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Steve F. Oberbauer

Department of Biological Sciences, Florida International University, oberbaue@fiu.edu

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Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests

Fabien H. Wagner¹, Bruno Hérault², Damien Bonal³, Clément Stahl^{4,5}, Liana O. Anderson⁶, Timothy R. Baker⁷, Gabriel Sebastian Becker⁸, Hans Beeckman⁹, Danilo Boanerges Souza¹⁰, Paulo Cesar Botosso¹¹, David M. J. S. Bowman¹², Achim Bräuning¹³, Benjamin Brede¹⁴, Foster Irving Brown¹⁵, Jesus Julio Camarero^{16,17}, Plínio Barbosa Camargo¹⁸, Fernanda C. G. Cardoso¹⁹, Fabrício Alvim Carvalho²⁰, Wendeson Castro²¹, Rubens Koloski Chagas²², Jérome Chave²³, Emmanuel N. Chidumayo²⁴, Deborah A. Clark²⁵, Flavia Regina Capellotto Costa²⁶, Camille Couralet⁹, Paulo Henrique da Silva Mauricio¹⁵, Helmut Dalitz⁸, Vinicius Resende de Castro²⁷, Jaçanan Eloisa de Freitas Milani²⁸, Edilson Consuelo de Oliveira²⁹, Luciano de Souza Arruda³⁰, Jean-Louis Devineau³¹, David M. Drew³², Oliver Dünisch³³, Giselda Durigan³⁴, Elisha Elifuraha³⁵, Marcio Fedele³⁶, Ligia Ferreira Fedele³⁶, Afonso Figueiredo Filho³⁷, César Augusto Guimarães Finger³⁸, Augusto César Franco³⁹, João Lima Freitas Júnior²¹, Franklin Galvão²⁸, Aster Gebrekirstos⁴⁰, Robert Gliniars⁸, Paulo Maurício Lima de Alencastro Graça⁴¹, Anthony D. Griffiths^{42,43}, James Grogan⁴⁴, Kaiyu Guan^{45,46}, Jürgen Homeier⁴⁷, Maria Raquel Kanieski⁴⁸, Lip Khoon Kho⁴⁹, Jennifer Koenig⁴³, Sintia Valerio Kohler³⁷, Julia Krepkowski¹³, José Pires Lemos-Filho⁵⁰, Diana Lieberman⁵¹, Milton Eugene Lieberman⁵¹, Claudio Sergio Lisi^{36,52}, Tomaz Longhi Santos²⁸, José Luis López Ayala⁵³, Eduardo Eijji Maeda⁵⁴, Yadvinder Malhi⁵⁵, Vivian R. B. Maria³⁶, Marcia C. M. Marques¹⁹, Renato Marques⁵⁶, Hector Maza Chamba⁵⁷, Lawrence Mbwambo⁵⁸, Karina Liana Lisboa Melgaço²⁶, Hooz Angela Mendivelso^{16,17}, Brett P. Murphy⁵⁹, Joseph J. O'Brien⁶⁰, Steven F. Oberbauer⁶¹, Naoki Okada⁶², Raphaël Pélissier^{63,64}, Lynda D. Prior¹², Fidel Alejandro Roig⁶⁵, Michael Ross⁶⁶, Davi Rodrigo Rossatto⁶⁷, Vivien Rossi⁶⁸, Lucy Rowland⁶⁹, Ervan Rutishauser⁷⁰, Hellen Santana²⁶, Mark Schulze⁷¹, Diogo Selhorst⁷², Williamar Rodrigues Silva⁷³, Marcos Silveira¹⁵, Susanne Spannl¹³, Michael D. Swaine⁷⁴, José Julio Toledo⁷⁵, Marcos Miranda Toledo⁷⁶, Marisol Toledo⁷⁷, Takeshi Toma⁷⁸, Mario Tomazello Filho³⁶, Juan Ignacio Valdez Hernández⁵³, Jan Verbesselt¹⁴, Simone Aparecida Vieira⁷⁹, Grégoire Vincent⁶⁴, Carolina Volkmer de Castilho⁸⁰, Franziska Volland¹³, Martin Worbes⁸¹, Magda Lea Bolzan Zanon⁸², and Luiz E. O. C. Aragão^{1,83}

¹Remote Sensing Division, National Institute for Space Research – INPE, São José dos Campos 12227-010, SP, Brazil

²CIRAD, UMR Ecologie des Forêts de Guyane, Kourou 97379, France

³INRA, UMR EEF 1137, Champenoux 54280, France

⁴INRA, UMR Ecologie des Forêts de Guyane, Kourou 97387, France

⁵Department of Biology, University of Antwerp, Wilrijk 2610, Belgium

⁶National Center for Monitoring and Early Warning of Natural Disasters – CEMADEN,

São José dos Campos 12.247-016, SP, Brazil

⁷School of Geography, University of Leeds, Leeds LS2 9JT, UK

⁸Institute of Botany, University of Hohenheim, 70593 Stuttgart, Germany

⁹Laboratory for Wood Biology and Xylarium, Royal Museum for Central Africa, Tervuren 3080, Belgium

¹⁰Programa de Pós-graduação em Ciências de Florestas Tropicais, Instituto Nacional de Pesquisas da Amazônia, Manaus 69067-375, AM, Brazil

¹¹Embrapa Florestas, Brazilian Agricultural Research Corporation, Colombo 83411-000, PR, Brazil

¹²School of Biological Sciences, University of Tasmania, Hobart 7001, Tasmania, Australia

¹³Institute of Geography, University of Erlangen-Nuremberg, 91058 Erlangen, Germany

¹⁴Laboratory of Geo-information Science and Remote Sensing, Wageningen University,

Wageningen 6708PB, the Netherlands

¹⁵Centro de Ciências Biológicas e da Natureza, Laboratóio de Botânica e Ecologia Vegetal, Universidade Federal Do Acre, Rio Branco 69915-559, AC, Brazil

¹⁶Instituto Pirenaico de Ecologia, Consejo Superior de Investigaciones Cientificas (IPE-CSIC), Zaragoza 50059, Spain

- ¹⁷Instituto Boliviano de Investigacion Forestal (IBIF), Santa Cruz de la Sierra 6204, Bolivia
- ¹⁸Centro de Energia Nuclear na Agricultura, Laboratóio de Ecologia Isotópica, Universidade de SÃo Paulo, Piracicaba 13416903, SP, Brazil
- ¹⁹Departamento de Botânica, Universidade Federal do Paraná, Curitiba 81531-980, PR, Brazil
- ²⁰Departamento de Botânica, Universidade Federal de Juiz de Fora (UFJF), Juiz de Fora 36015-260, MG, Brazil
- ²¹Programa de Pós-Graduação Ecologia e Manejo de Recursos Naturais, Universidade Federal do Acre,
- Rio Branco 69915-559, AC, Brazil
- ²²Departamento de Ecologia do Instituto de Biociências, Universidade de São Paulo (USP), São Paulo 05508-090, SP, Brazil
- ²³UMR 5174 Laboratoire Evolution et DiversitéBiologique, CNRS & UniversitéPaul Sabatier, Toulouse 31062, France
- ²⁴Biological Sciences Department, University of Zambia, Lusaka Box 32379, Zambia
- ²⁵Department of Biology, University of Missouri-St. Louis, Saint Louis 63121, MO, USA
- ²⁶Coordenação de Pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da Amazônia,

Manaus 69080-971, AM, Brazil

- ²⁷Departamento de Engenharia Florestal, Universidade Federal de Viçosa (UFV), Viçosa 36570-000, MG, Brazil
- ²⁸Departamento de Engenharia Florestal, Universidade Federal do Paraná, Curitiba 80210-170, PR, Brazil
- ²⁹Centro de Ciêcias Biológicas e da Natureza, Laboratório de Botânica e Ecologia Vegetal, Universidade Federal do Acre, Rio Branco 69915-559, AC, Brazil
- ³⁰Prefeitura Municipal de Rio Branco, Rio Branco 69900-901, AC, Brazil
- ³¹Département Hommes, Natures, Sociétés, Centre National de la Recherche Scientifique (CNRS) et UMR 208 Patrimoines Locaux et Gouvernance, Paris 75231 Cedex 05, France
- ³²Dept. Forest and Wood Science, University of Stellenbosch, Stellenbosch 7600, South Africa
- ³³Meisterschule Ebern für das Schreinerhandwerk, 96106 Ebern, Germany
- ³⁴Floresta Estadual de Assis, Assis 19802-970, SP, Brazil
- ³⁵Tanzania Forestry Research Institute (TAFORI), Dodoma P.O. Box 1576, Tanzania
- ³⁶Departamento de Ciências Florestais, Universidade de São Paulo, Escola Superior de Agricultura Luiz de Queiroz, Piracicaba 13418-900, SP, Brazil
- ³⁷Departamento de Engenharia Florestal DEF, Universidade Estadual do Centro-Oeste, Irati 84500-000, PR, Brazil
- ³⁸Departamento de Ciências Florestais, Centro de Ciências Rurais, Universidade Federal de Santa Maria, Santa Maria 97105-9000, RS, Brazil
- ³⁹Departamento de Botânica, Laboratório de Fisiologia Vegetal, Universidade de Brasília, Instituto de Ciências Biológicas, Brasília 70904-970, DF, Brazil
- ⁴⁰World Agroforestry Centre (ICRAF), Nairobi P.O. Box 30677-00100, Kenya
- ⁴¹Coordenação de Pesquisa em Ecologia, Instituto Nacional de Pesquisas da Amazônia,

Manaus C.P. 478 69011-970, AM, Brazil

- ⁴²Departement of Land Resource Management, Northern Territory Government, Palmerston NT 0831, Australia
- ⁴³Research Institute for Environment and Livelihoods, Charles Darwin University, Darwin NT 0909, Australia
- ⁴⁴Department of Biological Sciences, Mount Holyoke College, South Hadley 01075, MA, USA
- ⁴⁵Department of Earth System Science, Stanford University, Stanford 94305, CA, USA
- ⁴⁶Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana Champaign, Champaign 61801, USA
- ⁴⁷Department of Plant Ecology, Albrecht von Haller Institute of Plant Sciences, University of Göttingen, 37073 Göttingen, Germany
- ⁴⁸Departamento de Engenharia Florestal, Universidade do Estado de Santa Catarina UDESC, Lages 88520-000, SC, Brazil
- ⁴⁹Tropical Peat Research Institute, Biological Research Division, Malaysian Palm Oil Board, Selangor 43000, Malaysia
- ⁵⁰Departamento de Botânica, Instituto de Ciências Biologicas, Universidade Federal de Minas Gerais,

Belo Horizonte 31270-901, MG, Brazil

- ⁵¹Division of Science & Environmental Policy, California State University Monterey Bay, Seaside 93955, CA, USA
- ⁵²Departamento de Biologia, Universidade Federal de Sergipe, São Cristóvão 49100-000, Brazil
- ⁵³Programa Forestal, Colegio de Postgraduados, Montecillo 56230, México
- ⁵⁴Department of Geosciences and Geography, University of Helsinki, Helsinki 00014, Finland
- ⁵⁵School of Geography and the Environment, University of Oxford, Oxford OX1 3QY, UK
- ⁵⁶Departamento de Solos e Engenharia Agrícola, Universidade Federal do Paraná, Curitiba 80035-050, PR, Brazil
- ⁵⁷Laboratoria de Dendrochronologia y Anatomia de Maderas Espinoza, Universidad Nacional de Loja, Loja EC110103, Ecuador
- ⁵⁸Tanzania Forestry Research Institute (TAFORI), Morogoro P.O. Box 1854, Tanzania

Santa Cruz de la Sierra CP 6201, Bolivia

Correspondence to: Fabien Hubert Wagner (wagner.h.fabien@gmail.com)

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Abstract. The seasonal climate drivers of the carbon cycle in tropical forests remain poorly known, although these forests account for more carbon assimilation and storage than any other terrestrial ecosystem. Based on a unique combination of seasonal pan-tropical data sets from 89 experimental sites (68 include aboveground wood productivity measurements and 35 litter productivity measurements), their associated canopy photosynthetic capacity (enhanced vegetation index, EVI) and climate, we ask how carbon assimilation and aboveground allocation are related to climate seasonality in tropical forests and how they interact in the seasonal carbon cycle. We found that canopy photosynthetic capacity seasonality responds positively to precipitation when rainfall is < 2000 mm yr⁻¹ (water-limited forests) and to radiation otherwise (light-limited forests). On the other hand, independent of climate limitations, wood productivity and litterfall are driven by seasonal variation in precipitation and evapotranspiration, respectively. Consequently, light-limited forests present an asynchronism between canopy photosynthetic capacity and wood productivity. First-order control by precipitation likely indicates a decrease in tropical forest productivity in a drier climate in water-limited forest, and in current light-limited forest with future rainfall $<2000\,\mathrm{mm\,yr^{-1}}$.

1 Introduction

Tropical forests have a primary role in the terrestrial carbon (C) cycle. They constitute 54% of the total aboveground biomass carbon of Earth's forests (Liu et al., 2015) and account for half $(1.19 \pm 0.41 \, \text{PgC yr}^{-1})$ of the global carbon sink of established forests (Pan et al., 2011; Baccini et al.,

⁵⁹Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin NT 0909, Australia

⁶⁰Center for Forest Disturbance Science, USDA Forest Service, Athens 30607, GA, USA

⁶¹Department of Biological Sciences, Florida International University, Miami 33199, FL, USA

⁶²Graduate School of Agriculture, Kyoto University, Kyoto 606-8501, Japan

⁶³Institut Français de Pondicherry, Puducherry 6005001, India

⁶⁴UMR AMAP (botAnique et bioinforMatique de l'Architecture des Plantes), IRD, Montpellier 34398, France

⁶⁵Tree Ring and Environmental History Laboratory, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales – CONICET, Mendoza 5500, Argentina

⁶⁶Department of Earth and Environment, Southeast Environmental Research Center, Florida International University, Miami 33199, FL, USA

⁶⁷Departamento de Biologia Aplicada, FCAV, Universidade Estadual Paulista, UNESP, Jaboticabal 14884-000, SP, Brazil

⁶⁸UR B&SEF (Biens et services des écosystèmes forestiers tropicaux), CIRAD, Yaoundé BP 2572, Cameroon

⁶⁹School of Geosciences, University of Edinburgh, Edinburgh EH9 3FF, UK

⁷⁰CarboForExpert, Geneva 1211, Switzerland

⁷¹HJ Andrews Experimental Forest, Oregon State University, Blue River 97413, OR, USA

⁷²Ibama, Rio Branco 69907-150, AC, Brazil

⁷³PRONAT – Programa de Pós-Graduação em Recurso Naturais, Universidade Federal de Roraima – UFRR, Boa Vista 69310-000, RR, Brazil

⁷⁴School of Biological Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK

⁷⁵Departamento de Ciências Ambientais, Universidade Federal do Amapá, Macapá 68902-280, AP, Brazil

⁷⁶Embrapa Cocais, Brazilian Agricultural Research Corporation, São Luiz 65066-190, MA, Brazil

⁷⁷Instituto Boliviano de Investigacion Forestal (IBIF), Universidad Autonoma Gabriel René Moreno,

⁷⁸Department of Forest Vegetation, Forestry and Forest Products Research Institute (FFPRI), Ibaraki 305-8687, Japan

⁷⁹Núcleo de Estudos e Pesquisas Ambientais (NEPAM), Universidade Estadual de Campinas (UNICAMP), Campinas 13083-867, SP, Brazil

⁸⁰Embrapa Roraima, Brazilian Agricultural Research Corporation, Boa Vista 69301-970, RR, Brazil

⁸¹Crop Production Systems in the Tropics, Georg-August-University, 37077 Göttingen, Germany

⁸²Departamento de Engenharia Florestal, Centro de Educação Superior Norte, Universidade Federal de Santa Maria, Frederico Westphalen 98400-000, RS, Brazil

⁸³College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4RJ, UK

2012). Based on annual or multi-annual measurements of forest wood productivity, changes in carbon dynamics and functioning of the tropical trees have already been observed. While tropical forests have been acting as a long-term, net carbon sink, a declining trend in carbon accumulation has been recently demonstrated for Amazonia (Brienen et al., 2015). Furthermore, a positive change in water-use efficiency of tropical trees due to the CO2 increase over the past 150 years has also been observed (van der Sleen et al., 2015; Bonal et al., 2011). Currently, increasing evidence shows that the tropical forests present a seasonality in the assimilation and storage of carbon, associated with climate seasonality (Wu et al., 2016; Doughty et al., 2014; Rowland et al., 2014b, a, 2015; Wagner et al., 2014). However, the inherent problem of these studies is that they are based on only one site or one region, which renders it difficult to disentangle the potential climate drivers due to collinearity between climate variables. Moreover, the studies sometime focus on a single part of the carbon cycle that may lead to erroneous interpretation on forest productivity due to interactions among the carbon cycle components (Doughty et al., 2014). Understanding the seasonal drivers of the carbon cycle in a pan-tropical context by using the maximum information available on carbon storage and assimilation is therefore needed to assess the mechanisms driving changes in forest carbon use and predict tropical forest behaviour under future climate changes.

