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Do dynamic global vegetation models capture the seasonality of carbon fluxes in the Amazon basin? A data-model intercomparison

Running head: Seasonal C-flux simulations at Amazon forests

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Abstract

To predict forest response to long-term climate change with improved confidence requires that dynamic global vegetation models (DGVMs) be successfully tested against ecosystem response to short-term variations in environmental drivers, including regular seasonal patterns. Here, we used an integrated dataset from four forests in the Brasil flux network, spanning a range of dry season intensities and lengths, to determine how well four state-of-the-art models (IBIS, ED2, JULES, and CLM3.5) simulated the seasonality of carbon exchanges in Amazonian tropical forests. We found that most DGVMs poorly represented the annual cycle of gross primary productivity (*GPP*), of photosynthetic capacity (*Pc*), and of other fluxes and pools. Models simulated consistent dry season declines in *GPP* in the equatorial Amazon (Manaus K34, Santarem K67, and Caxiuanã CAX); a contrast to observed *GPP* increases. Model simulated dry season *GPP* reductions were driven by an external environmental factor, “soil water stress” and consequently by a constant or decreasing photosynthetic infrastructure (*Pc)*, while observed dry-season *GPP* resulted from a combination of internal biological (leaf-flush and abscission and increased *Pc*) and environmental (incoming radiation) causes. Moreover, we found models generally overestimated observed seasonal net ecosystem exchange (*NEE*) and respiration (*Re*) at equatorial locations. In contrast, a southern Amazon forest (Jarú RJA) exhibited dry season declines in *GPP* and *Re* consistent with most DGVMs simulations. While water-limitation was represented in models and the primary driver of seasonal photosynthesis in southern Amazonia, changes in internal biophysical processes, light harvesting adaptations (e.g. variations in leaf area index *(LAI)* and increasing leaf-level assimilation rate related to leaf demography), and allocation lags between leaf and wood, dominated equatorial Amazon carbon flux dynamics and were deficient or absent from current model formulations. Correctly simulating flux seasonality at tropical forests requires a greater understanding and the incorporation of internal biophysical mechanisms in future model developments.

1. Introduction

Dynamic global vegetation models (DGVMs) are the most widely used and appropriate tool for predicting large-scale responses of vegetation to future climate scenarios. However, to forecast the future of Amazonia under climate change remains a challenge. The previous generation of DGVMs produced projections for Amazonia's ecosystems that diverged widely, with outcomes ranging from large-scale forest die-back to forest resilience (Betts *et al.*, 2004, 2004; Friedlingstein *et al.*, 2006; Baker *et al.*, 2008). More recent DGVMs simulations showed the large-scale die-off scenario to be unlikely (Cox *et al.*, 2013), given (1) an improved model understanding of forest response to the negative effects of temperature -previously overestimated and now constrained (Cox *et al.*, 2013); and (2) current models being forced with updated climate projections (temperature and precipitation) bounded by observations that no longer demonstrate drastic climate changes in response to rising CO_2 in the tropics (Cox *et al.*, 2013; Huntingford *et al.*, 2013). Yet tropical forest response to climate change remains uncertain as models produce varying outcomes (Shao *et al.*, 2013) even without die-off. Some cutting-edge DGVMs projected forest degradation due to future deforestation and increasing temperature, with catastrophic consequences for the global climate based on climate-carbon cycle feedbacks (Wang *et al.*, 2013; Friend *et al.*, 2014; Wang *et al.*, 2014), while other DGVMs foresaw strong carbon sinks in these forests due to CO_2 fertilization of photosynthesis (Rammig *et al.*, 2010; Ahlström *et al.*, 2012; Huntingford *et al.*, 2013; Friend *et al.*, 2014). Although the effects of temperature, water limitation and CO_2 fertilization mechanisms remain uncertain, all DGVMs continue to agree that Amazonian forests play an important role in regulating the global carbon and water cycle (Eltahir & Bras, 1994; Werth & Avissar, 2002; Wang *et al.*, 2013, Wang *et al*. 2014; Ahlström *et al.*, 2015).

Key to reducing uncertainty in DGVMs is their systematic evaluation against observational datasets. This exercise enables the identification of model deficiencies through comparison with observed patterns in ecosystem processes, as well as the mechanisms underpinning such processes (Baker *et al.*, 2008; Christoffersen *et al.*, 2014). Recent model-data evaluations in tropical forests have focused on the cascade of ecosystem responses to long term droughts (Powell *et al.*, 2013) and the definition of spatial patterns in productivity and biomass (Delbart *et al.*, 2010; Castanho *et al.*, 2013). However, one important context for model assessment in tropical forests is in the seasonality of ecosystem water and carbon exchange, as observational datasets reveal axes of variation in productivity, biomass and/or forest function across space (da Rocha *et al.*, 2009; Restrepo-Coupe *et al.*, 2013) and/or through time (Saleska *et al.*, 2003; von Randow *et al.*, 2004; Hutyra *et al.*, 2007; Brando *et al.*, 2010). The most consistent temporal variation in tropical forests is the seasonality of water, energy, and carbon exchange, since all tropical ecosystems are seasonal in terms of insolation and a majority experience recurrent changes in precipitation, temperature and/or day length. Evaluation with respect to seasonality has typically focused on evapotranspiration (*ET*) (Shuttleworth, 1988; Werth & Avissar, 2002; Christoffersen *et al.*, 2014) and on net carbon exchange (*NEE*) (Baker *et al.*, 2008; von Randow *et al.*, 2013; Melton *et al.*, 2015). Where models compensated misrepresentations of gross primary productivity (*GPP*) in the *NEE* balance, by improving or adjusting the efflux term represented by heterotrophic (Melton *et al.*, 2015) or ecosystem respiration (Baker *et al.*, 2008) to available moisture among other strategies. Only recently have the seasonal dynamics of *GPP* drawn the attention of different groups (De Weirdt *et al.*, 2012; Kim *et al.*, 2012) and where Kim et al. (2012) demonstrated that a consequence of its incorrect derivation was to overestimate the vulnerability of tropical forests to climate extremes. Therefore, identifying discrepancies in observed *versus* modeled seasonality in carbon flux even when seasonal amplitudes are not large -as can be the case for evergreen tropical forests (see Albert et al. (in preparation) for cryptic phenology), can lead to important model developments with significant consequences -to obtain better projections of the fate of tropical ecosystems under present and future climate scenarios.

Analysis of eddy covariance datasets have shown that in non-water limited forests of Amazonia, the observed seasonality of *GPP* was not exclusively controlled by seasonal variations in light quantity (as has been demonstrated for *ET*) or water availability. Instead *GPP* was driven by a combination of incoming radiation and phenological rhythms influencing leaf quantity (measured as leaf area index; *LAI*) and quality (leaf-level photosynthetic capacity as a function of time since leaf flush) (Restrepo-Coupe *et al.*, 2013; Wu *et al.*, 2016). The lack of a direct correlation between *GPP* and climate suggests that ecosystem models that are missing sufficient detail of canopy leaf phenology will likely not capture seasonal productivity patterns. Accordingly, recent studies showed model simulations (ED2 and ORCHIDEE) to be deficient in terms of predicted seasonality in *GPP* and litter-fall, if missing leaf-demography and turnover as in Kim et al. (2012) and in De Weirdt et al. (2012), respectively. Between the two studies, only two sites (eastern (K67) and northeastern (CAX)) were represented, both of which experience very similar precipitation and light regimes. This further highlights the need for expanded evaluation of modeled seasonality of *GPP* across a range of sites spanning a broader range of climates and phenologies.

