Sunlight mediated seasonality in canopy structure and photosynthetic activity of Amazonian rainforests

2015 Environ. Res. Lett. 10 064014

(http://iopscience.iop.org/1748-9326/10/6/064014)

Environmental Research Letters

LETTER

Sunlight mediated seasonality in canopy structure and photosynthetic activity of Amazonian rainforests

Jian Bi[1,20], **Yuri Knyazikhin**[1,20], **Sungho Choi**[1], **Taejin Park**[1], **Jonathan Barichivich**[2], **Philippe Ciais**[3], **Rong Fu**[4], **Sangram Ganguly**[5], **Forrest Hall**[6], **Thomas Hilker**[7], **Alfredo Huete**[8], **Matthew Jones**[9], **John Kimball**[9], **Alexei I Lyapustin**[10], **Matti Mõttus**[11], **Ramakrishna R Nemani**[12], **Shilong Piao**[13,14], **Benjamin Poulter**[15], **Scott R Saleska**[16], **Sassan S Saatchi**[17,18], **Liang Xu**[17], **Liming Zhou**[19] **and Ranga B Myneni**[1]

[1] Department of Earth and Environment, Boston University, Boston, MA 02215, USA
[2] Climatic Research Unit, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK
[3] Laboratoire des Sciences du Climat et de l'Environnement, IPSL-LSCE, CEA-CNRS-UVSQ, 91191 Gif sur Yvette Cedex, France
[4] Department of Geological Sciences, The University of Texas at Austin, Austin, TX 78712, USA
[5] Bay Area Environmental Research Institute, NASA Ames Research Center, Moffett Field, CA 94035, USA
[6] Biospheric Sciences Laboratory, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA
[7] College of Forestry, Oregon State University, Corvallis, OR 97331, USA
[8] Plant Functional Biology and Climate Change Cluster, University of Technology Sydney, New South Wales 2007, Australia
[9] Numerical Terradynamic Simulation Group, The University of Montana, Missoula, MT 59812, USA
[10] Climate and Radiation Laboratory, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA
[11] Department of Geosciences and Geography, University of Helsinki, FI-00014, Helsinki, Finland
[12] NASA Advanced Supercomputing Division, Ames Research Center, Moffett Field, California 94035, USA
[13] Department of Ecology, Peking University, Beijing 100871, People's Republic of China
[14] Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100085, People's Republic of China
[15] Department of Ecology, Montana State University, Bozeman, MT 59717, USA
[16] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA
[17] Institute of the Environment and Sustainability, University of California, Los Angeles, CA 90095, USA
[18] Radar Science and Engineering section, Jet Propulsion Laboratory, California Institute of Technology, Pasadena, CA 91109, USA
[19] Department of Atmospheric and Environmental Sciences, University at Albany, State University of New York, Albany, New York 12222, USA
[20] These authors contributed equally to this work.

E-mail: jknjazi@bu.edu

Keywords: Amazonian rainforests, seasonality, remote sensing, MISR, MODIS

Supplementary material for this article is available online

OPEN ACCESS

RECEIVED
26 February 2015

REVISED
28 May 2015

ACCEPTED FOR PUBLICATION
1 June 2015

PUBLISHED
16 June 2015

Abstract

Resolving the debate surrounding the nature and controls of seasonal variation in the structure and metabolism of Amazonian rainforests is critical to understanding their response to climate change. *In situ* studies have observed higher photosynthetic and evapotranspiration rates, increased litterfall and leaf flushing during the Sunlight-rich dry season. Satellite data also indicated higher greenness level, a proven surrogate of photosynthetic carbon fixation, and leaf area during the dry season relative to the wet season. Some recent reports suggest that rainforests display no seasonal variations and the previous results were satellite measurement artefacts. Therefore, here we re-examine several years of data from three sensors on two satellites under a range of sun positions and satellite measurement geometries and document robust evidence for a seasonal cycle in structure and greenness of wet equatorial Amazonian rainforests. This seasonal cycle is concordant with independent observations of solar radiation. We attribute alternative conclusions to an incomplete study of the seasonal cycle, i.e. the dry season only, and to prognostications based on a biased radiative transfer model. Consequently, evidence of dry season greening in geometry corrected satellite data was ignored and the absence of evidence for seasonal variation in lidar data due to noisy and saturated signals was misinterpreted as evidence of the absence of changes during the dry season. Our results, grounded in the physics of radiative transfer, buttress previous reports of dry season increases in leaf flushing, litterfall, photosynthesis and evapotranspiration in well-hydrated Amazonian rainforests.

