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Variation are Essential for Accurate Modeling of
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The phenology of leaf quality and its within-canopy variation are essential for accurate modeling of photosynthesis in tropical evergreen forests

Running Head: Modeling tropical photosynthetic seasonality

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Abstract:

Leaf quantity (i.e. canopy leaf area index, LAI), quality (i.e. per-area photosynthetic capacity), and longevity all influence the photosynthetic seasonality of tropical evergreen forests. However, these components of tropical leaf phenology are poorly represented in most terrestrial biosphere models (TBMs). Here, we explored alternative options for the representation of leaf phenology effects in TBMs that employ the Farquahar, von Caemmerer & Berry (FvCB) representation of CO_2 assimilation. We developed a two-fraction leaf (sun and shade), two-layer canopy (upper and lower) photosynthesis model to evaluate different modeling approaches and assessed three components of phenological variations (i.e. leaf quantity, quality, and within-canopy variation in leaf longevity). Our model was driven by the prescribed seasonality of leaf quantity and quality derived from ground based measurements within an Amazonian evergreen forest. Modeled photosynthetic seasonality was not sensitive to leaf quantity, but was highly sensitive to leaf quality and its vertical distribution within the canopy, with markedly more sensitivity to upper canopy leaf quality. This is because light absorption in tropical canopies is near maximal for the entire year, implying that seasonal changes in LAI have little impact on total canopy light absorption; and because leaf quality has a greater effect on photosynthesis of sunlit leaves than light limited, shade leaves and sunlit foliage are more abundant in the upper canopy. Our two-fraction leaf, two-layer canopy model which accounted for all three phenological components was able to simulate photosynthetic seasonality, explaining ~90% of the average seasonal variation in eddy covariance derived CO_2 assimilation. This work identifies a parsimonious approach for representing tropical evergreen forest photosynthetic seasonality in TBMs that utilize the FvCB model of CO_2 assimilation, and highlights the importance of incorporating more

- 49 realistic phenological mechanisms in models that seek to improve the projection of future carbon
- 50 dynamics in tropical evergreen forests.

1. Introduction

Tropical evergreen forests play a dominant role in the global carbon, water, and energy cycles (Pan *et al.*, 2011; Fu *et al.*, 2013; Stark *et al.*, 2016). They account for around one-third of annual terrestrial photosynthesis (Beer *et al.*, 2010) and a quarter of the global aboveground carbon stock (Saatchi *et al.*, 2011; Aragao *et al.*, 2014). Therefore, even small errors in model representation of the carbon pools or fluxes in this biome will result in marked uncertainty in the projection of future climate (Friedlingstein *et al.*, 2006, 2014; Cox *et al.*, 2013; Huntingford *et al.*, 2013). A key area of uncertainty is our understanding and model representation of tropical evergreen forest seasonality, including seasonal leaf display as well as physiological function (Saleska *et al.*, 2003; Restrepo-Coupe *et al.*, 2013; Guan *et al.*, 2015). Most Terrestrial Biosphere Models (TBMs) have a mechanistic representation of CO₂ assimilation that is capable of simulating the response of photosynthesis to global change (e.g. increasing atmospheric CO₂ concentration). However, most of these models lack mechanistic representation of tropical forest photosynthetic seasonality (de Weirdt *et al.*, 2012, Kim *et al.*, 2012; Restrepo-Coupe *et al.*, 2017). To improve our ability to project the impact of global change on the terrestrial carbon cycle, we need to integrate model representation of the mechanisms that regulate tropical forest photosynthetic seasonality with an approach that is capable of mechanistically representing the response of photosynthesis to global change.

Within tropical evergreen forests, leaf production from field based studies (e.g. Wright & van Schaik, 1994; Girardin *et al.*, 2016), and canopy photosynthesis (i.e. gross primary productivity, GPP) derived from eddy flux towers (Saleska *et al.*, 2003; Hutyyra *et al.*, 2007; Restrepo-Coupe *et al.*, 2013) and satellites (Lee *et al.*, 2013; Guan *et al.*, 2015) consistently show seasonal variability. Importantly, this seasonal variation is not directly related to extrinsic

environmental variability (Bradley *et al.*, 2011; Guan *et al.*, 2015; Wu *et al.*, 2016a, 2017). Instead, increasing evidence has shown that tropical leaf phenology is a primary mechanism regulating seasonal carbon assimilation (Doughty & Goulden, 2008; Kim *et al.*, 2012; Restrepo-Coupe *et al.*, 2013; Wu *et al.*, 2016a, 2017). Here phenology refers to periodic cycles of leaf production, development and abscission within a forest canopy, which produces seasonal variability in leaf quantity (i.e. canopy leaf area index, LAI) and leaf quality (i.e. per-area leaf photosynthetic capacity), and includes the differential leaf turnover associated with the changes in leaf longevity within vertical canopy profiles. Despite a modest seasonality in leaf quantity (e.g. Doughty & Goulden, 2008; Brando *et al.*, 2010; Lopes *et al.*, 2016; Saleska *et al.*, 2016), many tropical evergreen forests exhibit substantial leaf turnover during the dry season when monthly precipitation is lower than the evaporative demand (Borchert, 1994; Wright & van Schaik, 1994; Wu *et al.*, 2016a; Lopes *et al.*, 2016). As a result, these forests have a strong seasonality in leaf quality because recently mature leaves have a higher photosynthetic capacity than the old leaves they replace (Kitajima *et al.*, 1997a; Doughty & Goulden, 2008; Wu *et al.*, 2016a). Importantly, this seasonal variation in leaf quality was recently shown to be one of the most important phenological mechanisms responsible for photosynthetic seasonality in tropical evergreen forests (Wu *et al.*, 2016a, 2017). However, this advance (e.g. Wu *et al.*, 2016a, 2017) was based on a light use efficiency model that can capture tropical forest photosynthetic seasonality but lacks the physiological and structural complexity that is necessary to project the response to the changing climate, particularly rising CO₂ concentration.

In addition to leaf quality and quantity, the within canopy variation in leaf longevity has been well documented in the tropics (e.g. Lowman, 1992; Miyaji *et al.*, 1997; Reich *et al.*, 2004). This large within-canopy variation in leaf phenological characteristics, with understory leaves

living two or more times longer than canopy leaves, may be attributed either to temporal niche partitioning between canopy trees and the understory (Messier *et al.*, 1998; Augspurger *et al.*, 2005; Richardson & O’Keefe, 2009), or to an adaptive response to large within-canopy variation in environmental variables (Wright *et al.*, 2006; Stark *et al.*, 2012, 2015; Niinemets *et al.*, 2015). As such, within-canopy variation in light and associated biotic properties have also been suggested as an important control on processes such as leaf development, energy balance, water use, and photosynthesis (Ellsworth & Reich, 1993; Baldocchi & Amthor, 2001; Stark *et al.*, 2012; Morton *et al.*, 2016).

Despite the importance of leaf phenology in regulating photosynthetic seasonality in the tropics, the combined effects of these three phenological components on tropical forest photosynthetic seasonality are either absent or have not been adequately represented in current TBMs (e.g. Restrepo-Coupe *et al.*, 2017). The majority of TBMs (e.g. Fisher *et al.*, 2015; Rogers *et al.*, 2017) utilize the Farquhar, von Caemmerer and Berry (1980) (FvCB) leaf scale mechanistic model of CO₂ assimilation to simulate carbon uptake together with a leaf to canopy scaling relationship, which often represents the whole forest canopy as sunlit and shade leaf fractions (e.g. dePury & Farquhar, 1997; Drewry *et al.*, 2010). Several modeling attempts have been proposed to improve the representation of photosynthetic seasonality. For example, some TBMs have included seasonal variation in LAI driven by water availability (Baker *et al.*, 2008; Powell *et al.*, 2013; Sitch *et al.*, 2015; Xu *et al.*, 2016; Restrepo-Coupe *et al.*, 2017); however, the representation of seasonal change in leaf quality and their vertical distribution has rarely been explored before. As a result, these models generally fail to adequately reproduce the photosynthetic seasonality of tropical evergreen forests, simulating a dry-season photosynthetic decrease as a consequence of increasing dry-season water stress, with eddy covariance derived

GPP showing the opposite trend (Saleska *et al.*, 2003; Baker *et al.*, 2008; de Goncalves *et al.*, 2013; Restrepo-Coupe *et al.*, 2017). Several other attempts have shown some improvement in the modeling performance of TBM-based photosynthetic seasonality by tuning model parameters to allow for seasonal variation in leaf photosynthetic capacity (e.g. de Weirdt *et al.*, 2012; Kim *et al.*, 2012). However, the assumptions made in these models, such as the application of the leaf economic spectrum to within-canopy relationships, require systematic evaluation (Messier *et al.*, 2016) or compared to field based metrics of both leaf phenology (e.g. leaf production and senescence) and GPP. The model-observation mismatch and the incomplete mechanistic evaluation highlight need for improving current TBMs which should include a mechanistic representation of leaf phenology effects on tropical evergreen forest photosynthesis that includes all three phenological components of leaf quantity, quality, and differential leaf turnover within a forest canopy.