If the improved representation of the dynamics of leaves and other carbon pools translates into more accurate simulations of seasonal *GPP* and/or the long-term carbon budget (De Weirdt *et al.*, 2012; Kim *et al.*, 2012; Melton *et al.*, 2015), then comparisons between observations and model derived seasonality of carbon allocation could provide insight into the mechanistic response of vegetation to climate and strategies to incorporate them into DGVMs. For example, critically evaluating the seasonality of net primary production of leaves (NPP_{leaf}) and wood (NPP_{wood}) in tandem with photosynthesis, will inform deficiencies in model allocation schemes and carbon pool residence times. Model net primary production (*NPP)* typically arises from the allocation of photosynthate to main organs, either as a constant fraction of *GPP* (Kucharik *et al.*, 2006), or according to fixed allometric rules (Sitch *et al.*, 2003). However, such a view of supply-limited growth has come into question recently (Würth *et al.*, 2005; Fatichi *et al.*, 2014). Thus as water, temperature, and nutrients can all impact cell expansion, there may be a temporary imbalance between carbon used for tissue growth and maintenance respiration *versus* carbon supplied by assimilation (photosynthesis) (Fatichi *et al.*, 2014). Patterns in seasonality of *GPP*, NPP_{leaf} and NPP_{wood}, therefore, potentially reveal the degree of coupling (or lack thereof) of these two carbon sinks (NPP_{wood} and NPP_{leaf}) with photosynthetic activity (*GPP*). Indeed, Doughty et al. (2014) used bottom-up estimates of the ecosystem carbon-budget at a forest in southwest Amazonia and showed that components of *NPP* varied independently of photosynthetic supply, which they interpreted in terms of theories of optimal allocation patterns. While an alternative interpretation of such patterns could simply refer to biophysical limitations on growth, which vary seasonally (Fatichi *et al.*, 2014), both studies suggest that modeling allocation as a function of *GPP* will likely fail to capture observed seasonality. Ground-based bottom-up estimates of primary productivity at a temporal resolution greater than a year (i.e., seasonal) are difficult if not impossible, principally because there is no accepted method for estimating whole-tree non-structural carbon (*NSC*) and its variation with seasons (Würth *et al.*, 2005; Richardson *et al.*, 2015). We propose coupling co-located top-down eddy flux estimates of *GPP* with bottom-up *NPP* estimates (NPP_{wood}, NPP_{leaf} and $NPP_{litter\text{-}fall}$) to circumvent this problem and to obtain a better informed view of the mechanisms (e.g. allocation schemes) models may incorporate or test against, to improve seasonal simulations of carbon fluxes and pools.

The focus of this study was to evaluate, for the first time, modeled seasonal cycles of different carbon pools and fluxes, including leaf area index (*LAI*), *GPP*, leaf fall, leaf flush, and wood production, with high resolution eddy flux estimates of *GPP* and ground-based surveys. We centered our study on a comparison between forests located in the equatorial Amazon (radiation- and phenology-driven) to a southern forest (driven by water availability) and explored the different model strategies to incorporate and simulate physical and ecological drivers. Here, we assessed four state-of-the art DGVMs in active development for use in coupled climate-carbon cycle simulations in terms of whether they could simultaneously determine patterns of growth and photosynthesis, thereby getting the ‘right answer for the right reason’. We conclude by proposing several approaches for improving model formulations and highlight the need for model-informed field campaigns and future experimental designs.

2. Methods

2.1. Site descriptions

We analyzed data from the Brazil flux network for four tropical forests represented by the southern site of Reserva Jarú (RJA), and three central Amazonia forests (~3ºS) from west to east: the Reserva Cuieiras near Manaus (K34), the Tapajós National forest, near Santarém (K67) , and the Caxiuanã National forest near Belém (CAX) (Fig. 1). For detailed site information see previous works by Restrepo-Coupe et al. (2013), and de Goncalves et al. (2009; 2013) and individual site publications (Araújo *et al.*, 2002; Carswell *et al.*, 2002; Malhi *et al.*, 2002; Saleska *et al.*, 2003; Kruijt *et al.*, 2004; von Randow *et al.*, 2004; Hutyra *et al.*, 2007; da Costa *et al.*, 2010; Baker *et al.*, 2013).

All study sites had mean annual precipitation (*MAP*) above 2000 mm year^{-1} (Fig. S1 and Table 1), based on the 1998-2014 satellite-derived precipitation from the Tropical Rainfall Measuring Mission (TRMM 3B43-v7 at a resolution of 0.25 deg) (Huffman *et al.*, 2007; NASA, 2014) (Fig. S10 for a comparison between observations and TRMM data). CAX and K34 have *MAP* over 2500 mm year^{-1}, 2572 and 2673 mm year^{-1}, respectively (Fig. S11). By contrast, at the southern forest of RJA and the equatorial forest of K67 *MAP* was

~2030 mm year^{-1}. Moreover, RJA has a 5-month dry season length (*DSL*) analogous to two of the central Amazon sites of CAX and K67 (4 to 5-months); however, longer than K34 site (1 to 2-months). Where the dry season was based on the 16-year TRMM series and defined as those periods where precipitation was less than ~100 mm month^{-1} (Sombroek, 2001; da Rocha *et al.*, 2004; Restrepo-Coupe *et al.*, 2013). The 100 mm month^{-1} threshold corresponds to ~90% of the observed annual maximum *ET* averaged across years (115±12 mm month^{-1}) and close to the mean seasonal *ET* (92±1.5 mm month^{-1}) at the four tropical forests here reported (Restrepo-Coupe *et al.*, 2013). RJA and K67 showed similar mean dry-season precipitation (46 mm month^{-1} at RJA and 64 mm month^{-1} at K67). However, the annual minimum averaged across the years 1998-2014 (*MiAP*) at RJA was 15 mm month^{-1} compared to a more benign dry season minimum of 36 mm month^{-1} at K67 (Fig. 1 and Table 1). Despite being located at a latitude further from the equator (10˚S) incoming photosynthetic active radiation (*PAR*) at the southern forest of Jarú, was less seasonal (low amplitude) if compared to the central Amazon forests (latitude ~3˚S) (Fig. 2). At RJA, peak top of the atmosphere radiation (*TOA*) was synchronous with the wet season –where we expected higher reflectance by clouds decreasing the surface available *PAR* (Fig. 2). All equatorial sites sat on highly weathered deep clay soils (>= 10 m), whereas RJA sat on a lower water storage capacity loamy sandy soil and a more shallow and variable profile, with depth to bedrock as shallow as 2-3 m (Hodnett *et al.*, 1996; Christoffersen *et al.*, 2014).

