



**HAL**  
open science

## Amazon forest response to repeated droughts

T. R. Feldpausch, O. L. Phillips, R. J. W. Brienen, E. Gloor, J. Lloyd, G. Lopez-Gonzalez, A. Monteagudo-Mendoza, Y. Malhi, A. Alarcón, P. Alvarez-Loayza, et al.

► **To cite this version:**

T. R. Feldpausch, O. L. Phillips, R. J. W. Brienen, E. Gloor, J. Lloyd, et al.. Amazon forest response to repeated droughts. *Global Biogeochemical Cycles*, 2016, 30 (7), pp.964-982. 10.1002/2015GB005133 . hal-01499063

**HAL Id: hal-01499063**

**<https://hal.science/hal-01499063v1>**

Submitted on 30 Mar 2017

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Copyright

## RESEARCH ARTICLE

10.1002/2015GB005133

## Special Section:

Trends and Determinants of the Amazon Rainforests in a Changing World, A Carbon Cycle Perspective

## Key Points:

- During the 2010 drought interval, Amazon forests did not gain biomass, regardless of whether forests experienced precipitation deficit anomalies
- Biomass losses were partially driven by a decline in productivity related to precipitation anomalies
- Pre-2010 droughts did not compound the effects of the 2010 drought

## Supporting Information:

- Supporting Information S1

## Correspondence to:

T. R. Feldpausch,  
T.R.Feldpausch@exeter.ac.uk

## Citation:

Feldpausch, T. R., et al. (2016), Amazon forest response to repeated droughts, *Global Biogeochem. Cycles*, 30, 964–982, doi:10.1002/2015GB005133.

Received 2 MAR 2015

Accepted 28 APR 2016

Accepted article online 30 APR 2016

Published online 1 JUL 2016

Corrected 19 AUG 2016

This article was corrected on 19 AUG 2016. See the end of the full text for details.

©2016. American Geophysical Union.  
All Rights Reserved.

## Amazon forest response to repeated droughts

T. R. Feldpausch<sup>1</sup>, O. L. Phillips<sup>2</sup>, R. J. W. Brienen<sup>2</sup>, E. Gloor<sup>2</sup>, J. Lloyd<sup>3,4</sup>, G. Lopez-Gonzalez<sup>2</sup>, A. Monteagudo-Mendoza<sup>5</sup>, Y. Malhi<sup>6</sup>, A. Alarcón<sup>7</sup>, E. Álvarez Dávila<sup>8</sup>, P. Alvarez-Loayza<sup>9</sup>, A. Andrade<sup>10</sup>, L. E. O. C. Aragao<sup>1,11</sup>, L. Arroyo<sup>12</sup>, G. A. Aymard C.<sup>13</sup>, T. R. Baker<sup>2</sup>, C. Baraloto<sup>14,15</sup>, J. Barroso<sup>16</sup>, D. Bonal<sup>17</sup>, W. Castro<sup>18</sup>, V. Chama<sup>5</sup>, J. Chave<sup>19</sup>, T. F. Domingues<sup>20</sup>, S. Fauset<sup>2</sup>, N. Groot<sup>2</sup>, E. Honorio Coronado<sup>2</sup>, S. Laurance<sup>21</sup>, W. F. Laurance<sup>21</sup>, S. L. Lewis<sup>2,22</sup>, J. C. Licona<sup>7</sup>, B. S. Marimon<sup>23</sup>, B. H. Marimon-Junior<sup>23</sup>, C. Mendoza Bautista<sup>24</sup>, D. A. Neill<sup>25</sup>, E. A. Oliveira<sup>23</sup>, C. Oliveira dos Santos<sup>23</sup>, N. C. Pallqui Camacho<sup>5</sup>, G. Pardo-Molina<sup>26</sup>, A. Prieto<sup>27</sup>, C. A. Quesada<sup>10</sup>, F. Ramírez<sup>28</sup>, H. Ramírez-Angulo<sup>29</sup>, M. Réjou-Méchain<sup>19</sup>, A. Rudas<sup>27</sup>, G. Saiz<sup>30</sup>, R. P. Salomão<sup>31</sup>, J. E. Silva-Espejo<sup>5</sup>, M. Silveira<sup>16</sup>, H. ter Steege<sup>32</sup>, J. Stropp<sup>33</sup>, J. Terborgh<sup>9</sup>, R. Thomas-Caesar<sup>34</sup>, G. M. F. van der Heijden<sup>35</sup>, R. Vásquez Martínez<sup>36</sup>, E. Vilanova<sup>37</sup>, and V. A. Vos<sup>38,39</sup>