1. Introduction

Understanding the seasonal variation in functioning of rainforests and its controls are requisite for understanding how rainforests will respond to climate change. *In situ* studies report counter-intuitive seasonal variation in wet equatorial Amazonian rainforests —higher photosynthetic and evapotranspiration rates and increased litterfall and leaf flushing during the Sunlight-rich dry season (Saleska *et al* 2003, da Rocha *et al* 2004, Goulden *et al* 2004, Rice *et al* 2004, Hasler and Avissar 2007, Hutyra *et al* 2007, Negrón Juárez *et al* 2009, Costa *et al* 2010, Jones *et al* 2014). Water limitation during the dry season is alleviated in these forests through deep roots and hydraulic redistribution (Nepstad *et al* 1994, Oliveira *et al* 2005). Satellite data, which cover a large area and span a long time period, support findings of *in situ* studies—higher radiometric greenness level and green leaf area during the dry season compared to the wet season (Xiao *et al* 2005, Huete *et al* 2006, Myneni *et al* 2007, Samanta *et al* 2012, Hilker *et al* 2014, Jones *et al* 2014, Maeda *et al* 2014). This convergent view of seasonality, parsed from several studies, shows how sunlight interacts with adaptive mechanisms to result in higher rates of leaf flushing, litterfall, photosynthesis and evapotranspiration in tropical forests if water limitation is absent (Wright and Van Schaik 1994, Restrepo-Coupe *et al* 2013, Borchert *et al* 2015, Guan *et al* 2015).

This community-consensual view was questioned in recent studies (Galvão *et al* 2011, Morton *et al* 2014). The studies claim that the dry season greening inferred from passive remote sensing data resulted from an artificial increase in forest canopy reflectance at near-infrared (NIR) wavelengths caused by variations in sun-satellite sensor geometry. Their analyses of satellite-borne lidar data suggested that these forests exhibited no seasonal variations in canopy structure or leaf area. Relying on model simulations to guide and imbue a physical meaning to the satellite data analysis, the studies conclude that Amazon rainforests maintain consistent structure and greenness during the dry season.

These contradictory results justify a re-examination of the same satellite data with the goal of assessing seasonality in wet equatorial Amazonian rainforests. In addition to data from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) on the Terra platform and the Geoscience Laser Altimeter System (GLAS) instrument onboard the Ice, Cloud and land Elevation Satellite (ICESat) used in (Morton *et al* 2014), we also include data from the MODIS instrument on Aqua and Multiangle Imaging Spectroradiometer (MISR) on the Terra satellite. The MISR sensor views the Earth's surface with nine cameras simultaneously, as opposed to the two MODIS sensors, which are capable of only one view each. This feature enables the rigorous use of the theory of radiative transfer in vegetation canopies—the fundamental theory that explains from first principles the mechanisms underlying the signals generated by the canopy and measured by a remote sensor (Knyazikhin *et al* 2005).

This study is focused on terra firme rainforests in central Amazonia that are relatively undisturbed by human activities (supplementary data and methods section 1, figure S1). The period June to May is treated as one seasonal cycle as per convention (Huete *et al* 2006, Morton *et al* 2014). It consists of a short dry season, June to October, and a long wet season thereafter (supplementary data and methods section 1). The following analysis of satellite borne sensor data addresses the question at the center of current debate —did previous studies (Xiao *et al* 2005, Huete *et al* 2006, Myneni *et al* 2007, Brando *et al* 2010, Samanta *et al* 2012) misinterpret changes in near-infrared (NIR) reflectance caused by seasonal changes in sun-satellite sensor geometry (figures S2 and S3) as seasonal variations in rainforest canopy structure and greenness (Galvão *et al* 2011, Morton *et al* 2014)?

