.5 Annual ratio between carbon stocks and fluxes

The ratio of respiration of a particular pool relative to its size is particularly instructive (Table 5) to evaluate the representation of the respiration process in the model. As can be seen at Caxiuana, K67 and M34, about 10 % of the carbon stored in the plants is respired annually and between 7 and 9 % of the litter and soil carbon content, depending on the site. As a whole, about 9 % of the total biomass (soil, litter and plant) is respired. These percentages are very well captured

**Table 5.** Mean annual autotrophic and heterotrophic carbon stocks and respiration flux deduced from the synthesis of observations (OBS) done by Malhi et al. (2009) and simulated by ISBA<sub>CC</sub> (simulations CTL and PS+R) at Caxiuana, K67 and M34. Stocks are in tCha<sup>-1</sup> and fluxes in tCha<sup>-1</sup> yr<sup>-1</sup>. The ratio defines the % of carbon respired per carbon pool.

		Caxiuana			Santarem K67			Manaus M34		
		Auto	Hetero	EcoS	Auto	Hetero	EcoS	Auto	Hetero	EcoS
Stocks	OBS	218.7	103.3	322	166.7	171.5	338.2	199.9	141.0	340.9
	PS+R	276.6	87.1	363.7	250.6	98.5	349.2	276.3	150.1	426.4
	CTL	89	27.7	116.7	74.3	29.9	104.2	93.5	51.6	145.1
Resp	OBS	21.4 ± 4.1	9.4 ± 0.8	30.1 ± 4.2	14.9 ± 4.2	14.9 ± 1.4	29.8 ± 4.4	19.8 ± 4.6	9.6 ± 1.2	29.3 ± 4.7
	PS+R	25.2	9.6	34.8	22.5	8.6	31.1	25.0	9.6	34.7
	CTL	33.9	3.2	37.2	30.3	2.8	33.1	32.2	3.5	35.7
Ratio %	OBS	9.8	9.1	9.4	8.9	8.7	8.8	9.9	6.8	8.6
	PS+R	9.1	11.0	9.6	9.0	8.7	8.9	9.0	6.4	8.1
	CTL	38.1	11.6	31.9	40.8	9.4	29.8	34.4	6.8	23.9

by the new (PS+R) version but totally misrepresented by the original scheme (CTL). Ecosystem respiration relative to the stock is 3 times too high although the absolute value was reasonable. Nevertheless, large uncertainties surrounds the seasonality of  $R_A$  (and consequently  $R_{ECO}$ ).

## 5 Conclusions

In this study, we proposed and evaluated revised parameterizations of the photosynthesis, its sensitivity to soil water stress and the  $R_A$  function in the ISBA<sub>CC</sub> LSM implemented in the CNRM ESM, over the Amazon forest. As far as the energy and water budgets are concerned, net radiation and soil water dynamics that are driven by observed atmospheric forcing are reasonably well simulated by ISBA<sub>CC</sub>. Our modifications of photosynthesis mainly allow the model to better capture the turbulent energy fluxes ( $H$  and  $LE$ ). While the mean carbon fluxes are slightly better captured with the revised parameterization, ISBA<sub>CC</sub> still struggles to capture the seasonality of the observed (NEE) or reconstructed ( $R_{ECO}$  and GPP) carbon fluxes. Interestingly, when ISBA<sub>CC</sub> is compared to the ORCHIDEE model based on different parameterizations, scores are systematically more site-dependent than model-dependent. This either suggests problems in the prescribed atmospheric forcing, or in the eddy-covariance measurements, unless both models do not account for a crucial process. Further investigations are thus needed.

Changes made to the parameterization of  $R_A$  improve the simulation of the CUE, in good agreement with the observations from Malhi et al. (2009) and Rowland et al. (2014). By enhancing the carbon storage, biomass pools become larger and more consistent with observations. However, increasing the carbon stock in ISBA<sub>CC</sub> by a factor of 3 between CTL and PS+R versions barely impacts the net carbon flux. This illustrates the weak link between carbon stocks and fluxes in the ISBA<sub>CC</sub> model and the need for further improvements.

There is no silver bullet for the parameterization of  $R_A$ , such as the Farquhar model for the carbon assimilation. Because  $R_A$  represents a large part of  $R_{ECO}$ , and  $R_{ECO}$  is crucial to determine the NEE, both annual amount and seasonality of  $R_A$  need to be correctly represented. Indeed, considering the relevance of  $R_{ECO}$  in the seasonal changes of the ecosystem carbon budget (Meir et al., 2008; Rowland et al., 2014), and not only over the Amazon forest (Atkin and Macherel, 2009; Atkin et al., 2014), there is an urgent need to better understand the main drivers of autotrophic respiration in a wide range of environmental conditions.