<sup>1</sup>Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK, <sup>2</sup>School of Geography, University of Leeds, Leeds, UK, <sup>3</sup>Department of Life Sciences, Imperial College London, Ascot, UK, <sup>4</sup>School of Marine and Tropical Biology, James Cook University, Cairns, Queensland, Australia, <sup>5</sup>Universidad Nacional San Antonio Abad del Cusco, Cusco, Peru, <sup>6</sup>Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK, <sup>7</sup>Instituto Boliviano de Investigación Forestal, Santa Cruz de la Sierra, Bolivia, <sup>8</sup>Fundación Con-Vida, Medellín, Colombia, <sup>9</sup>Center for Tropical Conservation, Duke University, Durham, North Carolina, USA, <sup>10</sup>National Institute for Research in Amazonia, Manaus, Brazil, <sup>11</sup>National Institute for Space Research, São Paulo, Brazil, <sup>12</sup>Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel René Moreno, Santa Cruz de la Sierra, Bolivia, <sup>13</sup>UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Guanare, Venezuela, <sup>14</sup>International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, Florida, USA, <sup>15</sup>INRA, UMR Ecologie des Forêts de Guyane, Kourou, French Guiana, <sup>16</sup>Universidade Federal do Acre, Rio Branco, Brazil, <sup>17</sup>INRA, UMR 1137 "Ecologie et Ecophysiologie Forestiere", Champenoux, France, <sup>18</sup>Graduate Program in Ecology and the Management of Natural Resources, Acre Federal University, Rio Branco, AC, Brazil, <sup>19</sup>Université Paul Sabatier CNRS, UMR 5174 Evolution et Diversité Biologique, Toulouse, France, <sup>20</sup>Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil, <sup>21</sup>Centre for Tropical Environmental and Sustainability Science and College of Science and Engineering, James Cook University, Cairns, Queensland, Australia, <sup>22</sup>Department of Geography, University College London, London, UK, <sup>23</sup>Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil, <sup>24</sup>FOMABO, Manejo Forestal en las Tierras Tropicales de Bolivia, Sacta, Bolivia, <sup>25</sup>Facultad de Ingeniería Ambiental, Universidad Estatal Amazónica, Puyo, Ecuador, <sup>26</sup>Universidad Autónoma del Beni, Campus Universitario, Riberalta, Bolivia, <sup>27</sup>Doctorado Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia, <sup>28</sup>Universidad Nacional de la Amazonía Peruana, Iquitos, Peru, <sup>29</sup>Facultad de Ciencias Forestales y Ambientales, Universidad de Los Andes, Mérida, Venezuela, <sup>30</sup>Institute of Meteorology and Climate Research, Karlsruhe Institute of Technology, Garmisch-Partenkirchen, Germany, <sup>31</sup>Museu Paraense Emílio Goeldi, Belém, Brazil, <sup>32</sup>Naturalis Biodiversity Center, Leiden, Netherlands, <sup>33</sup>Institute of Biological and Health Sciences, Federal University of Alagoas, Maceió, Brazil, <sup>34</sup>Iwokrama International Centre for Rainforest Conservation and Development, Georgetown, Guyana, <sup>35</sup>School of Geography, University of Nottingham, Nottingham, UK, <sup>36</sup>Jardín Botánico de Missouri, Prolongacion Bolognesi Mz.e, Pasco, Peru, <sup>37</sup>Instituto de Investigaciones para el Desarrollo Forestal, Universidad de Los Andes, Mérida, Venezuela, <sup>38</sup>Universidad Autónoma del Beni, Riberalta, Bolivia, <sup>39</sup>Centro de Investigación y Promoción del Campesinado Norte Amazónico, Riberalta, Bolivia