2. Data and methods

A detailed description of methods and data used is given in the supplementary information available at stacks.iop.org/ERL/10/064014/mmedia. A brief summary is provided here. The study region and the various data analysed in this study are detailed in the supplementary data and methods section 1–2. The sun-sensor geometry relevant to the discussion in this article is presented in the supplementary data and methods section 3. The theory of remote measurements and evaluation of NIR reflectance angular signatures (figure 3) and their interpretation is described in the supplementary data and methods section 4. A critical look at Morton *et al* 2014 analyses of MODIS and GLAS data is presented in the supplementary discussion. Abbreviations and symbols are listed in supplementary table S5.

3. Results and discussioin

3.1. Leaf area index seasonality

The seasonal cycle of green leaf area inferred from satellite data (figure 1(a)) exhibits rising values during the dry season (June to October), high values during the early part of the wet season (November to February) and decreasing values thereafter (March to May). This seasonal variation of about 20% is imposed on a base value of Leaf Area Index (LAI, one-sided green leaf area per unit ground area) of about 5.75, is greater than the uncertainty of the LAI product (0.66 LAI, Yang *et al* 2006) and is observed in nearly 70% of the rainforests in the study domain (figure S4(a)); the rest lacked valid data. Is this seasonal variation real or a misinterpretation of changes in satellite-sensor measurements caused by seasonal changes in sun position