The goal of this study was to develop an approach that would provide the sufficient phenological representation of the three components to capture the photosynthetic seasonality of a tropical evergreen forest in a mechanistic model framework that included the FvCB representation of CO₂ assimilation and a multilayer canopy. We accomplished this by evaluating the performance of model structures that incorporated the three different phenological mechanisms. We asked three questions: (1) Is seasonality of tropical forest photosynthesis reproduced by a model including leaf phenology? (2) What is the relative contribution of these three phenological components in controlling the seasonality of photosynthesis? (3) Finally, how do these three components regulate tropical forest photosynthetic seasonality?

Our approach was to modify existing canopy photosynthesis models to enable coupling with prescribed, field-based phenology of the leaf quantity and quality allowing us to simulate

canopy photosynthetic seasonality. In addition, we enabled representation of sun and shade leaf fractions and a two-layer canopy (upper and lower) to allow us to explore within-canopy phenological variation. As such, our model framework allowed us to assess how the three components of leaf phenology independently and jointly regulated canopy-scale photosynthetic seasonality. In order to evaluate the model performance and avoid other confounding factors in our analysis, such as seasonal and inter-annual environmental variation (Baldocchi & Amthor, 2001; Richardson *et al.*, 2007; Wu *et al.*, 2017), our target variable was GPP_{ref} , which is eddy covariance derived or modeled GPP under a reference environment. This enabled us to focus on the underlying physiological mechanisms and isolate the biological controls on GPP from seasonality in environmental variables (Wu *et al.*, 2017). The successful attribution of biological controls on tropical forest photosynthesis will not only improve modeling of photosynthesis in the tropics but also help assess the correct functional response to environmental variability.

2. Materials and Methods

2.1 Model evaluation

To evaluate model performance we used data from the Tapajós k67 eddy covariance (EC) tower site (with Fluxnet2015 ID of “BR-Sa1”; <http://fluxnet.fluxdata.org/data/download-data/>). The k67 EC tower site (54°58'W, 2°51'S) is located in the Tapajós National Forest, near Santarém, Pará, Brazil. Tapajós is an evergreen tropical forest on a well-drained clay-soil plateau (Rice *et al.*, 2004), with a mean upper canopy height of ~40 m (Hutyra *et al.*, 2007). Mean annual precipitation is ~2000 mm year⁻¹ with a 5-month dry season (monthly precipitation < monthly evapotranspiration) from approximately mid-July to mid-December (Hutyra *et al.*, 2007; Restrepo-Coupe *et al.*, 2013).

The k67 EC site included seven-full-year flux and meteorological measurements (years 2002-2005, and 2009-2011; Wu *et al.*, 2016a, 2017). Detailed descriptions of the instrumentation and data pre-processing protocol for the k67 EC data can be found in Hutyra *et al* (2007) and Restrepo-Coupe *et al* (2013). No gap-filling data was used in this study. Hourly EC measurements of net ecosystem exchange (NEE) was partitioned into ecosystem respiration (R_{eco}) and GPP following standard approaches (Hutyra *et al.*, 2007; Restrepo-Coupe *et al.*, 2013): Reco, which was averaged within monthly bins from valid nighttime hourly NEE during well-mixed periods (u^* criterion: ≥ 0.22 m/s), was also used as an estimate of average monthly daytime respiration, and GPP was estimated as $-(NEE - Reco)$. We did not use a temperature function to extrapolate nighttime NEE to daytime Reco, as is done at many higher latitude sites (e.g. Reichstein *et al.*, 2005), because nighttime temperature range within most months at k67 is too small to constrain such a function (Hutyra *et al.*, 2007). Also because Reco is composited by the two components: (1) the heterotrophic component (which is expected to have higher values in the daytime, due to higher temperature in the daytime than at night; Reichstein *et al.*, 2005), and (2) the autotrophic component, especially the part associated with foliar respiration (which is expected to have lower values in the daytime, due to light-inhibition of mitochondrial respiration in leaves; Heskell *et al.*, 2013; Wehr *et al.*, 2016), therefore, without the specific information about the relative contribution of these two components, we judged that our approach (using unmodified nighttime values as estimates for daytime Reco) was conservative – especially for a study of seasonality, for which potential errors in absolute value are less important.

In this study we used the reference GPP (GPP_{ref}) as our target variable and benchmark for model evaluation. GPP_{ref} represents the CO_2 assimilation of the canopy in the absence of environmental fluctuations and thus provides the capability to evaluate the phenological impact

on canopy-scale photosynthesis independent of other sources of variation. EC-derived GPP_{ref} was calculated as the monthly average of all seven-year EC-derived GPP measurements under a reference environmental condition, following Wu *et al* (2016a, 2017). The EC-derived GPP_{ref} here scales linearly with incident light-use-efficiency under the reference environment as used in Wu *et al* (2016a, 2017) (where it was called canopy-scale photosynthetic capacity). The reference environment for GPP_{ref} was taken as narrow bins of each climatic driver: canopy-top photosynthetically active radiation (PAR_0)= $1320 \pm 200 \mu\text{mol m}^{-2}\text{s}^{-1}$, diffuse light fraction= 0.4 ± 0.1 , vapor pressure deficit (VPD)= $0.87 \pm 0.20 \text{ kPa}$, air-temperature (T_{air})= $28 \pm 1 ^\circ\text{C}$, and solar zenith angle (SZA)= $30 \pm 5^\circ$, and 8.1% of all hourly EC-derived GPP measurements were selected under the reference environment (~ 20 measurements per month per year; almost equally distributed across months). We used the seven-year mean annual cycle of monthly EC-derived GPP_{ref} as a benchmark for model validation. The same reference environment is also used for our model simulation of canopy-scale GPP_{ref} (see "Model Framework" below).

2.2 Prescribed phenology

Three components of leaf phenology were examined in this study, including the quantity, the quality, and within-canopy variation in leaf turnover rates, all of which are tightly linked with seasonal variability in leaf production, development and abscission within a tropical forest canopy (Wu *et al.*, 2016a,b; Lopes *et al.*, 2016). Our prescribed, field-based leaf phenology data at the k67 site are the same as those used in Wu *et al* (2016a).

(1) Field data of canopy LAI, litterfall LAI, and new leaf LAI. The mean annual cycle of monthly canopy LAI (range: $5.35\text{--}6.15 \text{ m}^2 \text{ m}^{-2}$) was derived from tower-mounted camera image timeseries (Tetracam Agricultural Digital Camera, Tetracam, Inc., Gaomesville, FL; January

2010 to December 2011) using a camera-based tree inventory approach. For details about this approach, please refer to supplementary materials section 5 and Figs. S5 and S8 in Wu *et al* (2016a). The mean annual cycle of monthly litterfall LAI (range: 0.23–0.66 m² m⁻²) was derived by converting field observations of mass-based foliage litterfall (Mg biomass month⁻¹ ha⁻¹; bi-weekly measurements from 2001 to 2005; Brando *et al.*, 2010) of the same site into area-based litterfall LAI (m² m⁻² per month), with the formula of Litterfall LAI = mass-based Litterfall×SLA, applying a mean specific leaf area (SLA) of 0.816 ha Mg⁻¹ biomass (Malhado *et al.*, 2009). The mean annual cycle of monthly new leaf LAI production (in m² m⁻² per month) was estimated by using the formula of dLAI/dt + litterfall LAI, where dLAI/dt is the average canopy LAI change in the two months centered around LAI of each month (Wu *et al.*, 2016a).

(2) Field based leaf gas exchange measurements. Leaf level photosynthetic capacity, represented by the apparent maximum carboxylation capacity of Rubisco standardized to a reference temperature of 25°C ($V_{\text{cmax}25}$) (Bernacchi *et al.*, 2013), was derived from standard leaf gas exchange measurements of photosynthetic CO₂ response curves ($A-C_i$) for top-of-canopy sunlit leaves of five canopy trees at the k67 site (species and structural information for leaf samples are shown in Table S1; data are available from <http://datadryad.org/resource/doi:10.5061/dryad.8fb47>; see supplementary materials in Wu *et al*, 2016a for more details on these data). Briefly, the trees we targeted for $A-C_i$ curves represent the most abundant species that account for ~24% of the local basal area (Pyle *et al.*, 2008). Prior to gas exchange measurements, branches (of ~ 1m length) were assessed using arborist climbing methods, cut, then promptly but gently lowered to the ground with ropes, and re-cut under water at least once within 15 minutes of the initial harvest. Gas exchange was typically measured for leaves of each age category present on the branch. These sunlit leaves (n=27) were initially

classified into three age classes (Young, Mature, and Old) based on visual assessment of color, size, rigidity, and bud scars (when present) (Chavana-Bryant *et al.*, 2016), and then confirmed by in-situ leaf tagging and associated photographic imaging of leaves at known ages (from 10 days old up to 1 year old; see Wu *et al.*, 2016b for more details). These leaf age classes roughly correspond to a young age class (leaves of 1-2 months old), a mature age class (leaves of 3-5 months), and an old age class (leaves of ≥ 6 months). Very young leaves (recent leaf burst; e.g. Fig. S1 in Wu *et al.*, 2016b) were too small, delicate, or logistically challenging for photosynthesis measurements, therefore field derived leaf $V_{\text{cmax}25}$ of the young age class (which corresponds to the young leaves of late stage, big enough for Licor measurements) was then divided by two to provide an average across the distribution of the entire young age class. The five-species mean ($\pm$ standard deviation) $V_{\text{cmax}25}$ for these top-of-canopy sunlit leaves of young, mature, and old age classes were $6.8 (\pm 1.4)$, $36.5 (\pm 10.7)$, and $23.4 (\pm 5.1) \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively.

