

# The phenology of leaf quality and its within-canopy variation is essential for accurate modeling of photosynthesis in tropical evergreen forests

Jin Wu<sup>1</sup>  | Shawn P. Serbin<sup>1</sup> | Xiangtao Xu<sup>2</sup> | Loren P. Albert<sup>3</sup> | Min Chen<sup>4,5</sup> | Ran Meng<sup>1</sup> | Scott R. Saleska<sup>3</sup> | Alistair Rogers<sup>1</sup> 

<sup>1</sup>Environmental & Climate Sciences Department, Brookhaven National Laboratory, New York, NY, USA

<sup>2</sup>Department of Geosciences, Princeton University, Princeton, NJ, USA

<sup>3</sup>Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA

<sup>4</sup>Department of Global Ecology, Carnegie Institution for Science, Stanford, CA, USA

<sup>5</sup>Joint Global Change Research Institute, Pacific Northwest National Laboratory, College Park, MD, USA

## Correspondence

Jin Wu, Environmental & Climate Sciences Department, Brookhaven National Laboratory, Upton, New York, NY, USA.  
Email: jinwu@bnl.gov

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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 Farquhar, von Caemmerer & Berry (FvCB) representation of CO<sub>2</sub> 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<sub>2</sub> assimilation. This work identifies a parsimonious approach for representing tropical evergreen forest photosynthetic seasonality in TBMs that utilize the FvCB model of CO<sub>2</sub> assimilation and highlights the importance of incorporating more realistic phenological mechanisms in models that seek to improve the projection of future carbon dynamics in tropical evergreen forests.

## KEYWORDS

big leaf, gross primary productivity, leaf age, leaf area index, light use efficiency, multilayer, photosynthetic capacity, sun/shade

## 1 | INTRODUCTION

Tropical evergreen forests play a dominant role in the global carbon, water, and energy cycles (Fu et al., 2013; Pan et al., 2011; Stark et al., 2016). They account for around one-third of annual terrestrial photosynthesis (Beer et al., 2010) and a quarter of the global above-ground carbon stock (Aragão et al., 2014; Saatchi et al., 2011). 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 (Cox et al., 2013; Friedlingstein et al., 2006, 2014; 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 (Guan et al., 2015; Restrepo-Coupe et al., 2013; Saleska et al., 2003). Most Terrestrial Biosphere Models (TBMs) have a mechanistic representation of CO<sub>2</sub> assimilation that is capable of simulating the response of photosynthesis to global change (e.g., increasing atmospheric CO<sub>2</sub> concentration). However, most of these models lack mechanistic representation of tropical forest photosynthetic seasonality (Kim et al., 2012; Restrepo-Coupe et al., 2017; de Weirdt et al., 2012). 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., Girardin et al., 2016; Wright & Van Schaik, 1994), and canopy photosynthesis (i.e., gross primary productivity, GPP) derived from eddy flux towers (Hutyra et al., 2007; Restrepo-Coupe et al., 2013; Saleska et al., 2003) and satellites (Guan et al., 2015; Lee et al., 2013) 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., 2016; Wu, Guan et al., 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., 2016; Wu, Guan et al., 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., Brando et al., 2010; Doughty & Goulden, 2008; 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., 2016; 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 (Doughty & Goulden, 2008; Kitajima, Mulkey, & Wright, 1997a; Wu et al., 2016). 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., 2016; Wu, Guan et al., 2017). However, this advance (e.g., Wu et al., 2016; Wu, Guan et al., 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 CO<sub>2</sub> 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, Silva, & Paulo, 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 (Augspurger, Cheeseman, & Salk, 2005; Messier, Parent, & Bergeron, 1998; Richardson & O'Keefe, 2009), or to an adaptive response to large within-canopy variation in environmental variables (Niinemets, Keenan, & Hallik, 2015; Stark et al., 2012, 2015; Wright, Leishman, Read, & Westoby, 2006). 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 (Baldocchi & Amthor, 2001; Ellsworth & Reich, 1993; Morton et al., 2016; Stark et al., 2012).

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 CO<sub>2</sub> 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., Drewry et al., 2010; dePury & Farquhar, 1997). 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; Restrepo-Coupe et al., 2017; Sitch et al., 2015; Xu et al., 2016); 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 (Baker et al., 2008; de Gonçalves et al., 2013; Restrepo-Coupe et al., 2017; Saleska et al., 2003). 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., Kim et al., 2012; de Weirdt 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, McGill, Enquist, & Lechowicz, 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 CO<sub>2</sub> 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: (i) Is seasonality of tropical forest photosynthesis reproduced by a model including leaf phenology? (ii) What is the relative contribution of these three phenological components in controlling the seasonality of photosynthesis? (iii) 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. To evaluate the model performance and avoid other confounding factors in our analysis, such as seasonal and interannual environmental variation (Baldocchi & Amthor, 2001; Richardson et al., 2007; Wu, Guan et al., 2017), our target variable was GPP<sub>ref</sub>, 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, Guan 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 ~2,000 mm/year 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., 2016; Wu, Guan et al., 2017). Detailed descriptions of the instrumentation and data preprocessing 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<sub>eco</sub>) 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: (i) 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 (ii) 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, Atkin, Turnbull, & Griffin, 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<sub>ref</sub>) as our target variable and benchmark for model evaluation. GPP<sub>ref</sub> represents the CO<sub>2</sub> 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<sub>ref</sub> was calculated as the monthly average of all seven-year EC-derived GPP measurements under a reference environmental condition, following Wu et al. (2016); Wu, Guan et al. (2017). The EC-derived GPP<sub>ref</sub> here scales linearly with incident light-use efficiency under the reference environment as used in Wu et al. (2016); Wu, Guan et al. (2017) (where it was called canopy-scale photosynthetic capacity). The reference environment for GPP<sub>ref</sub> was taken as narrow bins of each climatic driver: canopy-top photosynthetically active radiation (PAR<sub>0</sub>) = 1320 ± 200 μmol m<sup>-2</sup> s<sup>-1</sup>, diffuse light fraction = 0.4 ± 0.1, vapor pressure deficit (VPD) = 0.87 ± 0.20 kPa, air-temperature (T<sub>air</sub>) = 28 ± 1°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 (Lopes et al., 2016; Wu et al., 2016; Wu, Chavana-Bryant et al., 2017). Our prescribed, field-based leaf phenology data at the k67 site are the same as those used in Wu et al. (2016).