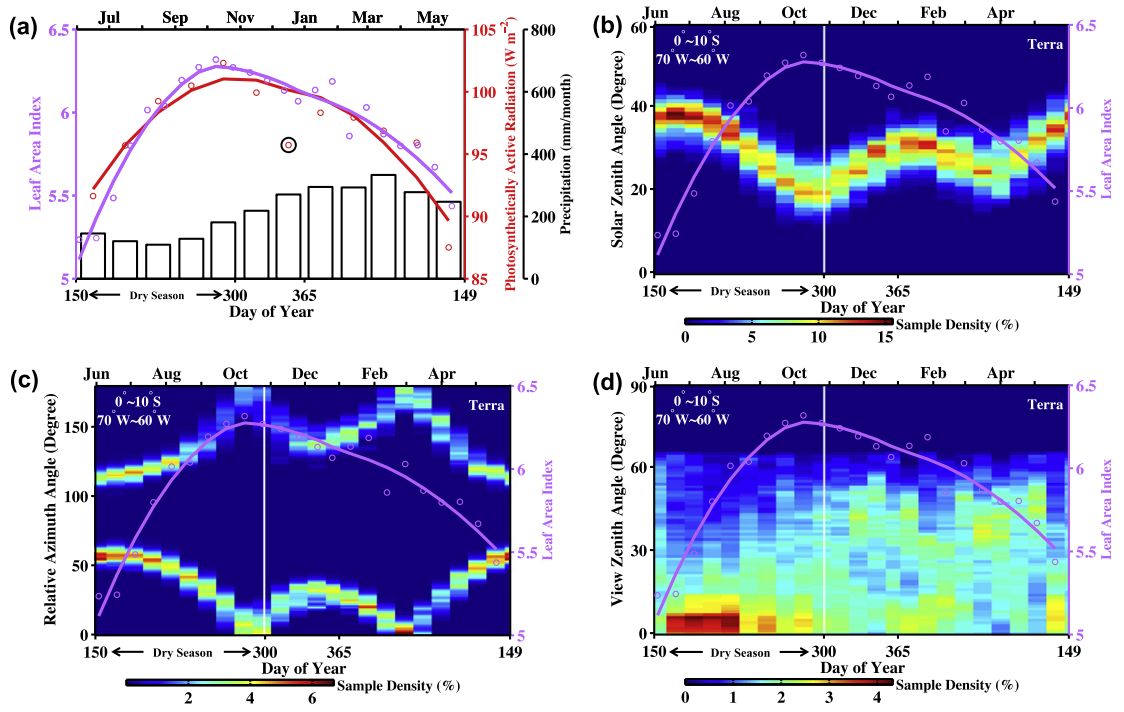

Figure 1. Seasonal variations in green leaf area of central Amazonian rainforests. (a) Seasonal cycles of Terra MODIS leaf area index (LAI), at-surface photosynthetically active radiation (PAR) from CERES, and TRMM precipitation. The PAR polynomial regression curve excludes the circled data point. The seasonal profiles represent average values over pixels that exhibited dry season greening in at least 4 out of 7 seasonal cycles analyzed (63% of all forest pixels). (b)–(d) Seasonal cycle of LAI, as in panel (a), contrasted against seasonal variations in (b) solar zenith angle, (c) sensor view relative azimuth angle and (d) view zenith angle.

in the sky and the manner in which the sensor measures reflected radiation ('sun-sensor geometry')? The answer requires an understanding of how this geometry changes during the seasonal cycle, which is described in the supplementary data and methods section 3.

The seasonal cycle of leaf area in figure 1(a) cannot be an artefact of seasonal changes in sun-sensor geometry because the algorithm with which leaf area is derived explicitly accounts for geometry changes, i.e. the algorithm is capable of differentiating between changes in measurements caused by leaf area changes and those caused by geometry changes (Knyazikhin *et al* 1999, Knyazikhin *et al* 1998). This is also evident from the fact that the seasonal cycle of leaf area does not track the seasonal course of either the Sun position in the sky (figure 1(b)) or the MODIS sensor sampling (figures 1(c) and (d)). Instead, it tracks independently obtained observations of seasonal variation in sunlight (figure 1(a)). This behavior is consistent with the idea that sunlight acts as a proximate cue for leaf production in moist tropical forests if water limitation is absent (Wright and Van Schaik 1994, Borchert *et al* 2015, Guan *et al* 2015). Thus, relatively high sunlight levels from absence of clouds during the dry season cause leaf area to increase, which in turn generates higher rates of photosynthesis (Saleska *et al* 2003, Da Rocha *et al* 2004, Restrepo-Coupe *et al* 2013, Gatti *et al* 2014). But, photosynthesis becomes decoupled from sunlight during the early to middle part of the wet season. This results in increasing rates of photosynthesis, which are possibly sustained by still sufficiently high levels of light and increasing leaf production (Restrepo-Coupe *et al* 2013). All three decrease rapidly thereafter. A bimodal seasonal cycle of LAI reported in one instance could be site-specific (figure 2 in Doughty and Goulden (2008)) as alternate *in situ* evidence does not exist (Restrepo-Coupe *et al* 2013, Xiao *et al* 2005, Asner *et al* 2000, Carswell *et al* 2002, Chave *et al* 2010, Malhado *et al* 2009, Negrón Juárez *et al* 2009).

3.2. Evidence for seasonality after sun-sensor geometry correction

The Enhanced Vegetation Index (EVI) is a proven proxy for the potential photosynthetic carbon fixation by vegetation (Xiao *et al* 2005, Huete *et al* 2006, Brando *et al* 2010). It is calculated from satellite-sensor measurements of reflected solar radiation at three different wavelength bands. These measurements depend on sun-sensor geometry, but this dependency can be eliminated by expressing the measurements in a fixed geometry (Morton *et al* 2014, Lyapustin *et al* 2012). The EVI calculated from MODIS sensor measurements in a fixed geometry, i.e. nadir viewing direction and 45° solar zenith angle, shows a distinct wet season decrease (figure 2(a)) and dry season increase (figure 2(b)). These changes are greater than a highly conservative estimate of the precision in 43% of the pixels during the wet season and 31% of the pixels