Despite long-term investigation of changes in forest aboveground biomass stock and carbon fluxes, the direct effect of climate on the seasonal carbon cycle of tropical forests remains unclear. Contrasting results have been reported depending on methods used. Studies show an increase of aboveground biomass gain in the wet season from direct measurement (biological field measurements), or, from indirect measurement, an increase of canopy photosynthetic capacity in the dry season (remote sensing, flux tower network) (Wagner et al., 2013). Several hypotheses have been proposed to explain these patterns. (i) Wood productivity, estimated from trunk diameter increment, is mainly controlled by rainfall and water availability and occurs preferentially during the wet season, even if carbon accumulation in the trees could be greater in the dry season than in the wet season, likely reflecting a tradeoff between maximum potential growth rate and hydraulic safety (Rowland et al., 2014b, a; Wagner et al., 2014). Seasonal variation in carbon allocation to the different parts of the plant (crown, roots) also contributes to optimising resource use and could explain the low synchronicity between wood productivity and carbon accumulation in the trees (Doughty et al., 2014, 2015; Rowland et al., 2014b). (ii) Litterfall peaks mainly occur during dry periods in response to two potential climate drivers: seasonal changes in daily insolation leading to production of new leaves and synchronous abscission of old leaves, and high evaporative demand and low water availability, which both induce leaf shedding in the dry season (Borchert et al., 2015; Zhang et al., 2014; Wright and Cornejo, 1990; Chave et al., 2010; Myneni et al., 2007; Jones et al., 2014; Bi et al., 2015); and (iii) Photosynthesis in these tropical forested regions is mainly limited by water and is sustained during the dry season above a threshold of 2000 mm of mean annual precipitation (Restrepo-Coupe et al., 2013; Guan et al., 2015). Water limitation is not the only known control, and other climate variables and internal carbon allocation have been demonstrated to drive photosynthetic capacity in tropical forests such as irradiance, temperature and leaf dynamics. Irradiance is directly and positively linked to plant photosynthetic capacity, carbon uptake and plant growth (Graham et al., 2003), while temperatures above 30 °C drive a reduction of photosynthetic capacity (Lloyd and Farquhar, 2008; Doughty and Goulden, 2008; Doughty, 2011). Recently, for non-waterlimited forests in Amazonia, Wu et al. (2016) showed that the increase in ecosystem photosynthesis during dry periods result from the synchronisation of new leaf growth and litterfall, shifting canopy composition towards younger more light-use efficient leaves.

Here, we determine the dependence of seasonal aboveground wood productivity, litterfall and canopy photosynthetic capacity (using the MODIS enhanced vegetation index (EVI) as a proxy) on climate across the tropics, and assess their interconnections in the seasonal carbon cycle. EVI strongly correlated with chlorophyll content and photosynthetic activity (Huete et al., 2002, 2006), and we used a corrected version of the index to account for sun-angle artifact (Morton et al., 2014; Wagner et al., 2015). While positive correlation of leaf flushing and EVI has already been reported in tropical forests (Brando et al., 2010; Wagner et al., 2013; Wu et al., 2016), Chavana-Bryant et al. (2016) have demonstrated in a tropical forest that EVI increased with leaf development (from youngest to the most mature cohorts), and then declined when leaves were at old and senescent stages. Here we assume that EVI represents the maturation of new leaves and that the highest value of EVI represents the highest greenness and canopy photosynthetic capacity, when leaves are fully mature. We use a unique satellite and groundbased combination of monthly data sets from 89 pan-tropical experimental sites (68 include aboveground wood productivity and 35 litter productivity measurements), their associated canopy photosynthetic capacity and climate to address the following questions. (i) Are seasonal aboveground wood productivity, litterfall productivity and photosynthetic capacity all dependent on climate? (ii) Does a coherent pan-tropical rhythm exist among these three key components of forest carbon fluxes? (iii) If so, is this rhythm primarily controlled by exogenous (climate) or endogenous (ecosystem) processes?

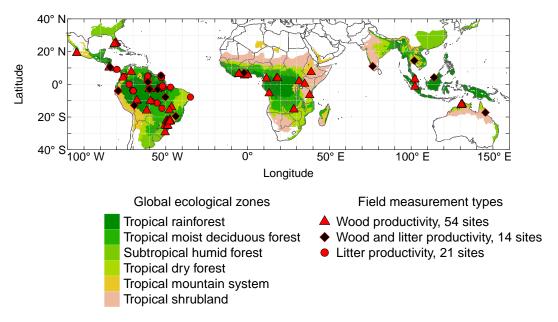


Figure 1. Geographical locations of the 89 observation sites with the field measurement types (wood productivity and/or litter productivity) and global ecological zones (FAO, 2012). Wood productivity is available for 68 sites (54 + 14), litter productivity for 35 sites (21 + 14), and EVI and climate for all the 89 studied sites (54 + 21 + 14).

2 Methods

2.1 Data sets

We compiled publications reporting seasonal wood productivity of tropical forests. Seasonal tree growth measurements in 68 pantropical forest sites, representing 14481 individuals, were obtained from published sources or directly from the authors (Table 1, Fig. 1). The data set consists of repeated seasonal measurements of tree diameter, mostly with dendrometer bands (94.1 %), electronic point surveys (4.4 %) or graduated tapes (1.5%). The names of all recorded species were checked using the Taxonomic Name Resolution Service and corrected as necessary (Boyle et al., 2013; Chamberlain and Szocs, 2013). Botanical identifications were made at the species level for 11 967 trees, at the genus level for 1613 trees, family level for 171 trees and unidentified for 730 trees. Wood density values were taken from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009) or from the authors, when measured on the sample (Table 1). Direct determination was available for 455 trees and species mean was assumed for an additional 8671 trees. For the remaining 5355 trees, we assumed genus mean (4639), family mean (136) or site mean (580) of wood density values as computed from the global database (Zanne et al., 2009). Palms, lianas and species from mangrove environments were excluded from the analysis. Diameter changes were converted to biomass estimates using a tropical forest biomass allometric equation – which uses tree height (estimated in the allometric equation if not available), tree diameter and wood density (Chave et al., 2014) – and then the mean monthly increment of the sample was computed for each sample. Recently, Cuny et al. (2015) showed that stem woody biomass production lags behind stem-girth increase by over 1 month in temperate coniferous forests, but here we assume that stemgirth increase represents woody biomass production as no such information is yet available for tropical forest trees. To detect the errors of overestimated or underestimated growth, the increment histogram of each site was plotted. For each suspected error, the increment trajectory of trees was then visually assessed to confirm the error. If the error was clearly identifiable, such as an abnormal increase (or decrease) in diameter values followed by a large decrease (or increase) of the same amplitude resulting from typographic errors, for example 28 whereas 2.8 was expected, the typographic error was corrected. When the typographic error was not clearly identifiable, the value was corrected with linear approximation with the mean increment of t+1 and t-1. In some cases there was an identifiable increase of diameter values (or decrease), but not followed by a decrease (or an increase) of the same amplitude. This pattern was associated to the repositioning of the dendrometer bands (reported in the source data set). In this case, the increment was deleted and set to zero and the new time series of cumulative diameter values were computed. As the diameter values are needed to compute biomass, this strategy was used to benefit of the full time series of diameter increment even after solving the error.

Seasonal litterfall productivity measurements from a previously published meta-analysis were used for South America (Chave et al., 2010) (description in Table 1 of Chave et al., 2010). In this data set, we used only monthly measurement

Table 1. Description of the study sites. For each site, continent (cont.) (Africa – Af, America – Am, Asia – As and Australia – Aus), country, full site name and geographical coordinates (long.-lat., in decimal degrees) are reported. The next column reports the site's type of measurements: wood productivity and litterfall (WP+LT) or only wood productivity (WP), the type of wood productivity measurements: dendrometer bands (DB) or electronic point dendrometers (EPD), the time scale of the measurements, the number of trees, the number of the dendrometers (EPD) and the dendrometers (EPD) are reported. species, the reference for the wood specific gravity (wsg), the period of the measurements, the mean diameter (mm) of the sample and the mean wood productivity in kg tree⁻¹ yr⁻¹

Reference	Cont.	Country	Site	Lat.	Long.	Type	Method	Timescale N_tree		N_sp	wsg	Duration	Diameter	dagb ± SE
Detienne and A. (1976)	Af	Cameroon	MBalmayo	3.515	11.501	WP	DB	bi-	_	-	Zanne et al. (2009)	1/1966–12/1970	491.8 (491.8–491.8)	41.24 ± 4.698
Detienne and A. (1976)	Af	CAR	MBaiki	3.812	17.881	WP	DB	weekly bi-	_	_	Zanne et al. (2009)	2/1969–11/1970	282.9 (282.9–282.9)	9.51 ± 1.651
								weekly						
Detienne and A. (1976)	Af	CAR	Mokinda	3.650	18.350	WP	DB	bi-	_	_	Zanne et al. (2009)	2/1969–12/1970	391.1 (391.1–391.1)	11.52 ± 2.771
Couralet et al. (2010)	Δf	DRC	Luki forest	-5 583	13 183	WÞ	J.	monthly	40	4	Zanne et al. (2009)	4/2006_8/2007	243 2 (121 4-456 9)	12 23 + 1 646
Krenkowski et al. (2011)	Δf	Ethionia	Minessa	7 433	38 867	WP	EBD 5	30 min	o d	,	Zanne et al (2009): Aerts	3/2008-1/2012	327 (168 3–582 1)	11 5 + 1 309
	;	1			0		ļ		,					I
Baker et al. (2003)	Af	Ghana	Bonsa River	5.333	-1.850	WP	DB	monthly	36	2	Zanne et al. (2009)	8/1997-12/1999	380.7 (107.2-824.3)	20.18 ± 0.976
Swaine et al. (1990)	Af	Ghana	GPR	5.908	0.061	WP	DB	monthly	12	7	Zanne et al. (2009)	1/1978-4/1979	112.4 (45.7–186.6)	1.05 ± 0.655
Lieberman (1982)	Af	Ghana	Pinkwae	5.750	-0.133	WP	DB	monthly	7	2	Zanne et al. (2009)	3/1978-4/1979	51.7 (34.8–91.7)	0.21 ± 0.188
Baker et al. (2003); Owusu-	Af	Ghana	Tinte Bepo	7.067	-2.100	WP + LP	DB	monthly	40	ယ	Zanne et al. (2009)	7/1997-1/1999	346.6 (172.9–780.5)	20.71 ± 1.498
Sekyere et al. (2006)	>	Time Const	Tamb	6017	n 022	W/D		an cardelly	3	5	7 (2000)	7/1072 12/1001	168 6 (717) 2025	2 74 - 0 221
Detienne and A. (1976)	Αf	Ivory Coast	Oume	6.383	-5.416	WP	DB	bi-	_	_ ;	Zanne et al. (2009)	4/1966-12/1970	550.4 (550.4–550.4)	25.12 ± 3.806
	,	:				;	1	weekly	1	3				
Omnais et al. (2013)	2	Ixciiya	Navallicga	0.250	1.000	1	į	шопшу	00	36	et al. (2012)	0/2003-12/2003	333 (20.3-1024.7)	11.22 ± 0.100
Elifuraha et al. (2008)	Af	Tanzania	Kitulangalo	-6.667	37.973	WP	DB	monthly	53	10	Zanne et al. (2009)	2/2007-8/2008	237.1 (71–632.3)	4.27 ± 1.239
Gliniars et al. (2013)	Af	Uganda	Budongo	1.750	31.500	WP	DB	monthly	312	2	Zanne et al. (2009); Becker et al. (2012)	1/2005–12/2009	230.7 (93.7–1163.8)	4.22 ± 0.115
Chidumayo (2005)	Af	Zambia	Makeni	-15.467	28.183	WP	DB	monthly	45	4	Zanne et al. (2009)	12/1996-6/2003	69.7 (28.2–167.7)	13.68 ± 0.633
Chidumayo (2005)	Af	Zambia	UNZA	-15.392	28.333	WP	DB	monthly	51	2	Zanne et al. (2009)	1/1997-5/2002	68.6 (30.7–340)	6.88 ± 0.329
Mendivelso et al. (2013)	Am	Bolivia	Inpa	-16.117	-61.717	WP	DB	monthly	43	5	Mendivelso et al. (2013)	8/2010-9/2011	162.5 (107.7–290.7)	3.67 ± 0.58
Dünisch et al. (2002)	Am	Brazil	Aripuana	-10.150	-59.433	WP	DB	monthly	60	2	Zanne et al. (2009)	10/1998-10/2001	413.3 (138.3-1120.4)	45.43 ± 1.442
Chagas et al. (2004)	Am	Brazil	Caetetus	-22.400	-49.700	WP	DB	monthly	70	7	Zanne et al. (2009)	2/1996-7/1997	203.2 (50.9-651)	5.91 ± 0.89
Castilho et al. (2012)	Am	Brazil	Caracarai	1.476	-61.019	WP + LP	DB	Ψ	2396	202	Zanne et al. (2009); Boan-	1/2013-3/2014	198.6 (34.3–1049.6)	4.55 ± 0.105
Melgaço (2014)	Am	Brazil	Ducke	-2.952	-59.944	WP + LP	DB	monthly bi-	1972	540	erges (2012) Zanne et al. (2009)	2/2013-2/2014	266.1 (97.3–1367.9)	11.67 ± 0.266
	•	:					į	monthly	1	:				
Fedele et al. (2004)	All	DIAZII	Dulatex	-22.417	-40.000	*	5	шопшу	1	1	Zamie et al. (2007)	1/1999-4/2000	231.7 (89.7-321.9)	13.37 ±0.540
Vieira et al. (2004)	Am	Brazil	FEC	-10.074	-67.627	WP	DB	monthly	313	76	Zanne et al. (2009)	11/2000-6/2008	433.9 (102.7–1388.2)	36.97 ± 0.558
Zanon and Finger (2010)	Am	Brazil	Flona SFP	-29.417	-50.404	WP	DB	monthly	96	_	Zanne et al. (2009)	2/2004-6/2006	413.1 (235.3–551)	37.48 ± 0.847
Carvalho (2009)	Am	Brazil	Iaciara	-14.065	-46.487	WP	DB	monthly	171	6	Zanne et al. (2009)	5/2007-11/2008	270.9 (39.3–1815.3)	18.37 ± 2.965
Rossatto et al. (2009)	Am	Brazil	IBGE	-15.945	-47.885	WP	DB	monthly	116	24	Zanne et al. (2009)	6/2006-5/2008	79.1 (35.7–261.5)	3.24 ± 0.156
Lisi et al. (2008); Ferreira-	Am	Brazil	Ibicatu	-22.783	-47.717	WP	DB	monthly	32	5	Zanne et al. (2009)	12/1998–5/2006	264.2 (109.1–462.1)	22.44 ± 0.882
Kohler et al. (2008)	Am	Brazil	Irati	-25.374	-50.575	WP	DB	φ	199	20	Zanne et al. (2009)	7/2002-6/2008	341.6 (100.5–983.1)	10.52 ± 0.179
de Castro (2014)	Αm	Brazil	Itatinoa	-23 043	-48 631	WÞ	DB.	monthly weekly	9	_	Zanne et al. (2009)	11/2012_12/2013	52 (45 7-62 9)	4 02 + 0 178
Toledo et al. (2012); Paula	Am	Brazil	Lagoa Santa	-19.543	-43.927	WP + LP	DB	monthly	28	_	Toledo et al. (2012)	10/2009-5/2011	322.8 (139.2–711.9)	9.63 ± 0.991
mid Edinos i mio (Eddi)														