**Abstract** The Amazon Basin has experienced more variable climate over the last decade, with a severe and widespread drought in 2005 causing large basin-wide losses of biomass. A drought of similar climatological magnitude occurred again in 2010; however, there has been no basin-wide ground-based evaluation of effects on vegetation. We examine to what extent the 2010 drought affected forest dynamics using ground-based observations of mortality and growth from an extensive forest plot network. We find that during the 2010 drought interval, forests did not gain biomass (net change:  $-0.43 \text{ Mg ha}^{-1}$ , confidence interval (CI):  $-1.11, 0.19, n = 97$ ), regardless of whether forests experienced precipitation deficit anomalies. This contrasted with a long-term biomass sink during the baseline pre-2010 drought period (1998 to pre-2010) of  $1.33 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  (CI:  $0.90, 1.74, p < 0.01$ ). The resulting net impact of the 2010 drought (i.e., reversal of the baseline net sink) was  $-1.95 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  (CI:  $-2.77, -1.18; p < 0.001$ ). This net biomass impact was driven by an increase in biomass mortality ( $1.45 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  CI:  $0.66, 2.25, p < 0.001$ ) and a decline in biomass productivity ( $-0.50 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , CI:  $-0.78, -0.31; p < 0.001$ ).

Surprisingly, the magnitude of the losses through tree mortality was unrelated to estimated local precipitation anomalies and was independent of estimated local pre-2010 drought history. Thus, there was no evidence that pre-2010 droughts compounded the effects of the 2010 drought. We detected a systematic basin-wide impact of the 2010 drought on tree growth rates across Amazonia, which was related to the strength of the moisture deficit. This impact differed from the drought event in 2005 which did not affect productivity. Based on these ground data, live biomass in trees and corresponding estimates of live biomass in lianas and roots, we estimate that intact forests in Amazonia were carbon neutral in 2010 ( $-0.07 \text{ Pg C yr}^{-1}$  CI:  $-0.42, 0.23$ ), consistent with results from an independent analysis of airborne estimates of land-atmospheric fluxes during 2010. Relative to the long-term mean, the 2010 drought resulted in a reduction in biomass carbon uptake of  $1.1 \text{ Pg C}$ , compared to  $1.6 \text{ Pg C}$  for the 2005 event.

## 1. Introduction

The Amazon Basin has seen increased climatic variability over the recent decades. Precipitation records and long-term river levels show that while in some regions there is an overall trend toward increased annual precipitation [Gloor *et al.*, 2013], the dry season in the south of the basin appears to become longer [Marengo *et al.*, 2011] and drier [Chou *et al.*, 2013]. In addition, temperature has increased over the recent years [e.g., Jiménez-Muñoz *et al.*, 2013]. There are large uncertainties in predictions of 21st century climate, with some models suggesting an increase in extreme dry events [Cox *et al.*, 2008], and a tendency for increasingly dry conditions during the dry season [Malhi *et al.*, 2009], while recent multimodel comparisons suggest an increase in total precipitation concentrated in the wet season [Kitoh *et al.*, 2013]. It is highly uncertain how forests of the Amazon Basin will respond to these changes. As the most extensive tropical forest on Earth, a biome storing more than 100 billion tons of carbon in biomass [Feldpausch *et al.*, 2012], changes in the Amazon forest may have large and global consequences. To date, there has been no basin-wide analysis based on long-term permanent forest plot data of tree-by-tree response to the 2010 event and to repeated precipitation anomalies.

River level and precipitation records indicate that parts of the Amazon Basin have experienced several anomalously dry periods over the last two decades [Coelho *et al.*, 2012; Espinoza *et al.*, 2011; Lewis *et al.*, 2011; Marengo *et al.*, 2008]. The most recent events in 2005, 2007, and 2010 left large regions of Amazonia anomalously dry, with each having a distinctive and complex spatial pattern (supporting information Figure S1). These recent droughts are not individually exceptional in the long term as river gauge data indicate dry years of similar or greater magnitude over the last century in 1916, 1926, and 1963 [Coelho *et al.*, 2012; Williams *et al.*, 2005]. Nevertheless, forest response to the 2005 dry period resulted in a reversal of a multidecadal trend in aboveground biomass gain, with the forests on average losing biomass [Phillips *et al.*, 2009]. The main cause of this loss was increased tree mortality, not a reduction in tree growth.