(3) The mean seasonality of leaf age demographics and leaf quality. The quality component of leaf phenology refers to per-area leaf photosynthetic capacity. At the canopy scale, leaf quality can be approximated by the age-dependency of leaf photosynthetic capacity (shown above) and the associated leaf age fraction (or leaf age-demography). Leaf age demographics were approximated by a three-LAI-age-class demography model (Wu *et al.*, 2016a), with the inputs from mean annual cycles of monthly canopy LAI and new leaf LAI (calculated above). The model-derived three LAI-age demographics include the LAI for a young age class (leaves of 1-2 months old, LAI_Y), a mature age class (leaves of 3-5 months, LAI_M), and an old age class (leaves of ≥ 6 months, LAI_O ; see Fig. 1), with the two optimized model parameters from Wu *et al.* (2016a) which define leaf residence time at young and mature age classes respectively. The

reason we use these optimized parameters here is because these parameters were consistent with our field observations of leaf aging processes (Chavana-Bryant *et al.*, 2016; Wu *et al.*, 2016b), as well as the roughly similar time interval of mature and old leaf age classes for field-based leaf gas exchange measurements.

In sum, the leaf quality was calculated by using a three-age-class leaf demography-ontogeny model as below (Wu *et al.*, 2016a).

$$L_{quality} = \frac{V_{cmax,Y} \times LAI_Y + V_{cmax,M} \times LAI_M + V_{cmax,O} \times LAI_O}{LAI_Y + LAI_M + LAI_O} \quad (1)$$

Where $L_{quality}$ is leaf quality, which represents age composition weighted leaf photosynthetic capacity, and $V_{cmax,Y}$, $V_{cmax,M}$, and $V_{cmax,O}$ represent leaf level V_{cmax} at young, mature and old age classes respectively.

2.3 Model framework

2.3.1 TBM-type canopy photosynthesis models (DF1997 and ML)

Sun-shade, big leaf, canopy photosynthesis models, which represent the whole forest canopy as a big leaf of the two fractions (sun versus shade), are commonly used in many TBMs, e.g. Community Land Model version 4.5 (CLM4.5; Oleson *et al.*, 2013) and the Joint UK Land Environmental Simulator version 4.5 (JULES4.5; Best *et al.*, 2011; Clark *et al.*, 2011; Harper *et al.*, 2016). Canopy photosynthesis is usually represented in these formulations by the two processes: a leaf scale mechanistic photosynthesis model and a leaf-canopy scaling relationship, which represents the whole forest canopy as sunlit and shade fractions using approaches such as dePury and Farquhar (1997; DF1997) or a multi-layer approach (Drewry *et al.*, 2010; ML). These processes are described in detail as below.

(1) A leaf scale mechanistic photosynthesis model. Here we couple a mechanistic FvCB based photosynthesis model with a stomatal conductance scheme (Medlyn *et al.*, 2011; Lin *et al.*, 2015) to simulate the leaf level photosynthesis response to the variability in both biotic (e.g. $V_{\text{cmax}25}$ and $J_{\text{max}25}$) and climatic (e.g. PAR, temperature and VPD) factors (details in Table S2). The Medlyn-type stomatal conductance model was selected because leaves/stomata respond to VPD rather than relative humidity. Therefore, the Medlyn-type stomatal conductance model will likely capture projected increases in VPD better than other alternatives (Rogers *et al.*, 2017). The only prescribed parameter of this stomatal conductance model is the stomatal slope, and here we used the value of 3.77 based on a recent meta-data analysis for tropical rainforest trees (Lin *et al.*, 2015). Additionally, we refer to Lloyd & Farquhar (2008) and Bernacchi *et al.* (2013) to describe the temperature effect on leaf photosynthesis. As such, this photosynthesis model has the capability to simulate the leaf level photosynthetic response to the current environmental variability, but also to the changing environmental drivers associated with global change (i.e. rising CO₂ concentration, temperature and VPD).

(2) The leaf to canopy scaling relationship represented by the DF1997 model. DF1997 simulates canopy photosynthesis as the sum of the photosynthetic rate contributed by the sunlit fraction (GPP_{sun}) and the shade fraction (GPP_{shade}) of a forest canopy respectively (eqn. 2).

$$GPP = GPP_{\text{sun}} + GPP_{\text{shade}} \quad (2)$$

The DF1997 model is operated by firstly determining the LAI, V_{cmax} and absorbed PAR for each canopy fraction, and then applying leaf level photosynthesis model (as above) to simulate the photosynthesis to each canopy fraction. Canopy total LAI (LAI_{tot}) is partitioned into the sunlit fraction (LAI_{sun}) and the shade fraction (LAI_{shade}), following Beer's law (eqns. 3-4; dePury & Farquhar, 1997; Chen *et al.*, 1999; Ryu *et al.*, 2011):

$$LAI_{sun} = \frac{1 - \exp\left(-\frac{k \times \Omega \times LAI_{tot}}{\cos(SZA)}\right)}{k / \cos(SZA)} \quad (3)$$

$$LAI_{shade} = LAI_{tot} - LAI_{sun} \quad (4)$$

where $k(=0.5)$ is the extinction coefficient, and Ω is the clumping index; $\Omega=0.66$ for tropical evergreen forest (He *et al.*, 2012) was used in this study.

DF1997 also partitions the canopy integrated V_{cmax} ($V_{cmax,tot}$) into the sunlit fraction ($V_{cmax,sun}$) and the shade fraction ($V_{cmax,shade}$) (see Table S3). Here we assumed that V_{cmax} declines exponentially within the canopy following Lloyd *et al* (2010) (see eqns. 5-6 below; Fig. 2).

$$V_{cmax,i} = V_{cmax,0} \times \exp(-k_n \times LAI_i) \quad (5)$$

$$k_n = \exp(0.00963 \times V_{cmax,0} - 2.43) \quad (6)$$

where $V_{cmax,0}$ is the V_{cmax} of leaves at the top of the canopy; and k_n describes the exponential decline of V_{cmax} against the given accumulated LAI from the top of the canopy (LAI_i). By tracking PAR at the top of the canopy (PAR_0), which is the sum of direct beam ($PAR_{b,0}$) and diffuse radiation ($PAR_{d,0}$) in the visible spectrum (i.e. 400-700 nm), DF1997 calculates its canopy absorbance by the sunlit fraction (PAR_{sun}) and by the shade fraction (PAR_{shade}), using Beer's law and Seller's (1987) two-stream approximation for canopy radiative transfer (dePury & Farquhar, 1997; Ryu *et al.*, 2011; Tables S4-S5).

To facilitate the simulation of photosynthetic seasonality with DF1997, we prescribed top-of-canopy $V_{cmax,0}$ (in eqn. 5), i.e. *Lquality* (eqn. 1), while assuming that vertical changes in V_{cmax} within a forest canopy follow a fixed exponential decline rate (as described by eqns. 5-6). The complete equation set for the DF1997 model is provided in Tables S2-S5.

(3) The leaf-canopy scaling relationship represented by the multi-layer model. ML is an alternative way to scale leaf-level function and simulate canopy photosynthesis. ML explicitly

resolves direct and diffuse radiation for sunlit and shade canopy fractions at each canopy layer using Seller's (1987) two-stream approximation for canopy radiative transfer. The number of canopy layers is prescribed as N , where initial results from a model sensitivity showed that GPP was insensitive to $N \geq 15$ (Fig. S1). We thus used $N=15$ for the following simulations. In addition, we calculated the LAI of the sunlit ($LAI_{sun,i}$) and the shaded ($LAI_{shade,i}$) fractions for each canopy layer i ($i=1, 2, \dots, N$), and their corresponding per-area radiation absorbed by the sunlit fraction ($PAR_{sun,i}$) and the shade fraction ($PAR_{shade,i}$). Last, ML calculated the V_{cmax} of each canopy layer ($V_{cmax,i}$) also using eqns. 5-6.

The leaf level photosynthesis model was then used to calculate the photosynthesis rate of each canopy fraction for given layer i : per-area photosynthesis rate for the sunlit ($GPP_{sun,area,i}$) and the shade ($GPP_{shade,area,i}$). The cumulative canopy photosynthesis rate was thus equal to the sum of area weighted photosynthesis rate of each layer:

$$GPP = \sum_{i=1}^N (GPP_{sun,area,i} \times LAI_{sun,i} + GPP_{shade,area,i} \times LAI_{shade,i}) \quad (7)$$

To facilitate the simulation of photosynthetic seasonality with ML, we also prescribed top-of-canopy $V_{cmax,0}$ (in eqn. 5), i.e. $Lquality$ (eqn. 1).

It is important to note that the models (DF1997 and ML) presented here can simulate leaf phenology effects of both quantity and quality components; however, none of these models accounted for within-canopy phenological variation, and assumed a constant leaf turnover (flushing and abscission) rate throughout the canopy. Additionally, in our model simulation, we assume that leaf temperature and VPD for the sunlit and shade canopy fractions are the same as the reference environment.