## Code availability

ISBA<sub>CC</sub> is part of the larger sea and land surface scheme SURFEX. The control version (CTL) of ISBA<sub>CC</sub> used here is part of SURFEX\_v7.2 (<http://www.cnrm.meteo.fr/surfex/>) and the modified version (PS+R) is part of SURFEX\_v8 that will be released before summer 2015.

*Acknowledgements.* The authors thank Rogério D. Bruno and Humberto R. da Rocha for access to 10 m soil moisture observations. Thanks are due to the two anonymous reviewers for their constructive comments.

Edited by: C. Sierra

## References

- Ahlström, A., Schurgers, G., Arneth, A., and Smith, B.: Robustness and uncertainty in terrestrial ecosystem carbon response to CMIP5 climate change projections, *Environ. Res. Lett.*, 7, 044008, doi:10.1088/1748-9326/7/4/044008, 2012.
- Anav, A., Friedlingstein, P., Kidston, M., Bopp, L., Ciais, P., Cox, P., Jones, C., Jung, M., Myneni, R., and Zhu, Z.: Evaluating the land and ocean components of the global carbon cycle in the CMIP5 Earth System Models, *J. Climate*, 26, 6801–6843, 2013.

- Aragao, L. E., Poulter, B., Barlow, J. B., Anderson, L. O., Malhi, Y., Saatchi, S., Phillips, O. L., and Gloor, E.: Environmental change and the carbon balance of Amazonian forests, *Biol. Rev.*, 89, 913–931, 2014.
- Araujo, A., Nobre, A., Kruijt, B., Elbers, J., Dallarosa, R., Stefani, P., von Randow, C., Manzi, A., Culf, A., Gash, J., Valentini, R., and Kabat, P.: Comparative measurements of carbon dioxide fluxes from two nearby towers in a central Amazonian rainforest: The Manaus LBA site, *J. Geophys. Res.*, 107, 58.1–58.20, 2002.
- Atkin, O. K. and Macherel, D.: The crucial role of plant mitochondria in orchestrating drought tolerance, *Ann. Bot. London*, 103, 581–597, 2009.
- Atkin, O. K., Meir, P., and Turnbull, M. H.: Improving representation of leaf respiration in large-scale predictive climate-vegetation models, *New Phytologist*, 202, 743–748, 2014.
- Aubinet, M., Grelle, A., Ibrom, A., Rannik, U., Moncrieff, J., Foken, T., Kowalski, A. S., Martin, P., Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grunwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., and Vesala, T.: Estimates of the annual net carbon and water exchange of forests: The Euroflux methodology, *Adv. Ecol. Res.*, 30, 113–175, 2000.
- Aubinet, M., Heinesch, B., and Longdoz, B.: Estimation of the carbon sequestration by a heterogeneous forest: night flux corrections, heterogeneity of the site and inter-annual variability, *Glob. Change Biol.*, 8, 1053–1097, 2002.
- Baldocchi, D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw U, K. T., Pilegaard, K., Schmid, H. P., Valentini, R., Verma, S., Vesala, S., Wilson, K., and Wofsy, S.: FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities, *B. Am. Meteorol. Soc.*, 82, 2415–2434, 2001.
- Baker, I. T., Prihodko, L., Denning, A. S., Goulden, M. L., Miller, S., and da Rocha, H. R.: Seasonal drought stress in the amazon: reconciling models and observations, *J. Geophys. Res.*, 113, 2005–2012, doi:10.1029/2007JG000644, 2008.
- Baker, I. T., Harper, A. B., da Rocha, H. R., Denning, A. S., Araújo, A. C., Borma, L. S., Freitas, H. C., Goulden, M. L., Manzi, A. O., Miler, S. D., Nobre, A. D., Restro-Coupe, N., Saleska S. R., Stöckli, R., von Randow, C., and Wofsy, S. C.: Surface ecophysiological behavior across vegetation and moisture gradients in tropical South America, *Agric. For. Meteorol.*, 182–183, 177–188, 2013.