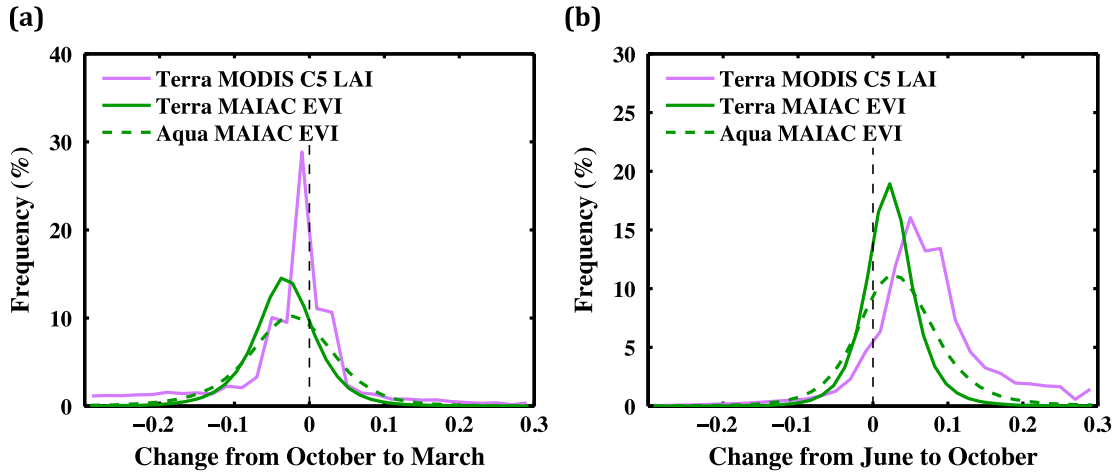

Figure 2. Wet and dry season changes in sun-sensor geometry corrected estimates of leaf area and greenness. Per-pixel changes in MODIS leaf area index (LAI) and MODIS MAIAC enhanced vegetation index (EVI) from (a) October to March and (b) June to October. LAI values are normalized by 10. The changes are calculated as the difference between the values in March and October, and October and June, respectively.

in the dry season. Here, the precision is estimated as the spatial standard deviation of the EVI data in the study domain. Analogous to EVI, pixel level estimates of green leaf area show a strong decrease in the wet season and increase during the dry season. The wet season decrease (figure 2(a)) suggests net leaf abscission, i.e. more older leaves dropped than those newly flushed, and the dry season increase indicates net leaf flushing (figure 2(b)), resulting in a sunlight mediated phenological behavior (Myneni *et al* 2007). The fact that both EVI and LAI show congruent changes during the seasonal cycle even though the Sun-sensor geometry effect is removed from measurements in different ways (Knyazikhin *et al* 1999, Knyazikhin *et al* 1998, Lyapustin *et al* 2012, Hilker *et al* 2014, Maeda *et al* 2014) is particularly noteworthy.

3.3. Evidence for seasonality from multiple sensors and geometries

Now we turn to satellite-sensor measurements of reflected solar radiation at the NIR wavelength band, which are at the heart of the controversy. These measurements are usually expressed as normalized quantities called reflectances (supplementary data and methods section 4.1–4.2). The geometric structure and radiation scattering properties of the rainforest canopy determine the magnitude and angular distribution of reflected radiation. The angular signatures of reflectance are therefore unique and rich sources of diagnostic information about rainforest canopies (Diner *et al* 1999). We first examine NIR angular signatures from the late dry season (October 15 to 30) and the middle part of the wet season (March 5 to 20). The Solar Zenith Angle (SZA) at the time when Terra (10:30 am) and Aqua (1:30 pm) satellites view the central Amazonian forests in March and October is between 20° and 30°. This variation minimally impacts the shape of angular signatures (supplementary data and methods section 4.4). MODIS and MISR sensors sample the rainforests very differently (figures S2(c)–(f); also see figure S1(c)). However, all the sensors record a distinct decrease in reflected NIR radiation in all view directions between October and March with no change in the overall shape of the angular signatures (figures 3(a) and (b)). Such a simple change in magnitude can only result from a change in canopy properties—this conclusion is based on the physics of how solar radiation interacts with foliage in vegetation canopies (supplementary data and methods section 4.3, figures S5(a) and (b)). The EVI, although evaluated from reflectances at NIR, red and blue wavelength bands, is tightly linked to NIR reflectance (Samanta *et al* 2012). Thus, the decrease in sun-sensor geometry corrected EVI (figure 2(a)) is in agreement with directly observed decreases in NIR angular signatures from October to March (figures 3(a) and (b)).