2.2. Eddy covariance methods

At the above-mentioned forests, climate, carbon, energy, water and momentum fluxes were measured by the eddy covariance (EC) method. Meteorological measurements included vapor pressure (*VPD)*, air temperature (T_{air}), *PAR*, and incoming and outgoing short and long wave radiation, among others. We estimated the cloudiness index (*CI*) -a proxy for light quality, based on the observed *PAR* and the theoretical *PAR* (PAR_{theo}). The PAR_{theo} was computed following Goudriaan (1986) top of the atmosphere radiation and scaled to fit monthly maximum observed *PAR* for the hour across years. The *CI* ranges from 0 to 1, from diffuse to direct irradiance dominating incoming *PAR* value, respectively:

$$CI = 1 - \frac{PAR_{obs}}{PAR_{theo}} \qquad \text{Equation 1}$$

Starting with half-hourly CO_2-flux data provided from each site's operator, we calculated net ecosystem exchange (*NEE* in µmol CO_2 m^{-2} s^{-1}), with fluxes to the atmosphere defined as positive. *NEE* was then filtered for low turbulence periods (u^*_{thresh}). For a detailed description of instrumentation, applied corrections, quality control procedures, the effect of u^*_{thresh} on *NEE* calculations, and for data processing refer to Restrepo-Coupe et al. (2013). Gross ecosystem exchange (*GEE*) was derived from tower measurements of daytime *NEE* by subtracting estimates of ecosystem respiration (R_e), which in turn we derived from the nighttime *NEE*. We assumed daytime R_e was the same as nighttime R_e, as we did not observed a statistically significant within-month correlation between nighttime hourly *NEE* and nighttime T_{air} (Restrepo-Coupe *et al.*, 2013). *GEE* is a negative value ($GEE = NEE - R_e$) as generally *NEE* is negative in the daytime, and R_e is positive (meteorological convention). We expressed ecosystem-scale photosynthesis, or gross ecosystem productivity (*GEP*), as negative *GEE* and assumed negligible re-assimilation of metabolic respiration CO_2 within the leaf and insignificant CO_2 recirculation below the EC system (Stoy *et al.*, 2006). For comparison with model output, we used *GEP* interchangeably with gross primary productivity (*GPP*).

We defined ecosystem photosynthetic capacity (*Pc*, gC m-2 d-1) as the 16-day *GPP* averaged over a fixed narrow range of reference climatic conditions following some of the modifications introduced by Wu et al. (2016) to *Pc* used in Restrepo-Coupe et al. (2013). For our analysis, *Pc* was estimated as the rate of carbon fixation under reference conditions defined by fixed narrow bins in: site specific day-time annual mean *PAR* ± 150 μmol m^{-2} s^{-1}, *VPD*, T_{air}, and *CI* ± 1.5 standard deviation from their respective means (see Table S1). Thus, *Pc*, by definition, removed the effect of day-to-day changes in available light, diffuse/direct radiation, photoperiod, temperature, and atmospheric demand from photosynthesis. The *Pc* has been shown to be a robust representation of the emergent photosynthetic infrastructure of the whole forest canopy (Wu *et al.*, 2016).

We looked at evapotranspiration (*ET,* mm d^{-1}) calculated as the latent heat flux (*LE,* W m^{-2}) measured at the tower multiplied by the latent heat of vaporization (λ, kJ kg^{-1}). We developed a Type II linear model between surface incident short wave radiation (SW_{down}, W m^{-2}) and the dependent variable, *ET*.

From the standard suite of climatic variables available for periods between 1999 and 2006 measured at each EC tower, meteorological drivers for the models were generated. According to Rosolem et al. (2008) the selected periods represent the mean climatological condition and exclude anomalous climatic events (e.g. 2010 El Niño-Southern Oscillation (ENSO) or 2005 drought as experienced at the southern Amazon). Variables included: SW_{down}; air temperature (T_{air}, °K); near surface specific humidity (Q_{air}, g kg^{-1}); rainfall

(*Precip*, mm month^{-1}); magnitude of near surface wind (*WS*, m s^{-1}), surface atmospheric pressure (*Pa*, hPa); surface incident longwave radiation (LW_{down}, W m^{-2}); and CO_2 concentration ($CO_{2\ air}$) was fixed at 375 ppm (de Goncalves *et al.*, 2009) (Fig. 2). Drivers were created for consecutive years where gaps were no greater than two months. All time series were subject to quality control and filled using other tower measurements (e.g. from a temperature profile), nearby sites and the variable's mean monthly diurnal cycle. We analyzed data for 2000-2005 for K34, 2002-2004 for K67, 2000-2002 for RJA and 1999-2003 for CAX. We restricted flux and meteorological observations and the calculation of seasonality to the above-mentioned dates in order to match model drivers and output.

Hourly fluxes (*GPP, NEE*, R_e, and *ET*) and meteorology were aggregated to 16-day time periods, assuming that at least 4 days were available with at least 21 hours of observations each. Gaps were not filled further and mean annual cycles were then calculated.

2.3. Field measurements

Although field measurements can be translated into carbon storage values (e.g. wood carbon pool from DBH inventories via allometric equations), we focus on departures from a base level because they reflect the seasonality of allocation. The following vegetation infrastructure descriptors and carbon pools were included in the analysis:

Leaf Area Index (*LAI*): model output was compared to *LAI* observations for Caxiuanã, CAX as reported by Metcalfe et al. (2007)), and for Santarem, K67 as by Brando et al. (2010). *LAI* was normalized from 0 to 1 ($LAI_{normalized}$) for purposes of presentation. Thus, in order to enhance and visualize any seasonal changes in LAI, independent of the observed or modeled absolute value, using Equation 2, where at time i, LAI_i was adjusted by LAI_{min} and LAI_{max} that corresponded to the minimum and maximum seasonal LAI, respectively:

$$LAI_{normalized(i)} = \frac{LAI_i - LAI_{min}}{LAI_{max} - LAI_{min}} \qquad \text{Equation 2}$$

Leaf litter-fall or net primary productivity allocated to litter-fall ($NPP_{litter\text{-}fall}$, gC m^{-2} d^{-1}): values corresponded to monthly litter-bed measurements at Manaus, K34 (here presented for the first time), and to those reported by Rice et al. (2004) for K67 and by Fisher et al. (2007) for CAX.

Modeled NPP_{leaf} followed a basic leaf balance model proposed by Restrepo-Coupe et al. (2013). Assuming the change in ecosystem Pc (dPc/dt) to be driven by 1) the loss or gain of leaves, $NPP_{litter\text{-}fall}$ and NPP_{leaf}, respectively (quantity); and 2) the changes in leaf-level carbon assimilation at saturating light ($SLA \times A_{max}$) related to age (quality). Therefore, solving for leaf production we obtained:

$$NPP_{leaf} = NPP_{litter-fall} + \frac{1}{A_{max}\, x\, SLA}\, x\, \frac{dPc}{dt} \qquad \text{Equation 3}$$

where specific leaf area (SLA) values were set to 0.0140 for K67 and CAX (Domingues *et al.*, 2005), 0.0164 m^2/gC for K34 (Carswell *et al.*, 2002). The A_{max} was reduced to reach 40% of the mean value at the time when leaf-fall reached its maximum (2-month linear gradient). Maximum A_{max} was set to 8.66 gC m^{-2} d^{-1} at K67 (Domingues *et al.*, 2005), and to 7.36 gC m^{-2} d^{-1} at K34 (Carswell *et al.*, 2000) and CAX.