1. Field data of canopy LAI, litterfall LAI, and new leaf LAI. The mean annual cycle of monthly canopy LAI (range: 5.35–6.15  $m^2/m^2$ ) was derived from tower-mounted camera image time series (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 (i.e., section 5 and Figures S5 and S8) in Wu et al. (2016). The mean annual cycle of monthly litterfall LAI (range: 0.23–0.66  $m^2/m^2$ ) was derived by converting field observations of mass-based foliage litterfall (Mg biomass month/ha; biweekly measurements from 2000 to 2005; Brando et al., 2010) of the same site into area-based litterfall LAI ( $m^2/m^2$  per month), with the formula of Litterfall LAI = mass-based Litterfall  $\times$  SLA, applying a mean specific leaf area (SLA) of 0.816 ha/Mg biomass (Malhado et al., 2009). The mean annual cycle of monthly new leaf LAI production (in  $m^2/m^2$  per month) was estimated using the formula of  $dLAI/dt +$  litterfall LAI, where  $dLAI/dt$  is the average canopy LAI change in the 2 months centered around LAI of each month (Wu et al., 2016).
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 ( $V_{cmax,25}$ ) (Bernacchi et al., 2013), was derived from standard leaf gas exchange measurements of photosynthetic  $CO_2$  response curves (A-C<sub>i</sub>) 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., 2016 for more details on these data). Briefly, the trees we targeted for A-C<sub>i</sub> 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 ~ 1 m length) were assessed using arborist climbing methods, cut, then promptly but gently lowered to the ground with ropes, and re-cut under water

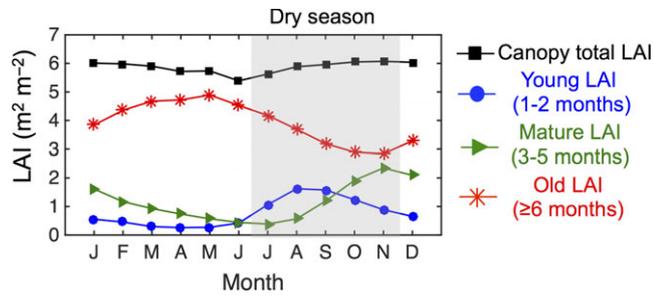
at least once within 15 min of the initial harvest. Gas exchange was typically measured for leaves of each age category present on the branch. These sunlit leaves ( $n = 27$ ) were initially classified into three age classes (Young, Mature, and Old) based on visual assessment of color, size, rigidity, and bud scars (when present) (Chavana-Bryant et al., 2017), 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, Chavana-Bryant et al., 2017 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  $\geq 6$  months). Very young leaves (recent leaf burst; e.g., Figure S1 in Wu, Chavana-Bryant et al., 2017) were too small, delicate, or logistically challenging for photosynthesis measurements; therefore, field-derived leaf  $V_{cmax,25}$  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)  $V_{cmax,25}$  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 ( $\pm 5.1$ )  $\mu mol CO_2 m^{-2} s^{-1}$ , 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., 2016), 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  $\geq 6$  months,  $LAI_O$ ) (see Figure 1), with the two optimized model parameters from Wu et al. (2016) 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., 2017; Wu, Chavana-Bryant et al., 2017), 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 using a three-age-class leaf demography-ontogeny model as below (Wu et al., 2016).

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

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.



**FIGURE 1** Mean annual cycles of monthly LAI in three age classes (three different color lines) at the Tapajós k67 site (adapted from figure 3a in Wu et al., 2016). The three-age LAI seasonality was modeled using the same leaf age residence time parameter as Wu et al. (2016), constrained to sum to total camera-observed LAI (black squares) at the same forest site. Shading indicates the dry season [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## 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 vs. shade), are commonly used in many TBMs, for example, 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 multilayer 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 (Lin et al., 2015; Medlyn et al., 2011) 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 metadata analysis for tropical rainforest trees (Lin et al., 2015). Additionally, we refer to Lloyd and 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  $\text{CO}_2$  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 ( $\text{GPP}_{\text{sun}}$ ) and the shade fraction ( $\text{GPP}_{\text{shade}}$ ) of a forest canopy, respectively (Equation 2).

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

The DF1997 model is operated by firstly determining the LAI,  $V_{\text{cmax}}$ , 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 ( $\text{LAI}_{\text{tot}}$ ) is partitioned into the sunlit fraction ( $\text{LAI}_{\text{sun}}$ ) and the shade fraction ( $\text{LAI}_{\text{shade}}$ ), following Beer's law (Equations 3 and 4; dePury & Farquhar, 1997; Chen, Liu, Cihlar, & Goulden, 1999; Ryu et al., 2011):

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

$$\text{LAI}_{\text{shade}} = \text{LAI}_{\text{tot}} - \text{LAI}_{\text{sun}} \quad (4)$$

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

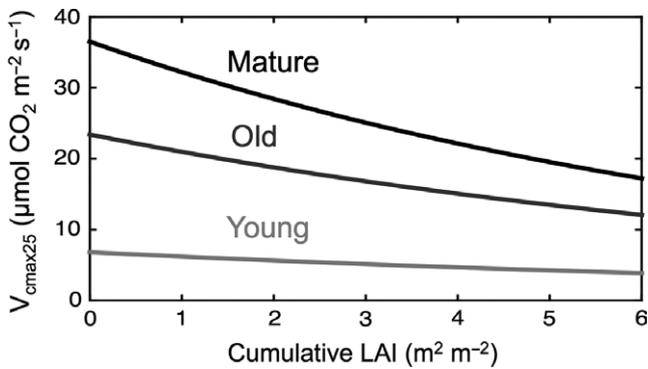
DF1997 also partitions the canopy integrated  $V_{\text{cmax}}$  ( $V_{\text{cmax,tot}}$ ) into the sunlit fraction ( $V_{\text{cmax,sun}}$ ) and the shade fraction ( $V_{\text{cmax,shade}}$ ) (see Table S3). Here we assumed that  $V_{\text{cmax}}$  declines exponentially within the canopy following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

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

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

where  $V_{\text{cmax},0}$  is the  $V_{\text{cmax}}$  of leaves at the top of the canopy; and  $k_n$  describes the exponential decline of  $V_{\text{cmax}}$  against the given accumulated LAI from the top of the canopy ( $\text{LAI}_i$ ). By tracking PAR at the top of the canopy ( $\text{PAR}_0$ ), which is the sum of direct beam ( $\text{PAR}_{\text{b},0}$ ) and diffuse radiation ( $\text{PAR}_{\text{d},0}$ ) in the visible spectrum (i.e., 400–700 nm), DF1997 calculates its canopy absorbance by the sunlit fraction ( $\text{PAR}_{\text{sun}}$ ) and by the shade fraction ( $\text{PAR}_{\text{shade}}$ ), using Beer's law and Seller's (1987) two-stream approximation for canopy radiative transfer (dePury & Farquhar, 1997; Ryu et al., 2011; Tables S4 and S5).