Table 1. Continued.

Reference	Cont.	Country	Site	Lat.	Long.	Type	Method	Timescale N_tree	tree N_sp	gsw qs	92	Duration	Diam	dagb ± SE
Grogan and Schulze	Am		Marajoara	-7.833	-50.267	WP+LP	DB	monthly			Zanne et al. (2009)	12/1996-11/2001	476.3 (137.1–1468.5)	66.5±1.769
(2012); Free et al. (2014)	4	Drozil	Douto Ecundina	21 022	17 467	W.D	gC	· Idanom	25	7.	(0000) To to came	13/1008 \$ /0006	214 9 (97 6 982 9)	20 02 ± 0 003
Fedele et al. (2004)	TIP.	Diazii	rono renena	-21.633	/0+./+-	1	d d	monum			unic et al. (2002)	12/1996-3/2000	514.0 (07.0-003.0)	20.63 ± 0.693
Kanieski et al. (2012, 2013) Silveira et al. (2014), Vieira	Am	Brazil Brazil	REPAR RHF	-25.587 -9.754	-49.346 -67.664	WP WP	DB DB	monthly monthly	87 253 8	4 Za 89 Za	Zanne et al. (2009) Zanne et al. (2009)	7/2009–10/2012 1/2005–6/2008	190.8 (81.7–325.1) 326.9 (103.3–1410.4)	5.27 ± 0.168 32.83 ± 1.297
et al. (2004)		:			000	9	á	-			(0000)	000000	000000000000000000000000000000000000000	- 10
Cardoso et al. (2012) Lisi et al. (2008); Ferreira-	Am Am	Brazil Brazil	Kio Cachoeira Santa Genebra	-25.314 -22.746	-48.690 -47.109	WP WP	DB	monthly monthly	121	2 Za 2 Za	Zanne et al. (2009) Zanne et al. (2009)	9/200 /-10/2008 9/2000-5/2006	135.5 (63.1–205.4) 260.5 (99–554.1)	16.25 ± 0.69 11.5 ± 0.75
Fedele et al. (2004) Lisi et al. (2008); Ferreira-	Am	Brazil	SRPQ	-21.667	-47.500	WP	DB	monthly	84	8 Za	Zanne et al. (2009)	2/2000–12/2006	275.4 (199.8–376.9)	18.66 ± 0.523
Fedele et al. (2004)		:					1					9		-
Vieira et al. (2004); Nepstad and Moutinho (2013)	Am	Brazil	Tapajos km67	-2.853	-54.955	WP	DB	monthly 1	1369 26	263 Za	Zanne et al. (2009)	6/1999–3/2006	326.2 (99–1997.6)	18.49 ± 0.35
Figueira et al. (2011); Nepstad and Moutinho (2013)	Am	Brazil	Tapajos km83	-3.017	-54.971	$\mathrm{WP} + \mathrm{LP}$	DB	weekly	734 12	1 <i>27</i> Za	Zanne et al. (2009)	11/2000-12/2004	345.6 (101.3–1135.2)	32.34 ± 0.412
Lisi et al. (2008); Ferreira-	Am	Brazil	Tupi	-22.723	-47.530	WP	DB	monthly	32	6 Za	Zanne et al. (2009)	12/1998–5/2006	224.9 (123.3–483.3)	16.04 ± 0.824
Chambers et al. (2013)	Am	Brazil	ZF-2	-2.967	-60.183	WP	DB	monthly	174	73 Za	Zanne et al. (2009)	7/2000–12/2001	222.6 (101.9–644.6)	5.74 ± 0.245
Mendivelso et al. (2013) O'Brien et al. (2008); Clark	Am	Colombia Costa Rica	Tulua La Selva	4.083 10.431	-76.200 -84.004	$\begin{array}{c} WP \\ WP + LP \end{array}$	DB DB	monthly monthly			Mendivelso et al. (2013) Zanne et al. (2009)	7/2010–8/2011 4/1997–5/2012	208.3 (129.4–338.4) 321.1 (100.3–743.1)	15.2 ± 0.858 37.38 ± 0.768
et al. (2010(@, 2009) Homeier (2012)	Δm	Costa Rica	PBAB	10.215	-84 507	W/D	A.C.	monthly	403		Zanna at al. (2000)	12/1999_4/2003	250 5 (103 3-1000 2)	5 79 + 0 101
Homeier et al. (2010, 2012); Roderstein et al. (2005); Brauning et al.	Am	Ecuador	RBSF	-3.978	770.67-	WP + LP	DB,EPD	monthly and 30– min		92 Za	Zanne et al. (2009)	7/1999–12/2011	182.3 (81.8–681.7)	3.22±0.059
(2002) Wagner et al. (2013); Stahl et al. (2010); Bonal et al. (2008)	Am	French Guiana	Paracou	5.279	-52.924	$\mathrm{WP} + \mathrm{LP}$	DB	bi- weekly	256	74 Ru Sta	Rutishauser et al. (2010); Stahl et al. (2010); Baraloto	4/2007–6/2010	337.8 (95.4–1001.6)	19.21 ± 0.389
Lopez-Ayala et al. (2006)	Am	Mexico	El Palmar	19.133	-104.467	WP	DB	bi-	23	2 Za	Zanne et al. (2009)	6/2002-8/2003	212.5 (81.3–500.5)	6.02 ± 0.981
Lopez-Ayala et al. (2006)	Am	Mexico	La Barcinera	19.150	-104.425	WP	DB	monuny bi-	41	1 Za	Zanne et al. (2009)	6/2002-8/2003	198.3 (96-416.4)	2.94 ± 0.808
Rowland et al. (2014b)	Am	Peru	Tambopata	-12.835	-69.285	WP + LP	DB		1167 28	287 Ro	(2014b);	10/2005-4/2011	221.5 (91.3–1966.3)	17.37 ± 0.22
Ross et al. (2003)	Am	USA	Big Pine Kev	24.671	-81.354	WP	DB	monthly monthly	15	Za 7 Za	Zanne et al. (2009) Zanne et al. (2009)	4/1990-11/1993	180.1 (112.8–299.3)	1.48 ± 0.166
Ross et al. (2003)	Am	USA	Key Largo	25.267	-80.324	WP	DB	monthly			Zanne et al. (2009)	12/1989-11/1993	175.4 (103.2–338.4)	2.52 ± 0.221
Ross et al. (2003) Ross et al. (2003)	Am	USA	Lignumvitae Key Sugarloaf Kev	24.903 24.625	-80.698 -81.543	W W	DB DB	monthly			Zanne et al. (2009) Zanne et al. (2009)	6/1990–11/1993 1/1990–11/1993	162.3 (99.9–376.6) 144.5 (101.7–226.6)	1.45 ± 0.279 1.35 ± 0.074
Worbes (1999)	Am	Venezuela	RFC	7.500	-71.083	WP	DB	monthly	52		Zanne et al. (2009)	4/1978–5/1982	256.9 (117.2–391.8)	21.04 ± 1.029
Pelissier and Pascal (2000); Pascal (1984)	As	India	Attapadi	11.083	76.450	WP + LP	DB	monthly		23 Za	Zanne et al. (2009)	3/1980–11/1983	172.7 (32–1250.9)	6.21 ± 0.655
Vincent (2012)	As	Indonesia	Muara Bungo	-1.523	102.273	WP	M				Zanne et al. (2009)	4/2004-5/2006	135 (53.3–175.5)	14.18 ± 0.608
Kho et al. (2013)	As	Malaysia	Lambir Beech	4.200	114.033	WP + LP	DB Pa	_	1048 33	334 KF	Kho et al. (2013)	6/2009–9/2010	224.9 (22–1367.1)	10.2 ± 0.314
Ohashi et al. (2009); Bun-	A A	Malaysia	SERS	14.500	102.300	WP + LP	DB DB	monthly			Zanne et al. (2009) Zanne et al. (2009)	3/2004–10/2006	386.7 (161.2–1075.6)	14.79 ± 0.300 4.38 ± 0.28
yavejchewin (1997) Prior et al. (2004)	Ā	Australia	Berry Springs	-12.700	131,000	WP	DB	monthly	88	6. Z.a	Zanne et al. (2009)	11/2000-5/2002	122.9 (24.2–287.9)	2.44+0.328
Drew et al. (2011)	Au	Australia	CSIRO	-12.411	130.920	WP	EPD	daily	~		Cause et al. (1989)	2/2009–5/2011	83 (61–109.7)	4.78 ± 0.34
Koenig and Griffiths (2012)	Αn	Australia	Gunn Point1	-12.194	131.147	WP	DB	monthly	9 (1 Za	Zanne et al. (2009)	4/2003-4/2005	105.3 (65.4–138.7)	1.03 ± 0.247
Koenig and Griffiths (2012)	Au Au	Australia	Gunn Point1B	12.121	131.035	WP	200	monthly	ه م	1 25	Zanne et al. (2009)	4/2003-4/2005	205.7 (87.2–324)	1.82 ± 0.823 1.56 ± 1.061
Koenig and Griffiths (2012)	n A	Australia	Gunn Point3	-12.184	131.028	WP	DB DB	monthly	ی ه	7 7	Zanne et al. (2009) Zanne et al. (2009)	4/2003-4/2003	206.9 (64.7–536.2) 107.4 (74.6–141.5)	1.36 ± 1.061 1.44 + 0.297
Brodribb et al. (2013)	Αn	Australia	Indian Island		130.507	WP	DB	3-	30 20	1 Za	Zanne et al. (2009)	6/2008-10/2010	233.9 (107.7–411.8)	3.72 ± 0.45
Prior et al. (2004)	Au	Australia	Leanyer	-12.404	130.898	WP	DB	monthly monthly	12		Zanne et al. (2009)	2/2001–5/2002	85 (21.1–189)	2.46 ± 0.604
Brodribb et al. (2013);	Αn	Australia	Mt Baldy	-17.269	145.423	$\mathrm{WP} + \mathrm{LP}$	DB	3-	20	1 Za	Zanne et al. (2009)	5/2008-8/2010	306.3 (171.9-598.4)	4.37 ± 0.516
Stocker et al. (1995)								monthly						

data from old-growth forests, as some sites have plots of both secondary and old-growth forests; flooded forests were excluded. In addition to these 23 sites, we compiled the seasonal leaf/litterfall data of 12 sites where we already had tree-growth measurements (Fig. 1 and Table 2). For these 35 sites, 26 had monthly leaf fall and 9 had monthly litterfall data (leaf fall, twigs usually less than 2 cm in diameter, flowers and fruits). The Pearson correlation coefficient between leaf fall and litterfall for the 20 sites where both data are available is 0.945 (Pearson test, t = 42.7597, dt = 218, t = 218

Enhanced vegetation index (EVI) was used as a proxy for canopy photosynthetic capacity in tropical forest regions (Huete et al., 2006; Guan et al., 2015). EVI for the 89 experimental sites (Fig. 1) was obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) MCD43 product collection 5 provided every 16 days at 500 m spatial resolution (from 4 May 2002 to 30 September 2014). Before computing the mean monthly EVI per site, we did a pixel selection in five steps. (i) Selection of all the pixels in a square of side 40 km, centred on the pixel containing each site (6561 pixels per site). This surface was selected to maximize the quantity of valid pixels to estimate monthly site's EVI, as, due to persistent cloud cover in tropical forest regions, valid observations of EVI are limited, producing incomplete time series of EVI values for a given pixel. (ii) In this area, the pixels containing the same or at least 90 % of the site land cover pixel were selected, based on MCD12Q1 for 2001-2012 at 500 m resolution (Justice et al., 1998). (iii) Thereafter, only the pixels forested in 2000 and without loss of forest and with tree cover above or equal to the site tree cover were retained using global forest cover loss 2000-2012 and Data mask based on Landsat data (Hansen et al., 2013). (iv) Only pixels with a range of ± 200 m the site altitude were retained, using NASA Shuttle Radar Topographic Mission (SRTM) data, which were reprocessed to fill in the original no-data holes (Jarvis et al., 2008). (v) For corrected reflectance computation we used quality index from 0 (good quality) to 3 (all magnitude inversions or 50% or less fill-values) extracted from MCD43A2. When required, data sets used to make the selection were aggregated to the spatial resolution of MCD43 product (500 m) and reprojected in the MODIS sinusoidal projection. The reflectance factors of red (0.620-0.670 µm, MODIS band 1), NIR (0.841–0.876 µm, MODIS band 2) and blue bands (0.459–0.479 µm, MODIS band 3) of the retained pixels were modelled with the RossThick-LiSparse-Reciprocal model parameters contained in the MCD43A1 product with view angle θ_v fixed at 0°, sun zenith angle θ_s at 30° and relative azimuth angle Φ at 0° and EVI was computed as shown in Eq. (1):

$$EVI = 2.5 \times \frac{NIR - red}{NIR + 6 \times red - 7.5 \times blue + 1}.$$
 (1)

To filter the time series, EVI above or below the 95 % confidence interval of the site's EVI values were excluded. Then, the 16-day time series were interpolated to a monthly time step. Finally, the interannual monthly mean of EVI for each site was computed. Further, the ΔEVI_{wet-dry} index was computed for each site, that is, the differences of wet- and dryseason EVI normalized by the mean EVI, whereas dry season is defined as months with potential evapotranspiration above precipitation (Guan et al., 2015). For the sites where evapotranspiration is never above precipitation, dry season was defined as months with normalized potential evapotranspiration above normalized precipitation. In this study ΔEVI_{wet-dry} computed from MODIS MCD43A1 is correlated with MOD13C1 (Amazonian sites: ρ_{Spearman} =0.90; pan-tropical sites: $\rho_{\text{Spearman}} = 0.86$) and MAIAC (Amazonian sites: $\rho_{\text{Spearman}} = 0.89$) products (Supplement Fig. S4).

