Vegetation chlorophyll estimates in the Amazon from multi-angle MODIS observations and canopy reflectance model


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As a preparatory study for future hyperspectral missions that can measure canopy chemistry, we introduce a novel approach to investigate whether multi-angle Moderate Resolution Imaging Spectroradiometer (MODIS) data can be used to generate a preliminary database with long-term estimates of chlorophyll. MODIS monthly chlorophyll estimates between 2000 and 2015, derived from a fully coupled canopy reflectance model (ProSAIL), were inspected for consistency with eddy covariance fluxes, tower-based hyperspectral images and chlorophyll measurements. MODIS chlorophyll estimates from the inverse model showed strong seasonal variations across two flux-tower sites in central and eastern Amazon. Marked increases in chlorophyll concentrations were observed during the early dry season. Remotely sensed chlorophyll concentrations were correlated to field measurements \((r^2 = 0.73)\) but the data deviated from the 1:1 line with root mean square errors (RMSE) ranging from 0.355 \(\mu g cm^{-2}\) (Tapajós tower) to 0.470 \(\mu g cm^{-2}\) (Manaus tower). The chlorophyll estimates were consistent with flux tower measurements of photosynthetically active radiation (PAR) and net ecosystem productivity (NEP). We also applied ProSAIL to mono-angle hyperspectral observations from a camera installed on a tower to scale modeled chlorophyll pigments to MODIS observations \((r^2 = 0.73)\). Chlorophyll pigment concentrations \((Chl_a + Chl_b)\) were correlated to changes in the amount of young and mature leaf area per month \((0.59 \leq r^2 < 0.64)\). Increases in MODIS observed \(Chl_a + Chl_b\) were preceded by increased PAR during the dry season \((0.61 < r^2 < 0.62)\) and followed by changes in net carbon uptake. We conclude that, at these two sites, changes in LAI, coupled with changes in leaf chlorophyll, are comparable with seasonality of plant productivity. Our results allowed the preliminary development of a 15-year time series of chlorophyll estimates over the Amazon to support canopy chemistry studies using future hyperspectral sensors.

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1. Introduction

Chlorophyll-based photosynthesis mediates up to 90% of the gas exchange between the terrestrial biosphere and the atmosphere (Ozanne et al., 2003; Sellers et al., 1996). However, in tropical regions, the controls on photosynthetic seasonality are less well understood than in temperate zones (Cleland et al., 2007; Wu et al., 2016). In Amazonia, in situ observations from eddy-flux towers (Hutyra et al., 2007; Restrepo-Coupe et al., 2013; Saleska et al., 2003) and field data (Doughty and Goulden, 2008; Zhang et al., 2010) suggest seasonal variations in gross carbon uptake also in evergreen vegetation. The processes driving these changes are only poorly represented in earth system models. In the absence of water limitation, oscillations in photosynthetic fluxes of evergreen tropical forests are likely a consequence of allocation of resources to growth of new leaves (Restrepo-Coupe et al., 2013; Wu et al., 2016). In equatorial forests, leaf flushing is correlated with increased light availability during the dry season while water supply is maintained through deep root systems (Nepstad et al., 1994). In contrast, more water-limited environments of southern Amazonia have shown photosynthesis decline during the dry season, likely in response to depletion of soil water (Guan et al., 2015).

Frequent satellite observations of vegetation biochemistry and leaf area may provide clues necessary to fully understand the seasonal rhythm of ecosystem metabolism. However, remote sensing of tropical regions has proven challenging and resulted in an extensive debate over sunlight and precipitation mediated changes in tropical regions (Bi et al., 2015; Morton et al., 2014; Samanta et al., 2012). Some studies (Huete et al., 2006; Myint et al., 2007; Zhou et al., 2014) have reported widespread and large seasonal variations between dry and wet season, whereas others have suggested no observational evidence for changes in tropical vegetation (Atkinson et al., 2011; Morton et al., 2014). The discrepancies can in part be attributed to errors in the estimation of atmospheric aerosol loadings and deficiencies in cloud screening (Hilker et al., 2015).