Climatologically, the 2010 event differed from 2005. While 2005 was bracketed by climatologically average years, the 2010 event was preceded by one of the wettest years in recent history (annual precipitation  $> 0.975$  quantile) [Gloor *et al.*, 2013]. Spatial footprints also differed, with 2005 drying being most pronounced in southwestern Amazonia, 2007 in southeastern Amazonia, and 2010 precipitation anomalies being more spatially dispersed (supporting information Figure S1). The 2010 drought occurred immediately following a number of anomalously hot dry seasons [Jiménez-Muñoz *et al.*, 2013], representing a possible intensification of climate stress for Amazonian forests. Inverse modeling of airborne measurements of carbon dioxide and carbon monoxide concentrations above Amazonia and weather reanalysis products indicated that the Amazon Basin neither gained nor lost carbon during 2010, while it was a net carbon sink in the relatively wet 2011 year for which measurements were also made [Gatti *et al.*, 2014; Laan-Luijckx *et al.*, 2015]. Data from a small number of plots indicated that mortality increased during the 2010 drought but that productivity was unaffected [Doughty *et al.*, 2015].

Tropical forest trees' physiological response to drought affects their carbon assimilation and allocation, as well as their mortality risk. Recent work has suggested a strong interdependence of hydraulic function, and metabolism, with drought affecting the ability of trees to mobilize and transport carbohydrates, produce defense compounds, and refill embolized xylem [McDowell *et al.*, 2011; O'Brien *et al.*, 2014]. Much of the existing work focuses on seedlings and temperate regions rather than the tropics, leaving major gaps in understanding of the physiological response to drought and the potential role of carbon starvation for tropical trees [Parker and Patton, 1975; Sala *et al.*, 2010], although recent research from one experimental drought

plot suggests that hydraulic stress plays a larger role than carbon starvation in initiating tree mortality [Rowland *et al.*, 2015]. At the tree level, by monitoring changes in carbon allocation to different tree components, there is some evidence to suggest that following drought, trees shift carbon allocation toward the canopy, and later, to fine roots [Doughty *et al.*, 2014]. The interaction of drought with high temperatures also appears to reduce tree growth [Clark *et al.*, 2010; Vlam *et al.*, 2014]. When stress becomes too great due to drought, tree mortality increases [Wang *et al.*, 2012]. Regardless of the exact mechanisms involved, it is clear that tree level physiological responses to drought substantially altered the carbon cycle of Amazonian forests during both the 2005 and the 2010 droughts [Brando *et al.*, 2008; Gatti *et al.*, 2014; Phillips *et al.*, 2009; Potter *et al.*, 2011].

If the climate of many tropical forests is shifting to one in which drought is a more frequent and/or intense phenomenon, we need to understand not only the impacts of single events but also the cumulative effects of repeated droughts. Two potentially opposing outcomes might be reasonably anticipated. First, if unusually severe water deficits result in increased mortality rates for already weakened trees “naturally” in decline (e.g., those that are competitively suppressed, drought intolerant, disease affected, or individuals reaching the end of their lifespan), then it may simply accelerate predestined mortality. In this scenario, the effect of the drought would be to concentrate mortality over short anomalously dry periods and thus potentially leave a forest of more vigorous, faster-growing individuals more likely to resist future physiological challenges once more normal rainfall patterns return. We call this the “inoculation” hypothesis, because the effect of the first drought (e.g., 2005 and 2007) is to (indirectly) confer on the remaining forest some resistance to the impact of future droughts.