To extract the monthly climate time series for the 89 experimental sites (Fig. 1), we used climate data sets from three sources: the Climate Research Unit (CRU) at the University of East Anglia (Mitchell and Jones, 2005), the Consortium for Spatial Information website (CGIAR-CSI, http: //www.cgiar-csi.org) and from NASA (Loeb et al., 2009). From the CRU, we used variables from the CRU-TS3.21 monthly climate global data set available at 0.5° resolution from 1901 to 2012: cloud cover (cld, unit: %); precipitation (pre, mm); daily mean, minimal and maximal temperatures (respectively tmp, tmn and tmx, °C); temperature amplitude (dtr, °C); vapour pressure (vap, hPa); and potential evapotranspiration (pet, mm). The maximum climatological water deficit (CWD) is computed with CRU data by summing the difference between monthly precipitation and monthly evapotranspiration only when this difference is negative (water deficit) (Chave et al., 2014). From the CGIAR-CSI, we used the Global High-Resolution Soil-Water Balance dataset, soil water content (swc, %) (Zomer et al., 2008). Additionally, we used monthly incoming radiation at the top of the atmosphere (rad, $W m^{-2}$) covering the period from 2000 to 2015 at 1° spatial resolution from the CERES instruments on the NASA Terra and Aqua satellites (Loeb et al., 2009) and monthly incoming radiation at the surface (rad_{surf}, W m⁻²) from CERES SYN1deg product computed for all-sky conditions, provided at 1° spatial resolution from 2000 to 2015. Monthly incoming radiation at the surface (shortwave radiation) refers to radiant energy with wavelengths in the visible, near-ultraviolet, and near-infrared spectra and is produced using MODIS data and geostationary satellite cloud properties (Kato et al., 2011). In addition to the temporal series of climate variables, we extracted the global ecological zones (GEZs) of the sites. These GEZs are defined by the Food and Agriculture Organization of the United Nations (FAO) and relies on a combination of climate and (potential) vegetation (FAO, 2012).

Because at some sites wood productivity or litterfall measurements are older than the EVI measurements (before 2002), and, for recent site measurements, climate data are

Table 2. Description of the study sites for litterfall measurements, adapted from Chave et al. (2010). For each site, reference of the article, continent, country, full site name and geographical coordinates (long.—lat., in degrees) are reported. The next column reports annual litterfall measurement of wood productivity and litterfall (WP+LP) or only Litterfall (LP), leaf fall (YES) or total litterfall (NO), the number of traps, the trap size, the total area sampled, the mean litterfall productivity in Mg ha⁻¹ yr⁻¹ and the duration.