New scaling approaches in combination with comprehensive field studies may help resolve some of these uncertainties and obtain a more biophysical understanding of the climatic and biological interactions during dry and wet periods. Most remote sensing time series use vegetation indices (VIs) for assessing vegetation responses to climate variables. While based on well-described physical principles, VIs are fundamentally empirical, because they are related to plant physiological traits, but do not explicitly model leaf-to-canopy radiative transfer. VI-derived vegetation greenness is therefore, dependent on soil and background effects, canopy structure and the view-illumination geometry (Galvão et al., 2013; Huete et al., 2006). Furthermore, VIs saturate in high biomass canopies (Moura et al., 2015).

Complementary to evidence of greenness derived from VIs, canopy reflectance (CR) models may provide new insights into seasonal variations of tropical vegetation. Canopy reflectance models couple radiative transfer theory with leaf optical models to simulate reflectance and transmittance of light through a canopy as a function of its constituents (Jacquemoud et al., 2009). When inverted, these models can provide estimates of biophysical quantities in an analytical fashion so that derived products are better scale-able in space and time. While CR models have existed for some time, their use over large areas has been hampered by the availability of suitable reflectance data. First, retrieval of biochemical estimates from inverse CR models depends on the quality of radiometric information in the visible and near infrared (NIR) spectrum and on the accuracy of atmospheric correction and cloud screening. Currently, orbital imaging spectrometers or hyperspectral sensors to measure canopy chemistry with 30 m spatial resolution and high signal-to-noise are not available for earth observation. Second, inverse modeling requires at least as many independent spectral observations as there are unknowns. Alternatively, these independent measurements can be obtained from multi-angle and multi-spectral observations. In this context, recently developed data processing techniques, such as the Multi-Angle Implementation of Atmospheric Correction Algorithm (MAIAC, Lyapustin et al., 2012), provide new opportunities for large scale model inversions by exploiting the multi-angle capacity of the Moderate Resolution Imaging Spectroradiometer (MODIS).

As a preparatory study for the Environmental Mapping and Analysis (EnMAP) planned for 2019 (Gunter et al., 2015), we investigate whether MODIS (MAIAC) multi-angle observations can be utilized to characterize changes in vegetation chlorophyll from an inverted canopy reflectance model. The idea is to compose a preliminary temporal database of vegetation chlorophyll over the Amazon that can serve as reference for future studies using hyperspectral sensors. We utilized ProSAIL, a fully coupled, canopy reflectance model of plant biophysical properties (Jacquemoud et al., 2009) that is among the most widely used and validated models in temperate and dense, tropical ecosystems (Galvão et al., 2013; Zhang et al., 2010). In Brazil, we focused our analysis on a large area of the Amazon (1000 × 1000 km) and on two flux-tower field stations (Manaus and Tapajós). MODIS derived estimates between 2000 and 2015 were inspected for consistency using eddy covariance derived fluxes, tower-based hyperspectral chlorophyll estimates, and field chlorophyll measurements to analyze seasonal patterns of pigment concentrations. By combining canopy reflectance model (ProSAIL) with multi-angle and directional observations from MODIS, the current approach is novel in providing an alternative to the use of empirical VIs to derive pigments and assess vegetation seasonality in the Amazon. It was also adapted to mono-angle observations acquired by a tower-mounted hyperspectral camera in Tapajós.

2. Methods

2.1. Study area

The study area has 1000 × 1000 km and includes the cities of Manaus and Santarém (Fig. 1). We also utilized data from two forest sites in the Brazilian Amazon: the Tapajós National Forest (k67-tower) in the state of Pará (2.85° S, 54.97° W) and the Reserva Cuiabá (k34-tower) in the state of Amazonas (2.81° S 60.21° W) (Fig. 1).

The sites span a gradient in precipitation and dry season length. The Tapajós forest is a moist primary forest with a mean precipitation of 2000 mm year−1 and an average dry season length of 4.7 months (Hutyra et al., 2007). The Reserva Cuiabá is a primary rain forest with an annual precipitation of 2600 mm and a dry season length of 2.4 months (Wu et al., 2016). Ground and eddy flux measurements at both sites have been collected since 1999 as part of the Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA).

2.2. Ground based and tower based measurements

In the Tapajós (k67) site, Eddy covariance (EC) estimates of net ecosystem productivity (NEP) and top-of-canopy photosynthetically active radiation (PAR) were collected between April 2001 and January 2006 (Hutyra et al., 2007). The estimates were downloaded as monthly daytime averages from the Oak Ridge National Laboratory’s Distributed Active Archive Center. The LBA project also provided field measurements of leaf area index (LAI) at k67 acquired between January and December 2004 (not all months were observed) (Costa and Cohen, 2013).