2.3.2 Modified TBM representation of canopy photosynthesis to allow for within-canopy phenological variation (a two-fraction leaf, two-layer canopy model)

Many field-based studies have indicated that leaf longevity could vary greatly depending on the growth environments (e.g. Wright *et al.*, 2006; Wu *et al.*, 2016b), with understory leaves displaying longer leaf longevity than upper canopy leaves (Lowman, 1992; Miyaji *et al.*, 1997; Reich *et al.*, 2004). This suggests that the leaf turnover rate in the upper canopy should be faster than that in the lower canopy and understory. However, the within-canopy phenological variation has not been explicitly accounted for until now. To accomplish this, we modified the ML model framework (via addition of a second, lower canopy layer) to allow explicit representation of within-canopy variation in leaf turnover, in addition to the sun and shade fractions that already allow for within-canopy physiological variation.

In this new model, we divided a forest canopy into the two layers: (1) the upper canopy layer with the cumulative LAI from 0 (top-of-canopy) to $2.5 \text{ m}^2 \text{ m}^{-2}$, and (2) the lower canopy layer including the remainder of the canopy. Both layers are assumed to have the same phenological pattern and timing, but the amount of leaf flush and litterfall that drives phenology is differentially allocated between them. This allocation between layers is specified by f_{top} , the fraction of observed leaf turnover (including leaf drop and flush) across the whole forest canopy attributed to leaves in the upper canopy layer, e.g. when $f_{\text{top}} = 0.7$, 70% of observed forest canopy leaf turnover (and associated amplitude of the LAI and L_{quality} variables) is attributed to the upper canopy layer and 30% to the lower canopy layer; under this case, the ratio of leaf turnover rate between upper canopy leaves and lower canopy leaves can be calculated as $(f_{\text{top}}/\text{LAI}_{\text{up}})/((1-f_{\text{top}})/\text{LAI}_{\text{low}})=2.8$, where $f_{\text{top}}=0.7$, LAI_{up} (or the average LAI for the upper canopy layer)= $2.5 \text{ m}^2 \text{ m}^{-2}$, and LAI_{low} (or the average LAI for lower canopy layer)= 3 m^2

m^{-2} . Since leaf longevity is an inverse of leaf turnover rate, therefore the leaf longevity for the lower canopy leaves is around 2.8 times longer than the upper canopy leaves when $f_{\text{top}}=0.7$. Our differentiation of these two canopy layers (upper and lower) at the LAI cutoff of $2.5 \text{ m}^2 \text{ m}^{-2}$ for the upper canopy is slightly arbitrary, but sensitivity analysis showed that our modeling results were largely insensitive to the LAI cutoff and exhibited only minor variation when LAI increased from 2 to $3 \text{ m}^2 \text{ m}^{-2}$ (Fig. S2).

2.4 Model experiments

We used our proposed two-fraction leaf, two-layer canopy model as the main modeling testbed for assessing the effect of different phenological components on modeled canopy photosynthetic seasonality. This is because previous studies (e.g. dePury and Farquhar, 1997; Bonan *et al.*, 2012) demonstrate that DF1997 and ML can simulate almost identical GPP fluxes at the canopy scale (which is also confirmed by our Fig. S3), and also because our proposed two-fraction leaf, two-layer canopy model here is identical to ML when no within-canopy phenological variation is considered but also enables to examine the effect of within-canopy phenological variation by varying f_{top} . First, we ran the model parameterized by all three components, aiming to explore how well the model with all phenological mechanisms can capture EC-derived GPP_{ref} seasonality. The model inputs for these phenological components include: (1) the leaf quantity based on field measurements of the mean annual cycle of monthly LAI, (2) the leaf quality based on field-derived seasonality of L_{quality} (as calculated by eqn. 1, weighted by field-measured age dependency of $V_{\text{cmax}25}$ and field-derived leaf age demographics), and (3) the within-canopy phenological variation, by assuming leaves of lower canopy layer had 2.8 times longer leaf longevity compared with that of upper canopy layer (or $f_{\text{top}}=0.7$), which is

consistent with the literature (e.g. Lowman, 1992; Miyaji *et al.*, 1997; Reich *et al.*, 2004). We also ran the models under two additional scenarios, aiming to explore the relative role of each phenological component on modeled photosynthetic seasonality, with that (1) the model is parameterized with the observed annual cycle of leaf quantity alone, while assuming neither within-canopy variation in leaf longevity nor seasonal variation in leaf quality, and that (2) the model is parameterized with the observed phenological cycles of leaf quantity and quality, while assuming a constant leaf turnover rate throughout the canopy. To further elucidate the mechanisms by which each phenological component regulates canopy photosynthetic seasonality, we also evaluated the GPP_{ref} sensitivity of the sunlit canopy fraction and the shade canopy fraction to the seasonal variation in leaf phenology (quantity and quality) and within-canopy variation in leaf longevity (by varying f_{top} from 0 to 1.0 with the increment of 0.1) respectively.

3. Results

3.1 Modeled GPP_{ref} seasonality parameterized by differential leaf phenological mechanisms

We used the two-fraction leaf, two-layer canopy model to explore how including model representation of the three different phenological components affected the ability of the models to simulate the canopy scale photosynthetic seasonality, as compared with EC-derived GPP_{ref} . Our results show that the model parameterized by all three phenological components (i.e. quantity, quality and within-canopy phenological variation) was best able to capture EC-derived photosynthetic seasonality (Fig. 3 and Table 1).

The seven-year mean annual cycle of EC-derived GPP_{ref} at the Tapajós k67 site showed an initial decline in the late wet season, and then an increase in the dry season (Fig. 3). The

models parameterized by leaf quantity alone or parameterized by both leaf quantity and quality displayed good agreement with the timing of EC-derived GPP_{ref} seasonality, but missed the depth or relative magnitude of GPP_{ref} seasonality: leaf quantity phenology alone explained only 19% of EC-derived GPP_{ref} seasonality for DF1997 (Table 1) and 17% for ML and the two-fraction leaf, two-layer canopy model (Table 1 and Fig. 3a); the modeled GPP_{ref} with both leaf quantity and quality (but no within-canopy phenological variation) explained ~80% of EC-derived GPP_{ref} seasonality for DF1997, ML, and the two-fraction leaf, two-layer canopy model (Table 1 and Fig. 3b). The modeled GPP_{ref} using the two-fraction leaf, two-layer canopy model with all three phenological components displayed the strongest agreement with the seasonal variability of EC-derived GPP_{ref} in both timing and relative magnitude ($R^2=0.90$; Table 1 and Fig. 3c).

3.2 Differential photosynthetic sensitivity to seasonal variation in leaf phenology between the sunlit canopy fraction and the shade canopy fraction

To better understand the mechanisms that underlie canopy-scale photosynthetic seasonality, we examined the photosynthetic sensitivity of the sunlit canopy fraction and the shade canopy fraction to seasonal variation in leaf phenology (quantity and quality). We theorized that the seasonal variation in GPP_{ref} is driven by changes in both canopy absorbed PAR (affecting RuBP regeneration limited photosynthesis in the FvCB model) and canopy integrated V_{cmax} (affecting Rubisco limited photosynthesis in the FvCB model). Fig. 4 summarizes our model diagnosis of these two pathways and their respective influence on modeled GPP_{ref} seasonality.

First we examined the seasonal dynamics of canopy absorbed PAR under reference environmental conditions (absolute value in Fig. 4a and relative value in Fig. S4). Our simulations showed that the PAR absorbed by the sunlit canopy fraction (PAR_{sun}), the shade canopy fraction (PAR_{shade}), and the entire canopy ($PAR_{sun} + PAR_{shade}$) all showed consistently low seasonal variability (<6%; Fig. 4a and Fig. S4), despite modest seasonal variability in leaf quantity (~12%; Fig. 4b). This is likely because tropical evergreen forests display consistently high leaf quantity over the annual cycle (e.g. LAI range: 5.35-6.15 m² m⁻² at the k67 site), and as such annual FAPAR is typically at or near saturation.

We then investigated the seasonal dynamics of canopy V_{cmax} , which is the integrated sum of leaf level V_{cmax} weighted by the total LAI attributed to the sunlit fraction and the shade fraction respectively (see eqns 3-5). Focusing first on the sunlit fraction, Fig. 4b highlights that the LAI_{sun} is generally stable (~1.5 m² m⁻²) through the annual cycle, despite the observed modest seasonality in total canopy leaf quantity ($LAI_{tot} = LAI_{sun} + LAI_{shade}$). As a consequence, the observed higher seasonal variability (~20%) in $V_{cmax, sun}$ (Fig. 4c) is primarily driven by leaf quality, which is associated with seasonal variation in leaf age demographics (Fig. 1 and eqn. 1). In addition, our results indicated that the higher seasonal variability (~25%) in $V_{cmax, shade}$ (Fig. 4c) is a consequence of seasonal variability in both LAI_{shade} (Fig. 4b) and leaf age demographics (Fig. 1 and eqn. 1).

Finally, we assessed the seasonal variability in GPP_{ref} as the joint response to the above two dynamics: canopy absorbed PAR and V_{cmax} . We used the FvCB model to calculate the GPP_{ref} of both fractions (sun vs. shade). Sensitivity analysis of the FvCB model (Fig. S5) showed that the canopy integrated absorbed PAR and canopy integrated V_{cmax} jointly regulated GPP_{ref} , with canopy integrated V_{cmax} dominating the GPP_{ref} response under high light condition (i.e.