Sabyer et al (2000) Am Grama Tirne Bepo 1607 -2.100 WP+1P YES 9 1 6 Sep±1133 Chewe et al (2000) Am Brazil Apart Bezalin Chewe et al (2000) Am Brazil	Marchan	Cont.	Country	Site	Lat.	Long.	Type	Type data	Trap number	Trap size	Total size	Mean \pm SE	Duration
Am Brazil Apjaiu Romina 2.567 -61.300 LP NO 6 1 6 Am Brazil Gnjaiu Romina 2.567 -60.300 LP NO 6 1 16 6 Am Brazil Cunicans Reserve Manaus -1.733 -67.150 LP ND 16 1 18 18 Am Brazil Cunicans Reserve Manaus -2.567 -60.017 LP ND 6 1 1 18 Am Brazil Jani Para L.1.785 -2.507 -60.017 LP NB 6 5 6.55 15 Am Brazil Jani Para L.1.000 -2.200 -2.000 PP NB 1 45 Am Brazil Manajous L.1.584 -2.200 MP+LP YES 10 0.25 15 Am Brazil Manajous L.1.533 L.2.500 MP+LP YES 10 0.25 15	Baker et al. (2003); Owusu-	Af	Ghana	Tinte Bepo	7.067	-2.100	WP + LP	YES	6		6	8.59 ± 1.123	1998/2000
Ann Brazil Apjau Rozania 2.567 -61,019 NO 6 1 6 Am Brazil Apjau Rozania 2.567 -61,019 NO 6 1 6 Am Brazil Cupitao Paco Para -1.733 -47,159 LP NO 16 1 6 Am Brazil Cupitao Paco Para -1.735 -47,159 LP NO 18 1 16 Am Brazil Cupitar Para Reserve -2.00 -54,000 LP ND 15 1.5 1.5 Am Brazil Ducke Drake -2.00 -54,000 LP ND 1.5 1.5 1.5 Am Brazil Manigorn L.100 -2.500 LP ND 2.0 2.5 2.5 2.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 1.5 </td <td>Sekyere et al. (2006)</td> <td></td>	Sekyere et al. (2006)												
Am Brazil BDFPP Reserve -2.560 -60,000 LP NO 18 1 18 Am Brazil Capitud Reserve -1.733 -47.150 LPP NO 16 1 18 Am Brazil Cancaranie Property 1-373 -47.150 LPP YES 25 0.25 18.75 Am Brazil Cunicias Reserve Manaus -2.567 -60.117 LP YES 25 0.25 15.55 Am Brazil Juri Para -1.080 -2.200 LP YES 10 0.25 15.55 Am Brazil Juri Para -1.000 -2.200 LP YES 20 0.25 15.55 Am Brazil Manajosan -1.0543 -2.200 PP YES 20 0.25 15.5 Am Brazil Manajosan -1.047 -2.807 PP YES 20 0.25 15.5 Am Colombia M	Chave et al. (2010)	Am	Brazil	Apiau Roraima	2.567	-61.300	LP	NO	9	-	9	8.91 ± 0.564	1988/1989
Am Brazil Capituo Pato Para 1-733 -471,30 LP NO 16 1 16 Am Brazil Carpituo Pato Para 1-735 -471,81	Chave et al. (2010)	Am	Brazil	BDFFP Reserve	-2.500	-60.000	LP	NO	18	1	18	6.59 ± 0.675	1999/2002
Am Brazil Custaeana 1.178 -61.019 WP+LP YES 75 0.25 18.75 Am Brazil Custaeana -1.785 -60.117 LP YES 25 0.25 15.5 Am Brazil Custaeana -2.567 -60.117 LP YES 10 0.25 15.5 Am Brazil Lucuea-Uria Reserve -2.507 -59.044 WP+LP YES 100 0.25 15.5 Am Brazil Lugoa Sama -1.000 -2.904 WP+LP YES 100 0.25 25 Am Brazil Manajosa -1.333 -59.047 WP+LP YES 10 0.25 25 Am Brazil Manajosa -1.333 -59.027 WP+LP YES 10 0.25 25 Am Brazil Manajosa -1.333 -2.927 WP+LP YES 10 0.25 25 Am Brazil Roombia </td <td>Chave et al. (2010)</td> <td>Am</td> <td>Brazil</td> <td>Capitao Paco Para</td> <td>-1.733</td> <td>-47.150</td> <td>LP</td> <td>ON</td> <td>16</td> <td>-</td> <td>16</td> <td>7.97 ± 0.6</td> <td>1979/1980</td>	Chave et al. (2010)	Am	Brazil	Capitao Paco Para	-1.733	-47.150	LP	ON	16	-	16	7.97 ± 0.6	1979/1980
Am Brazil Cucieria Reserve Manus -1.78 -51.466 LP VES 55 6.25 6.25 Am Brazil Cucieria Reserve Manus -2.567 -6.0117 LP ND 15 0.5 5.75 Am Brazil Cucieria Reserve -2.000 -54.000 LP YES 10 0.25 2.5 Am Brazil Lagou Sama -1.9543 -4.900 LP YES 10 0.25 2.5 Am Brazil Manade Piedade Pernanbuco -7.833 -2.927 MP+LP YES 10 0.25 2.5 Am Brazil Manade Piedade Pernanbuco -7.833 -2.927 MP+LP YES 10 0.25 2.5 Am Brazil Manadour -7.833 -2.927 MP+LP YES 10 0.25 2.5 Am Brazil Manuchan -7.833 -2.927 MP+LP YES 10 0.25 2.5 Am	Castilho et al. (2012)	Am	Brazil	Caracarai	1.476	-61.019	WP + LP	YES	75	0.25	18.75	5.36 ± 0.19	2012/2013
Am Brazil Curierie Reserve Mannas -2.567 -60.117 LP NO 15 0.5 7.5 Am Brazil Curierie Reserve -2.200 -5.900 -8.017 LP YEB 100 0.25 2.5 Am Brazil Lagou Santa -1.0543 -2.972 WP+LP YEB 100 0.25 2.5 Am Brazil Manajosan -2.1033 -9.987 LP YEB 100 0.25 2.5 Am Brazil Manajosan -3.133 -9.987 LP YEB 20 0.25 2.5 Am Brazil Robal Ace Prelade Pernanbeco -7.833 -9.987 LP YEB 20 0.25 2.5 Am Brazil Robal Mana de Prelade Pernanbeco -7.833 LP YEB 20 0.25 2.5 Am Brazil Robal Prepared Prepared Prepared Prepared Prepared Prepared Prepared Prepared	Chave et al. (2010)	Am	Brazil	Caxiuana	-1.785	-51.466		YES	25	0.25	6.25	6.17 ± 0.738	2005/2006
Am Brazil Curau-Una Reserve -2.000 -54,000 LP YES 45 1 45 Am Brazil Joacke -2.952 -59.944 WP+LP YES 100 0.25 2.5 Am Brazil Jagou Santan -1.004 -25.007 LP YES 100 0.25 2.5 Am Brazil Manajoara -1.333 -59.87 LP NO 20 0.25 2.5 Am Brazil Manajoara -1.04 -5.437 LP NO 20 0.25 2.5 Am Brazil Manajoara -1.041 -58.37 LP YES 10 0.25 2.5 Am Colombia Amazyacu -1.041 -58.57 LP YES 20 1.5 30 Am Colombia Amazyacu -1.041 -58.57 LP YES 20 1.5 1.5 Am Colombia Amazyacu -1.041<	Chave et al. (2010)	Am	Brazil	Cuieiras Reserve Manaus	-2.567	-60.117	LP	ON	15	0.5	7.5	8.03 ± 0.564	1979/1982
Am Bnzil Jucke -2.952 -59.944 WP+LP YES 100 0.25 2.5 Am Bnzil Jari Para -1.000 -2.200 LP YES 100 0.25 2.5 Am Bnzil Manaus -1.000 -2.200 LP YES 100 0.25 2.5 Am Bnzil Manaus -1.000 -2.200 LP YES 100 0.25 2.5 Am Bnzil Manaus -1.000 -2.200 LP YES 10 0.25 2.5 Am Bnzil Mova Xwamina -1.4683 -2.3275 LP YES 10 0.25 2.5 Am Bnzil Tonnopa -1.4683 -2.325 LP YES 20 0.25 2.5 Am Colombia Tonnopa -1.4683 -2.325 LP YES 20 0.5 1.5 Am Colombia Tonnopa -2.307	Chave et al. (2010)	Am	Brazil	Curua—Una Reserve	-2.000	-54.000	LP	YES	45	_	45	6.62 ± 0.799	1994/1995
Am Brazil Lagou Santa -1.000 -52.000 LP YES 100 0.25 25 Am Brazil Lagou Santa -1.05.43 -3.927 PP+LP YES 0.0 0.25 4 Am Brazil Manzjoara -3.133 -59.867 LP NO 20 0.25 5 Am Brazil Marajoara -3.133 -59.867 LP NO 20 0.25 5 Am Brazil Nova Xwantina -1.1465 -52.353 LP YES 10 0.25 25 Am Brazil Nova Xwantina -1.1412 -53.532 LP YES 10 0.25 25 Am Colombia Chinkique -1.1412 -53.532 LP YES 29 1.2 30 Am Colombia Chinkique LA -7.3491 PFLD YES 25 1.2 Am Colombia Chinkigue La Sebra	Melgaco (2014); Chave et al.	Am	Brazil	Ducke	-2.952	-59.944	WP + LP	YES	10	0.25	2.5	3.97 ± 0.197	1976/1977
Am Brazil Jari Pera -1,000 -52,000 LP YES 100 0.25 25 Am Brazil Manajoan -19,543 -43,927 WP+LP YES 100 0.25 25 Am Brazil Manajoan -19,543 -53,987 LP NO 20 0.25 5 Am Brazil Manajoan -1,144 -5,3867 LP YES 10 0.25 5 Am Brazil Rova Xavantina -1,141 -5,387 LP YES 10 0.25 5 Am Brazil Rova Maratina -1,141 -5,3875 LP YES 30 1 30 Am Colombia Calmopia Chindquete -0,047 WP+LP YES 30 1 30 Am Colombia Calmine Chindquete -0,047 WP+LP YES 30 1 30 Am Colombia Calmine Chin	(2010)												
Am Brazil Lagoa Santa -19.543 -43.927 WP+LP YES 20 0.25 4 Am Brazil Manauss -3.133 -59.267 WP+LP NOO 20 0.25 5 Am Brazil Mana de Picdade Pernambuco -7.833 -59.267 WP+LP NOO 20 0.25 5 Am Brazil Mana de Picdade Pernambuco -7.833 -24.397 LP YES 10 0.25 2.5 Am Brazil Sinop -14.655 LP YES 20 1 20 Am Colombia Trapajos -11.412 -58.757 LP YES 20 1 20 Am Colombia Trapajos -11.412 -58.752 LP YES 20 1 20 Am Colombia Gran Subma Guayana -11.412 -88.752 LP YES 25 1.5 1.5 Am Colombia Gran Subma Guayana </td <td>Chave et al. (2010)</td> <td>Am</td> <td>Brazil</td> <td>Jari Para</td> <td>-1.000</td> <td>-52.000</td> <td>LP</td> <td>YES</td> <td>100</td> <td>0.25</td> <td>25</td> <td>7.63 ± 0.896</td> <td>2004/2005</td>	Chave et al. (2010)	Am	Brazil	Jari Para	-1.000	-52.000	LP	YES	100	0.25	25	7.63 ± 0.896	2004/2005
Am Brazil Manaus -3.133 -59.867 LP NO 20 0.25 5 Am Brazil Marajoura -7.833 -50.267 WP+LP NO 20 0.25 1.5 Am Brazil Marajoura -7.833 -34.917 LP YES 10 0.25 2.5 Am Brazil Nova Xavanina -14.685 -25.335 LP YES 10 0.25 1.5 Am Brazil Sinop -14.685 -25.335 LP YES 10 1 16 Am Colombia Amacayacu -3.017 -34.917 WP+LP YES 24 0.5 12.5 Am Colombia Chiribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Critificar Central 4.833 -75.243 LP YES 24 0.5 12.5 Am Colombia Critifiquete	Toledo et al. (2012); Paula and	Am	Brazil	Lagoa Santa	-19.543	-43.927	WP + LP	YES	20	0.2	4	4.12 ± 0.331	1997/1998
Am Brazil Manaus -3.133 -59.867 LP NO 20 0.25 S Am Brazil Marajoara -3.838 1.P YES 10 0.25 S Am Brazil Nova Xwamina -14.685 -53.235 LP YES 10 0.25 2.5 Am Brazil Kio Jurnena -11.417 -88.767 LP YES 10 0.25 2.5 Am Colombia Tapajos -11.417 -88.767 LP YES 20 0.25 2.5 Am Colombia Tapajos -11.417 -88.767 LP YES 20 0.25 1.2 Am Colombia Amacyacu -3.017 -70.300 LP YES 24 0.5 1.2 Am Colombia Grindiquez Gentral 4.833 -75.25 LP YES 24 0.25 1.2 Am Colombia Grindiquez Gentral 4.833	Lemos Filho (2001))									
Am Brazil Marajoara -7.833 -50.267 WP+LP NO 50 1 50 Am Brazil Mova Xavanina -1.833 -34.917 LP YES 10 1.2 15 Am Brazil Rio Jurena -1.447 -58.375 LP YES 10 1.5 10 Am Brazil Rio Jurena -1.1417 -58.375 LP YES 10 1.5 10 Am Colombia Amacayacu -1.1417 -58.471 WP+LP YES 23 1.5 1.0 1.5 1.0 Am Colombia Amichique -1.1417 -58.471 WP+LP YES 24 0.5 1.2 4 Am Colombia Croulibra Central 4.833 LP YES 24 0.5 1.2 4 Am Colombia Craulibra Central 4.833 LP YES 25 0.5 1.5 Am Colo	Chave et al. (2010)	Am	Brazil	Manaus	-3.133	-59.867	LP	NO	20	0.25	5	7.24 ± 0.607	1997/1999
Am Brazil Mata de Piedade Pernanbuco -7.833 -34.917 LP YES 10 0.25 2.5 Am Brazil Nowa Kavantina -14.685 -52.335 LP YES 10 1 10 Am Brazil Rio Junena -11.412 -58.325 LP YES 10 1 10 Am Colombia Amacyacu -11.412 -53.325 LP YES 20 1 20 Am Colombia Amacyacu -11.412 -53.32 LP YES 25 1 10 1 Am Colombia Cardillera Central -3.71 -70.30 LP YES 25 7.5 Am Colombia Cardillera Central 4.833 -75.25 LP YES 25 7.5 Am Colombia Cardillera Central 4.833 -75.25 LP YES 25 7.5 Am Cobmbia Cardillera Central 4.833<	Grogan and Schulze (2012);	Am	Brazil	Marajoara	-7.833	-50.267	WP + LP	NO	50	1	50	3.53 ± 0.416	1998/2001
Am Brazil Mata de Pledade Pernanbuco 7.833 -34.917 LP YES 10 0.25 2.5 Am Brazil Nova Xxwantina -1.4885 -2.335 LP YES 10 1 10 Am Brazil Sinopurena -11.412 -55.325 LP YES 20 1 20 Am Colombia Tippijos -11.412 -55.325 LP YES 20 1 20 Am Colombia Chibriquete 0.07 -17.431 -7.433 LP YES 24 0.5 1.2 Am Colombia Cridilera Central -3.07 -75.52 LP YES 24 0.5 1.2 Am Colombia Grain Subana Guayana 5.117 -70.300 LP YES 24 0.5 1.2 Am Colombia Aselva 1.04.31 -84.004 WP+LP YES 25 0.5 1.2 Am F	Free et al. (2014)												
Am Brazil Nova Xavantina -14.685 -52.335 LP YES 10 1 10 Am Brazil Riop Iurnena -10.417 -83.767 LP YES 10 1 16 Am Brazil Tapajos -1.14.7 -83.767 LP YES 20 1 16 Am Colombia Chiribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Chiribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Chiribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Cara Sabana Guayana -3.96 -69.904 LP YES 24 0.5 12.5 Am Colombia Relva 10.431 -84.004 WP+LP YES 25 0.5 12.5 Am French Guinna Byaeva<	Chave et al. (2010)	Am	Brazil	Mata de Piedade Pernanbuco	-7.833	-34.917	LP	YES	10	0.25	2.5	11.05 ± 1.427	2003/2004
Am Brazil Rio Juruena —10417 —58767 LP YES 16 1 16 Am Brazil Sinop —11.412 —5.3.72 LP YES 20 1 20 Am Colombia Arnacayacu —3.017 —70.300 LP YES 25 0.55 12.5 Am Colombia Chritisquee 0.3717 —70.330 LP YES 24 0.55 12.5 Am Colombia Gran Sabana Guayama 5.117 —60.931 LP YES 24 0.55 12.5 Am Colombia Gran Sabana Guayama 5.117 —60.931 LP YES 29 0.55 12.5 Am Colombia Gran Sabana Guayama 5.117 —60.931 LP YES 30 0.55 12.5 Am Colombia Gran Sabana Guayama 5.117 —60.931 LP YES 30 0.55 12.5 Am Cosa Rica <td>Chave et al. (2010)</td> <td>Am</td> <td>Brazil</td> <td>Nova Xavantina</td> <td>-14.685</td> <td>-52.335</td> <td>LP</td> <td>YES</td> <td>10</td> <td>1</td> <td>10</td> <td>0.45 ± 0.091</td> <td>2002/2003</td>	Chave et al. (2010)	Am	Brazil	Nova Xavantina	-14.685	-52.335	LP	YES	10	1	10	0.45 ± 0.091	2002/2003
Am Brazil Sinop -11.412 -55.325 LP YES 20 1 20 Am Colombia Tapajos -3.017 -54.971 WP+LP YES 25 12.5 Am Colombia Chiribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Chiribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Caraillera Central 4.833 -75.525 LP YES 24 0.5 12.5 Am Colombia Caraillera Central 4.833 -75.525 LP YES 24 0.5 12.5 Am Colombia Caraillera Central 4.833 -79.04 WP+LP YES 26 0.5 12.5 Am Ecuador RBSF -23.978 -79.077 WP+LP YES 40 0.5 10.5 Am French Guiana Piste de Sain	Chave et al. (2010)	Am	Brazil	Rio Juruena	-10.417	-58.767	LP	YES	16	1	16	5.21 ± 1.514	2003/2004
Am Brazil Tapajos -3.017 -54.971 WP+LP YES 35 1 30 Am Colombia Chiribiquete -3.017 -7.4.33 LP YES 25 0.5 12.5 Am Colombia Chiribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Chribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Cordillera Central 4.833 -75.25 LP YES 30 0.5 12.5 Am Colombia Cordillera Central 4.833 -75.25 LP YES 30 0.5 12.5 Am Colombia Cordillera Central 4.833 -75.25 LP YES 9.5 4 4 9.5 12.5 12.5 12.5 12.5 12.5 12.5 12.5 12.5 12.5 12.5 12.5 12.5 12.5 12	Chave et al. (2010)	Am	Brazil	Sinop	-11.412	-55.325	LP	YES	20		20	5.27 ± 1.116	2002/2003
Am Colombia Amacayacu -3.71 -70.300 LP YES 24 0.5 12.5 Am Colombia Chiribiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Gran Sabana Guayana 5.117 -60.933 LP YES 24 0.5 12.5 Am Colombia Zafire La Selva -73.96 -60.931 LP YES 25 0.5 12.5 Am Colombia Zafire La Selva -73.96 -60.931 LP YES 25 0.5 12.5 Am Ecuador RESF -3.978 -73.07 WP+LP YES 40 0.5 12.5 Am French Guiana Paracou 5.279 -52.924 WP+LP YES 40 0.5 10 Am French Guiana BCI Plateau 5.174 -73.86 LP YES 40 0.55 10 Am </td <td>Figueira et al. (2011); Nepstad</td> <td>Am</td> <td>Brazil</td> <td>Tapajos</td> <td>-3.017</td> <td>-54.971</td> <td>WP + LP</td> <td>YES</td> <td>30</td> <td>1</td> <td>30</td> <td>5.54 ± 0.533</td> <td>2000/2003</td>	Figueira et al. (2011); Nepstad	Am	Brazil	Tapajos	-3.017	-54.971	WP + LP	YES	30	1	30	5.54 ± 0.533	2000/2003
Am Colombia Amacayacu -3717 -70.300 LP YES 25 0.5 12.5 Am Colombia Chirbiquete 0.067 -72.433 LP YES 24 0.5 12.5 Am Colombia Craillear Central 4.833 LP NO 8 0.5 4 Am Colombia Zafire 1.0431 -84.004 WP+LP YES 15.2 12.5 Am Colombia Zafire 1.0431 -84.004 WP+LP YES 16.2 0.5 12.5 Am Ecuador RBSF -3.978 -79.077 WP+LP YES 10.1 1.92 Am French Guiana Piste de Saint Elie 5.279 -52.924 WP+LP YES 40 0.45 18 Am French Guiana Piste de Saint Elie 5.333 -52.924 WP+LP YES 40 0.45 18 Am French Guiana Piste de Saint Elie 5.333	and Moutinho (2013)												
Am Colombia Chirthiquete 0.067 -72.433 LP YES 24 0.5 12 Am Colombia Cordillera Central 4.833 -75.525 LP YES 30 0.25 7.5 Am Colombia Zaffre -3.996 -69.904 LP YES 25 0.5 12.5 Am Colombia Zaffre -3.978 -79.077 WP+LP YES 162 0.25 12.5 Am Ecuador RBSF -3.978 -79.077 WP+LP YES 10 0.16 1.95 Am French Guiana Nouragues 5.279 -52.924 WP+LP YES 40 0.5 1.9 Am French Guiana Piste de Saint Elie 5.279 -52.924 WP+LP YES 40 0.45 1.8 Am French Guiana Piste de Saint Elie 5.233 -53.024 WP+LP YES 40 0.45 1.8 Am <t< td=""><td>Chave et al. (2010)</td><td>Am</td><td>Colombia</td><td>Amacayacu</td><td>-3.717</td><td>-70.300</td><td>LP</td><td>YES</td><td>25</td><td>0.5</td><td>12.5</td><td>6 ± 0.31</td><td>2004/2006</td></t<>	Chave et al. (2010)	Am	Colombia	Amacayacu	-3.717	-70.300	LP	YES	25	0.5	12.5	6 ± 0.31	2004/2006
Am Colombia Cordillera Central 4.833 -75.525 LP YES 30 0.25 7.5 Am Colombia Grain Sabana Guayana 5.117 -60.933 LP NO 8 0.25 7.5 Am Colombia Zafire -3.996 -98.904 WP+LP YES 162 0.25 12.5 Am Ecuador RBSF -3.978 -79.077 WP+LP YES 162 0.25 12.5 Am French Guiana Nouragues -73.978 -79.077 WP+LP YES 40 0.16 1.92 Am French Guiana Paracou 5.279 -52.924 WP+LP YES 40 0.45 18 Am French Guiana BCT Plateau -12.835 -85.924 WP+LP YES 40 0.45 18 Am French Guiana BCT Plateau -12.835 -69.284 WP+LP YES 40 0.25 10 Am	Chave et al. (2010)	Am	Colombia	Chiribiquete	0.067	-72.433	LP	YES	24	0.5	12	5.62 ± 0.528	1999/2002
Am Colombia Gran Sabana Guayana 5.117 -60.933 LP NO 8 0.5 4 Am Colombia Zafire -3.996 -69.904 LP YES 25 0.5 12.5 Am French Guiana Nouragues -3.978 -79.077 WP+LP YES 10 0.16 1.92 Am French Guiana Piste de Saint Elie 5.279 -52.924 WP+LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.279 -52.924 WP+LP YES 40 0.45 18 Am French Guiana BCI Plateau -12.835 -52.924 WP+LP YES 40 0.25 10 Am French Guiana BCI Plateau -12.835 -69.285 WP+LP YES 40 0.25 10 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 0.25 12.5	Chave et al. (2010)	Am	Colombia	Cordillera Central	4.833	-75.525	LP	YES	30	0.25	7.5	3.36 ± 0.211	1986/1987
Am Colombia Zafire -3.996 -69.904 LP YES 25 0.5 12.5 Am Costa Rica La Selva 10.431 -84.004 WP+LP YES 162 0.5 12.5 Am French Guiana Nouragues 4.084 -52.680 LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.233 -52.924 WP+LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.233 -53.033 LP YES 40 0.45 18 Am Perul Tambopata -12.835 -69.285 WP+LP YES 5 0.25 10 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 40 0.25 10 As India Attapadi 2.103 76.450 WP+LP YES 50 0.25 50 As Malay	Chave et al. (2010)	Am	Colombia	Gran Sabana Guayana	5.117	-60.933	LP	ON	~	0.5	4	5.23 ± 0.449	1999/2000
Am Costa Rica La Selva 10431 -84.004 WP + LP YES 162 0.25 40.5 Am Ecuador RBSF -3.978 -79.077 WP + LP YES 12 0.16 1.92 Am French Guiana Piste de Saint Elie 5.279 -52.924 WP + LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.333 -52.924 WP + LP YES 40 0.45 18 Am French Guiana Piste de Saint Elie 5.333 -52.924 WP + LP YES 40 0.45 18 Am Perud Tambopata -12.835 -69.285 WP + LP YES 25 0.25 0.25 Am Venezuela Attapadi 11.083 76.450 WP + LP YES 50 0.25 10 As India Attapadi Lambir 4.200 114.033 WP + LP YES 50 0.25 12.5	Chave et al. (2010)	Am	Colombia	Zafire	-3.996	-69.904	LP	YES	25	0.5	12.5	5.2 ± 0.383	2004/2006
Am French Guiana Nouragues 4.084 -52.680 LP YES 40 0.5 20 Am French Guiana Paracou 5.279 -52.924 WP+LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.333 -53.033 LP YES 40 0.5 18 Am Peru Tambopata 1.12.835 -69.285 WP+LP YES 60 1 60 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As Midia Attapadi Lambir 4.200 114.033 WP+LP YES 50 0.25 50 As Thailand SERS Aberth YES 50 0.25 12.5 Au Australia Attaged 14.500 10.1933 WP+LP YES 50 0.25 12.5 Australia Australia Attaged <td>O'Brien et al. (2008); Clark</td> <td>Am</td> <td>Costa Rica</td> <td>La Selva</td> <td>10.431</td> <td>-84.004</td> <td>WP + LP</td> <td>YES</td> <td>162</td> <td>0.25</td> <td>40.5</td> <td>6.73 ± 0.314</td> <td>1997/2011</td>	O'Brien et al. (2008); Clark	Am	Costa Rica	La Selva	10.431	-84.004	WP + LP	YES	162	0.25	40.5	6.73 ± 0.314	1997/2011
Am French Guiana Nouragues 4.084 -52.680 LP YES 40 0.5 20 Am French Guiana Nouragues 4.084 -52.680 LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.279 -52.924 WP+LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.333 -52.924 WP+LP YES 60 1 60 Am Panama BCI Plateau 9.154 -79.846 LP NO 40 0.25 10 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 0.25 6.25 As India Attapadi 11.083 76.450 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 114.033 WP+LP YES 50 0.25 12.5 As Tha	et al. (2010(@, 2009)												
Am French Guiana Nouragues 4.084 -52.680 LP YES 40 0.5 20 Am French Guiana Paracou 5.279 -52.924 WP+LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.333 -53.934 LP YES 60 1 60 Am Panama BCI Plateau 9.154 -79.846 LP YES 60 1 60 Am Peru Tambopata -12.835 -69.285 WP+LP YES 25 6.25 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 50 0.25 12.5 Au Australia <	Homeier et al. (2010, 2012);	Am	Ecuador	RBSF	-3.978	-79.077	WP + LP	YES	12	0.16	1.92	4.35 ± 0.21	2001/2002
Am French Guiana Nouragues 4.084 -52.680 LP YES 40 0.5 20 Am French Guiana Paracou 5.279 -52.924 WP+LP YES 40 0.5 1 Am French Guiana Piste de Saint Elie 5.333 -53.033 LP YES 60 1 60 Am Panama BCI Plateau 9.154 -79.846 LP NO 40 0.25 10 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 114.033 WP+LP YES 50 0.25 12.5 As Thailand Australia Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	Roderstein et al. (2005); Braun-												
Am French Guiana Nouragues 4.084 -52.680 LP YES 40 0.5 20 Am French Guiana Paracou 5.279 -52.924 WP+LP YES 40 0.5 20 Am French Guiana Piste de Saint Elie 5.333 -53.033 LP YES 60 1 60 Am Panama BCI Plateau 9.154 -79.846 LP NO 40 0.25 10 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 50 0.25 12.5 As Thailand Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	ing et al. (2009)												
Am French Guiana Piste de Saint Elie 5.373 -52.924 WP+LP YES 60 1 60 Am Panama BCI Plateau 9.154 -79.846 LP NO 40 0.25 10 Am Peru Tambopata -12.835 -69.285 WP+LP YES 25 0.25 10 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 50 0.25 12.5 Au Australia Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	Chave et al. (2010)	Am	French Guiana	Nouragues	4.084	-52.680	LP	YES	40	0.5	20	5.88 ± 0.64	2001/2008
Am French Guiana Piste de Saint Elie 5.333 -53.033 LP YES 60 1 60 Am Panama BCI Plateau 9.154 -79.846 LP NO 40 0.25 10 Am Venezuela Tambopata -12.835 -69.285 WP+LP YES 25 0.25 6.25 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 50 0.25 12.5 Au Australia Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	Wagner et al. (2013); Stahl et al.	Am	French Guiana	Paracou	5.279	-52.924	WP + LP	YES	40	0.45	18	4.77 ± 0.311	2003/2011
Am French Guiana Piste de Saint Elie 5.333 -53.033 LP YES 60 1 60 Am Panama BCI Plateau 9.154 -79.846 LP NO 40 0.25 10 Am Peru Tambopata -12.835 -69.285 WP+LP YES 25 0.25 10 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 50 0.25 12.5 Au Australia Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	(2010); Bonal et al. (2008)												
Am Panama BCI Plateau 9.154 -79.846 LP NO 40 0.25 10 Am Peru Tambopata -12.835 -69.285 WP+LP YES 25 0.25 10 As India Attapadi 11.083 76.450 WP+LP YES 100 0.5 50 As Malaysia Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 50 0.25 12.5 Au Australia Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	Chave et al. (2010)	Am	French Guiana	Piste de Saint Elie	5.333	-53.033	LP	YES	09	1	09	5.04 ± 0.608	1978/1981
Am Peru Tambopata -12.835 -69.285 WP+LP YES 25 0.25 6.25 Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi 11.083 76.450 WP+LP YES 100 0.5 50 As Malaysia Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 25 1 25 Au Australia Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	Wieder and J.S. (1995)	Am	Panama	BCI Plateau	9.154	-79.846	LP	NO	40	0.25	10	12.88 ± 0.941	1986/1990
Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi 11.083 76.450 WP+LP YES 100 0.5 50 As Malaysia Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 25 1 25 Au Australia Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	Rowland et al. (2014b); Chave	Am	Peru	Tambopata	-12.835	-69.285	WP + LP	YES	25	0.25	6.25	7.16 ± 0.607	2005/2006
Am Venezuela San Ignacio de Yuruani 5.000 -61.017 LP NO 10 1 10 As India Attapadi 11.083 76.450 WP+LP YES 100 0.5 50 As Malaysia Lambir 4.200 114.033 WP+LP YES 50 0.25 12.5 As Thailand SERS 14.500 101.933 WP+LP YES 25 1 25 Au Australia Mt Baldy -17.269 145.423 WP+LP YES 60 0.65 39	et al. (2010)												
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not yet available (after 2012), all the data sets were averaged monthly by site. Then, in order to remove the site effect on the mean and the variance of the variables and to analyse only seasonality, all the variables were centred on zero and scaled to a variance of 1 by site. That is, for a given variable of a site, monthly values were subtracted by their annual mean and divided by their annual standard deviation. The obtained normalized variable had a mean of 0 and a variance of 1, but the time variation in the variable time-series, that is in our case the seasonality, remained completely unchanged.