Leaf level measurements of vegetation chlorophyll were collected within the flux tower footprint on November 13–15, 2012. Using tree climbing to harvest branches from the upper canopy.
the leaves were cut and immediately placed in liquid nitrogen. The absorbance at 663 and 647 nm of the supernatant was used to estimate chlorophyll-a and chlorophyll-b concentrations following the protocol of Lichtenthaler (1987). From five common canopy tree species at Tapijos k67 site, 53 leaves were sampled in situ from both sunlit (canopy top) and deeply shade environments (5–10 m depth within the canopy). The leaves were also classified by three different leaf age classes (young: leaf age <2 months old; mature: 3–6 months old; old: >6 months old), with 1–3 replicates for each leaf age class.

In order to test the ability to scale ground measurements of chlorophyll, we also utilized data from the SOC-710 portable hyperspectral imaging system (Surface Optics Corporation, San Diego, CA, USA) that was mounted at a height of 61 m on the k67 eddy covariance tower. The SOC-710 is a 12-bit camera (low-noise silicon-based CCD) with spectral resolution of 4.7 nm. It operates in normal lighting conditions with variable exposure times and gain. The camera acquires data from 385 to 1050 nm in 128 spectral bands. Seventeen hyperspectral SOC-710 images were carefully selected and screened for data quality and clear sky conditions between July 27 and October 29, 2012. Reflectance measurements were calibrated using a Teflon panel. Images were acquired at an angle of 45° off-nadir around solar noon to minimize shading differences within the canopy.

In the Manaus (k34) site, NEP and PAR for the Cueiras reserve were available between 1999 and 2006 as monthly averages. Field measurements of vegetation chlorophyll were obtained within the flux tower footprint between April and November of 2015 and 203 leaves were sampled in situ within the tree canopies and classified by species, leaf age (young, mature, old) and light environment (sunlit/shaded and understorey). Leaves were cut and immediately kept on ice until laboratory analysis. The absorbance at 663 nm (Chl a) and 645 nm (Chl b) was measured using the Ultrospec 2100 pro UV/visible (Amersham, Biosciences, Cambridge, UK).

2.3. MODIS observations

We obtained MODIS (MAIAC) observations for a 1000 × 1000 km area spanning both tower sites between 2000 and 2015. Detailed descriptions of the MAIAC algorithm and of the assessment of errors and uncertainties are provided by Lyapustin et al. (2012) and Hilker et al. (2015), respectively. We utilized daily, 1 km surface reflectance products of MODIS bands 1–12 together with the sun-observer geometry of the individual observations as input data to ProSAIL.

The MAIAC quality information was used. Data were quality screened using the MAIAC quality flags in order to filter clouds or observations with high aerosol content. Only high quality pixels were selected.

2.4. Inversion of the ProSAIL canopy model from MODIS and hyperspectral tower data

ProSAIL is a combination of the PROSPECT leaf optical properties model and the SAIL canopy bidirectional reflectance model (Jacquemoud et al., 2009). Coupling of PROSPECT and SAIL as implemented in ProSAIL allows the assessment of canopy biochemistry through model inversion using multi-angle reflectance observations. Different optimization techniques are available. In this study, we used a modified Levenberg-Marquardt algorithm (implemented in the “minpack” c-library) to calculate the Jacobian matrix from forward-difference approximation (Moré et al., 1980).

Leaf area was not retrieved from PROSAIL model inversion, but instead estimated as a linear function of anisotropy of the Enhanced Vegetation Index (EVI) calculated from forward and backscatter reflectance and validated against field data, following the approach by Moura et al. (2015). Briefly, canopy structure affects the directional scattering of light and this scattering is observable from multi-angle observations. We utilized the RTLS BRDF model (Roujean et al., 1992) to derive forward and backscatter reflectance of the EVI and obtained LAI as linear function of the difference between them.