Wood net primary productivity (NPP_{wood}) was based on stem wood increment measurements (diameter at breast height, DBH) as reported by Rice et al. (2004) at K67, Chambers et al. (2013) at K34, and da Costa et al. (2010) at CAX. No data was available for RJA.

2.4. Dynamic global vegetation models (DGVMs)

We presented output from four state-of-the-art dynamic global vegetation models. All DGVMs were process based (e.g. photosynthesis, respiration, and evapotranspiration) and able to simulate the fluxes of carbon, water, and energy between the atmosphere and the land surface (see Table S2 and S3). The model simulations were run as part of the Interactions between Climate, Forests, and Land Use in the Amazon Basin: Modeling and Mitigating Large Scale Savannization project (Powell *et al.*, 2013).

To standardize all physical parameters within the models so as to focus on agreements and discrepancies among the different biomass schemes, all four DGVMs used the same soil hydrology properties (including free drainage conditions), and soil physical parameters and depths. The spin-up protocol consisted in running each model from near-bare-ground until variations in soil moisture, slow soil carbon, and above ground biomass were less than 0.5% (defined as average change for the last cycle of meteorological forcing as compared to the previous cycle). Atmospheric CO_2 concentrations were set to pre-industrial values (278 ppm) and later increased to present day starting in 1715 (considered as the first year after stabilization). Radiation was split between direct and diffuse following Goudriaan (1977). We summarized each DGVM's carbon flux, and vegetation dynamics formulation in Table S2 and S3, and briefly describe the four models in this section:

Ecosystem Demography model version 2 (ED2): The model explicitly tracked the dynamics of fine-scale ecosystem structure and function, including net ecosystem productivity (*NEP*), carbon partitioning, and growth and mortality dynamics (Medvigy *et al.*, 2009). It used four PFTs for the tropics, a 10-minute time step for the ecosystem model, and *LAI* was defined on a daily basis. The dynamics of individual plant cohorts (photosynthesis, mortality, transpiration, carbon allocation, etc.) were tracked independently. Canopy structure was dynamic in the model and depended on the number and size of the cohorts (canopy layers were not prescribed). ED2 tracked three different soil carbon pools for each layer (fast, slow and structural), water extraction depth varies according to plant functional types (PFTs). The model did not include hydraulic redistribution. The ED2 model photosynthesis parameterization was adjusted to improve the model's representation of diurnal, daily average, and seasonal *GPP* and *NPP* using data from a single site (K34).

Integrated Biosphere Simulator (IBIS): The tropical rainforest vegetation in IBIS is a composite of four plant functional types -”tropical evergreen tree”, “tropical deciduous tree”, “C3 grass”, and “C4 grass”, that compete for water and light. The model simulated hourly carbon fluxes using the Ball-Berry-Farquhar equations (Farquhar *et al.*, 1980). *LAI* was calculated annually using fixed allocation coefficient to the leaves (0.3) and fixed residence times (12 months), although a water stress function could seasonally drop leaves in the case of the tropical deciduous trees. Biomass was integrated over the year using a similar procedure (Foley *et al.*, 1996). The IBIS used here, simulated six soil layers with a total depth of 8 m; water extraction by the roots varied by layer, and was controlled by a root distribution parameter. IBIS required 76 parameters to be specified, of those 14 were related to soil, 12 were specific to each of the nine PFTs, and 50 were related to morphological and biophysical characteristics of vegetation.

Community Land Model-Dynamic Global Vegetation Model version 3.5 (CLM3.5): The predecessor to the current CLM4-CNDV model (Gotangco Castillo *et al.*, 2012), which is the land component of the Community Earth System Model (CESM). CLM3.5 runs were set using a prognostic phenology, which incorporated recent improvements to its canopy interception scheme, new parameterizations for canopy integration, a TOPMODEL-based model for runoff, canopy interception, soil water availability, soil evaporation, water table depth determination by the inclusion of a groundwater model, and nitrogen constraints on plant productivity (without explicit nitrogen cycling) (Oleson *et al.*, 2008). The model treated the canopy as a weighted average (by their respective *LAI*s) of sunlit and shaded leaves. The leaf phenology subroutine of this model for tropical forests applied only to the Broadleaf Deciduous Tree (BDT) PFT fraction (“raingreen” PFT), but all CLM3.5 simulations reported here were >95% tropical Broadleaf Evergreen Tree (BET) fractional PFT cover. The allocation scheme for this model dictated that leaf turnover for the tropical BET (at a rate of 0.5 yr^{-1}) be replaced instantaneously with new leaf production to maintain fixed allometric relationships (Sitch *et al.*, 2003); therefore, seasonality of *LAI* was not possible for these simulations.

Joint UK Land Environment Simulator (JULES): The UK community land surface model as described in Best et al., (2011) and Clark et al., (2011). Simulations for this study were conducted using JULES v2.1 which did not simulate drought deciduous vegetation. The model represents five PFTs globally, of which the “evergreen broad-leaved tree” PFT dominates over Amazonia. Gross leaf-level photosynthesis was based on Collatz et al. (1991, 1992) and was calculated as the smoothed minimum of three potentially limiting rates: a rubisco-limited, a light-limited, and the rate of transport of photosynthetic assimilates. Plant respiration was simulated as a function of tissue temperature and nitrogen concentrations. Soil moisture stress effects were incorporated by scaling potential net photosynthesis rate with a simple β factor (Cox *et al.*, 1999; Powell *et al.*, 2013). Leaf-level photosynthesis was coupled to stomatal conductance using the formulation by Jacobs (1994). Photosynthesis was scaled from leaf to canopy using a 10-layer canopy model which adopts the 2-stream approximation of radiation interception from Sellers (1985). *NEP* was partitioned into a fraction used for growth and a fraction used for the ‘spreading’ of vegetation. Carbon for growth was allocated to three vegetation pools (wood, roots, leaves) following specific allometric relationships between pools (Clark *et al.*, 2011).

DGVMs output followed the LBA-Data Model Intercomparison Project (LBA-DMIP) protocol (de Goncalves *et al.*, 2009); however, it includes some additional variables related to water limitation (e.g. soil water availability factor or soil water “stress”), land use change (e.g. additional carbon pools), and disturbance (e.g. mortality) (Powell *et al.*, 2013). Here, we present soil water “stress” (*FSW*) values, calculated following Ju et al. (2006). By definition *FSW* ranging from 0 to 1 is a measure of the water available to roots, where

FSW=1, is no stress.

Models were compared to observations based on the timing and amplitude metrics of their annual cycle. Statistical descriptors as correlation coefficient (R), root-mean-square difference, and the ratio of model-observations standard deviations were calculated for the 16-day time series for multiple years and summarized using the Taylor diagrams (Taylor, 2001).