To facilitate the simulation of photosynthetic seasonality with DF1997, we prescribed top-of-canopy  $V_{\text{cmax},0}$  (in Equation 5), that is,  $L_{\text{quality}}$  (Equation 1), while assuming that vertical changes in  $V_{\text{cmax}}$  within a forest canopy follow a fixed exponential decline rate (as described by Equations 5 and 6). The complete equation set for the DF1997 model is provided in Tables S2–S5.



**FIGURE 2** Vertical change in leaf-level  $V_{cmax25}$  with cumulative LAI from canopy top to forest floor, using the Equations 5 and 6, following Lloyd et al. (2010). Three color lines represent leaves at three age classes (Young: 1–2 months; Mature: 3–5 months; Old:  $\geq 6$  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., 2016)

3. The leaf-canopy scaling relationship represented by the multilayer 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  $N \geq 15$  (Figure 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 Equations 5 and 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 Equation 5), that is,  $L_{quality}$  (Equation 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, Chavana-Bryant et al., 2017), 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: (i) the upper canopy layer with the cumulative LAI from 0 (top-of-canopy) to  $2.5 \text{ m}^2/\text{m}^2$ , and (ii) 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  $ftop$ , the fraction of observed leaf turnover (including leaf drop and flush) across the whole forest canopy attributed to leaves in the upper canopy layer, for example, when  $ftop = 0.7$ , 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  $(ftop/LAI_{up})/((1-ftop)/LAI_{low}) = 2.8$ , where  $ftop = 0.7$ ,  $LAI_{up}$  (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) =  $3 \text{ m}^2/\text{m}^2$ . As 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  $ftop = 0.7$ . 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  $3 \text{ m}^2/\text{m}^2$  (Figure S2).

## 2.4 | Model experiments

We used our proposed two-fraction leaf, two-layer canopy model as the main modeling test bed for assessing the effect of different phenological components on modeled canopy photosynthetic seasonality. This is because previous studies (e.g., Bonan, Oleson,

Fisher, Lasslop, & Reichstein, 2012; dePury & Farquhar, 1997) demonstrate that DF1997 and ML can simulate almost identical GPP fluxes at the canopy scale (which is also confirmed by our Figure 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<sub>ref</sub> seasonality. The model inputs for these phenological components include: (i) the leaf quantity based on field measurements of the mean annual cycle of monthly LAI, (ii) the leaf quality based on field-derived seasonality of  $L_{quality}$  (as calculated by Equation 1, weighted by field-measured age dependency of  $V_{cmax25}$  and field-derived leaf age demographics), and (iii) 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  $f_{top} = 0.7$ ), 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 (i) 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 (ii) 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<sub>ref</sub> 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.

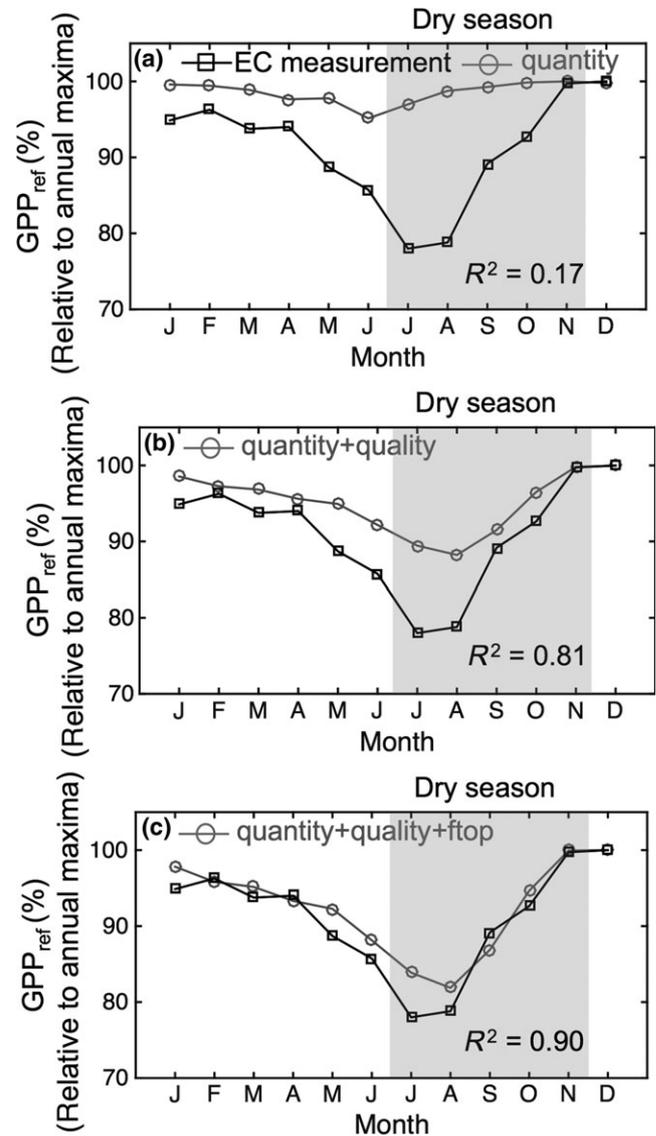
### 3 | RESULTS

#### 3.1 | Modeled GPP<sub>ref</sub> 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<sub>ref</sub>. 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 (Figure 3 and Table 1).

The seven-year mean annual cycle of EC-derived GPP<sub>ref</sub> at the Tapajós k67 site showed an initial decline in the late wet season, and then an increase in the dry season (Figure 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<sub>ref</sub> seasonality, but missed the depth or relative magnitude of GPP<sub>ref</sub> seasonality: leaf quantity phenology alone explained only 19% of EC-derived GPP<sub>ref</sub> seasonality for DF1997 (Table 1) and 17% for ML and the two-fraction leaf, two-layer canopy model (Table 1 and Figure 3a); the modeled GPP<sub>ref</sub> with both leaf quantity and quality (but no within-canopy phenological variation) explained



**FIGURE 3** Seasonal variation in EC-derived GPP<sub>ref</sub> (seven-year mean annual cycle; black squares) and modeled GPP<sub>ref</sub> (gray circles) incorporating different phenological components, using the two-fraction leaf, two-layer canopy model. (a) modeled GPP<sub>ref</sub> parameterized by seasonal variation in leaf quantity (or LAI) only; (b) modeled GPP<sub>ref</sub> 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<sub>ref</sub> parameterized by seasonal variation in leaf quantity and quality, and differential leaf turnover rates within a forest canopy (i.e.,  $f_{top} = 0.7$ ). 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

~80% of EC-derived  $GPP_{ref}$  seasonality for DF1997, ML, and the two-fraction leaf, two-layer canopy model (Table 1 and Figure 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 ( $R^2 = .90$ ; Table 1 and Figure 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). Figure 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 Figure 4a and relative value in Figure 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%; Figures 4a and S4), despite modest seasonal variability in leaf quantity (~12%; Figure 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  $m^2/m^2$  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 Equation 3–5). Focusing first on the sunlit fraction, Figure 4b highlights that the  $LAI_{sun}$  is generally stable (~1.5  $m^2/m^2$ ) 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  $V_{cmax, sun}$  (Figure 4c) is primarily driven by leaf quality, which is associated with seasonal variation in leaf age demographics (Figure 1 and