PAR $>800 \mu\text{mol m}^{-2} \text{s}^{-1}$) while canopy integrated absorbed PAR dominated GPP_{ref} response under low light condition (i.e. PAR $<400 \mu\text{mol m}^{-2} \text{s}^{-1}$). Given that the sunlit fraction could consistently capture sufficient PAR to photosaturate photosynthesis ($\sim 860 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig. 4a) over the annual cycle, the seasonal variability in $\text{GPP}_{\text{ref, sun}}$ closely tracked the seasonality of $V_{\text{cmax, sun}}$ (Figs. 4c,d), which is mostly determined by the phenology of leaf quality (Figs. 4b,c). On the other hand, since the shade fraction typically receives sub-saturating light ($\sim 300 \mu\text{mol m}^{-2} \text{s}^{-1}$; Fig. 4a) over the annual cycle, $\text{GPP}_{\text{ref, shade}}$ is primarily limited by the capacity for RuBP regeneration (Fig. S5). As a result, modeled $\text{GPP}_{\text{ref, shade}}$ seasonality is small ($\sim 7\%$; Fig. S6), which is comparable with the relative seasonal change in $\text{PAR}_{\text{shade}}$ ($\sim 6\%$; Fig. S4), but far less than the relative seasonality in $V_{\text{cmax, shade}}$ (25% ; Fig. 4c). The canopy total GPP_{ref} thus showed an intermediate seasonal variation, with the relative magnitude of annual change falling in between that of the two fractions (absolute value in Fig. 4d and relative value in Fig. S6).

3.3 Model sensitivity of canopy photosynthesis to within-canopy phenological variations

Finally, we used the two-fraction leaf, two-layer canopy model to explore the extent to which within-canopy phenological variations could affect modeled photosynthetic seasonality. We show that although the timing of the modeled GPP_{ref} seasonality follows observed LAI and LAI-age-demography (Fig. 1) and was independent of within-canopy phenological variation (i.e. ftop), the relative magnitude of the modeled GPP_{ref} seasonality is highly sensitive to ftop (Fig. 5a). As ftop increases (more leaf turnover is partitioned to the upper canopy), the relative magnitude of modeled GPP_{ref} seasonality increases (Fig. 5a). Meanwhile, the correlation between modeled and EC-derived GPP_{ref} seasonality also increases with ftop and reaches near saturation when $\text{ftop} \geq 0.7$ ($R^2=0.90$; Fig. 5b). The underlying reason is associated with the

differential photosynthetic sensitivity to leaf quality allocated to the two canopy layers (upper vs. lower): as shown in Fig. 4, only the photosynthetic rate of the sunlit fraction (mostly occupied in the upper canopy layer) is predominantly Rubisco limited and therefore, the photosynthetic rate of the upper canopy layer shows high sensitivity to leaf quality.

4. Discussion

Accurate model representation of the effects of leaf phenology on ecosystem photosynthesis is a critical need for TBMs in general (Richardson *et al.*, 2012) and is essential, necessary first step for capturing the timing and magnitude of seasonal variation in tropical forest carbon fluxes (Restrepo-Coupe *et al.*, 2013, 2017; Fu *et al.*, 2013; Christoffersen *et al.*, 2014; Wu *et al.*, 2016a). Here we developed a parsimonious approach to effectively couple the effects of leaf phenology (i.e. quantity, quality and within-canopy variation) to the FvCB model for simulating canopy-level photosynthetic seasonality. Our approach could be parameterized and adopted within TBMs where it would enable improved representation and projection of the response of tropical evergreen forest photosynthesis to global change.

Our results demonstrated that the proposed model (two-fraction leaf, two-layer canopy) could effectively simulate EC-derived photosynthetic seasonality, only if the quality component of leaf phenology was incorporated (Fig. 3 and Table 1). This is also consistent with previous field-based remote sensing studies (Doughty & Goulden, 2008; Brando *et al.*, 2010; Lopes *et al.*, 2016; Saleska *et al.*, 2016), which highlight that variation in photosynthetic efficiency and the spectral reflectance properties of leaves (Roberts *et al.*, 1998; Chavana-Bryant *et al.*, 2016; Wu *et al.*, 2016a,b) may significantly contribute to explaining the satellite-detected dry season “green-up” in tropical evergreen forests. In addition, our finding supports previous work which

showed that model representation of photosynthetic seasonality could be improved by tuning model parameters to allow for seasonal variation in photosynthetic capacity, i.e. leaf quality (Kim *et al.*, 2012; de Weirt *et al.*, 2012).

Although the models with different leaf phenological components were all able to simulate the seasonal photosynthetic trend, the relative magnitude of modeled GPP_{ref} seasonality varied strongly across the models (Fig. 3). The approach of incorporating all phenological components (i.e. quantity, quality, and within-canopy variation) displayed the strongest agreement with local EC-derived GPP_{ref} , while the approaches incorporating only part of the three phenological components (e.g. leaf quantity alone in Fig. 3a and leaf quantity and quality alone in Fig. 3b) only explained around half or less of the observed relative annual change magnitude. These differences in model performance can be attributed to differential photosynthetic sensitivity of the sunlit canopy fraction and the shade canopy fraction to seasonal variation in leaf quantity, quality and within-canopy phenological variation, explained as below:

Leaf quantity. Our results show that there is only a weak effect of the quantity component of leaf phenology on GPP_{ref} (Table 1). This is because tropical evergreen forests consistently have high leaf quantity throughout the annual cycle (Myneni *et al.*, 1997; Doughty & Goulden, 2008; Brando *et al.*, 2010; Morton *et al.*, 2014; Bi *et al.*, 2015; Lopes *et al.*, 2016; Wu *et al.*, 2016a), and therefore the observed small seasonal changes in leaf quantity had little impact on FAPAR seasonality (Fig. 4a and Fig. S4), and thus had little impact on GPP_{ref} seasonality.

Leaf quality. Our results show that the phenology of leaf quality is one of the dominant drivers of canopy photosynthetic seasonality in tropical evergreen forests (Table 1), confirming recent work (Wu *et al.*, 2016a). Using an FvCB-type canopy photosynthesis model (i.e. two-fraction leaf, two-layer canopy model), we demonstrate that both light absorption and canopy

integrated V_{cmax} regulate canopy-scale photosynthesis rate (Fig. S5). However, only the upper, sunlit canopy fraction with sufficient light availability and absorption are limited by Rubisco (i.e. are light saturated) and show sensitivity to seasonal variation in leaf quality (i.e. V_{cmax} ; Figs. 4, S5 and S6). In contrast, the shaded canopy fraction is predominantly limited by light and not by photosynthetic capacity, and consequently, increasing photosynthetic capacity in the shaded canopy fraction has little to no impact on the modeled GPP_{ref} . In other words, our results confirm the differential photosynthetic sensitivity to leaf quality between the sunlit and shade canopy fractions. Our finding is thus not consistent with the assumption made by Doughty & Goulden (2008), who assumed constant photosynthetic rates of the sunlit and shade canopy fractions with a single scalar to account for seasonal variation in leaf quality, and may explain why the approach of Doughty & Goulden (2008) overestimates the leaf quality effect for the shade canopy fraction.

Within-canopy phenological variation. Differential photosynthetic sensitivity of the sunlit and shade canopy fractions to leaf quality (as shown in Fig. 4) suggests that the return on investment for a new leaf is far greater if that leaf is flushed in the upper, sunlit canopy than in the shade, which was subsequently confirmed by our model sensitivity analysis of ftop (Fig. 5). This model sensitivity analysis demonstrated that by allowing for differential leaf turnover rates within the canopy, especially when attributing the majority of leaf turnover to the upper canopy, our model (two-fraction leaf, two-layer canopy) could markedly improve the model representation of photosynthetic seasonality (Figs. 3, 5). Importantly, our prescribed higher leaf turnover rate in the upper canopy (i.e. $\text{ftop}=0.7$) is also consistent with field-based studies in the tropics which show that the longevity of upper canopy leaves is markedly shorter than that of lower canopy leaves (Lowman, 1992; Miyaji *et al.*, 1997; Reich *et al.*, 2004).

Our analysis of the two-fraction leaf, two-layer canopy model further show that when the majority of leaf turnover is allocated to the upper canopy, the whole forest tends to become more Rubisco-limited and thus approaches a simpler one-layer big-leaf assumption, such as the model presented in Wu *et al* (2016a). This explains why the simple model of Wu *et al* (2016a), which does not contain explicit representation of within-canopy physiological and phenological variation, still captured the seasonal cycle of GPP_{ref} in tropical evergreen forests. The approach of Wu *et al* (2016a), which is based on empirical relationships, is a valuable approach for broad-scale remotely sensed monitoring of tropical forest carbon cycling but lacks the capacity to project tropical forest responses under future climates and global change. Thus a light-use efficiency approach (e.g. Wu *et al.*, 2016a) is not as valuable for use within TBMs that typically utilize the FvCB formulation of photosynthesis to simulate leaf and canopy photosynthesis (Rogers *et al.*, 2017). Since TBMs need to project the response of photosynthesis to rising CO_2 , temperature, VPD and drought, they require more sophisticated approaches where key model inputs, such as V_{cmax} , may be derived from trait databases, remote sensing, or internally generated (i.e. prognostic) allowing coupling to biogeochemical processes (e.g. Fisher *et al.*, 2015; Serbin *et al.*, 2015; Ali *et al.*, 2016). Therefore, to accurately represent canopy photosynthetic processes in tropical forests under a changing climate we advocate the use of the approach outlined here, i.e. the two-fraction leaf, two-layer canopy model coupled to an FvCB formulation with model representation of the three components of leaf phenology we identify here.