3. Results

3.1. Gross primary productivity (*GPP*) and ecosystem photosynthetic capacity (*Pc*)

The observed annual cycle of ecosystem-scale *GPP* showed two divergent patterns: (1) increasing levels of photosynthetic activity (*GPP*) as the dry season progresses in the equatorial Amazon (K34, K67 and CAX) where *MiAP* was 103, 60 and 37 mm month^{-1}, respectively, and maximum radiation was synchronous with low precipitation; and (2) declining productivity as the dry-season advanced in the southern forest (RJA) where radiation was somewhat aseasonal and *MiAP* was less than half its central Amazon counterparts (14 mm month^{-1}) (Fig. 3). By contrast, at all sites, model simulations showed peak *GPP* seasonality at the end of wet season with declining *GPP* during the dry season (Fig. 3). The reduced dry season *GPP* observed at the southern Amazon forest of Jarú (RJA) was consistent with increasing degrees of water limitation. At the sites in the equatorial Amazon (K34, K67 and CAX), modeled soil water “stress” (*FSW*; Fig. 2) (where *FSW*=1, no stress) acted to reduce model *GPP* during the dry season, even as observed *Pc* increased following higher levels of incoming solar radiation (*PAR*; Fig. 2 and *Pc*; Fig.

4). Similar to *GPP*, models tended to achieve good *Pc* representation at RJA (Fig. S7). However, simulated *Pc* at the equatorial Amazon forest sites remained unchanged (IBIS and JULES) or decreasing gradually from the middle of the wet season to the end of the dry period at K67 (ED2 and CLM3.5) (Fig. 4).

FSW reached an all-site minimum at RJA by the end of the dry season (Fig. 2) and corresponded with a decrease in model *ET* not seen on the EC measurements (Fig. 3). With the exception of CAX, seasonal observations of *ET* at all of the sites showed very little seasonality and remained close to 92 mm month^{-1} (3 mm d^{-1}). In general, DGVMs were able to capture the seasonality of *ET*; however, they overestimated the dry-period reduction in water exchange at RJA and in the case of K34 and CAX overestimated *ET* absolute values (Fig. S9). By contrast, a very simple linear regression driven by SW_{down} was able to represent ~83% of the seasonality of *ET* (Fig. 3).

3.2 Carbon allocation

We explored different DGVMs approaches to simulate the phenology of carbon allocation, in particular measures of plant metabolism (ecosystem photosynthetic capacity, *Pc* as proxy), standing biomass (wood increment, leaf-production and the balance of gain and loss of leaves), and additions to soil organic matter (leaf-fall), in an attempt understand the model-data discrepancies on the estimates of *GPP*, R_e, and *NEE* (Fig. S7 and S8).

Our results indicated that none of the models was able to capture or replicate the observed dry-season *LAI* changes at the equatorial Amazon forests EC locations (Fig. 4). In addition, with the exception of ED2, the annual mean *LAI* values were unrealistically high

(Baldocchi *et al.*, 1988; Gower *et al.*, 1999; Asner *et al.*, 2003; Sakaguchi *et al.*, 2011). In contrast, with some model phenology schemes that assumed *LAI* and T_{air} to be positively correlated, we observed non-statistically significant positive and negative regressions at CAX and K67, respectively (R^2<0.1; p-value >0.1) (Fig. S6).

In the field, leaf litter-fall plays an important role in determining the seasonality of *LAI*, *Pc* (as per Equation 3), heterotrophic respiration and soil carbon pools. Data for the central Amazon forests show a highly seasonal leaf-fall cycle (Chave *et al.*, 2010), with maximum leaf mortality at the beginning of the dry season at CAX and in the middle of the dry period at K67 (Fig. 4). At equatorial sites, peak litter-fall corresponded to a maximum in SW_{down}, where we observed a statistically significant linear regression between SW_{down} and $NPP_{litter-fall}$ with a coefficient of determination, R^2 equal to 0.34 at K34, 0.21 at K67, and 0.6 at CAX (p<0.01) (Fig. S2). With the exception of ED2, which included a drought-deciduous phenology and consequentially seasonal variations in leaf abscission, seasonality in $NPP_{litter-fall}$ was not resolved in most DGVMs (Fig. 4).

Estimates of leaf-production (increase in the amount of young-high photosynthetic capacity leaves) from the observations at K67 forest showed peak NPP_{leaf} in the dry season in contrast to most simulations. In general, NPP_{leaf} was: (1) constant in most models; (2) allocated at the end of the year, similar to $NPP_{liter-fall}$; or (3) declining, in particular during the strong K67 dry season (Fig. 4). Even if counterintuitive, at some of the equatorial Amazon sites key leaf-demography processes (e.g. leaf-fall and leaf-flush) and/or *LAI*, increased in tandem during the dry season.

In contrast to NPP_{leaf}, NPP allocation to wood growth was aseasonal at K34; however at K67 NPP_{wood} peaked during the wet season, displaying opposite seasonality and being out-of-phase with NPP_{leaf}. This pattern seemed to be different at CAX, with maximum NPP_{leaf} at the beginning of the dry season, ahead of NPP_{wood} which steadily increased as the dry season progressed and was maintained at high levels for the first half of the wet season. At this site precipitation was significantly seasonal (wet season was the rainiest of all equatorial sites) and the amplitude of the seasonal cycle of SW_{down} was the largest of all Brasil flux central Amazon locations. By contrast, models simulated a peak in NPP_{wood} at CAX and K67 that corresponded to the beginning of the dry season. The seasonality of model NPP_{wood} was absent at the three equatorial forests and only significant differences between the wet and dry periods were reported at RJA, where all simulations showed minimum NPP_{wood} at the end of the dry season.

Our analysis shows a statistically significant negative linear regression between SW_{down} and NPP_{wood} with a coefficient of determination, R^2 equal to 0.58 at K67 and 0.63 at CAX ($p<0.01$) (Fig. S3). Non-significant correlation was found between SW_{down} and NPP_{wood} or precipitation and NPP_{wood} at K34 -the wettest and least seasonal of the four studied forests.

Seasonal observations of the different NPP components and GPP showed a lack of temporal synchrony between them. Nor was a shared allocation pattern among forests – each exhibited different phenologies (Fig. 5). At some sites (CAX and K67), there was a statistically significant correlation (~1 to 2-month lag, NPP_{leaf} ahead) between GPP and NPP_{leaf} (Fig. S5). However, there was no temporal correspondence between GPP and NPP_{wood}. By comparison, model allocation (NPP_{leaf}, $NPP_{litter\text{-}fall}$ and NPP_{wood}) and GPP was coupled at most models (Fig. 5).

3.3. Ecosystem respiration (R_e) and net ecosystem exchange (*NEE*)

Similar to *GPP*, the timing and amplitude of ecosystem respiration (R_e) seasonality at RJA was well captured by most DGVMs (Fig. S7); however, at equatorial Amazon sites all simulations overestimated R_e (Fig. 3). In particular, during the months for which R_e reached a minimum -the wet season at CAX and the dry season at K67, model R_e showed opposite seasonality to observations. The imbalance between predicted R_e and *GPP* translated into an underestimation of the observed net ecosystem uptake (negative *NEE*), with the models predicting a positive *NEE* (strong carbon source), in particular, at K34 and CAX. More importantly, the seasonality of *NEE* in the equatorial forests (K34, K67 and CAX) was missed, with the DGVMs foreseeing a greater carbon loss during the dry season, as opposed to those observed during the September-December period (Fig. 3).