The 89 sites represent a large sample of tropical forests under different tropical and subtropical climates corresponding to six global ecological tropical zones (FAO, 2012): tropical rain forest (TAr, 41 sites), tropical moist deciduous forest (TAwa, 23 sites), tropical dry forest (TAwb, 14 sites), tropical mountain systems (TM, 7 sites), tropical shrubland (TBSh, 1 site) and subtropical humid forest (SCf, 3 sites).

2.2 Data analysis

2.3 Effect of stem hydration on wood productivity

Changes in tree circumference measured with dendrometers are commonly used to characterise seasonal wood productivity. However, accelerated changes in circumference increments during the onset of the wet season can be caused by bark swelling as stems become hydrated (Stahl et al., 2010). Similarly, bark shrinking during dry periods can mask any secondary growth and even lead to negative growth increments (Stahl et al., 2010; Baker et al., 2002). Stem shrinkage during dry periods may be an important limitation of this work (Sheil, 2003; Stahl et al., 2010), as negative monthly growth values exist at almost all the study sites. Since the measurements are stem radius or circumference changes rather than wood formation, it is difficult to distinguish between true wood formation and hydrological swelling and shrinking. Direct measurements of cambial growth, such as pinning and micro-coring, currently represent the most reliable techniques for monitoring seasonal wood formation; however, all these methods are highly time-consuming, which severely restricts their applicability for collecting large data sets (Makinen et al., 2008; Trouet et al., 2012). Nevertheless, some observations already exist to compare growth from dendrometers and cambial growth at a seasonal scale for the same trees. In a tropical forest in Ethiopia experiencing a strong seasonality, high-resolution electronic dendrometers have been combined with wood anatomy investigation to describe cambial growth dynamics (Krepkowski et al., 2011). These authors concluded that water scarcity during the long dry season induced cambial dormancy (Krepkowski et al., 2011). Furthermore, after the onset of the rainy season, (i) bark swelling started synchronously among trees, (ii) bark swelling was maximum after few rainy days, and (iii) evergreen trees were able to quickly initiate wood formation. In a laboratory experiment of trunk section desiccation, Stahl et al. (2010) have shown a decrease in the diameter of the trunk sections ranging from 0.08 to 1.73 % of the initial diameter. This decrease was significantly correlated with the difference in water content in the bark, but not with the difference in water content in sapwood. The variation in the diameter of the trunk sections were observed when manipulating the chamber relative air humidity from 90 to 40 %. However, these values are not representative of the in situ French Guiana climatic conditions, which is where the trunk sections have been collected and where relative humidity never falls below 70 %. Negative increments were reported for onequarter of their sample with dendrometers measurements in the field. Recently, at the same site, some authors showed that biomass increments were highly correlated between the first and last quantiles of trunk bark thickness and between the first and the last quantile of trunk bark density, thereby suggesting that secondary growth is driven by cambial activity (Wagner et al., 2013) and not by water content in bark. At Paracou, a recent study showed a decrease or stop in the cambial growth for some species during the dry season, based on analysis of tree rings (Morel et al., 2015).

In a temperate forest, Makinen et al. (2008) simultaneously using dendrometer pinning and micro-coring on Norway spruce and Scots pine, Makinen et al. (see Figs. 3 and 5 in 2008) showed that a lag of 2 weeks exists between the growth measured by dendrometers, but the general pattern of growth is highly correlated. In La Selva (Costa Rica), where there is no month with precipitation below 100 mm, a seasonal variation is reported, thereby suggesting a seasonality only driven by cambial growth. In conclusion, swelling and shrinking exist and could result from different biotic and abiotic causes, cell size, diameter, bark thickness and relative air humidity (Stahl et al., 2010; Baker et al., 2002). To test how swelling and shrinking affect our results, we made first a linear model of wood productivity with precipitation as a single predictor with all the data, and then a similar linear model discarding the first month of the wet season (first month with precipitation > 100 mm) and the first month of the dry season (precipitation < 100 mm). Here, we assume that swelling occurs in the first month of the wet season and shrinking occurs in the first month of the dry season, as already observed. The removal of the first month of dry and wet seasons (defined, respectively, as the first month with precipitation > 100 mm and the first month with precipitation < 100 mm) did not affect the results of the linear model of wood productivity as a function of precipitation, that is, intercepts and slopes are not significantly different in both models (overlaps of the 95 % confidence interval of coefficients and parameters, Table 3).

2.4 Seasonality analysis

To address the first question "Are seasonal aboveground wood productivity, litterfall productivity and photosynthetic capacity dependent on climate?", we analysed with linear models the relationship between our variable of interest

Table 3. Coefficient of the linear model of wood productivity with the precipitation; with all data $m_{\rm WP}$ or after removing the first month of the dry season and wet season (defined, respectively, as the first month with precipitation > 100 mm and the first month with precipitation < 100 mm), $m_{\rm WP, -init}$.

Model	Parameter	Value	2.5 % CI*	97.5 % CI*	p value	R^2
$m_{ m WP}$	(Intercept)	-0.001	-0.05	0.05	0.982	0.433
	precipitation	0.66	0.64	0.74	< 0.0001	
m_{WPinit}	(Intercept)	-0.03	-0.08	0.02	0.284	0.466
, ,	precipitation	0.67	0.61	0.72	< 0.0001	

^{*:} confidence intervals of the model parameters

(wood productivity, litterfall productivity and photosynthetic capacity) and each climate variable at each site and at t, t-1month and t + 1 month. These lags were chosen to account for variations between years in the climate seasonality, as we used in our analysis the average climate per site. For example, if the tree diameter increments were measured during a year with a wet-season initiation delayed by 1 month in relation to the average year, a lag of 1 month could exist in the relation of the tree diameter increments and the monthly averages of precipitation used in linear models. The results were classified for each variable as a count of sites with significantly positive, negative or non-significant results. To enable between-sites comparison, when the overall link was negative, the linear model was then run with the climate variable multiplied by -1. For a given climate variable, a site with a significant association at only one of the time lags (-1, 0)or 1) was classified as significant. This strategy enables us to highlight the potential drivers of our variable of interest, which are the climate variables with a constant relation with the variable of interest in all the sites. Climate variable with no effect, or effect due to a particular correlation with a potential driver at some sites, will show changes in the sign of the relation with the variable of interest. Then, a McNemar test was run to compare the proportion of our classification (negative, positive or no relationship) between all paired combinations of climate variables accounting for dependence in the data, that is, to compare not only the proportion of positive, negative and no significant effect between two climate variables and the variable of interest but also to detect if the sites in each of the classes (positive, negative and no significant effect) were similar. In order to summarise all the relations between the climate variables, a table (similar to a correlation table) containing all paired combination p values of the McNemar test was built. In this table a p value < 0.05indicate that a different association between the two climate variables and the variables of interest cannot be rejected. To determine which climate variables explain the same part of variance and to enable interpretation, a cluster analysis was performed on the table of p values of the McNemar test using Ward distance. Climate variables in the same cluster indicate that they share a similar relation with the variable of interest.

When the climate variable with direct effect was identified, we built a linear model to predict wood and litter productivity seasonality with climate in all sites. For EVI, two climate variables were identified and their influence was dependent on the site values of $\Delta EVI_{wet-dry}$. To find the $\Delta EVI_{wet-dry}$ threshold of main influence of each variable, the R^2 of the linear relationship EVI as a function of the climate variable for different values of $\Delta EVI_{wet-drv}$ threshold were computed. R^2 was computed for the sample above or below $\Delta EVI_{wet-dry}$ depending on the relationship of each variable to the threshold. The optimal threshold of $\Delta EVI_{wet-drv}$ for climate variable influence on normalized EVI was defined by a break in the decrease of R^2 values. Optimal thresholds were then used to define the range of $\Delta EVI_{wet-dry}$ where EVI is influenced by one of the climate variables, the other and by both. To find the best linear combination of variables that contains the maximum information to predict EVI, we ran an exhaustive screening of the candidate models with the identified climate variables and their interactions with the $\Delta EVI_{wet-dry}$ classes using a stepwise procedure based on the Bayesian information criterion, BIC (Schwarz, 1978).

To address the second question "Does a coherent pantropical rhythm exist among these three key components of the forest carbon fluxes?", we analysed the linear relationship between wood, litter productivity and canopy photosynthetic capacity. The non-parametric Mann-Whitney test was used to determine the association between wood/litter productivity and photosynthesis rhythmicity depending on site limitations.

To address the third question – is the rhythm among these three key components of the forest carbon controlled by exogenous (climate) or endogenous (ecosystem) processes? – we analysed the linear relationship between $\Delta EVI_{wet\text{-}dry}$ and mean annual precipitation, as well as the relationship between $\Delta EVI_{wet\text{-}dry}$, $\Delta wood$ productivity_{wet\text{-}dry} and $\Delta litter$ productivity_{wet\text{-}dry} and maximum climatological water deficit (CWD). $\Delta EVI_{wet\text{-}dry}$, $\Delta wood$ productivity_{wet\text{-}dry} and $\Delta litter$ productivity_{wet\text{-}dry} indices are the differences of wet- and dry-season variable values normalized by the mean of the variable, where the dry season is defined as months with potential evapotranspiration above precipitation.