Our work also highlights three important directions for future advances in model representation of tropical evergreen forest photosynthesis. First, to minimize additional sources of uncertainty when exploring approaches for the modeling of tropical forest photosynthetic

seasonality we utilized observed leaf phenology (e.g. Fig. 1). However, the ultimate mechanisms that regulate seasonal variation in both tropical leaf quantity and quality are still largely unknown. An improved and prognostic understanding and model representation of the mechanisms that drive seasonal and inter-annual changes in leaf quantity and quality, i.e. the drivers of broader-scale (i.e. regional and global) tropical evergreen forest phenology, will be a key component in new models that seek to improve projections of carbon dynamics and potential climate feedbacks in the tropics (Wu *et al.*, 2016a).

Second, our demonstration of the importance of leaf phenology effects on tropical forest photosynthetic seasonality relied on modeled and EC-derived GPP_{ref} . This simplification was essential to enable us to elucidate fundamental mechanisms connecting annual patterns of leaf phenology with physiology, but is not appropriate when simulating forest responses to climate over time or in response to climatic perturbations. Since canopy photosynthesis is jointly determined by extrinsic environmental variability and changes in intrinsic photosynthetic machinery (Farquhar *et al.*, 1980; Collatz *et al.*, 1991; Sellers *et al.*, 1992; dePury & Farquhar, 1997; Baldocchi & Amthor, 2001; Dai *et al.*, 2003; Medvigy *et al.*, 2009; Wu *et al.*, 2016a; Rogers *et al.*, 2017), there is a great need to improve our understanding and model representation of the fundamental physiological responses to environmental variability, particularly rising atmospheric CO₂ concentration, temperature, VPD and changes in precipitation, but also light capture and utilization by the forest canopy (Rogers *et al.*, 2017). It will be critical to link advances in understanding of leaf phenology and physiology in future TBMs, particularly in tropical evergreen forests.

Finally, our study also highlights that one of the most practical challenges limiting studies in the tropics is the limited availability of observations (Schimel *et al.*, 2015). For example, there

is very little information available on the within-canopy (i.e. light-dependent vs. height-dependent) and seasonal (i.e. continuous, age-dependency) variation in leaf physiology, phenology, biochemical traits, and optical properties in the tropics (e.g. Kitajima *et al.*, 1997b; Chavana-Bryant *et al.*, 2016; Wu *et al.*, 2016b); even less is known about the spatial heterogeneity in the relationship among photosynthetic capacity, leaf traits, canopy structure, phenology, and climate across broader-scale (i.e. regional and global) tropical forests (e.g. Kumagai *et al.*, 2006; Kenzo *et al.*, 2015; Wu *et al.*, 2016b). As a consequence, some important physiological mechanisms might be underrepresented in current models. For example, the study presented by Kitajima *et al.* (1997b) showed that leaf level V_{cmax} (at mature age class) for the same tropical tree species can vary depends on the timing (i.e. wet or dry season) when leaves are produced. This approach, also known as seasonal leaf phenotypes, suggested that leaf level photosynthetic capacity should be modeled as a function of the timing when leaves are produced, in addition to leaf age which has been explored in this paper. Our model framework has sufficient flexibility to incorporate this additional component of photosynthetic seasonality, but would require extensive field data and subsequent model evaluation to validate our approach.

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Author Contributions:

J.W., A.R., S.P.S., and X.X. designed the research. J.W. and S.P.S. developed the Matlab and R codes of canopy photosynthesis model. J.W. performed the data analysis. J.W. drafted the manuscript, and A.R., S.P.S., S.R.S, X.X., L.P.A., M.C., and M.R. contributed to writing the final version.

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Main Figures and Tables

Table 1. Correlations between the seasonality of eddy covariance derived GPP_{ref} and the seasonality of modeled GPP_{ref} using three different models parameterized by four different inputs of leaf phenology. R^2 for coefficient of determination; p, or p-value, for significance of the test; within-canopy phenological variation for the two-fraction leaf, two-layer canopy model was parameterized when $f_{top}=0.7$; NA for not applicable.

Model\Phenology	Quantity	Quality	Quantity+Quality	Quantity+Quality+Within-Canopy Variation
DF1997	($R^2=0.19$; $p=0.041$)	($R^2=0.69$; $p<0.0001$)	($R^2=0.80$; $p<0.0001$)	NA
ML	($R^2=0.17$; $p=0.042$)	($R^2=0.72$; $p<0.0001$)	($R^2=0.81$; $p<0.0001$)	NA
Two-fraction leaf, two-layer canopy	($R^2=0.17$; $p=0.042$)	($R^2=0.72$; $p<0.0001$)	($R^2=0.81$; $p<0.0001$)	($R^2=0.90$; $p<0.0001$)

Caption for Main Figures

Figure 1. Mean annual cycles of monthly LAI in three age classes (three different color lines) at the Tapajós k67 site (adapted from Fig. 3A in Wu *et al.*, 2016a). The three-age LAI seasonality was modeled using the same leaf age residence time parameter as Wu *et al.* (2016a), constrained to sum to total camera-observed LAI (black squares) at the same forest site. Shading indicates the dry season.

Figure 2. Vertical change in leaf level $V_{\text{cmax}25}$ with cumulative LAI from canopy top to forest floor, using the eqns. 5-6, following Lloyd *et al.* (2010). Three color lines represent leaves at three age classes (Young: 1-2 months; Mature: 3-5 months; Old: ≥ 6 months) respectively. $V_{\text{cmax}25}$ of three age classes at the top of the canopy are derived from leaf level gas exchange measurements at the Tapajós k67 site ($n=5$ tree species; also see Wu *et al.*, 2016a).

Figure 3. Seasonal variation in EC-derived GPP_{ref} (seven-year mean annual cycle; black squares) and modeled GPP_{ref} (grey circles) incorporating different phenological components, using the two-fraction leaf, two-layer canopy model. (a) modeled GPP_{ref} parameterized by seasonal variation in leaf quantity (or LAI) only; (b) modeled GPP_{ref} parameterized by seasonal variation in both leaf quantity and quality, while assuming a constant leaf turnover rate throughout the vertical canopy profile; (c) modeled GPP_{ref} parameterized by seasonal variation in leaf quantity and quality, and differential leaf turnover rates within a forest canopy (i.e. $f_{\text{top}}=0.7$). Shading indicates the dry season; f_{top} refers to the fraction of observed leaf turnover across the whole forest canopy attributed to leaves in the upper canopy layer.

Figure 4. Differential photosynthetic sensitivity of the canopy sunlit fraction and the canopy shade fraction to seasonal variation in leaf quantity (Fig. 1) and leaf quality (Fig. 1 and eqn. 1) at the Tapajós k67 site assessed by using the two-fraction leaf, two-layer canopy model under the reference environment: (a) canopy absorbed PAR, (b) canopy LAI, (c) canopy integrated V_{cmax} , and (d) canopy GPP_{ref} . Data are shown for total canopy (black circles), the sunlit canopy fraction (black triangles) and the shaded canopy fraction (grey triangles); canopy-scale V_{cmax} (of per-ground area) is the sum of canopy LAI weighted by leaf level V_{cmax} (see Table S3 for equations), and since the LAI of the shade canopy fraction is higher than the LAI of the sunlit canopy fraction, as such V_{cmax} of the shade canopy fraction is higher than V_{cmax} of the sunlit canopy fraction; shading indicates the dry season.

Figure 5. Assessing the effect of within-canopy phenological variation (i.e. f_{top}) on canopy photosynthetic seasonality using the two-fraction leaf, two-layer canopy model. (a) Modeled annual cycles of GPP_{ref} (relative to annual maxima) under different f_{top} values from 0.2 to 1.0; and (b) R^2 between modeled and EC-derived GPP_{ref} seasonality plotted against f_{top} . Shading indicates dry season; f_{top} refers to the fraction of observed leaf turnover across the whole forest canopy attributed to leaves in the upper canopy layer.

Caption for Supplementary Figures and Supplementary Tables

Figure S1. The sensitivity of modeled canopy-scale GPP using the multi-layer model (ML) to the number of layers used for model simulation, under (a) highly cloudy environment ($PAR_{b,0}=10.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ vs. $PAR_{d,0}=260.3 \mu\text{mol m}^{-2} \text{s}^{-1}$), (b) intermediate cloudy environment ($PAR_{b,0}=743.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ vs. $PAR_{d,0}=268. \mu\text{mol m}^{-2} \text{s}^{-1}$), and (c) clear sky environment ($PAR_{b,0}=1850.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ vs. $PAR_{d,0}=173.7 \mu\text{mol m}^{-2} \text{s}^{-1}$). For model simulation, $PAR_{b,0}$ for canopy surface direct beam and $PAR_{d,0}$ for canopy surface diffuse beam; solar zenith angle= 30° , $LAI=6 \text{ m}^2 \text{m}^{-2}$, leaf temperature= 28°C ; ambient CO_2 concentration= 380 ppm ; $V_{\text{cmax}25}=40 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$.