Equation 1). In addition, our results indicated that the higher seasonal variability (~25%) in  $V_{cmax, shade}$  (Figure 4c) is a consequence of seasonal variability in both  $LAI_{shade}$  (Figure 4b) and leaf age demographics (Figure 1 and Equation 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 (Figure 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.,  $PAR > 800 \mu mol m^{-2} s^{-1}$ ) while canopy integrated absorbed PAR dominated  $GPP_{ref}$  response under low light condition (i.e.,  $PAR < 400 \mu mol m^{-2} s^{-1}$ ). Given that the sunlit fraction could consistently capture sufficient PAR to photosaturate photosynthesis (~860  $\mu mol m^{-2} s^{-1}$ ; Figure 4a) over the annual cycle, the seasonal variability in  $GPP_{ref, sun}$  closely tracked the seasonality of  $V_{cmax, sun}$  (Figure 4c,d), which is mostly determined by the phenology of leaf quality (Figure 4b,c). On the other hand, as the shade fraction typically receives subsaturating light (~300  $\mu mol m^{-2} s^{-1}$ ; Figure 4a) over the annual cycle,  $GPP_{ref, shade}$  is primarily limited by the capacity for RuBP regeneration (Figure S5). As a result, modeled  $GPP_{ref, shade}$  seasonality is small (~7%; Figure S6), which is comparable with the relative seasonal change in  $PAR_{shade}$  (~6%; Figure S4), but far less than the relative seasonality in  $V_{cmax, shade}$  (25%; Figure 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 Figure 4d and relative value in Figure S6).

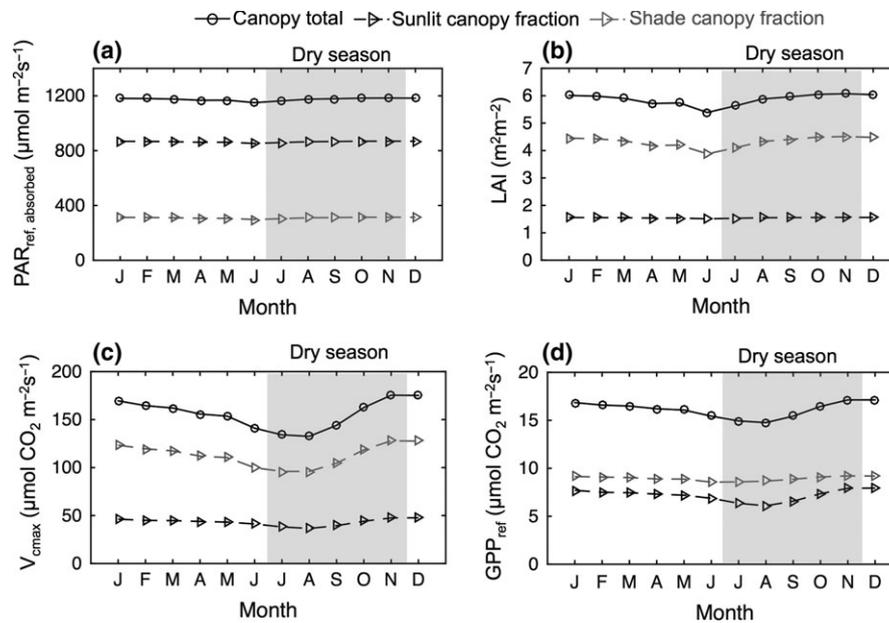
### 3.3 | Model sensitivity of canopy photosynthesis to within-canopy phenological variations

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 (Figure 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 (Figure 5a). As ftop increases (more leaf turnover is partitioned to the upper canopy), the relative magnitude of modeled  $GPP_{ref}$  seasonality increases (Figure 5a). Meanwhile, the correlation between

**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

Model\Phenology	Quantity	Quality	Quantity + Quality	Quantity + Quality + Within-Canopy variation
DF1997	$R^2 = .19$ ; $p = .041$	$R^2 = .69$ ; $p < .0001$	$R^2 = .80$ ; $p < .0001$	NA
ML	$R^2 = .17$ ; $p = .042$	$R^2 = .72$ ; $p < .0001$	$R^2 = .81$ ; $p < .0001$	NA
Two-fraction leaf, two-layer canopy	$R^2 = .17$ ; $p = .042$	$R^2 = .72$ ; $p < .0001$	$R^2 = .81$ ; $p < .0001$	$R^2 = .90$ ; $p < .0001$

$R^2$  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 ftop = 0.7; NA for not applicable.



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

modeled and EC-derived  $\text{GPP}_{\text{ref}}$  seasonality also increases with  $f_{\text{top}}$  and reaches near saturation when  $f_{\text{top}} \geq 0.7$  ( $R^2 = .90$ ; Figure 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 Figure 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.