- Ball, J. T., Woodrow, I. E., and Berry, J. A.: A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions, in: *Progress in Photosynthesis Research*, vol. 4, edited by: Biggins, J., Martinus Nijhoff, the Netherlands, 221–224, 1987.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rodenbeck, C., Arain, M. A., Baldocchi, D., Bonan, G. B., Bondeau, A., Cescatti, A., Lasslop, G., Anders, L., Lomas, M., Luyssaert, S., Margolis, H., Oleson, K. W., Rouspard, O., Veenendaal, E., Viovy, N., Williams, C., Woodward, F. I., and Papale, D.: Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate, *Science*, 329, 834–838, doi:10.1126/science.1184984, 2010.
- Berthelot, M., Friedlingstein, P., Ciais, P., Dufresne, J.-L., and Monfray, P.: How uncertainties in future climate change predictions translate into future terrestrial carbon fluxes, *Glob. Change Biol.*, 11, 959–970, doi:10.1111/j.1365-2486.2005.00957.x, 2005.
- Bonal, D., Bosc, A., Ponton, S., Goret, J. Y., Burban, B., Gross, P., Bonnefond, J. M., Elbers, J., Longdoz, B., Epron, D., Guehl, J. M., and Granier, A.: Impact of severe dry season on net ecosystem exchange in the neotropical rainforest of french guiana, *Glob. Change Biol.*, 14, 1917–1933, doi:10.1111/j.1365-2486.2008.01610.x, 2008.
- Bonan, G. B., Lawrence, P. J., Oleson, K. W., Levis, S., Jung, M., Reichstein, M., Lawrence, D. M., and Swenson, S. C.: Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data, *J. Geophys. Res.*, 116, G02014, doi:10.1029/2010JG001593, 2011.
- Bonan, G. B., Oleson, K. W., Fisher, R. A., Lasslop, G., and Reichstein, M.: Reconciling leaf physiological traits and canopy flux data: use of the TRY and FLUXNET databases in the Community Land Model version 4, *J. Geophys. Res.*, 117, G02026, doi:10.1029/2011JG001913, 2012.
- Bruno, R. D., da Rocha, H. R., de Freitas, H. C., Goulden, M. L., and Miller, S. D.: Soil moisture dynamics in an eastern Amazonian tropical forest, *Hydrol. Processes*, 20, 2477–2489, doi:10.1002/hyp.6211, 2006.
- Calvet, J.: Investigating soil and atmospheric plant water stress using physiological and micrometeorological data, *Agric. For. Meteorol.*, 103, 229–247, 2000.
- Calvet, J. C. and Soussana J., F.: Modelling CO<sub>2</sub>-enrichment effects using an interactive vegetation SVAT scheme, *Agr. For. Meteorol.*, 108, 129–152, 2001.
- Calvet, J. C., Noilhan, J., Roujean, J. L., Bessemoulin, P., Cabelluene, M., Olioso, A., and Wigneron, J. P.: An interactive vegetation SVAT model tested against data from six contrasting sites, *Agr. Forest Meteorol.*, 92, 73–95, 1998.
- Calvet, J. C., Rivalland, V., Picon-Cochard, C., and Guehl, J. M.: Modelling forest transpiration and CO<sub>2</sub> fluxes response to soil moisture stress, *Agr. For. Meteorol.*, 124, 143–156, 2004.
- Carré, D., Roujean, J. L., Lafont, S., Calvet, J. C., Boone, A., Decharme, B., Delire, C., and Gastellu-Etchegorry, J. P.: A canopy radiative transfer scheme with explicit FAPAR for the interactive vegetation model ISBA-A-gs: impact on carbon fluxes, *J. Geophys. Res.-Biogeosci.*, 118, 1–16, doi:10.1002/jgrg.20070, 2013.
- Chambers, J. Q., Tribuzy, E. S., Toledo, L. C., Crispim, B. F., Higuchi, N., dos Santos, J., Araujo, A. C., Kruijt, B., Nobre, A. D., and Trumbore, S. E.: Respiration from a tropical forest ecosystem: partitioning of sources and low carbon use efficiency, *Ecol. Appl.*, 14, S72–S88, 2004.
- Costa, M. H., Biajoli, M. C., Sanches, L., Malhado, A. C. M., Hutyra, L. R., Da Rocha, H. R., Aguiar, R. G., and De Araújo, A. C.: Atmospheric versus vegetation controls of Amazonian tropical rain forest evapotranspiration: Are the wet and seasonally dry rain forests any different?, *J. Geophys. Res.-Biogeosci.*, 115, 1–9, doi:10.1029/2009JG001179, 2010.
- Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A., and Totterdell, I. J.: Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model, *Nature*, 408, 184–187, 2000.