4. Discussion

In this study, we found that dynamic global vegetation models poorly represented the annual cycle of carbon flux dynamics for the Amazon evergreen tropical forest sites with eddy covariance towers. In particular, at equatorial Amazonia, observations showed an increase in *GPP, Pc*, and/or *LAI* during the dry season. In contrast, DGVMs simulated constant or declining *GPP* and *Pc*, and in general, assumed no seasonal cycling in *LAI* (Fig. 4). The disparity between model and *in situ* measurements of *GPP* indicated that there is a bias in the modeled ecosystem response to climate and a lack of understanding of which drivers, meteorological (e.g. light or water) or phenological (e.g. leaf demography) or a combination thereof, control ecosystem carbon flux. Moreover, a mismatch between seasonal observations of carbon pools and allocation strategies (NPP_{leaf}, NPP_{wood}, $NPP_{litter-fall}$) and model results highlights the importance of phenology as an essential tool for understanding productivity within the tropical forest of the Amazon (see Delpierre et al. (2015) for a compleate description of model allocation schemes).

4.1 Seasonality of gross primary productivity (*GPP*), and other carbon fluxes

We observed the greatest discrepancies between measured and model predicted *GPP*, R_e, and *NEE* at central Amazon sites, where productivity is hypothesized to be primarily controlled by a combination of light availability and phenology (Restrepo-Coupe *et al.*, 2013; Wu *et al.*, 2016). By contrast, models were able to capture the “correct” seasonality at the southern forest of RJA, a site that shows significant signs of water limitation. However, at RJA the amplitude of the annual cycle were overestimated by most DGVMs, which assume lower than expected *GPP* during the dry season. Our results suggest that, while models have improved their ability to simulate water stress, their ability to simulate light-based growth strategies is still an issue.

Satellite phenology studies have shown annual precipitation values and the length of the dry season to be important factors when determining ecosystem response (Guan *et al.*, 2015). Nevertheless, K67 and RJA share similar rainfall values, with *MAP* of 2030 mm year^{-1}, dry season precipitation (*DSP*) of 50 mm month^{-1}, and a 4 to 5 month dry period, only the minimum annual precipitation differs, having RJA *MiAP* of 14 compared to 37 mm month^{-1} measured at K67. Moreover, increasing levels of incoming light at K67 and other equatorial sites during the dry season provided an opportunity for vegetation to increase productivity under the existent precipitation regime, as rainfall delivered more than 60% of ecosystem water needs assuming a monthly ~100 mm requirement (*DSP* >64 mm month^{-1}). For central Amazon tropical forests, observed increases in *GPP*, *Pc*, and allocation patterns, linked to light harvesting strategies, were concurrent with the reported maxima in incoming in solar radiation (Malhado *et al.*, 2009; Restrepo-Coupe *et al.*, 2013) or/and increasing insolation and photoperiod (including flushing and flowering as in Wright & van Schaik (1994) and Borchert et al. (2015)). Our results show that the observed NPP_{leaf} and *Pc* annual cycle is consistent with canopy ‘greenness’ seasonality detected by remote sensing. Although controversial (Samanta et al., 2010; Morton et al., 2014), many satellite derived vegetation indices analysis (Huete et al., 2006; Saleska et al., 2007, 2016; Guan et al., 2015) show evidence of similar leaf phenology, as well as phenocam (Wu et al., 2016), and ground-based studies (Chavana-Bryant et al., 2016; Girardin et al., 2016). By comparison, at RJA, there was no tradeoff between light, precipitation and atmospheric demand, as solar radiation was somewhat aseasonal (with a maximum at the beginning of the wet season) and dry season rainfall values (*MiAP*) reached less than 10% of mean tropical forest *ET*.

Although our study focuses solely on the rainforest biome, we report how small differences on the timing and amplitude of the precipitation and radiation cycle and their relationship (light versus water availability) resulted in different paterns in the allocation and carbon uptake seasonallity among the four sites (e.g. photosynthetic capacity *versus* leaf flush). Scaling from site to basin, across gradients in cloudiness and precipitation and correspondent variations in seasonality found within the greater Amazonia, will require a rigorous exercise in understanding climate and vegetation controls to carbon flux across a continuum of light and water driven seasonalities (leaf, wood, flower, fruit, and root allocation among other plant growth strategies), thus, beyond the scope of this analysis. Moreover, the fluxes discussed here represent the ecosystem responses to climatology and the community dominant allocation strategies, we acknoledge the different phenological responses by “light-adapted” tree species at RJA or “water-adapted” species at equatorial sites (e.g. individual leaf phenology and traits as reported in Chavana-Bryant et al. (2016) and Lopes et al. (2016)). Future work should explore the ability of DGVMs to capture forest biological controls to productivity during anomalous meteorological conditions (e.g. dry versus wet years) and interannual variability.

4.2 Carbon allocation strategies

Models include *LAI* in the vegetation dynamics module using a variety of strategies: (1) prescribed *LAI* values from remote sensing sources; (2) dynamic calculation of daily *LAI* (e.g. ED2)*;* and (3) *LAI* is fixed annually and the DGVMs allocates any changes in leaf quantity at the end of the year, when next year's carbon balance and *LAI* values will be calculated (e.g. CLM3.5) (Table S3). This last approach may need to be re-evaluated given the importance of phenology as an ecosystem productivity driver. Models that dynamically calculate *LAI* generally rely on defining a range of values for each PFT (Clark *et al.*, 2011), where the actual index will depend mostly on the phenological status of the vegetation type –a function of temperature. Although some evergreen ecosystems do respond to temperature thresholds (e.g. positive correlation between T_{air} and *LAI,* and a threshold at $T_{air}>0$ or “heat sum” has been identified for conifer and deciduous forests at temperate areas (Khomik *et al.*, 2010; Delpierre *et al.*, 2015)), *LAI* and *Pc* at the tropical ecosystems studied here, did not exhibit a statistically significant correlation with T_{air}. Moreover, model *LAI* values were unreasonably 2+ units above observed values

(Baldocchi *et al.*, 1988; Gower *et al.*, 1999; Asner *et al.*, 2003; Sakaguchi *et al.*, 2011). Some models assumed *LAI* value above six (IBIS, CLM3.5 and JULES), the theoretical limit of *LAI* (assuming no clumping and planar leaf angle distribution) according to Beer's law. Similar to previous findings by Christoffersen et al. (2014) regarding DGVMs performance when simulating water fluxes, some of the model deficiencies could be resolved by changing the parameterization of each PFT, such as the case of maximum and minimum *LAI* values. However, a true improvement will only come if we increase the frequency and coverage of our measurements, and a better understanding of the carbon allocation, mechanisms that control the change in *LAI,* and the balance between loss due to abscission, leaf production, and other ecosystem processes.