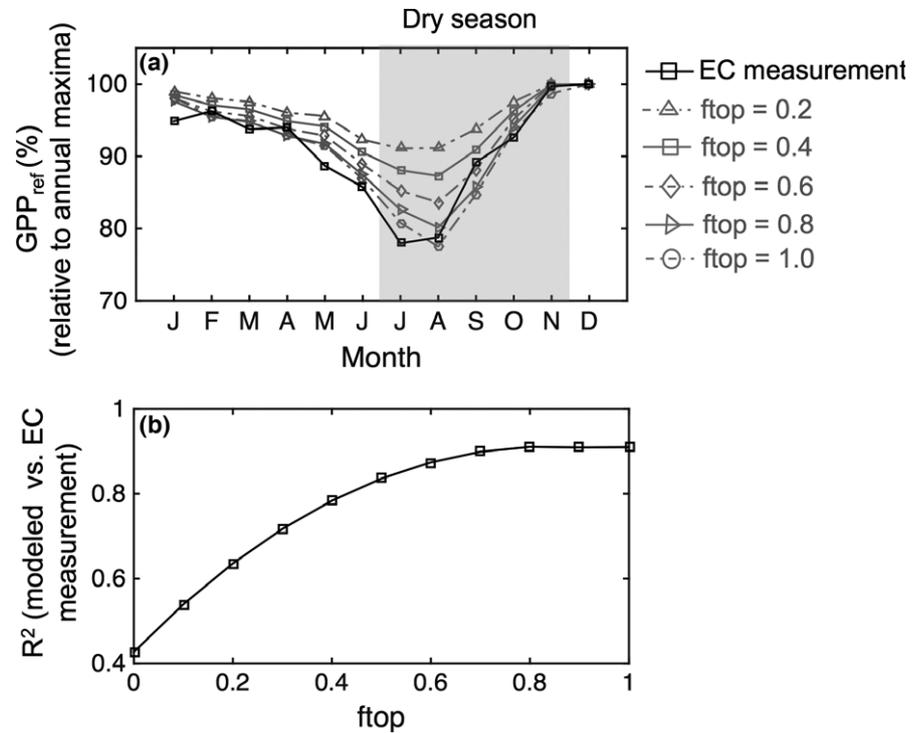
## 4 | DISCUSSION

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 (Christoffersen et al., 2014; Fu et al., 2013; Restrepo-Coupe et al., 2013, 2017; Wu et al., 2016). 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 (Figure 3 and Table 1). This is also consistent with previous field-based remote sensing studies (Brando et al., 2010; Doughty & Goulden, 2008; Lopes et al., 2016; Saleska et al., 2016), which highlight that variation in photosynthetic efficiency and the spectral reflectance properties of leaves (Chavana-Bryant et al., 2017; Roberts et al., 1998; Wu et al., 2016; Wu, Chavana-Bryant et al., 2017) 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, that is, leaf quality (Kim et al., 2012; de Weirdt 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  $\text{GPP}_{\text{ref}}$  seasonality varied strongly across the models (Figure 3). The approach of incorporating all phenological components (i.e., quantity, quality, and within-canopy variation) displayed the strongest agreement with local EC-derived  $\text{GPP}_{\text{ref}}$ , while the approaches incorporating part of the three phenological components (e.g., leaf quantity alone in Figure 3a and leaf quantity and quality alone in Figure 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



**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

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 (Bi et al., 2015; Brando et al., 2010; Doughty & Goulden, 2008; Lopes et al., 2016; Morton et al., 2014; Myneni et al., 2007; Wu et al., 2016), and therefore, the observed small seasonal changes in leaf quantity had little impact on FAPAR seasonality (Figures 4a and 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., 2016). 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 (Figure 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.,  $V_{cmax}$ ; Figures 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 and 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 and 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 Figure 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  $f_{top}$  (Figure 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 (Figures 3 and 5). Importantly, our prescribed higher leaf turnover rate in the upper canopy (i.e.,  $f_{top} = 0.7$ ) 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. (2016). This explains why the simple model of Wu et al. (2016), 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. (2016), 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., 2016) 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). As TBMs need to project the response of photosynthesis to rising CO<sub>2</sub>, 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., Ali et al., 2016; Fisher et al., 2015; Serbin et al., 2015). Therefore, to accurately represent canopy photosynthetic processes in tropical forests under a changing climate we advocate the use of the approach outlined here, that is, 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., Figure 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 interannual changes in leaf quantity and quality, that is, 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., 2016).

Second, our demonstration of the importance of leaf phenology effects on tropical forest photosynthetic seasonality relied on modeled and EC-derived GPP<sub>ref</sub>. 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. As canopy photosynthesis is jointly determined by extrinsic environmental variability and changes in intrinsic photosynthetic machinery (Baldocchi & Amthor, 2001; Collatz et al., 1991; Dai et al., 2003; Farquhar et al., 1980; Medvigy et al., 2009; dePury & Farquhar, 1997; Rogers et al., 2017; Sellers et al., 1992; Wu et al., 2016), there is a great need to improve our understanding and model representation of the fundamental physiological responses to environmental variability, particularly rising atmospheric CO<sub>2</sub> 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., Chavana-Bryant et al., 2017; Kitajima, Mulkey, & Wright, 1997b; Wu, Chavana-Bryant et al., 2017); 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., Kenzo et al., 2015; Kumagai et al., 2006; Wu, Chavana-Bryant et al., 2017). 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.

## REFERENCES

- Ali, A. A., Xu, C., Rogers, A., Risher, R. A., Wullschlegel, S. D., Massoud, E.C., ... Wilson, C. J. (2016). A global scale mechanistic model of photosynthetic capacity (LUNA V1. 0). *Geoscientific Model Development*, 9, 587–606.
- Aragão, L. E. O. C., Poulter, B., Barlow, J. B., Anderson, L. O., Malhi, Y., Saatchi, S., ... Gloor, E. (2014). Environmental change and the carbon balance of Amazonian forests. *Biological Reviews*, 89, 913–931.
- Augsburger, C. K., Cheeseman, J. M., & Salk, C. F. (2005). Light gains and physiological capacity of understorey woody plants during phenological avoidance of canopy shade. *Functional Ecology*, 19, 537–546.
- Baker, I. T., Prihodko, L., Denning, A. S., Goulden, M., Miller, S., & da Rocha, H. R. (2008). Seasonal drought stress in the Amazon: Reconciling models and observations. *Journal of Geophysical Research: Biogeosciences*, 113, G00B01. <https://doi.org/10.1029/2007jg000644>