To avoid over-representation of sites with the "same climate" (that is, to account for spatial and temporal autocorrelation in the climate data) cross correlation (positive and negative) were computed within sites for the monthly climate variables rad, pre, pet, dtr, tmn and tmx. The site's annual values of the same climate variables were added in the table. After scaling and centring the table, the Euclidian distance between each site and the mean table of all other sites (barycentre) was computed. We defined the weight of each site as the distance to the other divided by the maximum distance to the other. This distance was used as a weight in the linear models.

All analysis were performed in R (Team, 2014).

3 Results

3.1 Climate footprint in seasonal carbon assimilation and storage

A direct and dominant signal of precipitation seasonality was found in seasonality of wood productivity for 59 out of the 68 sites (86.8%) where wood productivity data were available (cluster of variables in Fig. 2a with temperature amplitude (dtr), cloud cover (cld), precipitation (pre) and soil water content (swc), Sect. 2.2 and Supplement Table S1). All the variables in this cluster are wet season indicators: low temperature amplitude, high precipitation, high soil water content and high cloud cover. Two other clusters of climate variables are apparently associated with wood productivity. However, the climate variables that better explained wood productivity in these two clusters, vapour pressure (vap) and mean temperature (tmp), respectively, are highly correlated with precipitation in the clusters (Fig. 2a and Tables S3-S4). In spite of this dominant signal, these are outliers in our data, that exhibit no relationship or a negative relationship with precipitation (Appendix A1). Four of the five sites that have no dry season (months with precipitation below 100 mm) were amongst these outliers.

It is interesting to note that 48.0% of the monthly wood productivity is explained by the single variable "precipitation" (model $m_{\rm WP}$ in Table 4). The linear model with monthly precipitation only ($m_{\rm WP}$) was able to reproduce the seasonality of the majority of the sites analysed (Fig. 3a). No monthly lag between predicted and observed seasonality was observed for 35 sites. For 63 sites, a lag between -2 and +2 months was observed (Fig. 4a).

Canopy photosynthetic capacity, as estimated by EVI, for the 89 experimental sites, displayed an intriguing pattern with monthly precipitation, apparently related to the difference of $\Delta \text{EVI}_{\text{wet-dry}}$ (Fig. 5a), an indicator of the dry season evergreen state maintenance (Guan et al., 2015), computed as the difference between the mean EVI of the wet season ($p_{\text{re}} \geq \text{pet}$) and of the dry season ($p_{\text{re}} < \text{pet}$) (Sect. 2.1). This pattern can be explained by a change in the climate pa-

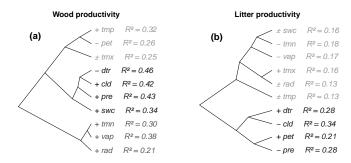


Figure 2. Dendrogram of the climate seasonality associations with the seasonality of wood productivity (a) and litterfall (b). The global sign and R^2 of the linear relationship between wood and litter productivity and the following climate variable is given. + indicates a positive correlation between the climate variable and wood or litter productivity in all the sites, - a negative correlation in all the sites, while \pm indicates positive correlation for a portion of the sites while negative for the other. Climate variables in the same cluster are highly correlated, that is, they produce the same prediction in terms of values and effects for the same sites. Different shades of grey indicate the relative strength of associations for each cluster with seasonality of wood or litter productivity, black indicates the strongest association. cld: cloud cover; pre: precipitation; rad: solar radiation at the top of the atmosphere; tmp, tmn and tmx are respectively the daily mean, minimal and maximal temperatures; dtr: temperature amplitude; vap: vapour pressure; pet: potential evapotranspiration; and swc: relative soil water content.

rameters that mainly control photosynthesis, from precipitation in water-limited sites ($\Delta EVI_{wet-dry} > 0.0378$, Fig. 5b) to maximal temperature in light-limited site ($\Delta EVI_{wet-drv}$ < -0.0014, Figs. 5c and S1). Sites with mixed influence of precipitation and temperature are found between the range of $\Delta EVI_{wet-dry}$ [-0.0014; 0.0378] (Fig. 6 for the definition of the thresholds). In our sample, the shift in climate control depends on the annual water availability. That is, sites are not water-limited above 2000 mm yr⁻¹ of mean annual precipitation (Fig. 5d), as previously observed (Guan et al., 2015). Rather, they are light-limited as shown by the relationship between photosynthetic capacity and maximal temperature (Fig. 5c). Light-limited sites are located in Amazonia, in the south of Brazil and in south-east Asia (Fig. 7). For all the sites, maximal temperature is highly correlated with incoming solar radiation at the surface ($r_{Pearson} = 0.80$, p < 0.0001), approximating solar energy available for the plants (Fig. 8). With the model mBIC_{EVI} (Table 4), precipitation, maximal temperatures and their thresholds explained 54.8 % of the seasonality of photosynthetic capacity (Fig. 3c). For 39 sites, no seasonal lag between predicted and observed seasonality of canopy photosynthetic capacity was observed using the model mBIC_{EVI}. However, a majority of the sites (82 sites) appeared to have a lag between -2 and +2 months (Fig. 4c). The model failed to reproduce the seasonality for seven sites (one water-limited, one light-limited and five mixed sites).

Table 4. Intercepts and slopes of the fitted linear models for seasonal wood production (m_{WP}) , litterfall (m_{lit}) and EVI $(mBIC_{EVI})$; with the seasonal climate variables: precipitation (pre), cloud cover (cld) and maximal temperature (tmx). Light-, water- and mixed limitation indicate the limitation of the sites and are defined with the value of $\Delta EVI_{wet-dry}$ (Fig. 6 for the definition of the thresholds).

Model	Components	Coefficien (std. error)	t value	p value	R^2
Wood production (m_{WP})	Intercept	0.0005 (0.0249)	0.02	0.9833	0.480
F (WI)	Precipitation	0.6869 (0.0260)	26.40	< 0.0001	
Litterfall (m_{lit})	Intercept	0.0000 (0.0389)	0.00	0.9999	0.317
(\'`\'II(\'	Cloud cover	-0.5685 (0.0407)	-13.98	< 0.0001	
	Intercept	0.0000 (0.0197)	0.00	0.9999	
	Maximal temperature in light-limited sites	0.7643 (0.0396)	19.28	< 0.0001	
EVI (mBIC _{EVI})	Maximal temperature in sites with mixed limitations	0.1683 (0.0545)	3.09	0.0020	0.548
	Maximal temperature in water-limited sites	-0.1100 (0.0275)	-4.00	< 0.0001	-
	Precipitation in sites with mixed limitation	0.3697 (0.0545)	6.78	< 0.0001	-
	Precipitation in water-limited sites	0.8149 (0.0275)	29.60	< 0.0001	-

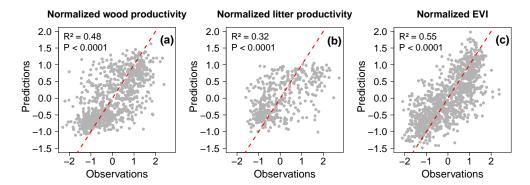


Figure 3. Observed vs. predicted monthly wood productivity under the model only with precipitation, m_{WP} (a); litterfall productivity under the model only with cloud cover, m_{lit} (b); and EVI the model only with precipitation, maximal temperature and site limitations, mBIC_{EVI} (c). The red dashed line is the identity line y = x. Parameters of the models are given in Table 4.

For 27 out of the 35 sites (77.1%) where litter data were available, litter productivity was associated with dry season indicators (lack of precipitation, high evaporation, low soil water content and high temperature amplitude, Fig. 2b). Surprisingly, we found that cloud cover (cld), an indirect variable, was the best single predictor of litterfall seasonality (Table 4). Direct effects are observed only for potential evapotranspiration (pet) and temperature amplitude (dtr) (Fig. 2b and Table S5). A second cluster of climate variables is associated with litter productivity but a key variable in this subgroup, minimal temperature (tmn), is correlated with cloud cover (cld) (Table S7). Despite this dominant signal, outliers showing no relationship with cld exist in our data (Ap-

pendix A2). The predictive model with cloud cover as a single variable (Table 4) explains 31.7% of the variability and performs well to reproduce the seasonality of litterfall productivity (Figs. 3b and 4b).

At a pan-tropical scale, 48 % of the variability of monthly aboveground wood productivity (Fig. 3a and Table 4) and 31.7 % of the monthly litterfall seasonality can be linearly explained with a single climate variable (Fig. 3b). The relationship between photosynthetic capacity (EVI) and climate is more complex; however, 54.8 % of the monthly EVI variability can be linearly explained with only two climate variables, precipitation and maximal temperature (Fig. 3c).

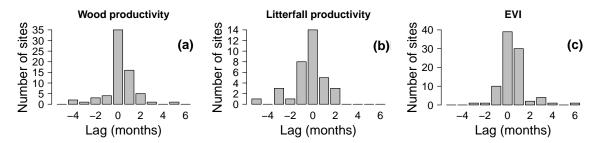


Figure 4. Cross correlation between observations and predictions of wood production (a), litterfall (b) and EVI (c) with the linear models parameters (Table 4). A cross correlation of zero month indicates a similar seasonal pattern in the time series of observations and predictions.

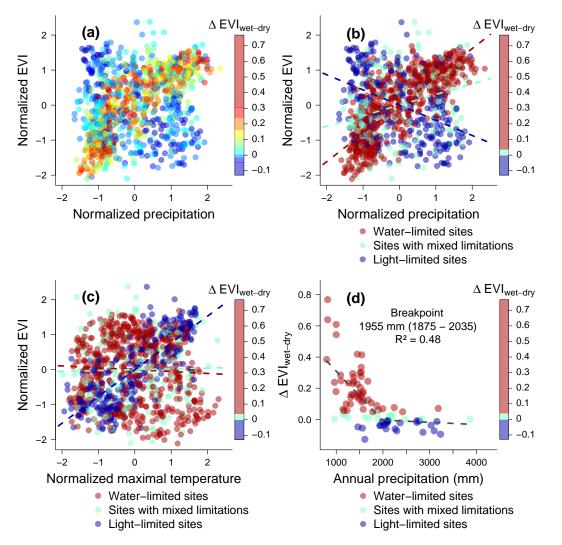


Figure 5. Monthly associations of EVI with precipitation (a, b), maximal temperatures (c), and association of $\Delta \text{EVI}_{\text{wet-dry}}$ with mean annual precipitation (d). In (a) colours represent the value of $\Delta \text{EVI}_{\text{wet-dry}}$ while in (b), (c) and (d) colours represent $\Delta \text{EVI}_{\text{wet-dry}}$ grouped by the following classes: water-limited sites ($\Delta \text{EVI}_{\text{wet-dry}} > 0.0378$), sites with mixed limitations ($\Delta \text{EVI}_{\text{wet-dry}} = -0.0014$) and light-limited sites ($\Delta \text{EVI}_{\text{wet-dry}} < -0.0014$). The dashed lines in (b) and (c) represent the linear relationship between climate variable and observed EVI for water-limited sites, sites with mixed limitations and light-limited sites. Parameters of the models are given in Table S8. The dashed lines in (d) represents the best regression model with a breakpoint between $\Delta \text{EVI}_{\text{wet-dry}}$ and mean annual precipitation.

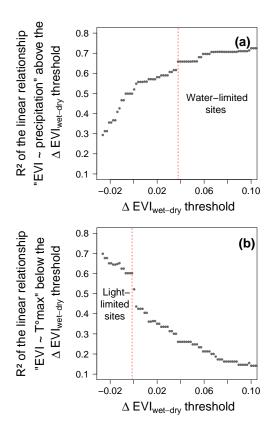


Figure 6. Threshold of $\Delta EVI_{wet-dry}$ used to define "water-limited" sites (a) and "light-limited" sites (b). Sites with $\Delta EVI_{wet-dry}$ between the two thresholds had a mixed influence of the two climate variables and were qualified as "mixed". The names of the classes represent the main climate limitations deduced from the climate control on canopy photosynthetic capacity observed in our results. The y axis represents the R^2 values of the linear models normalized EVI as a function of normalized precipitation (a) and as a function of maximal temperature (b), respectively for the sample with $\Delta EVI_{wet-dry}$ above the threshold (a) and below the threshold (b). Optimal threshold of $\Delta EVI_{wet-dry}$ for climate variable influence on normalized EVI was defined by a break in the decrease of R^2 values, which is represented by red dashed lines.

3.2 Decoupling wood productivity, litter productivity and canopy photosynthetic capacity seasonality

In sites where both measurements were available, we observed a negative relationship between wood productivity and litterfall (Fig. 9, supported by linear analysis, Fig. S2). This relationship is consistent across the tropics and constant for all our sites (Fig. 10c), independently of the site water or light limitations (Mann-Whitney test, U = 746, p = 0.0839). Wood productivity and litterfall are mainly driven by only one climate driver in our results, precipitation and cloud cover respectively. The seasonality of these climate drivers are coupled for all the sites, where maximum precipitation occurs in the wet season while minimum cloud cover occurs in the dry season.

In water-limited forests, the seasonality EVI and above-ground wood production are synchronous for the majority of the sites (Fig. 10a), as a consequence of their relationship with precipitation. However, aboveground wood production is better explained by precipitation than EVI (R^2 of 0.503 and 0.451 respectively).

Conversely, in light-limited sites and forests with mixed limitations (mixed forests), EVI is weakly coupled with the seasonality of wood productivity (respectively p = 0.0633, $R^2 = 0.017$ and p = 0.0124, $R^2 = 0.055$). Therefore, we conclude that the relationship between EVI and wood productivity depends on site limitations (Mann-Whitney test, U = 874.5, p = 0.0012).

The relationship between EVI and litter production is not constant (Fig. 10b), and also depends on site limitations (Mann-Whitney test, $U=1016.5,\ p<0.001$). EVI is consistently negatively associated with litterfall production for water-limited forests ($p<0.001,\ R^2=0.510$), reflecting forest "brown-down" when litterfall is maximal. Litter production is slightly better explained by cloud cover than EVI (R^2 of 0.533 and 0.510 respectively), and they predict the same effect for the same site (McNemar test, p=0.999). No significant associations are found between EVI and litter in forests with mixed limitations ($p=0.8531,\ R^2<0.0001$) and in light-limited forests ($p=0.4309,\ R^2<0.0001$).

 $\Delta EVI_{wet-dry}$ and $\Delta wood$ productivity_{wet-dry} are dependent on annual water availability (Figs. 11a–b and 5d). $\Delta wood$ productivity_{wet-dry} is close to zero and could be negative for light-limited sites; the amplitude of the seasonality is driven by the annual water availability. The values for $\Delta wood$ productivity_{wet-dry} in south-east Asia are all negative. This is consistent with the negative or null associations of wood productivity and precipitation at these sites (Appendix A1). Δ litter productivity_{wet-dry} is poorly correlated with maximum climatological water deficit (CWD).