In the observations, *Pc* values increased during the dry season at all central Amazon sites (Restrepo-Coupe *et al.*, 2013; Saleska *et al.*, 2016). Elevated *Pc* can be achieved through leaf flush, as younger leaves have higher leaf carbon assimilation at saturating light (A_{max}) compared to old leaves (Sobrado, 1994; Wu *et al.*, 2016), or by changes in leaf herbivory, *epiphyllous* growth, and stress, among other factors. Alternatively, *Pc* can be increased through a surge in canopy infrastructure (quantity of leaves) measured as leaf area index (*LAI*) (Doughty & Goulden, 2008). Our observations suggested a combination of these two processes or *Pc* mostly driven by the presence of younger leaves, as we observed a small increase in *LAI* at K67 during the dry season (0.7 m^2/m^2 ~10% of annual mean) and a gradual decline at CAX, respectively. In order to address the relationship between leaf demography (leaf age distribution) and carbon fluxes, we presented the seasonality of *in situ* observations of NPP_{leaf} and compared it to model estimates. We have shown that, at the equatorial Amazon estimated NPP_{leaf} was synchronous with the seasonality of SW_{down}

(Fig. S4 and S12). Thus, increasing light may trigger new leaf production as part of a light-based growth strategy missed by the DGVMs evaluated here (Wright & van Schaik, 1994; Restrepo-Coupe *et al.*, 2013; Borchert *et al.*, 2015). Some vegetation schemes have introduced a time-dynamic carbon allocation: to leaves, generic roots, coarse and fine roots, etc. However, even if models assign NPP_{leaf} varying turnover time from 243 days to a maximum of 2.7 years, the timing of leaf production seems to be missed. The counterintuitive mechanism observed at some central Amazon forests where all or most of the leaf-demography processes (leaf-fall, leaf-flush and *LAI*) increase during the dry season, constitutes an important challenge for modelers and plant physiologists. An appropriate model representation and further studies are required of: (1) the leaf lifespan (Malhado *et al.*, 2009), (2) the seasonality of leaf age distribution (e.g. sun and shade leaf cohorts: young, mature, old), (3) the effect of leaf-fall on increasing light levels at lower layers of the canopy, and (4) the relationship between leaf age and physiology (Albert *et al.*, in preparation), to properly characterize Amazon basin leaf phenology and associated changes in productivity. Thus, an homogeneous age cohort where all leaves have similar ability to assimilate carbon can contribute to the model simulated aseasonal *Pc* and *GEP* seasonality driven only by water availability.

Previous studies have linked the robustness of model predictions of the terrestrial ecosystem carbon response to climate change projections to the uncertainty of the different carbon pools within the models (Ahlström *et al.*, 2012). Observations show that the seasonality of allocation (e.g. $NPP_{litter\text{-}fall}$) and leaf-demography (e.g. NPP_{leaf}) are closely related to the fast and slow soil carbon pools (input) and ecosystem respiration. Decomposition of $NPP_{litter\text{-}fall}$ initiates the transfer of carbon to the soil microbial and the slow and passive pools in many models and determines heterotrophic respiration. Similarly, autotrophic respiration (maintenance and growth) also will be driven by live tissue allocation (NPP_{wood}, NPP_{leaf}, and NPP_{roots}). Therefore, R_e will depend on a well-characterized phenological response of litter and woody debris, wood and leaf accumulation, and the soil carbon pools. Still, in some models and according to a set of prescribed allometric relationships for each PFT, leaves, fine roots and stems *NPP* are allocated at the end of each simulated year. Thus, to improve simulation-data agreement and to generate reliable projections for ecosystem response to climate perturbations, the next generation of models must include a basic mechanistic understanding of the environmental controls on ecosystem metabolism that goes beyond correlations (e.g. NPP_{leaf} *versus* SW_{down}, $NPP_{liter\ fall}$ *versus Precip*) and addresses the long time adaptation to climate and their seasonality. We highlight the need for extended EC measurements accompanied by seasonal based biophysical inventories, as both datasets complement and inform each other.

The seasonal patterns in *GPP* and *NPP* (leaf and wood); show to be (1) aseasonal at K34; (2) near-synchronous at CAX; and (3) out-of-phase at K67. By comparison, along a wet to dry ecosystems continuum, seasonal observations at flooded forests showed reduced production of new leaves and lower photosynthetic assimilation during the inundation period and NPP_{wood} and NPP_{leaf} their peak then shifted into the dry season (Parolin, 2000; Dezzeo *et al.*, 2003) and no single pattern has been described for dry tropical forests other than $NPP_{leaf\text{-}fall}$ increasing during the dry period (Murphy & Lugo, 1986). The *GPP*, NPP_{leaf} and NPP_{wood} dry-season maxima at CAX may be interpreted in terms of a combination of mechanisms: (1) optimal allocation patterns (Doughty *et al.*, 2014) -- in sync photosynthetic activity and carbon allocation driven by dry-season light increases; and (2) reflect biophysical limitations (Fatichi *et al.*, 2014) --wet season conditions (e.g. low radiation and high soil moisture content), drive both leaves and wood to be produced during the dry season (leaf anteceding). By comparison, the NPP_{wood} patterns observed at K67 where dry-season *MiAP* is ~50% of mean annual *ET* may reflect biophysical limitations on the sink tissue (e.g. cell turgor and cell division in cambial tissues) --water availability as a driver (Wagner *et al.*, 2012; Rowland *et al.*, 2013), or/and an allocation strategy that favors NPP_{leaf} to NPP_{wood}. At K67 and K34 forests, the timing of *GPP versus* NPP_{wood} highlights the importance of non-structural carbon (*NSC*) (Fatichi *et al.*, 2014) and difficulties faced by more mechanistic DGVMs.

Here we reported a contrast between seasonal *ET* and *GPP* in terms of the former being simply described (mostly) by variations in radiation and the latter being a more complex function of leaf demography and environmental drivers (Restrepo-Coupe *et al.*, 2013; Wu *et al.*, 2016). In particular at RJA, *GPP* shows significant decrease during the dry season, yet *ET* is essentially invariant, indicating large seasonal variations in ecosystem water use efficiency (*WUE~GPP/ET*). These changes in *WUE* could be associated with seasonal variations in the leaf age distribution as shown in Wu et al. (2016) for K67 and K34. This hypothesis predicts that old leaves would require the same amount of water per unit intercepted radiation, but on average do less photosynthesis. A different biophysical explanation relates to ecosystem-average stomatal conductivity (*Gs*), as *Gs* would be determined by either changes in *LAI* or in climate (e.g. low Q_{air} or soil moisture) that may reach a minimum during the dry season. Decreasing *Gs* reduces *GPP* and transpiration (*T*), but not necessarily in proportion. Furthermore, *ET* includes *T* and surface and wet leaf evaporation (*E*), where *ET=E+T*. At RJA soil water may contribute to some of the *ET* given the shallow loamy sand profile (1.2–4.0m deep) characteristic of the site; moreover, water table depth is unknown and may similarly play an important role (Restrepo-Coupe *et al.*, 2013; Christoffersen *et al.*, 2014). Future work should address the acuracy of *ET* observations (energy balance closure), the partition between *E* and *T,* leaf-level seasonal changes in *WUE,* and ecosystem *Gs* at *RJA* and other forests.