The estimated LAI values were then used to constrain the model inversion and retrieve canopy biochemistry (model unknowns: Chlorophyll_{a+b}, Carotenoids, Canopy water, Nitrogen) based on daily directional MODIS reflectance observed within that month. While our inversion approach yields all model unknowns as output, we focused our analysis on the chlorophyll estimates. The estimates prior to May 2002 were solely based on MODIS/Terra data and, after this date, on Terra and Aqua. To reduce the number of necessary inversions, we first identified groups of pixels of similar nadir reflectance and leaf area (Fig. 2). This was accomplished through normalizing the directional reflectance of MODIS bands 1–12 to a view zenith angle (VZA) of 0° and solar zenith angle (SZA) of 45°, using the Ross-Thick Li-Sparse (RTLS) kernels (Roujean et al., 1992) provided in MAIAC. The BRDF normalization was applied only to identify groups of pixels with similar reflectance characteristics. The model inversion itself was still run using the observed, directional reflectance. Second, a hierarchical clustering algorithm was applied to calculate similarity and dissimilarity of all pixels and across all reflectance bands using standardized z-scores. Finally, a subset of 100 pixels was randomly selected from within each group and from as wide a range of observations angles as possible to run the inverse model for a given month based on MAIAC directional reflectance and estimated LAI. Since ProSAIL accounts for the sun-viewing geometry, the use of directional reflectance, therefore, maximizes the number of independent observations.

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Estimates of chlorophyll were also computed from the SOC-710 hyperspectral camera images using all 128 bands. Similar to the process described for MODIS, pixel observations were grouped into areas with similar reflectance values using hierarchical clustering, assuming a LAI of 6.0 m² m⁻² (Costa and Cohen, 2013; Wu et al., 2016). No multi-angular observations were available from the tower-based camera. Therefore, chlorophyll estimates were derived using reflectance data clustered for similar shade fractions instead. Differences in canopy shading were obtained using the sequential maximum angle convex cone (SMACC) algorithm (Gruninger et al., 2004) to determine spectral end members and the abundance of canopy shading on a per pixel basis for each date.

Finally, independent estimates of measurement uncertainties are difficult to acquire at 1 km spatial resolution. In this study, we obtained uncertainties of surface reflectance from day to day reflectance variability in all 12 bands for all months within the observation period (Hilker et al., 2012). Error propagation and uncertainties in remotely sensed vegetation chlorophyll were then inferred by running repeated model inversions (n = 100) and randomly varying input surface reflectance by the observed intra-monthly range of MODIS reflectance values.

3. Results

The strong linear relationship between field-measured LAI and MODIS acquired from MODIS anisotropy at the Tapajós site confirmed the ability of MODIS anisotropy to describe seasonal changes in vegetation leaf area (Fig. 3). The measured LAI underestimated the field observations by about 0.3 m² m⁻². Part of the bias in LAI may stem from the differences in footprint size of the two measurement types.

ProSAIL modeled vegetation chlorophyll (ChlA+B) from multi-angle MODIS observations varied by up to 15 μg cm⁻² seasonally. Wet season (February 2004) ChlA+B averaged about 35.0 μg cm⁻² across the study area (Fig. 4A), whereas the end-of-dry season (October 2004) mean was about 38.3 μg cm⁻² (Fig. 4B), which represents a 10% change in mean Chl concentration. Data gaps were more common during the wet season than during the dry period due to extensive cloud cover.

Both sites exhibited clear seasonal variations in chlorophyll concentrations with values ranging between 30 and 40 μg cm⁻² (Fig. 5). The mean error of chlorophyll estimates was 1.04 μg cm⁻² at Manaus and 1.10 μg cm⁻² at Tapajós. The seasonal amplitude in chlorophyll was notably larger at Tapajós (8 μg cm⁻² per year at k67 vs. 4 μg cm⁻² per year at k34), which corresponds well with the drier climate and the longer dry season encountered in this part of the basin.

Fig. 6A shows a true color composite obtained by the hyperspectral camera in August 5, 2012, with the SOC-710 bands centered at 666 nm (red), 563 nm (green) and 487 nm (blue). The main species encountered within the camera footprint were indicated. From the SMACC analysis, we considered “shaded” pixels as those with more than 0.6 shadow fraction, while “sunlit” pixels were defined as those with less than 0.3 shadow fraction (Fig. 6B). Only regions with more than 60% shading were used. Hierarchical clustering identified 598 groups of pixels with similar reflectance. Excluding the shaded portions of the scene, modeled chlorophyll estimates between the species varied from 32 to 50 μg cm⁻². Manilkara huberi showed the highest mean ChlA+B concentrations (46.8 μg m⁻²). Mean values for Erisma uncinatum and Chamaecrista xinguensis were 45.5 and 43.4 μg cm⁻², respectively (Fig. 6C).