Figure S2. The sensitivity analysis of LAI cutoff (which divides the canopy into upper and lower canopy layers) on modeled canopy-scale GPP_{ref} seasonality parameterized by field derived leaf quantity and quality by using the two-fraction leaf, two-layer canopy model under three different f_{top} values: (a) $f_{\text{top}}=0.4$, (b) $f_{\text{top}}=0.6$, and (c) $f_{\text{top}}=0.8$. Three color lines represent different LAI cutoff. Shading indicates the dry season.

Figure S3. Cross model comparisons for canopy-scale GPP-PAR relationship between DF1997 (red line) and ML (black line). For model simulation, solar zenith angle= 30° , $LAI=6 \text{ m}^2 \text{m}^{-2}$, leaf temperature= 28°C ; ambient CO_2 concentration= 380 ppm ; $V_{\text{cmax}25}=40 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$.

Figure S4. Average annual cycle of modeled FAPAR (relative to annual maxima) using the two-fraction leaf, two-layer canopy model at the Tapajós k67 site under three scenarios: whole canopy (black circles), the sunlit canopy fraction (black triangles), and the shade canopy fraction (grey triangles). Shading indicates the dry season.

Figure S5. GPP-PAR relationship simulated by the FvCB model under each given $V_{\text{cmax}25}$ (in $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$; represented as different color lines).

Figure S6. Average annual cycle of GPP_{ref} (relative to annual maxima) at the Tapajós k67 site under four scenarios: eddy covariance derived GPP_{ref} (red line), and modeled GPP_{ref} by using the two-fraction leaf, two-layer canopy model for the whole canopy (black circles), for the canopy of sunlit fraction (black triangles), and for the canopy of shade fraction (grey triangles). Shading indicates the dry season.

Table S1. Individual canopy trees for leaf gas exchange measurements of top-of-canopy sunlit leaves in 2012 campaign at the Tapajós k67 site (adapted from Wu *et al.*, 2016a). Species represented by these individuals account for 23.7% of basal area of vegetative community at the k67 site. NA for not applicable.

Scientific name	Family	Maximum canopy height (m)	Basal area abundance	Leaf age class	Number of leaves	$V_{\text{cmax}25}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)
<i>Erisma uncinatum</i> Warm.	Vochysiaceae	40	10.1%	Young	3	15.1
				Mature	3	26.3
				Old	3	21.1
<i>Chamaecrista scleroxylon</i> (Ducke) H.S.Irwin & Barneby <i>Chamaecrista xinguensis</i>	Leguminosae-Caesalpinioideae	27	4.47%	Young	1	11.2
				Mature	1	35.8
				Old	1	17.9
<i>Manilkara huberi</i> (Ducke) A.Chev.	Sapotaceae	37	6.54%	Young	1	13.7
				Mature	1	34.6
				Old	1	33.0
<i>Tachigali eriopetala</i> (Ducke) L.G.Silva & H.C.Lima	Leguminosae-Caesalpinioideae	44	1.55%	Young	2	14.0
				Mature	2	56.7
				Old	2	23.2
<i>Ocotea sp.</i>	Lauraceae	38	1.06%	Young	NA	NA
				Mature	2	29.0
				Old	4	21.4

Table S2. Modified equations of the Farquhar, von Caemmerer and Berry (FvCB; Farquhar *et al.*, 1980) leaf photosynthesis model, coupled with Medlyn type stomatal conductance scheme (Medlyn *et al.*, 2011). Symbols of constant are defined in Table S6, and values of the Rubisco parameters are given in Table S7.

Equations	Definition	No.	Ref.
$GPP_l = \min\{A_v, A_j, A_s\} - R_l$	Leaf level gross primary productivity (GPP, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	1	A
$A_v = \max\{V_{c\max} \times \frac{C_i - \Gamma_*}{C_i + K'}, 0\}$	Rubisco-limited photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	2	A
$K' = K_C \times (1 + \frac{O}{K_O})$	Effective Michaelis-Menten Constant	3	A
$A_j = \max\{J \times \frac{C_i - \Gamma_*}{4 \times (C_i + 2 \times \Gamma_*)}, 0\}$	Electron-transport limited rate of photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	4	A
$J_e = \Phi_{PSII, \max} \times \alpha \times \beta \times Q$	The rate of whole electron transport ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	5	C
$J = \frac{J_e + J_{\max} - \sqrt{(J_e + J_{\max})^2 - 4 \times \Theta \times J_e \times J_{\max}}}{2 \times \Theta}$	The rate of electrons through the thylakoid membrane ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	6	A
$A_s = 0.5 \times V_{c\max}$	Triose phosphate export limited rate of photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	7	B
$Parameter = Parameter_{25} \times \exp(\frac{(T_K - 298) \times \Delta H_a}{R \times T_K \times 298})$	Temperature functions for parameters that are based on Rubisco kinetic properties and do not have an optimum within a biologically significant temperature range (K_C , K_O , Γ_* , R_l , and in most cases $V_{c\max 25}$)	8	C
$J_{\max} = J_{\max 25} \times \frac{e^{-\frac{T_L - T_{opt}}{\Omega_T}}}{e^{-\frac{25 - T_{opt}}{\Omega_T}}}$	Temperature function for maximum electron transport rate, $J_{\max}$	9	C, D
$\Omega_T = 11.6 + 0.18 \times T_{opt}$	Coefficient for temperature function of $J_{\max}$	10	C, D
$J_{\max 25} = 1.67 \times V_{c\max 25}$	Linear scaling relationship between $J_{\max 25}$ and $V_{c\max 25}$	11	E, F
$T_K = T_l + 273.15$	Leaf temperature in Kelvin	12	C
$R_{l25} = 0.015 \times V_{c\max 25}$	Leaf dark respiration at 25°C ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	13	E
$g_s = 1.6 \times (1 + \frac{g_1}{\sqrt{VPD}}) \times \frac{GPP_l}{C_a}$ $GPP_l = g_s \times (C_a - C_i)$ $\Rightarrow C_i = C_a \times (1 - \frac{1}{1.6 \times (1 + \frac{g_1}{\sqrt{VPD}})})$	Use optimal stomatal model to estimate internal CO ₂ concentration (C_i) from atmospheric CO ₂ concentration (C_a) and vapor pressure deficit (VPD)	14	G

A: Farquhar *et al.*, 1980; B: Ryu *et al.*, 2011; C: Bernacchi *et al.*, 2013; D: June *et al.*, 2004; E: Bonan *et al.*, 2014; F: Medlyn *et al.*, 2002; G: Medlyn *et al.*, 2011.

Table S3. Modified equations of V_{cmax} for the canopy of sunlit and shade fractions. Symbols of constant are defined in Table S6, and values of the Rubisco parameters are given in Table S7.

Equations	Definition	No.	Ref.
$V_{cmax,tot} = \frac{V_{cmax,0}}{k_n} \times (1 - \exp^{(-k_n \times LAI_{tot})})$	Canopy total V_{cmax} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	15	A
$V_{cmax,sun} = \frac{V_{cmax,0} \times \Omega}{k_n + k_b \times \Omega} \times (1 - \exp^{(-(k_n + k_b \times \Omega) \times LAI_{tot})})$	V_{cmax} for the canopy of sunlit cohort ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	16	A, B
$V_{cmax,shade} = V_{cmax,tot} - V_{cmax,sun}$	V_{cmax} for the canopy of shade cohort ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	17	A, B
$k_n = \exp^{(0.00963 \times V_{cmax,0} - 2.43)}$	Coefficient of V_{cmax} decline within a forest canopy	18	H
$k_b = \frac{0.5}{\cos(SZA)}$	Beam radiation extinction coefficient of the canopy	19	A

A: Farquhar *et al.*, 1980; B: Ryu *et al.*, 2011; H: Lloyd *et al.*, 2010.

Table S4. Modified equations of absorbed photosynthetically active radiation (PAR) by the canopy of sunlit and shade fractions. Symbols of constant are defined in Table S6, and values of the Rubisco parameters are given in Table S7.