- Cox, P. M., Pearson, D., Booth, B. B., Friedlingstein, P., Huntingford, C., Jones, C. D., and Luke, C. M.: Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability, *Nature*, 494, 341–344, 2013.
- Dalmonech, D., Foley, A. M., Anav, A., Friedlingstein, P., Friend, A. D., Kidston, M., Willeit, M., and Zaehle, S.: Challenges and opportunities to reduce uncertainty in projections of future atmospheric CO<sub>2</sub>: a combined marine and terrestrial biosphere perspective, *Biogeosciences Discuss.*, 11, 2083–2153, doi:10.5194/bgd-11-2083-2014, 2014.
- da Rocha, H. R., Goulden, M. L., Miller, S. D., Menton, M. C., Pinto, L. D., de Freitas, H. C., and Silva Figueira, A. M.: Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia, *Ecol. Applic.*, 14, S22–S32, 2004.
- da Rocha, H. R., Manzi, A. O., Cabral, O. M., Miller, S. D., Goulden, M. L., Saleska, S. R., Restro-Coupe, N., Wofsy, S. C., Borma, L. S., Artaxo, P., Vourlitis, G., Nogueira, J. S., Cardoso, F. L., Nobre, A. D., Kruijt, B., Freitas, H. C., von Randow, C., Aguiar, R. G., and Maia, J. F.: Patterns of water and heat flux across a biome gradient from tropical forest to savanna in Brazil, *J. Geophys. Res. Biogeo.*, 114, G00B12, doi:10.1029/2007JG000640, 2009.
- Decharme, B., Douville, H., Boone, A., Habets, F., and Noilhan, J.: Impact of an exponential profile of saturated hydraulic conductivity within the ISBA LSM: simulations over the Rhone basin, *J. Hydrometeorol.*, 7, 61–80, 2006.
- Decharme, B., Boone, A., Delire, C., and Noilhan, J.: Local evaluation of the Interaction between Soil Biosphere Atmosphere soil multilayer diffusion scheme using four pedotransfer functions, *J. Geophys. Res.*, 116, 1984–2012, 2011.
- Decharme, B., Martin, E., and Faroux, S.: Reconciling soil thermal and hydrological lower boundary conditions in land surface models, *J. Geophys. Res.-Atmos.*, 118, 1–16, 2013.
- de Rosnay, P., Bruen, M., and Polcher, J.: Sensitivity of surface fluxes to the number of layers in the soil model used in GCMs, *Geophys. Res. Lett.*, 27, 3329–3332, doi:10.1029/2000GL011574, 2000.
- de Rosnay, P., Polcher, J., Bruen, M., and Laval, K.: Impact of a physically based soil water flow and soil-plant interaction representation for modeling large-scale land surface processes, *J. Geophys. Res.-Atmos.*, 107, 4118, doi:10.1029/2001JD000634, 2002.
- Desai, A. R., Richardson, A. D., Moffat, A. M., Kattge, J., Hollinger, D. Y., Barr, A., Falge, E., Noormets, A., Papale, D., Reichstein, M., and Stauch, V. J.: Cross site evaluation of eddy covariance GPP and RE decomposition techniques, *Agr. Forest Meteorol.*, 148, 821–838, doi:10.1016/j.agrformet.2007.11.012, 2008.
- De Weirdt, M., Verbeeck, H., Maignan, F., Peylin, P., Poulter, B., Bonal, D., Ciais, P., and Steppe, K.: Seasonal leaf dynamics for tropical evergreen forests in a process-based global ecosystem model, *Geosci. Model Dev.*, 5, 1091–1108, doi:10.5194/gmd-5-1091-2012, 2012.
- Domingues, T. F., Berry, J. A., Martinelli, L. A., Ometto, J., and Ehleringer, J. R.: Parameterization of canopy structure and leaf-level gas exchange for an eastern Amazonian tropical rain forest (Tapajós National Forest, Para, Brazil), *Earth Interact.*, 9, EI149, doi:10.1175/EI149.1, 2005.
- Domingues, T. F., Martinelli, L. A., and Ehleringer, J. R.: Ecophysiological traits of plant functional groups in forest and pasture ecosystems from eastern Amazonia, Brazil, *Plant Ecol.*, 193, 101–112, 2007.
- Eltahir, E. and Bras, R. L.: Precipitation recycling in the Amazon Basin, *Q. J. Roy. Meteorol. Soc.*, 120, 861–880, 1994.
- Espírito-Santo, F. D. B., Gloor, M., Keller, M., Malhi, Y., Saatchi, S., Nelson, B., Junior, R. C. O., Pereira, C., Lloyd, J., Frohling, S., Palace, M., Shimabukuro, Y. E., Duarte, V., Mendoza, A. M., López-González, G., Baker, T. R., Feldpausch, T. R., Brienen, J. W., Asner, P., Boyd, D. S., and Phillips, O. L.: Size and frequency of natural forest disturbances and the Amazon forest carbon balance, *Nature communications*, 5, 3434, doi:10.1038/ncomms4434, 2014.
- Farquhar, G. D., von Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C3 species, *Planta*, 149, 78–90, 1980.
- Field, C. B. and Mooney, H. A.: The photosynthesis-nitrogen relationship in wild plants, in: *The Economy of Plant Form and Function*, edited by: Givnish, T. J., Cambridge University Press, Cambridge, 25–55, 1986.
- Fisher, R. A., Williams, M., da Costa, A. L., Malhi, Y., da Costa, R. F., Almeida, S., and Meir, P.: The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment, *Glob. Change Biol.*, 13, 2361–2378, 2007.
- Foley, J. A., Prentice, C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., and Haxeltine, A.: An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics, *Global Biogeochem. Cycles*, 10, 603–628, doi:10.1029/96GB02692, 1996.
- Foley, J. A., Costa, M. H., Delire, C., Ramankutty, N., and Snyder, P.: Green surprise? How terrestrial ecosystems could affect earth's climate, *Front. Ecol. Environ.*, 1, 38–44, 2003.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Brovkin, V., Cadule, P., Doney, S., Eby, M., Fung, I., Bala, G., John, J., Jones, C., Joos, F., Kato, T., Kawamiya, M., Knorr, W., Lindsay, K., Matthews, H. D., Raddatz, T., Rayner, P., Reick, C., Roeckner, E., Schnitzler, K. G., Schnur, R., Strassmann, K., Weaver, A. J., Yoshikawa, C., and Zeng, N.: Climatecarbon cycle feedback analysis: results from the C4MIP model inter-comparison, *J. Climate*, 19, 3337–3353, 2006.
- Fu, R., Yin, L., Li, W., Arias, P. A., Dickinson, R. E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., Fisher, R. A., and Myneni, R. B.: Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection, *P. Natl. Acad. Sci. USA*, 110, 18110–18115, doi:10.1073/pnas.1302584110, 2013.
- Gatti, L. V., Miller, J. B., D'Amelio, M. T. S., Martinewski, A., Basso, L. S., Gloor, M. E., Wofsy, S., and Tans, P.: Vertical profiler of CO<sub>2</sub> above eastern Amazonia suggest a net carbon flux to the atmosphere and balanced biosphere between 2000 and 2009, *Tellus B*, 20, 581–594, doi:10.1111/j.1600-0889.2010.00484.x, 2010.
- Gatti, L. V., Gloor, M., Miller, J. B., Doughty, C. E., Malhi, Y., Domingues, L. G., Basso, L. S., Martinewski, A., Correia, C. S. C., and Borges, V. F.: Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements, *Nature*, 506, 76–80, 2014.