Hyperspectral camera observations closely matched in rank chlorophyll measurements obtained in the field (Fig. 7A). A highly significant linear relationship (r² = 0.98, p < 0.05) was observed between the field samples, categorized into species, sunlit and shaded vegetation, and the camera observations that best matched the sampling date (September 25, 2012). The field observations were averaged by species and shade/sun status. The total number of samples presented in Fig. 7A (n = 4) appears small, but results are average values based on all 53 field observations. We also investigated the potential to scale tower observations in time by matching the sequence of SOC-710 images available at k67 between July and September to the corresponding MODIS overpasses. The results confirmed a highly significant linear correlation (r² = 0.73, p < 0.05) also in the temporal domain (Fig. 7B). The relationship was systematically biased, as camera-based ChlA+B varied between 42 and 52 μg cm⁻², whereas seasonal changes observed by MODIS ranged only between 36 and 38 μg cm⁻², possibly due
Fig. 4. Seasonal variation in ProSAIL derived concentrations of vegetation chlorophyll (Chl$_{a+b}$) in February (A) and October (B) 2004. The location of the k34 (Manaus) and k67 (Tapajós) towers is illustrated as red triangles.

Fig. 5. Time series of ProSAIL derived Chl$_{a+b}$ observed at Manaus (A) and Tapajós (B) between 2000 and 2014 (3 km radius around the tower). The gray area represents the estimated uncertainty range calculated as standard deviation of the propagated range of reflectance observed within a month.

Fig. 6. (A) Illustration of SOC-710 hyperspectral imagery in a true color composite. The three main species delineated in the camera footprint are Manilkara huberi (in red), Erisma uncinatum (in blue) and Chamaecrista xinguensis (in yellow). (B) Corresponding shadow fraction endmember modeled using the SMACC algorithm; and (C) Chl$_{a+b}$ estimates [µg cm$^{-2}$] obtained from ProSAIL. The calibration panel is visible at the bottom of the image (excluded from analysis). The red polygons in (B) represent areas with more than 60% shading.
Fig. 7. (A) Relationship between field measured vegetation chlorophyll at k67, categorized by species, sunlit and shaded leaves (average of 53 observations), and modeled ChlA+B using the camera image that best matched the field sampling date (September 25, 2012). (B) Relationship between k67 tower-based ChlA+B using the full time series of camera observations (x-axis) between July 27 and October 29 and ChlA+B estimates obtained from the corresponding MODIS overpasses (y-axis). The RMSE is 0.355 µg cm⁻².

Fig. 8. Relationship between vegetation chlorophyll measured at k34, categorized into sunlit and shaded foliage, and corresponding MODIS ChlA+B (y-axis) acquired over the same month. The acquisition dates are color coded by day of year (DOY). The RMSE is 0.470 µg cm⁻².

to differences in shadow fractions resulting from the very different pixel size observed by the two instruments. Observations made at the Tapajós site were confirmed also for Manaus (Fig. 8). At k34, no tower-mounted hyperspectral camera was available. However, chlorophyll observations acquired repeatedly over seven months provided an opportunity to relate field measurements to MODIS observations directly. While the ProSAIL applied to tower hyperspectral data underestimated the field measured chlorophyll at k67 (Fig. 7b), it overestimated this constituent when using MODIS data at k34 (Fig. 8). Differences in offsets observed in Figs. 6b and 7 may be explained by the distinct footprint sizes of the two measurement types (tower and satellite) and by the difficulties to model shading on each dataset.

MODIS derived ChlA+B estimates were closely related to incoming PAR measured at the top of the k34 and k67 flux towers between 2000 and 2006 (Fig. 8). Values shown are daytime monthly averages. We included a one-month lag in our analysis to allow for a response time of the chlorophyll build-up. ChlA+B values from a given month were related to PAR values from the previous month (Fig. 9).

Comparison between monthly averaged NEP and monthly MODIS ChlA+B showed similar seasonal patterns at k34 (Fig. 10A) and k67 (Fig. 10B). At Manaus (k34), ChlA+B concentrations increased from a minimum average of 31 µg cm⁻² observed in May to 39 µg cm⁻² in August. After that, a steady decline was observed toward the beginning of the next dry season. At Tapajós (k67), mean ChlA+B concentrations showed a minimum value of 32 µg cm⁻² in May and increased to about 39 µg cm⁻² in September. In both sites, the standard deviation decreased from the wet to the dry season.