The wet season reduction in greenness is inconsistent with the hypothesis of invariant dry season greenness. Indeed the net loss of leaf area, without a corresponding net gain elsewhere during the seasonal cycle, will result in rainforests without leaves in a few years. If wet Amazonian forests somehow maintain consistent canopy structure and greenness during the dry season, then they must be either aseasonal or the entire seasonal cycle must be confined to the wet season, but this argument lacks empirical support. The question then arises whether variations in angular signatures of forest reflectance during the dry season support this inference?

Therefore, let us now consider NIR reflectances from early (25 June to 10 July) and the late dry season (15 October to 30 October) when both sun position in the sky and sensor sampling vary significantly (figures S2(a)–(d); also see figure S1(c)). MODIS and MISR measurements are made at significantly higher SZA in June (~35°–40°) compared to October (~20°–30°).

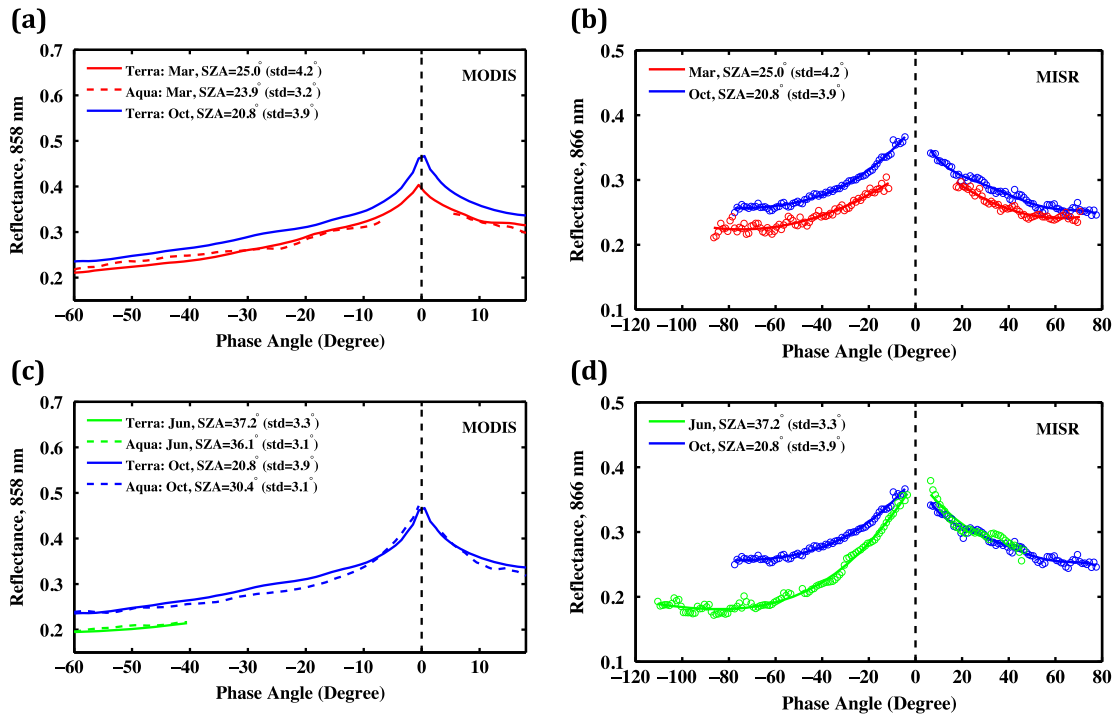

Figure 3. Seasonal changes in angular signatures of near-infrared (NIR) reflectance from three satellite borne sensors. Angular signatures of NIR reflectance in March (5 Mar to 20 Mar), June (25 Jun to 10 Jul) and October (15 Oct to 30 Oct). The Aqua MODIS signature for October is shown in panel (c) for clarity. The phase angle is the angle between the directions to the Sun and sensor (figure S1(c)).