- Gibelin, A. L., Calvet, J. C., Roujean, J. L., Jarlan, L., and Los, S. O.: Ability of the land surface model ISBA-A-gs to simulate leaf area index at the global scale: Comparison with satellites products, *J. Geophys. Res.*, 11, D18102, doi:10.1029/2005JD0066911, 2006.
- Gibelin, A. L., Calvet, J. C., and Viovy, N.: Modelling energy and CO<sub>2</sub> fluxes with an interactive vegetation, land surface model, Evaluation at high and middle latitudes, *Agr. For. Meteorol.*, 148, 1611–1628, 2008.
- Gloor, M., Gatti, L., Brienen, R., Feldpausch, T. R., Phillips, O. L., Miller, J., Ometto, J. P., Rocha, H., Baker, T., de Jong, B., Houghton, R. A., Malhi, Y., Aragão, L. E. O. C., Guyot, J.-L., Zhao, K., Jackson, R., Peylin, P., Sitch, S., Poulter, B., Lomas, M., Zaehle, S., Huntingford, C., Levy, P., and Lloyd, J.: The carbon balance of South America: a review of the status, decadal trends and main determinants, *Biogeosciences*, 9, 5407–5430, doi:10.5194/bg-9-5407-2012, 2012.
- Good, P., Jones, C., Lowe, J., Betts, R., and Gedney, N.: Comparing tropical forest projections from two generations of Hadley Centre Earth System models, HadGEM2-ES and HadCM3LC, *J. Climate*, 26, 495–511, 2013.
- Goudriaan, J.: A simple and fast numerical method for the computation of daily totals of crop photosynthesis, *Agric. For. Meteorol.*, 38, 249–254, 1986.
- Goudriaan, J., van Laar, H. H., van Keulen, H., and Louwarse, W.: Photosynthesis, CO<sub>2</sub> and plant production, in: *Wheat growth and modelling*, edited by: Day, W. and Atkin, R. K., NATO AS/ Series A, vol. 86, Plenum Press, New York, 107–122, 1985.
- Goulden, M. L., Miller, S. D., da Rocha, H. R., Menton, M. C., de Freitas, H. C., Figueira, A. M. E. S., and de Sousa, C. A. D.: Diel and seasonal patterns of tropical forest CO<sub>2</sub> exchange, *Ecol. Appl.*, 14, 42–54, 2004.
- Grant, R., Huttyra, L., and Oliveira, R.: Modeling the carbon balance of Amazonian rain forests: resolving ecological controls on net ecosystem productivity, *Ecol. Monogr.*, 79, 445–463, 2009.
- Hollinger, D. Y. and Richardson, A. D.: Uncertainty in eddy covariance measurements and its application to physiological models, *Tree Physiol.*, 25, 873–885, 2005.
- Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L. M., Sitch, S., Fisher, R. A., Lomas, M., Walker, A. P., Jones, C. D., Booth, B. B. B., Malhi, Y., Hemming, D., Kay, G., Good, P., Lewis, S. L., Phillips, O. L., Atkin, O. K., Lloyd, J., Gloor, E., Zaragoza-Castells, J., Meir, P., Betts, R., Harris, P. P., Nobre, C., Marengo, C., and Cox, P. M.: Simulated resilience of tropical rainforests to CO<sub>2</sub>-induced climate change, *Nat. Geosci.*, 6, 268–273, 2013.
- Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., and Schulze, E. D.: A global analysis of root distributions for terrestrial biomes, *Oecologia*, 108, 389–411, 1996.
- Jacobs, C. M. J.: Direct impact of atmospheric CO<sub>2</sub> enrichment on regional transpiration, PhD thesis, Agricultural University, Wageningen, 1994.
- Joetzjer, E., Douville, H., Delire, C., and Ciais, P.: Present-day and future Amazonian precipitation in global climate models: CMIP5 versus CMIP3, *Clim. Dynam.*, 41, 2921–2936, 2013.