- Baldocchi, D. D., & Amthor, J. S. (2001). Canopy photosynthesis: history. In J. Roy, B. Saugier, & H. A. Mooney (Eds.), *Terrestrial global productivity* (pp. 9–31). Waltham, MA: Academic Press.
- Beer, C., Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., ... Papale, D. (2010). Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate. *Science*, *329*, 834–838.
- Bernacchi, C. J., Bagley, J. E., Serbin, S. P., Ruiz-Vera, U. M., Rosenthal, D. M., & Vanloocke, A. (2013). Modelling C3 photosynthesis from the chloroplast to the ecosystem. *Plant, Cell & Environment*, *36*, 1641–1657.
- Best, M. J., Pryor, M., Clark, D. B., Rooney, G. G., Essery, R. L. H., Menard, C. B., ... Harding, R. J. (2011). The Joint UK Land Environment Simulator (JULES), model description—Part 1: Energy and water fluxes. *Geoscientific Model Development*, *4*, 677–699.
- Bi, J., Knyazikhin, Y., Choi, S., Park, T., Barichivich, J., Ciais, P., ... Myneni, R. B. (2015). Sunlight mediated seasonality in canopy structure and photosynthetic activity of Amazonian rainforests. *Environmental Research Letters*, *10*, 064014. <https://doi.org/10.1088/1748-9326/10/6/064014>
- Bonan, G. B., Oleson, K. W., Fisher, R. A., Lasslop, G., & Reichstein, M. (2012). Reconciling leaf physiological traits and canopy flux data: Use of the TRY and FLUXNET databases in the Community Land Model version 4. *Journal of Geophysical Research: Biogeosciences*, *117*, G02026. <https://doi.org/10.1029/2011JG001913>
- Borchert, R. (1994). Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, *75*, 1437–1449.
- Bradley, A. V., Gerard, F. F., Barbier, N., Weedon, G. P., Anderson, L. O., Huntingford, C., ... Arai, E. (2011). Relationships between phenology, radiation and precipitation in the Amazon region. *Global Change Biology*, *17*, 2245–2260.
- Brando, P. M., Goetz, S. J., Baccini, A., Nepstad, D. C., Beck, P. S. A., & Christman, M. C. (2010). Seasonal and interannual variability of climate and vegetation indices across the Amazon. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 14685–14690.
- Chavana-Bryant, C., Malhi, Y., Wu, J., Asner, G. P., Anastasiou, A., Enquist, B. J., ... Gerard, F. F. (2017). Leaf aging of Amazonian canopy trees as revealed by spectral and physiochemical measurements. *New Phytologist*, *214*, 1049–1063.
- Chen, J. M., Liu, J., Cihlar, J., & Goulden, M. L. (1999). Daily canopy photosynthesis model through temporal and spatial scaling for remote sensing applications. *Ecological Modelling*, *124*, 99–119.
- Christoffersen, B. O., Restrepo-Coupe, N., Arain, M. A., Baker, I. T., Cestaro, B. P., Ciais, P., ... Saleska, S. R. (2014). Mechanisms of water supply and vegetation demand govern the seasonality and magnitude of evapotranspiration in Amazonia and Cerrado. *Agricultural and Forest Meteorology*, *191*, 33–50.
- Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., ... Cox, P. M. (2011). The Joint UK Land Environment Simulator (JULES), model description—Part 2: Carbon fluxes and vegetation dynamics. *Geoscientific Model Development*, *4*, 701–722.
- Collatz, G. J., Ball, J. T., Grivet, C., & Berry, J. A. (1991). Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: A model that includes a laminar boundary layer. *Agricultural and Forest Meteorology*, *54*, 107–136.
- Cox, P. M., Pearson, D., Booth, B. B., Friedlingstein, P., Huntingford, C., Jones, C. D., & Luke, C. M. (2013). Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature*, *494*, 341–344.
- Dai, Y., Zeng, X., Dickinson, R. E., Baker, I., Bonan, G. B., Bosilovich, M. G., ... Yang, Z.-L. (2003). The common land model. *Bulletin of the American Meteorological Society*, *84*, 1013–1023.
- Doughty, C. E., & Goulden, M. L. (2008). Seasonal patterns of tropical forest leaf area index and CO<sub>2</sub> exchange. *Journal of Geophysical Research: Biogeosciences*, *113*, G00B06. <https://doi.org/10.1029/2007jg000590>
- Drewry, D. T., Kumar, P., Long, S., Bernacchi, C., Liang, X.-Z., & Sivapalan, M. (2010). Ecohydrological responses of dense canopies to environmental variability: 1. Interplay between vertical structure and photosynthetic pathway. *Journal of Geophysical Research: Biogeosciences*, *115*, G04022. <https://doi.org/10.1029/2010JG001340>
- Ellsworth, D. S., & Reich, P. B. (1993). Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia*, *96*, 169–178.
- Farquhar, G. D., von Caemmerer, S., & Berry, J. A. (1980). A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C3 species. *Planta*, *149*, 78–90.
- Fisher, R. A., Muszala, S., Versteinstein, M., Lawrence, P. J., Xu, C., McDowell, N., ... Bonan, G. (2015). Taking off the training wheels: The properties of a dynamic vegetation model without climate envelopes. *Geoscientific Model Development Discussion*, *8*, 3293–3357.
- Friedlingstein, P., Cox, P., Betts, R., Bopp, L., von Bloh, W., Cadule, P., ... Zeng, N. (2006). Climate-carbon cycle feedback analysis: Results from the C4MIP model intercomparison. *Journal of Climate*, *19*, 3337–3353.
- Friedlingstein, P., Meinshausen, M., Arora, V. K., Jones, C. D., Anav, A., Liddicoat, S. K., & Knutti, R. (2014). Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *Journal of Climate*, *27*, 511–526.
- Fu, R., Yin, L., Li, W., Arias, P. A., Dickinson, R. E., Huang, L., ... Myneni, R. B. (2013). Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 18110–18115.
- Girardin, C. A., Malhi, Y., Doughty, C. E., Metcalfe, D. B., Meir, P., del Aguila-Pasquel, J., ... Rowland, L. (2016). Seasonal trends of Amazonian rainforest phenology, net primary productivity, and carbon allocation. *Global Biogeochemical Cycles*, *30*, 700–715.
- de Gonçalves, L. G., Borak, J. S., Costa, M. H., Saleska, S. R., Baker, I., Restrepo-Coupe, N., & Muza, M. N. (2013). Overview of the large-scale biosphere-atmosphere experiment in Amazonia Data Model Intercomparison Project (LBA-DMIP). *Agricultural and Forest Meteorology*, *182*, 111–127.
- Guan, K., Pan, M., Li, H., Wolf, A., Wu, J., Medvigy, D., ... Lyapustin, A. I. (2015). Photosynthetic seasonality of global tropical forests constrained by hydroclimate. *Nature Geoscience*, *8*, 284–289.
- Harper, A., Cox, P., Friedlingstein, P., Wiltshire, A. J., Jones, C. D., Sitch, S., ... van Bodegom, P. (2016). Improved representation of plant functional types and physiology in the Joint UK Land Environment Simulator (JULES v4. 2) using plant trait information. *Geoscientific Model Development Discussions*, *9*, 2415–2440.
- He, L., Chen, J. M., Pisek, J., Schaaf, C. B., & Strahler, A. H. (2012). Global clumping index map derived from the MODIS BRDF product. *Remote Sensing of Environment*, *119*, 118–130.
- Heskel, M. A., Atkin, O. K., Turnbull, M. H., & Griffin, K. L. (2013). Bringing the Kok effect to light: A review on the integration of daytime respiration and net ecosystem exchange. *Ecosphere*, *4*, 1–14.
- Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L. M., Sitch, S., Fisher, R., ... Cox, P. M. (2013). Simulated resilience of tropical rainforests to CO<sub>2</sub>-induced climate change. *Nature Geoscience*, *6*, 268–273.
- Hutyra, L. R., Munger, J. W., Saleska, S. R., Gottlieb, E., Daube, B. C., Dunn, A. L., ... Wofsy, S. C. (2007). Seasonal controls on the exchange of carbon and water in an Amazonian rain forest. *Journal of Geophysical Research: Biogeosciences*, *112*, G03008. <https://doi.org/10.1029/2006JG000365>
- Kenzo, T., Inoue, Y., Yoshimura, M., Yamashita, M., Tanaka-Oda, A., & Ichie, T. (2015). Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. *Oecologia*, *177*, 191–202.
- Kim, Y., Knox, R. G., Longo, M., Medvigy, D., Hutyra, L. R., Pyle, E. H., ... Moorcroft, P. R. (2012). Seasonal carbon dynamics and water fluxes in an Amazon rainforest. *Global Change Biology*, *18*, 1322–1334.