4 Discussion

We have found a remarkably strong climate signal in the seasonal carbon cycle components studied across tropical forests. While wood and litterfall production appear to be dependent on a single major climate driver across the tropics (water availability), the control of photosynthetic capacity varies according to the increase in annual water availability, shifting from water-only to light-only drivers.

Minimum aboveground wood production tends to occur in the dry season. While this result is not new (Wagner et al., 2014), here we confirm this pattern with a large database of wood production measurements (68 sites). Months with the lowest water availability are less favourable for cell expansion, as water stress is known to inhibit this process, as observed in dry tropical sites (Borchert, 1999; Krepkowski et al., 2011). This pattern is found in water-limited, mixed and light-limited sites. At the very end of the water availabil-

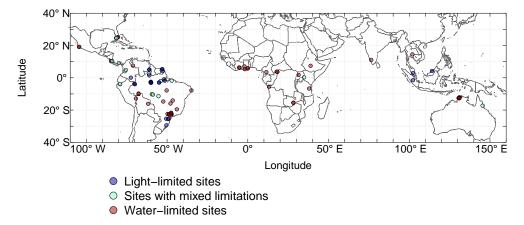


Figure 7. Locations and climate limitations of the 89 experimental sites. water-limited sites ($\Delta EVI_{wet-dry} > 0.0378$), sites with mixed limitations ($\Delta EVI_{wet-dry} = 0.0014$), (Fig. 6 for the definition of the thresholds).

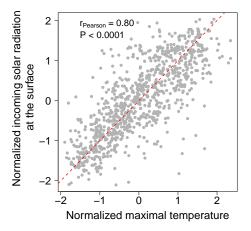


Figure 8. Association between normalized maximal temperature from Climate Research Unit and normalized incoming solar radiation at the surface from CERES. Monthly incoming solar radiation at the surface (incident shortwave radiation) refers to radiant energy with wavelengths in the visible, near-ultraviolet, and near-infrared spectra and is produced using MODIS data and geostationary satellite cloud properties (Kato et al., 2011). The red dashed line is the identity line y = x.

ity gradient (wettest ones), some sites have no relationship or a negative relationship with monthly precipitation, as observed in Lambir, Malaysia (Kho et al., 2013). These sites, three in south-east Asia and one in southern Brazil, have no marked dry season, defined as months with precipitation below 100 mm. These relationships with monthly precipitation could reflect cambial dormancy induced by soil water saturation, as observed in Amazonian floodplain forests (Schöngart et al., 2002), and/or be related to limited light availability due to persistent cloud cover. However, for these ultra wet sites, the lack of field data limits the analysis of the effects of climate on the seasonality of aboveground wood production.

Maximum litterfall, for most of our sites, occurs during the months of minimum cloud cover during the dry season. It is known that the gradient from deciduous to evergreen forests is related to water availability, with the evergreen state sustained during the dry season above a mean annual precipitation threshold of approximately 2000 mm yr⁻¹ (Guan et al., 2015). The litterfall peak occurs when evaporative demand is highest. The maintenance of litterfall seasonality in the light-limited sites could be driven mostly by a few large/tall canopy trees shedding leaves, mainly in response to high evaporative demand. This can explain why litterfall occurs in the dry season and is decoupled from EVI, a parameter that integrates the entire canopy (Fig. 10b). On the other hand, in water-limited sites, most of the trees shed their leaves, thereby resulting in a litterfall signal coupled with EVI "brown-down" (Fig. 10b).

Canopy photosynthetic capacity has different climate controls depending on water limitations (Fig. 5). As already observed, in sites with mean annual precipitation below $2000 \,\mathrm{mm}\,\mathrm{yr}^{-1}$ (Fig. 5d), photosynthetic capacity is highly associated with water availability (Guan et al., 2015) and highly dependent on monthly precipitation (Fig. 5b). This seems to confirm that longer or more intense dry seasons can lead to a dry-season reduction in photosynthetic rates (Guan et al., 2015). In addition to the control by water availability (Guan et al., 2015; Bowman and Prior, 2005; Hilker et al., 2014), we demonstrated that for sites where water is not limiting, photosynthetic capacity depends on maximal temperatures, which reflects available solar energy or daily insolation at the forest floor (Fig. 8). For these sites, the EVI peak occurs at the same time as the maximal temperature peak, which supports the hypothesis of the detection of a leaf flushing signal induced by a preceding increase of daily insolation (Borchert et al., 2015). This result is also consistent with flux-tower-based GPP estimates in neotropical forests (Restrepo-Coupe et al., 2013; Guan et al., 2015; Bonal et al., 2008). If the increase in EVI is a proxy of leaf

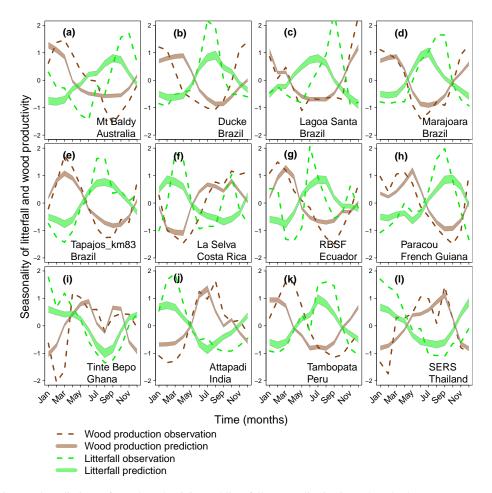


Figure 9. Observations and predictions of wood productivity and litterfall seasonality in sites where both measurements were available. The outliers in our analysis, Lambir and Caracarai, are not represented. *y* axis have no units as the variables were normalized.

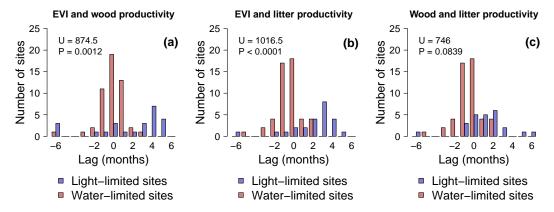


Figure 10. Cross-correlation between monthly EVI and wood productivity (**a**), EVI and litter productivity (**b**) and wood and litter productivity (**c**) for water- and light-limited sites. The x axis indicates the time-lag to get the maximum correlation between the variables. When no observations were available for wood and litter productivity, predictions from the climatic model were used (Table 4). To facilitate graphical representation, cross-correlation (**a**) is positive, while (**b**) and (**c**) are negative. A positive cross-correlation at lag of 1 month indicates a similar seasonal pattern in the time series with a time lag of 1 month, while a negative cross-correlation at lag 1 month indicates an opposite seasonal pattern with a time lag of 1 month. All the water-limited and light-limited sites were represented (respectively 50 and 24 sites) as only 4 water-limited sites in (**a**) and 3 in (**b**), and only 2 light-limited sites in (**c**) have no statistically significant cross-correlation.

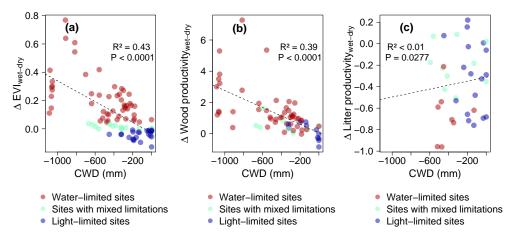


Figure 11. Associations between site's $\Delta EVI_{wet-dry}$ (a), $\Delta wood$ productivity_{wet-dry} (b) and $\Delta litter$ productivity_{wet-dry} (c) with the environmental variable maximum climatological water deficit (CWD). Dashed lines are the regression lines. $\Delta EVI_{wet-dry}$, $\Delta wood$ productivity_{wet-dry} and $\Delta litter$ productivity_{wet-dry} indices are the differences of mean of the wet- and dry-season of the variable normalized by the annual mean, where dry season is defined as months with potential evapotranspiration above precipitation (Guan et al., 2015). For the sites where evapotranspiration is never above precipitation, dry season is defined as months with normalized potential evapotranspiration above normalized precipitation.

maturation, as already observed in a tropical forest of southern Peru (Chavana-Bryant et al., 2016), our result supports the satellite-based hypothesis that temporal adjustment of net leaf flush occurs to maximize water and radiation use while reducing drought susceptibility (Myneni et al., 2007; Jones et al., 2014; Bi et al., 2015). However, more detailed data on the leaves dynamics would be necessary to confirm these assumptions.

We demonstrated that the seasonality of aboveground wood production and litterfall are coupled, while photosynthetic capacity seasonality can be decoupled from wood and litterfall production seasonality depending on the local water availability (Fig. 10).

Further, our results show that carbon allocation to wood is prioritized in the wet season, independently of the site conditions (water- or light-limited). This priority has also been shown in forests impacted by droughts, where trees prioritised wood production by reducing autotrophic respiration even when photosynthesis was reduced as a consequence of water shortage (Doughty et al., 2015). However, there is still a lack of information on a wider scale regarding how trees prioritise the use of non-structural carbohydrates. The potential decoupling of carbon assimilation and carbon allocation found here seems to indicate a complex and indirect mechanism driving carbon fluxes in the trees. Some experimental results showed that endogenous and phenological rhythms can define the prioritisation in carbon allocation and may be more important drivers of the carbon cycle seasonality than climate in tropical forests (Malhi et al., 2014; Doughty et al., 2014; Morel et al., 2015). This corroborates other results that indicate that growth is not limited by carbon supply in tropical forests (Körner, 2003; van der Sleen et al., 2015; Wurth et al., 2005). However, even if these results are in accordance with our results for light-limited sites, it must be noted that they cannot be generalized to water-limited sites, where climate constrains both photosynthetic capacity and wood productivity.

Canopy photosynthetic capacity and aboveground wood production appear to be predominantly driven by climate at seasonal and annual scales, thereby suggesting exogenous drivers (Figs. 5 and 11). However, if litterfall was driven by climate only, its pattern would be more predictable, with a linear relationship between annual water availability (CWD) and Δ litter productivity_{wet-dry} such as for wood production (Fig. 11b-c), which would translate into a massive peak in the dry season. Even with the litterfall peak occurring mainly in the dry season, another part of the variation seems to be related to endogenous drivers. Such endogenous effects have already been observed in tropical forests, for example, seasonality of root production prioritised over leaf production in a dry site in Bolivia or leaf production occurrence during wet months in French Guiana (Doughty et al., 2014; Morel et al., 2015). The lag between peak of litterfall in dry season and minimum photosynthetic capacity of the canopy we observe for light-limited sites (Fig. 10b) could reflect a mixture of bud sets and bud breaks with a relative weak synchronism due to the high diversity of species involved and the weakness of the seasonal signal of solar insolation. Our results are consistent with a seasonal cycle timed to the seasonality of solar insolation, but with an additional noise due to leaf renewal and/or net leaf abscission during the entire year unrelated to climate variations (Borchert et al., 2015; Myneni et al., 2007; Jones et al., 2014; Bi et al., 2015). While photosynthetic capacity and wood productivity appear mostly exogenously driven, litterfall association with climate at seasonal and annual scales suggest both exogenous and endogenous processes. It remains the case that the unexplained variability of photosynthetic capacity and wood productivity seasonality could be link to endogenous drivers, but more investigations are needed to demonstrate it.

In this study, we use EVI as an index of seasonality of canopy photosynthetic capacity based on the previously demonstrated correlation between canopy photosynthetic capacity from the MODIS sensor and solar-induced chlorophyll fluorescence (SIF) at a pan-tropical scale (Guan et al., 2015) and from the correlation between $\Delta \text{EVI}_{\text{wet-dry}}$ from MODIS MOD13C1, MCD43A1 and MAIAC products (Fig. S4). Here, we show how satellite and field data can be used to infer characteristics of tropical forests carbon cycle in a consistent framework. To go further, it is necessary to determine the real amount of photosynthetic products in order to describe quantitatively the seasonal carbon cycle in tropical forests.

5 Conclusions

In summary, the seasonality of carbon assimilation and allocation through photosynthetic capacity and aboveground wood production is consistently and directly related to climate in tropical forested regions. Notably, we found that regions without annual water limitations exhibit a decoupled carbon assimilation and storage cycle, which highlight the complexity of carbon allocation seasonality in the tropical trees. Although seasonal carbon allocation to aboveground wood production is driven by water, whether the seasonality of photosynthetic capacity is driven by light or water depends on the limitations of site water availability.

In a drier climate, from our results we can make the following assumptions. (i) In water-limited forests, the reduction of the wet period duration could lead to a time reduction of favourable conditions for carbon assimilation and allocation. (ii) In current light-limited forests with future precipitation below to the $2000 \, \mathrm{mm} \, \mathrm{yr}^{-1}$ threshold, the intensification of the dry period could suppress the canopy photosynthetic capacity increase during this high solar radiation period, reducing carbon assimilation and making these forests shift to water-limited forests. However, in light-limited forests with future precipitation above the $2000 \, \mathrm{mm} \, \mathrm{yr}^{-1}$ threshold, as cloud cover has been shown to limits net CO₂ uptake and growth of tropical forest trees (Graham et al., 2003), it remains uncertain how reduction of cloud cover will affect the productivity.

Appendix A: Description of outliers

A1 Wood productivity outliers

Despite this dominant signal, outliers exist in our data showing negative (3 sites) or no relationship (6 sites) with precipitation. Due to the correlation of climate variables at the site scale, it is difficult to interpret each site alone; however, some groups arose in these outlier sites. The first group, the two sites Itatinga and Pinkwae, contains only saplings measurements. The second group, the sites with no month with precipitation below 100 mm, includes Lambir (Malaysia). Muara Bungo (Indonesia), Pasoh (Malaysia), Flona SFP (Brazil). The third group includes two mountain sites, Tulua and Munessa. For Munessa, there is evidence of cambial growth related to precipitation Krepkowski et al. (2011); however, the sample we used comprises two species known to have different sensitivity to rainfall. The monthly mean of the sites' wood productivity could be responsible for the lack of rainfall-related pattern. Finally, for Caracarai (Brazil), there was a lack of 6-month data encompassing the beginning and middle of the wet season, which has been linearly interpolated to the month; however, due to the important sampling effort, we initially chose to keep this data set.

A2 Litterfall productivity outliers

Only one site, BDFFP, showed no apparent relationship between litter productivity and cloud cover (Fig. S3). This site is in a fragmented forest where fragmentation is known to affect litterfall (Vasconcelos and Luizão, 2004). For the other outlier, they all have a peak of litterfall correlated with pet or cld (Fig. S3). Three different groups can be observed: (i) sites which have another peak of litterfall during the year (Cueiras, La Selva, Gran Sabana), (ii) sites with very skew litterfall peaks followed by an important decrease in litterfall, while the climate conditions are optimal for litterfall productivity from the viewpoint of the linear model (Capitao Paco, Rio Juruena and RBSF) and (iii) sites which have two peaks of pet, but litterfall occurs only during one of them (Apiau Roraima, Gran Sabana).

Appendix: Data availability

The data and the code to reproduce the analysis and the figures are freely available upon request to the corresponding author.

The Supplement related to this article is available online at doi:10.5194/bg-13-2537-2016-supplement.

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