- Joetzjer, E., Delire, C., Douville, H., Ciais, P., Decharme, B., Fisher, R., Christoffersen, B., Calvet, J. C., da Costa, A. C. L., Ferreira, L. V., and Meir, P.: Predicting the response of the Amazon rainforest to persistent drought conditions under current and future climates: a major challenge for global land surface models, *Geosci. Model Dev.*, 7, 2933–2950, doi:10.5194/gmd-7-2933-2014, 2014.
- Jones, C., Robertson, E., Arora, V., Friedlingstein, P., Shevliakova, E., Bopp, L., Brovkin, V., Hajima, T., Kato, E., Kawamiya, M., Liddicoat, S., Lindsay, K., Reick, C. H., Roelandt, C., Segschneider, J., and Tjiputra, J.: Twenty-first-century compatible CO<sub>2</sub> emissions and airborne fraction simulated by CMIP5 Earth System Models under four representative concentration pathways, *J. Climate*, 26, 4398–4413, 2013.
- Keenan, T. F., Hollinger, D. Y., Bohrer, G., Dragoni, D., Munger, J. W., Schmid, H. P., and Richardson, A. D.: Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise, *Nature*, 499, 324–327, doi:10.1038/nature12291, 2013.
- Kim, Y., Knox, R. G., Longo, M., Medvigy, D., Huttyra, L. R., Pyle, E. H., Wofsky, S. C., Bras, R. L., and Moorcroft, P. R.: Seasonal carbon dynamics and water fluxes in an Amazon rainforest, *Glob. Change Biol.*, 18, 1322–1334, 2012.
- Krinner, G., Viovy, N., de Noblet-Ducoudre, N., Ogee, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch, S., and Prentice, I.: A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system, *Global Biogeochem. Cy.*, 19, 1–33, 2005.
- Kucharik, C. J., Foley, J. A., Delire, C., Fisher, V. A., Coe, M. T., Lenters, J. D., Young-Molling, C., Ramankutty, N., Norman, J. M., and Gower, S. T.: Testing the performance of a dynamic global ecosystem model: water balance, carbon balance, and vegetation structure, *Global Biogeochem. Cycles*, 14, 795–825, 2000.
- Kruijt, B., Elbers, J. A., von Randow, C., Araújo, A. C., Oliveira, P. J., Culf, A., Manzi, A. O., Nobre, A. D., Kabat, P., and Moors, E. J.: The robustness of eddy correlation fluxes for Amazon rain forest conditions, *Ecol. Appl.*, 14, 101–113, 2004.
- Lemaire, G. and Gastal, F.: N Uptake and Distribution in Plant Canopies, in: *Diagnosis of the Nitrogen Status in Crops*, edited by: Lemaire, G., Springer-Verlag, Heidelberg, 3–43, doi:10.1007/978-3-642-60684-7\_1, 1997.
- Lewis, S. L., Lloyd, J., Sitch, S., Mitchard, E. T., and Laurance, W. F.: Changing ecology of tropical forests: evidence and drivers, *Annu. Rev. Ecol., Evolution, Systematics*, 40, 529–549, 2009.
- Lloyd, J. and Taylor, J. A.: On the temperature dependence of soil respiration, *Functional Eco.*, 8, 315–323, 1994.
- Malhi, Y., Wood, D., Baker, T. R., Wright, J., Phillips, O. L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Monteagudo, A., Neill, D. A., Núñez-Vargas, P., Pitman, N. C. A., Quesada, C. A., Salomão, R., Silva, J. N. M., Torres Lezama, A., Terborgh, J., Vásquez Martínez, R., and Vinceti, B.: The regional variation of aboveground live biomass in old growth Amazonian forests, *Glob. Change Biol.*, 12, 1107–1138, 2006.
- Malhi, Y., Aragao, L. E. O., Metcalfe, D. B., Paiva, R., Quesada, C. A., Almeida, S., Anderson, L., Brando, P., Chamber, J. Q., and da Costa, A. C. L.: Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests, *Glob. Change Biol.*, 15, 1255–1274, 2009.