- Kitajima, K., Mulkey, S., & Wright, S. (1997a). Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. *American Journal of Botany*, *84*, 702–708.
- Kitajima, K., Mulkey, S., & Wright, S. (1997b). Seasonal leaf phenotypes in the canopy of a tropical dry forest: Photosynthetic characteristics and associated traits. *Oecologia*, *109*, 490–498.
- Kumagai, T., Ichie, T., Yoshimura, M., Yamashita, M., Kenzo, T., Saitoh, T. M., ... Komatsu, H. (2006). Modeling CO<sub>2</sub> exchange over a Bornean tropical rain forest using measured vertical and horizontal variations in leaf-level physiological parameters and leaf area densities. *Journal of Geophysical Research: Atmospheres*, *111*, D10107. <https://doi.org/10.1029/2005jd006676>
- Lee, J. E., Frankenberg, C., van der Tol, C., Berry, J. A., Guanter, L., Boyce, C. K., ... Saatchi, S. (2013). Forest productivity and water stress in Amazonia: Observations from GOSAT chlorophyll fluorescence. *Proceedings of the Royal Society of London B: Biological Sciences*, *280*, 20130171.
- Lin, Y. S., Medlyn, B. E., Duursma, R. A., Prentice, I. C., Wang, H., Baig, S., ... Wingate, L. (2015). Optimal stomatal behaviour around the world. *Nature Climate Change*, *5*, 459–464.
- Lloyd, J., & Farquhar, G. D. (2008). Effects of rising temperatures and [CO<sub>2</sub>] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*, 1811–1817.
- Lloyd, J., Patino, S., Paiva, R. Q., Nardoto, G. B., Quesada, C. A., Santos, A. J. B., ... Mercado, L. M. (2010). Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. *Biogeosciences*, *7*, 1833–1859.
- Lopes, A. P., Nelson, B. W., Wu, J., de Alencastro Graça, P. M. L., Tavares, J. V., Prohaska, N., ... Saleska, S.R. (2016). Leaf flush drives dry season green-up of the Central Amazon. *Remote Sensing of Environment*, *182*, 90–98.
- Lowman, M. D. (1992). Leaf growth dynamics and herbivory in five species of Australian rain-forest canopy trees. *Journal of Ecology*, *80*, 433–447.
- Malhado, A. C., Costa, M. H., de Lima, F. Z., Portilho, K. C., & Figueiredo, D. N. (2009). Seasonal leaf dynamics in an Amazonian tropical forest. *Forest Ecology and Management*, *258*, 1161–1165.
- Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton, C. V. M., ... Wingate, L. (2011). Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biology*, *17*, 2134–2144.
- Medvigy, D., Wofsy, S. C., Munger, J. W., Hollinger, D. Y., & Moorcroft, P. R. (2009). Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research: Biogeosciences*, *114*, G01002. <https://doi.org/10.1029/2008JG000812>
- Messier, J., McGill, B. J., Enquist, B. J., & Lechowicz, M. J. (2016). Trait variation and integration across scales: Is the leaf economic spectrum present at local scales? *Ecography*, *39*, 001–013. <https://doi.org/10.1111/ecog.02006>
- Messier, C., Parent, S., & Bergeron, Y. (1998). Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. *Journal of Vegetation Science*, *9*, 511–520.
- Miyaji, K., Silva, W. S., & Paulo, T. A. (1997). Longevity of leaves of a tropical tree, *Theobroma cacao*, grown under shading, in relation to position within the canopy and time of emergence. *New Phytologist*, *135*, 445–454.
- Morton, D. C., Nagol, J., Carabajal, C. C., Rosette, J., Palace, M., Cook, B. D., ... North, P. R. J. (2014). Amazon forests maintain consistent canopy structure and greenness during the dry season. *Nature*, *506*, 221–224.
- Morton, D. C., Rubio, J., Cook, B. D., Gastellu-Etchegorry, J.-P., Longo, M., Choi, H., ... Keller, M. (2016). Amazon forest structure generates diurnal and seasonal variability in light utilization. *Biogeosciences*, *13*, 2195–2206.
- Myneni, R. B., Yang, W., Nemani, R. R., Huete, A. R., Dickinson, R. E., Knyazikhin, Y., ... Salomonson, V. V. (2007). Large seasonal swings in leaf area of Amazon rainforests. *Proceedings of the National Academy of Sciences*, *104*, 4820–4823.
- Niinemets, Ü., Keenan, T. F., & Hallik, L. (2015). A worldwide analysis of within-canopy variations in leaf structural, chemical and physiological traits across plant functional types. *New Phytologist*, *205*, 973–993.
- Oleson, K. W., Lawrence, D. M., Bonan, G. B., Flanner, M. G., Kluzek, E., Lawrence, P. J., ... Thornton, P. E. (2013). *Technical description of version 4.5 of the Community Land Model (CLM)*. NCAR Tech. Note NCAR/TN-503 + STR. National Center for Atmospheric Research, Boulder, CO, 422 pp. <https://doi.org/10.5065/d6rr1w7m>, 2013.
- Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., ... Hayes, D. (2011). A large and persistent carbon sink in the world's forests. *Science*, *333*, 988–993.
- Powell, T. L., Galbraith, D. R., Christoffersen, B. O., Harper, A., Imbuzeiro, H. M. A., Rowland, L., ... Moorcroft, P. R. (2013). Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytologist*, *200*, 350–365.
- dePury, D. G. G., & Farquhar, G. D. (1997). Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. *Plant, Cell & Environment*, *20*, 537–557.
- Pyle, E. H., Santoni, G. W., Nascimento, H. E., Hutrya, L. R., Vieira, S., Curran, D. J., ... Wofsy, S. C. (2008). Dynamics of carbon, biomass, and structure in two Amazonian forests. *Journal of Geophysical Research: Biogeosciences*, *113*, G00B08. <https://doi.org/10.1029/2007jg000592>
- Reich, P. B., Uhl, C., Walters, M. B., Prugh, L., & Ellsworth, D. S. (2004). Leaf demography and phenology in Amazonian rain forest: A census of 40 000 leaves of 23 tree species. *Ecological Monographs*, *74*, 3–23.
- Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., ... Valentini, R. (2005). On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. *Global Change Biology*, *11*, 1424–1439.
- Restrepo-Coupe, N., da Rocha, H. R., Hutrya, L. R., da Araujo, A. C., Borma, L. S., Christoffersen, B., ... Saleska, S. R. (2013). What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network. *Agricultural and Forest Meteorology*, *182*, 128–144.
- Restrepo-Coupe, N., Levine, N., Christoffersen, B. O., Albert, L. P., Wu, J., Costa, M. H., ... Saleska, S. R. (2017). Do dynamic global vegetation models capture the seasonality of carbon fluxes in the Amazon basin? A data-model intercomparison. *Global Change Biology*, *23*, 191–208.
- Rice, A. H., Pyle, E. H., Saleska, S. R., Hutrya, L., Palace, M., Keller, M., ... Wofsy, S. C. (2004). Carbon balance and vegetation dynamics in an old-growth Amazonian forest. *Ecological Applications*, *14*, 55–71.
- Richardson, A. D., Anderson, R. S., Arain, M. A., Barr, A. G., Bohrer, G., Chen, G., ... Xue, Y. (2012). Terrestrial biosphere models need better representation of vegetation phenology: Results from the North American Carbon Program Site Synthesis. *Global Change Biology*, *18*, 566–584.
- Richardson, A. D., Hollinger, D. Y., Aber, J. D., Ollinger, S. V., & Braswell, B. H. (2007). Environmental variation is directly responsible for short-but not long-term variation in forest-atmosphere carbon exchange. *Global Change Biology*, *13*, 788–803.
- Richardson, A. D., & O'Keefe, J. (2009). Phenological differences between understory and overstory. In A. Noormets, (Ed.), *Phenology of ecosystem processes* (pp. 87–117). New York: Springer.
- Roberts, D. A., Nelson, B. W., Adams, J. B., & Palmer, F. (1998). Spectral changes with leaf aging in Amazon caatinga. *Trees*, *12*, 315–325.
- Rogers, A., Medlyn, B. E., Dukes, J. S., Bonan, G., vonCaemmerer, S., Dietze, M. C., ... Zaehle, S. (2017). A roadmap for improving the representation of photosynthesis in Earth System Models. *New Phytologist*, *213*, 22–42.