The magnitude and shape of angular signatures are impacted when both canopy properties and SZA vary. However, a higher or equal reflectance at lower SZA relative to reflectance at higher SZA always indicates an increase in leaf area and foliage scattering properties according to the physics of radiation interaction in vegetation (supplementary data and methods section 4.4–4.5, figures S5(c)–(f)). This is observed clearly in MISR data (figure 3(d)) because this sensor views the Earth's surface with nine cameras simultaneously, as opposed to the two MODIS sensors (figure 3(c)), which are capable of only one view each (figure S3). Further, the juxtaposition of the two angular signatures in figure 3(d) is significantly different than that predicted by theory for the case of identical canopies (supplementary data and methods section 4.6). Thus, the NIR angular signatures in figure 3(d) indicate a change in vegetation structure (LAI) and greenness (EVI) during the dry season.

4. Conclusions

Satellite data indicate a distinct sunlight-mediated seasonality in leaf area and photosynthetic carbon fixation over unstressed rainforests in central Amazonia. This seasonal cycle is not an artefact of seasonal changes in sun position in the sky or how the satellite-sensor measures the reflected radiation field. The spatially expansive remote sensing data agree with available *in situ* data. A better understanding of how the rainforests will respond to climate change depends on future ground campaigns as satellite data can complement, but not substitute, field data.

Acknowledgments

This study was supported by NASA Earth Science Division.

Author contributions

J B, Y K, S C and T P performed the analyses. RBM wrote the initial draft. All authors contributed with ideas to the analyses and with writing the article. The authors declare no conflict of interest.

References

Asner G P, Townsend A R and Braswell B H 2000 Satellite observation of El Nino effects on Amazon forest phenology and productivity *Geophys. Res. Lett.* **27** 981–4

Brando P M, Goetz S J, Baccini A, Nepstad D C, Beck P S and Christman M C 2010 Seasonal and interannual variability of climate and vegetation indices across the Amazon *Proc. Natl Acad. Sci. USA* **107** 14685–90

Borchert R, Calle Z, Strahler A H, Baertschi A, Magill R E, Broadhead J S, Kamau J, Njoroge J and Muthuri C 2015 Insolation and photoperiodic control of tree development near the equator *New Phytol.* **205** 7–13

Carswell F *et al* 2002 Seasonality in CO2 and H2O flux at an eastern Amazonian rain forest *J. Geophys. Res. Atmos.* **107** LBA43–1

Chave J *et al* 2010 Regional and seasonal patterns of litterfall in tropical South America *Biogeosciences* **7** 43–55

Costa M H *et al* 2010 Atmospheric versus vegetation controls of Amazonian tropical rain forest evapotranspiration: are the

wet and seasonally dry rain forests any different? *J. Geophys. Res. Biogeosci.* **115** G04021

Da Rocha H R, Goulden M L, Miller S D, Menton M C, Pinto L D, De Freitas H C and Silva Figueira A M E 2004 Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia *Ecol. Appl.* **14** S22–32

Diner D J, Asner G P, Davies R, Knyazikhin Y, Muller J P, Nolin A W, Pinty B, Schaaf C B and Stroeve J 1999 New directions in earth observing: scientific applications of multiangle remote sensing *Bull. Am. Meteorol. Soc.* **80** 2209–28

Doughty C E and Goulden M L 2008 Seasonal patterns of tropical forest leaf area index and CO_2 exchange *J. Geophys. Res. Biogeosci.* **113** G00B06

Galvão L S, Dos Santos J R, Roberts D A, Breunig F M, Toomey M and De Moura Y M 2011 On intra-annual EVI variability in the dry season of tropical forest: a case study with MODIS and hyperspectral data *Remote Sens. Environ.* **115** 2350–9

Gatti L *et al* 2014 Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements *Nature* **506** 76–80

Goulden M L, Miller S D, Da Rocha H R, Menton M C, De Freitas H C, Silva Figueira A M E and De Sousa C D 2004 Diel and seasonal patterns of tropical forest CO_2 exchange *Ecol. Appl.* **14** S42–54

Guan K *et al* 2015 Photosynthetic seasonality of global tropical forests constrained by hydroclimate *Nature Geosci.* **8** 284–9