- Malhi, Y., Doughty, C., and Galbraith, D.: The allocation of ecosystem net primary productivity in tropical forests, *Philos. T. R. Soc. B*, 366, 3225–3245, 2011.
- Marengo, J. A., Tomasella, J., Alves, L. M., Soares, W. R., and Rodriguez, D. A.: The drought of 2010 in the context of historical droughts in the Amazon region, *Geophys. Res. Lett.*, 38, L12703, doi:10.1029/2011GL047436, 2011.
- Meir, P., Grace, J., and Miranda, A. C.: Leaf respiration in two tropical rainforests: constraints on physiology by phosphorus, nitrogen and temperature, *Funct. Ecol.*, 15, 378–387, 2001.
- Meir, P., Metcalfe, D. B., Costa, A. C. L., and Fisher, R. A.: The fate of assimilated carbon during drought: impacts on respiration in Amazon rainforests, *Philos. T. Roy. Soc. B*, 363, 1849–1855, doi:10.1098/rstb.2007.0021, 2008.
- Mercado, L. M., Lloyd, J., Dolman, A. J., Sitch, S., and Patiño, S.: Modelling basin-wide variations in Amazon forest productivity – Part 1: Model calibration, evaluation and upscaling functions for canopy photosynthesis, *Biogeosciences*, 6, 1247–1272, doi:10.5194/bg-6-1247-2009, 2009.
- Metcalfe, D. B., Meir, P., Aragao, L. E. O. C., Lobo-do-Vale, R., Galbraith, D., Fisher, R. A., Chaves, M. M., Maroco, J. P., da Costa, A. C. L., de Almeida, S. S., Braga, A. P., Gonçalves, P. H. L., de Athaydes, J., da Costa, M., Portela, T. T. B., de Oliveira, A. A. R., Malhi, Y., and Williams, M.: Shifts in plant respiration and carbon use efficiency at a large-scale drought experiment in the eastern Amazon, *New Phytol.*, 187, 608–621, 2010.
- Nachtergaele, F., van Velthuisen, H., Verelst, L., and Wiberg, D.: Harmonized World Soil Database, Version 1.2, FAO, IIASA, ISRIC, ISSCAS, JRC, available at: <http://www.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/> (last access: 15 November 2012), 2012.
- Noilhan, J. and Mahfouf, J.-F.: The ISBA land surface parameterisation scheme, *Glob. Planet Chang.*, 13, 145–159, 1996.
- Noilhan, J. and Planton, S.: A simple parameterization of land surface processes for meteorological models, *Mon. Weather Rev.*, 117, 536–549, 1989.
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., and Hayes, D.: A large and persistent carbon sink in the world's forests, *Science*, 333, 988–993, 2011.
- Parton, W., Stewart, J., and Cole, C.: Dynamics of C, N, P and S in grassland soils: a model, *Biogeochemistry*, 5, 109–131, 1988.
- Phillips, O. L., Lewis, S. L., Baker, T. R., Chao, K. J., and Higuchi, N.: The changing Amazon forest, *Philos. T. R. Soc. B: Biological Sciences*, 363, 1819–1827, 2008.
- Potter, C. S. and Klooster, S. A.: Detecting a terrestrial biosphere sink for carbon dioxide: interannual ecosystem modeling for the mid 1980s, *Clim. Change*, 42, 489–503, 1999.
- Pyle, E. H., Santoni, G. W., Nascimento, H. E. M., Hutyra, L. R., Vieira, S., Curran, D. J., van Haren, J., Saleska, S. R., Chow, V. Y., Carmago, P. B., Laurance, W. F., and Wofsy, S. C.: Dynamics of carbon, biomass, and structure in two amazonian forests, *J. Geophys. Res.-Biogeosci.*, 113, G00b08, doi:10.1029/2007jg000592, 2008.
- Randerson, J. T., Hoffman, F. M., Thornton, P. E., Mahowald, N. M., Lindsay, K., Lee, Y.-H., Nevison, C. D., Doney, S. C., Bonan, G., Stoeckli, R., Covey, C., Running, S. W., and Fung, I. Y.: Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models, *Glob. Change Biol.*, 15, 2462–2484, 2009.