Seasonal changes in ChlA+B were well correlated with new green leaf production published in previous works (Fig. 11). ChlA+B followed new leaf production closely ($r^2 = 0.64$ and 0.59 for k34 and k67, respectively). Prior to month 3, new leaf production increased with chlorophyll concentrations, while between months 3 and 5 no change in new leaf production was observed. ChlA+B declined with a shift of leaf demography toward older leaf area. Starting in month 5, the strong increase in ChlA+B coincided with a strong increase in new leaf production, indicating higher chlorophyll concentration in young and mature leaves than in older ones.

Seasonal patterns observed in ChlA+B were different from vegetation greenness observed by conventional VIS. In Fig. 12, EVI and NDVI were derived from the same MODIS MAIAC data product, but were calculated using BRDF normalized (BRFn) observations (SZA = 45°; VZA = 0°). Both vegetation indices showed seasonal variations. However, changes in NDVI were more similar to those observed in ChlA+B, but onset and peak of greening occurred earlier, in April.

4. Discussion

Our unique approach using multi-angle MODIS observations and canopy reflectance model makes two important contributions for the remote sensing of pigment retrievals. The first contribution is to provide a preliminary long-term time series of MODIS (MAIAC)-based chlorophyll estimates over the Amazon. This database can be further refined through robust validation in order to support future canopy chemistry studies provided by the planned hyperspectral missions having much better spatial/spectral resolution than MODIS (e.g., EnMAP) but with lower temporal resolution. Despite the need of more samples for robust validation, the convergence of evidences observed during the comparison between chlorophyll estimates and flux tower measurements allow us to observe seasonal changes in the ability of plants to absorb photosynthetically active radiation.

Light absorption of plants is a function of the amount and the efficiency of the photosynthetic surface area. While several studies have reported increases in leaf surface area during the dry season
Fig. 9. Relationship with a one-month lag between photosynthetically active radiation (PAR) measured at the top of the eddy flux towers (2000–2006) and corresponding MODIS estimates of Chl_{A+B} in Manaus (A) and Tapajós (B).

Fig. 10. Seasonality of Chl_{A+B} (in black, left y-axis) and NEP (in red, right y-axis) at the k34 (A) and k67 (B) sites. Observations were averaged across multiple years to illustrate the mean seasonal signal. The error bars represent the standard deviations of the monthly mean observations. The gray areas represent the dry season (precipitation < 100 mm month⁻¹).

Fig. 11. Seasonal dynamics of Chl_{A+B} concentrations (black, left axis) and vegetation leaf area (gray axis), partitioned in young leaves, mature leaves and old leaves (data from Wu et al., 2016) for the k34 (A) and k67 (B) sites. The figure also shows the seasonal dynamics of new leaf production (in red) (r² = 0.64 and 0.59 for k34 and k67, respectively). The gray areas represent the dry season (precipitation <100 mm month⁻¹).
(Hilker et al., 2015; Huete et al., 2006; Myneni et al., 2007), the photosynthetic efficiency of this surface area is largely not accounted for in current photosynthesis models (Wu et al., 2016). Absorption efficiency is tightly linked to the concentration of chlorophyll within a leaf (Junker and Ensminger, 2016). Such measures of “leaf efficiency”, however, are not easily acquired using VIs. Results of Fig. 12 have shown that seasonal patterns of chlorophyll are much more related to changes in the NDVI than the EVI, because the EVI largely dependent on the NIR reflectance (Galvão et al., 2013). Results provided in Figs. 5–7 have demonstrated that field measurements of vegetation chlorophyll agreed in rank with ProSAIL estimates from multi-angle MODIS data.

The second contribution of our work is to provide new opportunities for inferring leaf demography and support evidence for it as driver of seasonality in tropical forests. Leaf chlorophyll concentrations are closely linked to leaf age (Doughty and Goulden, 2008). Spatially contiguous estimates of ChlA+B can deliver insights into the proportion of young leaves emerging in a given month. The increase in new leaf production (Fig. 11) was consistent with an increase in ChlA+B at both research sites, whereas increase in the proportion of old leaf area resulted in a decrease of ChlA+B observed by MODIS. This different behavior with leaf age is consistent with previous observations concluding that ChlA+B is withdrawn from older leaves in preparation for new leaf production (Hortonsteiner, 2006). As a result, at 1 km pixel size, changes in leaf chlorophyll concentrations can be interpreted as shifts in the proportion of leaves with higher ChlA+B versus those with lower ChlA+B concentrations in addition to changes in leaf area.