Hasler N and Avissar R 2007 What controls evapotranspiration in the Amazon basin? *J. Hydrometeorol.* **8** 380–95

Hilker T *et al* 2014 Vegetation dynamics and rainfall sensitivity of the Amazon *Proc. Natl Acad. Sci. USA* **111** 16041–6

Huete A R *et al* 2006 Amazon rainforests green-up with sunlight in dry season *Geophys. Res. Lett.* **33** L06405

Hutyra L R *et al* 2007 Seasonal controls on the exchange of carbon and water in an Amazonian rain forest *J. Geophys. Res. Biogeosci.* **112** G03008

Jones M O, Kimball J S and Nemani R R 2014 Asynchronous Amazon forest canopy phenology indicates adaptation to both water and light availability *Environ. Res. Lett.* **9** 124021

Knyazikhin Y *et al* 1999 MODIS leaf area index (LAI) and fraction of photosynthetically active radiation absorbed by vegetation (FPAR) product (MOD15) *Algorithm Theoretical Basis Document* (https://lpdaac.usgs.gov/products/modis_products_table/mcd15a2)

Knyazikhin Y, Martonchik J, Myneni R, Diner D and Running S 1998 Synergistic algorithm for estimating vegetation canopy leaf area index and fraction of absorbed photosynthetically active radiation from MODIS and MISR data *J. Geophys. Res. Atmos.* **103** 32257–75

Knyazikhin Y, Marshak A and Myneni R B 2005 Three-dimensional radiative transfer in vegetation canopies and cloud-vegetation interaction *Three Dimensional Radiative Transfer in the Cloudy Atmosphere* ed A Marshak and A B Davis (Berlin, Heidelberg: Springer) pp 617–51

Lyapustin A I *et al* 2012 Multi-angle implementation of atmospheric correction for MODIS (MAIAC): 3. Atmospheric correction *Remote Sens. Environ.* **127** 385–93

Maeda E E, Heiskanen J, Aragão L E O C and Rinne J 2014 Can MODIS EVI monitor ecosystem productivity in the Amazon rainforest? *Geophys. Res. Lett.* **41** 7176–83

Malhado A, Costa M H, de Lima F Z, Portilho K C and Figueiredo D N 2009 Seasonal leaf dynamics in an Amazonian tropical forest *For. Ecol. Manage.* **258** 1161–5

Morton D C *et al* 2014 Amazon forests maintain consistent canopy structure and greenness during the dry season *Nature* **506** 221–4

Myneni R B *et al* 2007 Large seasonal swings in leaf area of Amazon rainforests *Proc. Natl Acad. Sci. USA* **104** 4820–3

Negrón Juárez R I, da Rocha H R, Goulden M L and Miller S D 2009 An improved estimate of leaf area index based on the histogram analysis of hemispherical photographs *Agric. For. Meteorol.* **149** 920–8

Nepstad D C *et al* 1994 The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures *Nature* **372** 666–9

Oliveira R S, Dawson T E, Burgess S S and Nepstad D C 2005 Hydraulic redistribution in three Amazonian trees *Oecologia* **145** 354–63

Restrepo-Coupe N *et al* 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 *Agric. For. Meteorol.* **182** 128–44

Rice A H *et al* 2004 Carbon balance and vegetation dynamics in an old-growth Amazonian forest *Ecol. Appl.* **14** 55–71

Saleska S R *et al* 2003 Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses *Science* **302** 1554–7

Samanta A *et al* 2012 Seasonal changes in leaf area of Amazon forests from leaf flushing and abscission *J. Geophys. Res. Biogeosci.* **117** G01015

Wright S J and Van Schaik C P 1994 Light and the phenology of tropical trees *Am. Nat.* **143** 192–9

Xiao X *et al* 2005 Satellite-based modeling of gross primary production in a seasonally moist tropical evergreen forest *Remote Sens. Environ.* **94** 105–22

Yang W *et al* 2006 MODIS leaf area index products: from validation to algorithm improvement *IEEE Trans. Geosci. Remote Sens.* **44** 1885–98