- Reich, P. B., Tjoelker, M. G., Machado, J. L., and Oleksyn, J.: Universal scaling of respiratory metabolism, size and nitrogen in plants, *Nature*, 439, 457–461, 2006.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grunwald, T., Havrankova, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J. M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., and Valentini, R.: On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm, *Glob. Change Biol.*, 11, 1424–1439, doi:10.1111/j.1365-2486.2005.001002.x, 2005.
- Rice, A. H., Pyle, E. H., Saleska, S. R., Hutyra, L., Palace, M., Keller, M., de Camargo, P. B., Portilho, K., Marques, D. F., and Wofsy, S. C.: Carbon balance and vegetation dynamics in an old-growth amazonian forest, *Ecol. Appl.*, 14, 55–71, doi:10.1890/02-6006, 2004.
- Rowland, L., Hill, T. C., Stahl, C., Siebicke, L., Burban, B., Zaragoza-Castells, J., Ponton, S., Bonal, D., Meir, P., and Williams, M.: Evidence for strong seasonality in the carbon storage and carbon use efficiency of an Amazonian forest, *Glob. Change Biol.*, 20, 979–991, doi:10.1111/gcb.12375, 2014.
- Ruimy, A., Dedieu, G., and Saugier, B.: Turc: A diagnostic model of continental gross primary productivity and net primary productivity, *Global Biogeochem. Cy.*, 10, 269–285, doi:10.1029/96gb00349, 1996.
- Saleska, S. R., Miller, S. D., Matross, D. M., Goulden, M. L., Wofsy, S. C., da Rocha, H. R., de Camargo, P. B., Crill, P., Daube, B. C., de Freitas, H. C., Hutyra, L., Keller, M., Kirchhoff, V., Menton, M., Munger, J. W., Pyle, E. H., Rice, A. H., and Silva, H.: Carbon in amazon forests: Unexpected seasonal fluxes and disturbance-induced losses, *Science*, 302, 1554–1557, 2003.
- Shuttleworth J. W., Gash J. H. C., Lloyd C. R. Moore, C. J., Roberts, J., Marques, A. D., Fisch, G., Silva, V. D., Ribeiro, M. D. G., Molion, L. C. B., Sa, L. D. D., Nobre, J. C. A., Cabral, O. M. R., Patel, S. R., and Demoraes, J. C.: Eddy correlation measurements of energy partition for Amazonian forest, *Q. J. Roy. Meteorol. Soc.*, 110, 1143–1162, 1984.
- Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W., and Sykes, M. T.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, *Glob. Change Biol.*, 9, 161–185, 2003.
- Taylor, K. E. Summarizing multiple aspects of model performance in a single diagram, *J. Geophys. Res.*, 106, 7183–7192, doi:10.1029/2000JD900719, 2001.
- Valentini, R., Matteucci, G., Dolman, A. J., Schulze, E. D., Rebmann, C., Moors, E. J., Granier, A., Gross, P., Jensen, N. O., and Pilegaard, K.: Respiration as the main determinant of carbon balance in European forests, *Nature*, 404, 861–865, 2000.
- Van Heemst, H. D. J.: Potential crop production, in: *Modelling of Agricultural Production: Weather, Soil and Crops. Simulation Monographs*, edited by: Van Keulen, H. and Wolf, J., Pudoc, Wageningen, 1986.
- Verbeeck, H., Peylin, P., Bacour, C., Bonal, D., Steppe, K., and Ciais, P.: Seasonal patterns of CO<sub>2</sub> fluxes in Ama-

zon forests: Fusion of eddy covariance data and the ORCHIDEE model, *J. Geophys. Res. Biogeosci.*, 116, G02018, doi:10.1029/2010JG001544, 2011.

Wilson, K., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Berbigier, P., Bernhofer, C., Ceulemans, R., Dolman, H., Field, C., Grelle, A., Ibrom, A., Law, B. E., Kowalski, A., Meyers, T., Moncrieff, J., Monson, R., Oechel, W., Tenhunen, J., Valentini, R., and Verma, S.: Energy balance closure at FLUXNET sites, *Agric. For. Meteorol.*, 113, 223–243, 2002.