4.3 Final considerations for model improvement

This study identified three main tropical forest responses to climatic drivers that if understood could reduce the model *versus* observation *GPP* discrepancies. These are (1) light harvest adaptation schemes (Graham *et al.*, 2003); (2) response to water availability; and (3) allocation strategies (lags between leaf and wood) (Fig. 6). We propose thorough (1) optimization patterns and (2) thresholds (limitation) to obtain the seasonality of the different carbon pools. For example, models could incorporate some of the recent findings: (1) leaf demography as a function of light environment as in Wu et al. (2016) and in Mahlado et al. (2009), and (2) leaf phenology (greenness) seasonal patterns driven by soil moisture availability as a function of *MAP* threshold as in Guan et al. (2015). However, less has been reported about other processes and reservoirs different than NPP_{leaf} (e.g. flowering, and fruit maduration). In particular, our study lacks belowground information, as data that explores the seasonality of root allocation at tropical sites is scarce and difficult to interpret (see Delpierre et al. (2015) for root phenology at boreal and temperate forests). Future work should address this important carbon-pool and the corresponding model ability to simulate the seasonality of belowground processes.

To ensure models are obtaining the right answers for the right reasons, the robustness of a DGVM should be determined by its ability to simulate from hours to decades. The logical progression of model development starts by testing at daily scales where the environmental variability (amplitude of the daily cycle) is greater than within a year (amplitude of the seasonal cycle), and then test their ability to simulate seasonality as the variability is greater than across years (amplitude of the annual cycle) (Richardson *et al.*, 2007). If DGVMs are able to capture seasonal carbon flux observations, it would increase our confidence that models could perform at longer time scales (e.g. interannual variability), which is key to predict the future of tropical forests under a changing climate. Moreover, individual modeling groups could further study model variability, including sensitivity tests on parameter optimizations (constrained by observations), thus to reduce the uncertainty related to DGVM parametrization.

Climate models have come a long way, from the 1970 when the first land surface scheme was introduced in order to represent the atmosphere-biosphere interaction by partitioning ocean from dry land (Manabe & Bryan, 1969). Simulations of water, energy and carbon fluxes based on the response of different plant functional types to climate drivers and disturbance signifies a great step forward in weather prediction and the study of future climates under the effect of land cover changes and atmospheric CO_2 enrichment (Pitman, 2003; Niu & Zeng, 2012). Models are constrained in their development given the high computational needs and the multiple processes that need to be accounted for on a three dimensional grid from *LAI* seasonality, to ground water flux, to leaf level parameterization, there is a tradeoff and a “priority list”. This study highlights some of the advances in tropical forest simulations of carbon and water fluxes and aims to identify future opportunities, as the inclusion of light harvesting and allocation strategies in an attempt to improve *GPP* and *NPP* predictions.

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List of Tables

Table 1. Precipitation at Amazon basin study sites. Based on the Tropical Rainfall Measuring Mission (TRMM) (NASA, 2014) for the years 1998 to 2014.

List of Figures

Figure 1. Locations of eddy covariance tower study sites at the Amazon Basin *sensu-stricto (Eva & Huber (eds), 2005)*. Minimum monthly precipitation (mm month^{-1}) from the Tropical Rainfall Measuring Mission (TRMM) (NASA, 2014) based on an annual composite for the years 1998 to 2014.

Figure 2. From top to bottom annual cycle of daily average observed climatic variables: incoming photosynthetic active radiation (*PAR*; μmol m^{-2} s^{-1}, black line right y-axis) and precipitation (*Precip*; mm month^{-1}, dark gray bars left y-axis), top of the atmosphere incoming radiation (*TOA*; W m^{-2}, blue line right y-axis) (not a driver). From left to right study sites (from wet to dry) near Manaus (K34), Caxiuanã (CAX), Santarém (K67), and Reserva Jarú southern (RJA) forests. Gray shaded area is dry season as defined using satellite derived measures of precipitation (TRMM: 1998-2014). Second row LSM drivers: near surface specific humidity (Q_{air}; g kg^{-1}, black line left y-axis) and temperature (T_{air}; °C, blue line right y-axis). Lower panel depicts model ecosystem-scale of model soil moisture “stress” (*FSW*, where 1=no stress). Simulations from ED2 (blue), IBIS (red), CLM3.5 (green), and JULES (purple).

Figure 3: Annual cycle of daily average ecosystem-scale photosynthesis (*GPP*; gC m^{-2} d^{-1}), ecosystem respiration (R_e; gC m^{-2} d^{-1}), net ecosystem exchange (*NEE*; gC m^{-2} d^{-1}), and

evapotranspiration (*ET*; mm month^{-1}). From left to right study sites (from wet to dry) near Manaus (K34), Caxiuanã (CAX), Santarém (K67), and Reserva Jarú southern (RJA) forests. Observed (black + dark gray uncertainty) and simulated by models (colors). Dashed black line at *ET* panels corresponds to a linear model where the independent variable is incoming radiation (SW_{down}). Gray shaded area is dry season as defined using satellite derived measures of precipitation (TRMM: 1998-2014). Simulations from ED2 (blue), IBIS (red), CLM3.5 (green), and JULES (purple).

Figure 4. From top to bottom annual cycle of daily average ecosystem photosynthetic capacity (*Pc; gC* m^{-2} d^{-1}), leaf area index (*LAI;* m^{2} m^{-2}), normalized *LAI* (its value constrained between 0 and 1 in order to better track its changes), net primary productivity (*NPP;* m^{-2} d^{-1}) allocated to leaves -leaf flush (NPP_{leaf}; m^{-2} d^{-1}), *NPP* allocated to litter-fall ($NPP_{litter\text{-}fall}$; gC m^{-2} d^{-1}). Lower row *NPP* allocated to wood (NPP_{wood}; gC m^{-2} d^{-1}). Gray shaded area is dry season as defined using satellite derived measures of precipitation (TRMM: 1998-2014). From left to right study sites (from wet to dry) near Manaus (K34), Caxiuanã (CAX), Santarém (K67), and Reserva Jarú southern (RJA) forests. Observed (black) *versus* simulated by models (colors). Simulations from ED2 (blue), IBIS (red), CLM3.5 (green), and JULES (purple). Dashed green lines (CLM3.5) at $NPP_{litter\text{-}fall}$ and NPP_{leaf}, indicate average values for comparison purposes (models allocated at the end of the year as indicated by continuous line).

Figure 5. From top to bottom, annual cycle observed (black) and model simulations from JULES (purple), CLM3.5 (green), IBIS (red), and ED2 (blue). Normalized (by its seasonal maximum) annual cycle of daily average ecosystem-scale photosynthesis (GPP/GPP_{max})

(continuous line), net primary productivity (*NPP*) allocated to leaves -leaf flush (NPP_{leaf} /$NPP_{leaf\ max}$), *NPP* allocated to litter-fall ($NPP_{litter\text{-}fall}$ /$NPP_{litter\text{-}fall\ max}$), and *NPP* allocated to wood (NPP_{wood} /$NPP_{wood\ max}$). From left to right study sites (from wet to dry) near Manaus (K34), Caxiuanã (CAX), Santarém (K67), and Reserva Jarú southern (RJA) forests. Gray shaded area is dry season as defined using satellite derived measures of precipitation (TRMM: 1998-2014).

Figure 6. Ecosystem response to climate seasonality selection of biological adaptive mechanisms: light harvest adaptations (green tones), allocation strategies (orange tones), and water limitation (blue tones). Mechanisms classified when possible into resource optimization (Opt) and biophysical limitations (Lim).