Equations	Definition	No.	Ref.
$Q_{tot} = (1 - \rho_{cb}) \times PAR_{b,0} \times (1 - \exp^{-k'_b \times LAI_{tot} \times \Omega}) + (1 - \rho_{cd}) \times PAR_{d,0} \times (1 - \exp^{-k'_d \times LAI_{tot} \times \Omega})$	Canopy absorbed total radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	20	A, B
$Q_{b,sun} = PAR_{b,0} \times (1 - \sigma) \times (1 - \exp^{-k'_b \times LAI_{tot} \times \Omega})$	The absorbed incoming beam radiation by sunlit leaves ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	21	A, B
$Q_{d,sun} = PAR_{d,0} \times (1 - \rho_{cd}) \times (1 - \exp^{-(k'_d + k'_b) \times LAI_{tot} \times \Omega})$	The absorbed incoming diffuse radiation by sunlit leaves ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	22	A, B
$Q_{s,sun} = PAR_{b,0} \times [(1 - \rho_{cb}) \times (1 - \exp^{-(k'_b + k'_b) \times LAI_{tot} \times \Omega}) \times \frac{k'_b}{k'_b + k'_b} - (1 - \sigma) \times (1 - \exp^{-2 \times k'_b \times LAI_{tot} \times \Omega}) \times \frac{1}{2}]$	The absorbed incoming scattered radiation by sunlit leaves ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	23	A, B
$Q_{sun} = Q_{b,sun} + Q_{d,sun} + Q_{s,sun}$	Canopy absorbed total radiation for sunlit leaves ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	24	A, B
$Q_{shade} = Q_{tot} - Q_{sun}$	Canopy absorbed total radiation for shade leaves ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	25	A, B
$k'_b = \frac{0.46}{\cos(SZA)}$	Beam and scattered beam radiation extinction coefficient	26	A
$k'_d = 0.719$	Diffuse and scattered diffuse radiation extinction coefficient	27	A

A: Farquhar *et al.*, 1980; B: Ryu *et al.*, 2011.

972 **Table S5.** Equations to calculate incoming photosynthetically active radiation (PAR) over a
973 canopy. R_{short} denotes total short-wave radiations from in-situ observations. P denotes observed
974 air pressure and P_0 denotes standard air pressure.

Equations	Definition	No.	Ref.
$R_{b,vis} = \frac{600 \times e^{-0.185 \times \frac{P}{P_0} \times m}}{m}$	Expected beam visible radiation under clear sky ($W\ m^{-2}$)	28	N
$R_{d,vis} = \frac{0.4 \times (600 - R_{b,vis} \times m)}{m}$	Expected diffuse visible radiation under clear sky ($W\ m^{-2}$)	29	N
$R_{b,nir} = \frac{720 \times e^{-0.06 \times \frac{P}{P_0} \times m} - w}{m}$	Expected diffuse visible radiation under clear sky ($W\ m^{-2}$)	30	N
$R_{b,nir} = \frac{720 \times e^{-0.06 \times \frac{P}{P_0} \times m} - w}{m}$	Expected diffuse near-infrared radiation under clear sky ($W\ m^{-2}$)	31	N
$f_{PAR} = \frac{R_{b,vis} + R_{d,vis}}{R_{b,nir} + R_{d,nir} + R_{b,vis} + R_{d,vis}}$	The fraction of total PAR over total incoming radiation (f_{PAR})	32	N
$f_{PAR,b} = \frac{R_{b,vis}}{R_{b,vis} + R_{d,vis}} \times (1 - (\frac{0.9 - \frac{R_{short}}{R_{b,nir} + R_{d,nir} + R_{b,vis} + R_{d,vis}}}{0.7})^2)$	The fraction of beam PAR over total PAR ($f_{PAR,b}$)	33	N
$PAR_{b,0} = R_{short} \times f_{PAR} \times f_{PAR,b}$	The canopy top photosynthetically active radiation in beam light ($PAR_{b,0}$)	34	N
$PAR_{d,0} = R_{short} \times f_{PAR} \times (1 - f_{PAR,b})$	The canopy top photosynthetically active radiation in diffuse ($PAR_{d,0}$) light	35	N
$w = 1320 \times 10^{-1.195 + 0.4459 \times \log_{10} m - 0.0345 \times (\log_{10} m)^2}$	Expected water absorbance of near-infrared radiation in the atmosphere ($W\ m^{-2}$)	36	N
$m = \cos(SZA)^{-1}$	Parameter calculated from solar zenith angle (SZA)	37	N

975 N: Weiss & Norman, 1985.

Table S6. Table of constants used in leaf and canopy level photosynthesis model.

Symbols	Definition	Values	Ref.
C_i	Inter-cellular CO ₂ concentration (=0.7*ambient CO ₂ concentration; $\mu\text{mol mol}^{-1}$)	266	A
O	Oxygen concentration (mmol mol^{-1})	205	A
α	Leaf absorbance	0.85	A, C
β	Fraction of photosystem II to photosystem I	0.5	A, C
$\Phi_{PSII, \max}$	Maximum quantum efficiency of PSII photochemistry	0.7	C
Θ	Curvature term	0.7	A, E
R	Universal gas constant ($\text{J mol}^{-1} \text{K}^{-1}$)	8.314	A
$V_{c \max 25}$	Maximal carboxylation rate at 25°C ($\mu\text{mol/m}^2/\text{s}$)	Observation	K
T_{opt}	Optimal leaf temperature for $J_{\max}$ (°C)	35	I
$V_{c \max, 0}$	Maximal carboxylation rate for leaves at canopy surface ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Observation	K
Ω	Clumping index	0.66	J
LAI_{tot}	Canopy total leaf area index (m^2/m^2)	Observation	K
ρ_{cb}	Canopy reflection coefficient for beam radiation	0.029	A
ρ_{cd}	Canopy reflection coefficient for diffuse radiation	0.036	A
σ	Leaf scattering coefficient of radiation	0.15	A
g1	Slope for stomatal conductance model	3.77	L

A: Farquhar *et al.*, 1980; C: Bernacchi *et al.*, 2013; E: Bonan *et al.*, 2014; I: Lloyd & Farquhar, 2008; J: He *et al.*, 2005; K: Wu *et al.*, 2016a; L: Lin *et al.*, 2015.

Table S7. The values for c and ΔH_a (activation energy) describing the temperature response of the five parameters used to predict CO₂ uptake by leaves during Rubisco-limited photosynthesis in leaf level FvCB model (see Table S4) (reference: M: Bernacchi *et al.*, 2001).

Parameter	Value at 25°C	c (dimensionless)	ΔH_a (kJ mol ⁻¹)
R_l (μmol/m ² /s)	R_{l25}	18.72	46.39
$V_{c\max}$ (μmol/m ² /s)	$V_{c\max 25}$	26.35	65.33
Γ_* (μmol/m ² /s)	42.75	19.02	37.83
K_C (μmol/m ² /s)	404.9	38.05	79.43
K_O (mmol/m ² /s)	278.4	20.30	36.38

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Figure 1. Mean annual cycles of monthly LAI in three age classes (three different color lines) at the Tapajós k67 site (adapted from Fig. 3A in Wu et al., 2016a). The three-age LAI seasonality was modeled using the same leaf age residence time parameter as Wu et al (2016a), constrained to sum to total camera-observed LAI (black squares) at the same forest site. Shading indicates the dry season.

144x62mm (300 x 300 DPI)

Figure 2. Vertical change in leaf level V_{cmax25} with cumulative LAI from canopy top to forest floor, using the eqns. 5-6, following Lloyd et al (2010). Three color lines represent leaves at three age classes (Young: 1-2 months; Mature: 3-5 months; Old: ≥ 6 months) respectively. V_{cmax25} of three age classes at the top of the canopy are derived from leaf level gas exchange measurements at the Tapajós k67 site ($n=5$ tree species; also see Wu et al., 2016a).

112x65mm (300 x 300 DPI)

Figure 3. Seasonal variation in EC-derived GPPref (seven-year mean annual cycle; black squares) and modeled GPPref (grey circles) incorporating different phenological components, using the two-fraction leaf, two-layer canopy model. (a) modeled GPPref parameterized by seasonal variation in leaf quantity (or LAI) only; (b) modeled GPPref parameterized by seasonal variation in both leaf quantity and quality, while assuming a constant leaf turnover rate throughout the vertical canopy profile; (c) modeled GPPref parameterized by seasonal variation in leaf quantity and quality, and differential leaf turnover rates within a forest canopy (i.e. ftop=0.7). Shading indicates the dry season; ftop refers to the fraction of observed leaf turnover across the whole forest canopy attributed to leaves in the upper canopy layer.

Figure 4. Differential photosynthetic sensitivity of the canopy sunlit fraction and the canopy shade fraction to seasonal variation in leaf quantity (Fig. 1) and leaf quality (Fig. 1 and eqn. 1) at the Tapajós k67 site assessed by using the two-fraction leaf, two-layer canopy model under the reference environment: (a) canopy absorbed PAR, (b) canopy LAI, (c) canopy integrated V_{cmax} , and (d) canopy GPP_{ref} . Data are shown for total canopy (black circles), the sunlit canopy fraction (black triangles) and the shaded canopy fraction (grey triangles); canopy-scale V_{cmax} (of per-ground area) is the sum of canopy LAI weighted by leaf level V_{cmax} (see Table S3 for equations), and since the LAI of the shade canopy fraction is higher than the LAI of the sunlit canopy fraction, as such V_{cmax} of the shade canopy fraction is higher than V_{cmax} of the sunlit canopy fraction; shading indicates the dry season.

219x137mm (300 x 300 DPI)

Figure 5. Assessing the effect of within-canopy phenological variation (i.e. f_{top}) on canopy photosynthetic seasonality using the two-fraction leaf, two-layer canopy model. (a) Modeled annual cycles of GPP_{ref} (relative to annual maxima) under different f_{top} values from 0.2 to 1.0; and (b) R^2 between modeled and EC-derived GPP_{ref} seasonality plotted against f_{top} . Shading indicates dry season; f_{top} refers to the fraction of observed leaf turnover across the whole forest canopy attributed to leaves in the upper canopy layer.

157x120mm (300 x 300 DPI)