The seasonal signal observed from MODIS ChlA+B, compared to the high level of species diversity found at both sites, provides evidence of synchronized leaf flushing early during the dry season. Previous results have found that net leaf flushes are asynchronous in regions with short dry seasons and become more synchronous across a west-to-east longitudinal moisture gradient of increasing dry season length. Wu et al. (2016) estimated that the effect of combined new leaf growth shifting canopy composition toward younger, more light-use efficient leaves, explains about 27% increases in ecosystem productivity. This is consistent with the increase in ChlA+B, in response to an increase in tower measured PAR (Fig. 9), followed by an increase in net photosynthesis (Fig. 10). The findings presented in Figs. 8 and 9 allow the conclusion that canopy chlorophyll and leaf area are important drivers of seasonality in tropical forest productivity (Restrepo-Coupe et al., 2013).

The observed increase in chlorophyll together with an increase in PAR (Fig. 9) and before an increase in NPP (Fig. 10) allows the conclusion that new leaf production drives the seasonal increase in productivity during the dry season months. Therefore, our study supports the view that low radiation during wet season is a growth limiting factor (Brando et al., 2010; Huete et al., 2006; Hutrya et al., 2007; Myneni et al., 2007; Samanta et al., 2012) but suggests that the observed increase in productivity during the dry season is preceded by a distinct light-response. This light response increases the absorption efficiency of the leaf surface area (Fig. 10) in addition to canopy leaf area (Myneni et al., 2007). Taken together, these changes suggest significant seasonal variation in standing canopy photosynthetic capacity (Restrepo-Coupe et al., 2013). Not accounting for these changes may result either in underestimation of the seasonal dynamics of tropical vegetation or in overestimation of the effect of sunlight on photosynthesis.

![Fig. 12](image-url) Seasonal changes in ChlA+B (in black) plotted against NDVI (top line, in red) and EVI (bottom line, in red) for k34 Manaus (A and C) and k67 Tapajós (B and D). The analysis averages years between 2000 and 2015, excluding the extreme drought years of 2005 and 2010. The gray areas represent the dry season (precipitation <100 mm month$^{-1}$).
By adjusting the input variables in ProSAIL, the current approach can be applied to other tropical forests of the world. However, for any scenario, robust validation of the chlorophyll estimates is still the greatest challenge due to the need of intensive fieldwork to represent the MODIS footprint size. For instance, our MODIS estimates performed in the 1000 × 1000 km area were just supported by a small number of leaves collected around two towers in the Amazon (53 leaves in Tapajós and 203 leaves in Manaus). The strategy of validation can be facilitated with the use of the upcoming hyperspectral EnMAP data (30 m spatial resolution) and with a network of hyperspectral cameras mounted over other towers in the Amazon. Despite the uncertainties, our seasonal estimates were consistent with flux tower measurements of PAR and NEP.

5. Conclusions

We have shown that Chl_{a+b} concentrations over the Amazon can be estimated from multi-angle, multi-temporal, multi-spectral MODIS observations through inversion of canopy radiative transfer models at regional scales and over multiple years. The current approach was adapted also to mono-angle hyperspectral observations using hierarchical clustering to reduce the number of necessary inversions, and linear spectral unmixing to compute shadow fractions, as demonstrated in the data analysis of the tower-mounted hyperspectral camera. The field chlorophyll measurements were under- and overestimated by ProSAIL using the camera and MODIS data, respectively. Despite the uncertainties and the need of a more robust validation, our results have demonstrated strong seasonal changes in the capacity of leaves to absorb PAR across two tropical forest sites selected to be representative of a broad range of tropical vegetation. This capacity is a function of both, the amount and the chlorophyll concentration within the photosynthetic surface area, and is an important driver of growth performance and vegetation phenology.

We conclude that multi-angle and directional observations from MODIS can help scale vegetation phenology and seasonal controls on ecosystem productivity systematically in space and time. In addition, our long-term chlorophyll estimates comprise an important preliminary database to support future studies in the Amazon using the upcoming EnMAP mission with greater number of bands and better spatial resolution than MODIS but with lower revisit time of the scene. It also contributes to other hyperspectral missions having larger swath width (145 km) such as the planned Hyperspectral Infrared Imager (HyspIRI) (Hochberg et al., 2015).

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