- Ryu, Y., Baldocchi, D. D., Kobayashi, H., van Ingen, C., Li, J., Black, T. A., ... Rouspard, O. (2011). Integration of MODIS land and atmosphere products with a coupled-process model to estimate gross primary productivity and evapotranspiration from 1 km to global scales. *Global Biogeochemical Cycles*, 25, GB4017. <https://doi.org/10.1029/2011gb004053>
- Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A., Salas, W., ... Morel, A. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences*, 108, 9899–9904.
- Saleska, S. R., Miller, S. D., Matross, D. M., Goulden, M. L., Wofsy, S. C., da Rocha, H. R., ... Silva, H. (2003). Carbon in Amazon forests: Unexpected seasonal fluxes and disturbance-induced losses. *Science*, 302, 1554–1557.
- Saleska, S. R., Wu, J., Guan, K., Araujo, A. C., Huete, A., Nobre, A. O., & Restrepo-Coupe, N. (2016). Brief Communications Arising: Dry season greening of Amazon forests. *Nature*, 531, E4–E5.
- Schimel, D., Pavlick, R., Fisher, J. B., Asner, G. P., Saatchi, S., Townsend, P., ... Cox, P. (2015). Observing terrestrial ecosystems and the carbon cycle from space. *Global Change Biology*, 21, 1762–1776.
- Sellers, P. J. (1987). Canopy reflectance, photosynthesis, and transpiration. II. The role of biophysics in the linearity of their interdependence. *Remote Sensing of Environment*, 21, 143–183.
- Sellers, P. J., Berry, J. A., Collatz, G. J., Field, C. B., & Hall, F. G. (1992). Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of Environment*, 42, 187–216.
- Serbin, S. P., Singh, A., Desai, A. R., Dubois, S. G., Jablonski, A. D., Kingdon, C. C., ... Townsend, P. A. (2015). Remotely estimating photosynthetic capacity, and its response to temperature, in vegetation canopies using imaging spectroscopy. *Remote Sensing of Environment*, 167, 78–87.
- Sitch, S., Friedlingstein, P., Gruber, N., Jones, S. D., Murray-Tortarolo, G., Ahlstrom, A., ... Myneni, R. (2015). Recent trends and drivers of regional sources and sinks of carbon dioxide. *Biogeosciences*, 12, 653–679.
- Stark, S. C., Breshears, D. D., Garcia, E. S., Breshears, D. D., Garcia, E. S., Law, D. J., ... Redmond, M. D. (2016). Toward accounting for ecoclimate teleconnections: Intra-and inter-continental consequences of altered energy balance after vegetation change. *Landscape Ecology*, 31, 181–194.
- Stark, S. C., Enquist, B. J., Saleska, S. R., Leitold, V., Schiatti, J., Longo, M., ... Oliveira, R. C. (2015). Linking canopy leaf area and light environments with tree size distributions to explain Amazon forest demography. *Ecology Letters*, 18, 636–645.
- Stark, S. C., Leitold, V., Wu, J. L., Hunter, M. O., de Castilho, C. V., Costa, F. R. C., ... Saleska, S. R. (2012). Amazon forest carbon dynamics predicted by profiles of canopy leaf area and light environment. *Ecology Letters*, 15, 1406–1414.
- Wehr, R., Munger, J. W., McManus, J. B., Nelson, D. D., Zahniser, M. S., Davidson, E. A., ... Saleska, S. R. (2016). Seasonality of temperate forest photosynthesis and daytime respiration. *Nature*, 534, 680–683.
- de Weirdt, M., Verbeeck, H., Maignan, F., Peylin, P., Poulter, B., Bonal, D., ... Steppe, K. (2012). Seasonal leaf dynamics for tropical evergreen forests in a process-based global ecosystem model. *Geoscientific Model Development*, 5, 1091–1108.
- Wright, I. J., Leishman, M. R., Read, C., & Westoby, M. (2006). Gradients of light availability and leaf traits with leaf age and canopy position in 28 Australian shrubs and trees. *Functional Plant Biology*, 33, 407–419.
- Wright, S. J., & Van Schaik, C. P. (1994). Light and the phenology of tropical trees. *American Naturalist*, 143, 192–199.
- Wu, J., Albert, L. P., Lopes, A. P., Restrepo-Coupe, N., Hayek, M., Wiedemann, K. T., Guan, K., ... Saleska, S. R. (2016). Leaf development and demography explain photosynthetic seasonality in Amazon evergreen forests. *Science*, 351, 972–976.
- Wu, J., Chavana-Bryant, C., Prohaska, N., Serbin, S. P., Guan, K., Albert, L. P., ... Saleska, S. R. (2017). Convergence in relationships between leaf traits, spectra and age across diverse canopy environments and two contrasting tropical forests. *New Phytologist*, 214, 1033–1048.
- Wu, J., Guan, K., Hayek, M., Restrepo-Coupe, N., Wiedemann, K. T., Xu, X., ... Saleska, S. R. (2017). Partitioning controls on Amazon forest photosynthesis between environmental and biotic factors at hourly to inter-annual timescales. *Global Change Biology*, 3, 1240–1257.
- Xu, X., Medvigy, D., Powers, J. S., Becknell, J. M., & Guan, K. (2016). Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist*, 212, 80–95.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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