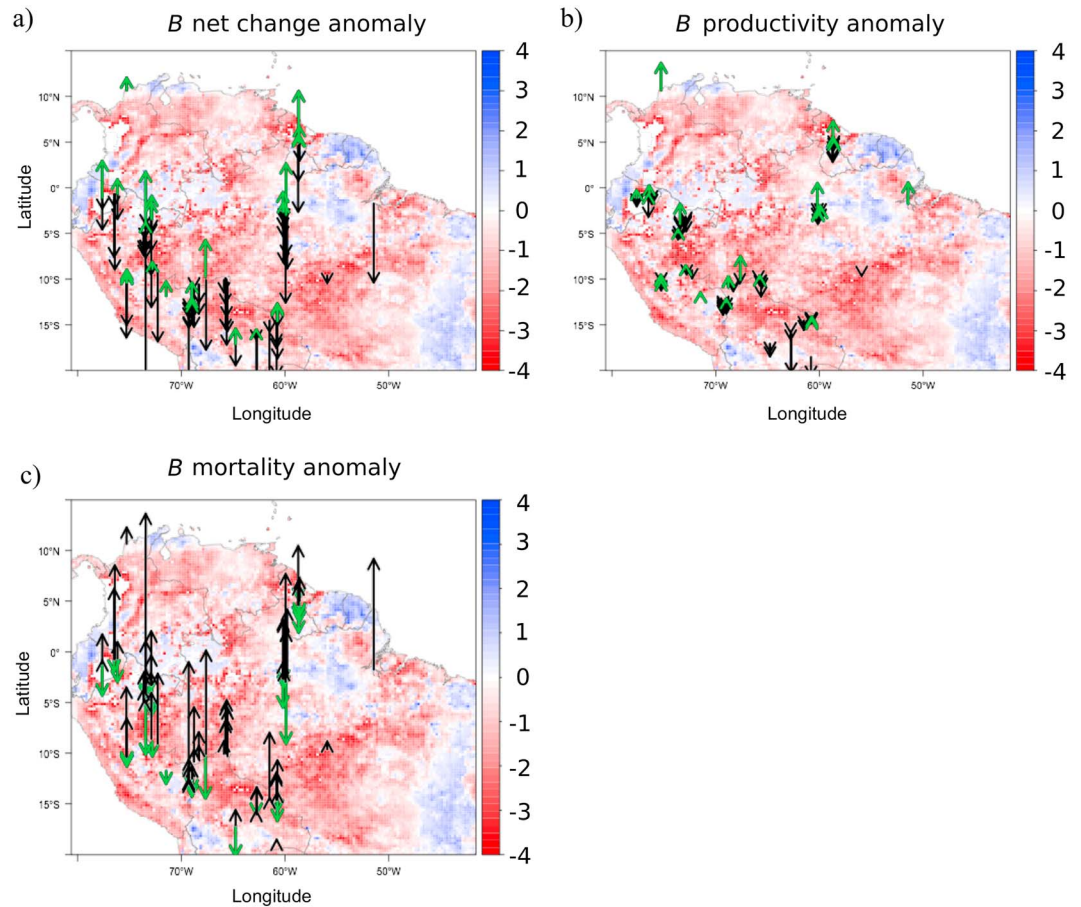
Alternatively, it could also be argued that successive droughts might act in concert, for example, through repeated episodes of irreversible damage from embolism [Anderegg *et al.*, 2014], and hydraulic fatigue [Rowland *et al.*, 2015], or by continual drawdown of carbohydrate reserves as a result of reduced photosynthetic rates [Doughty *et al.*, 2015]. In such a scenario, the first drought may weaken but not kill a large number of trees, making them vulnerable to repeated droughts of similar magnitude [Brando *et al.*, 2008]. We call this the “degradation” hypothesis, because the initial drought is expected to degrade trees’ ability to respond to later physiological challenges. This is conceptually similar to the “mortality spiral” toward tree death suggested by Franklin *et al.* [1987]. Consistent with this, experimental drought studies showed that drought effects may take a number of years to be expressed, with the mortality impacts of two drought experiments in eastern Amazonia only becoming clear after two or three seasons of experimental moisture depletion [Brando *et al.*, 2008; da Costa *et al.*, 2010; Rowland *et al.*, 2015].

Forest demography studies [Condit, 1995; Phillips *et al.*, 2010b; Williamson *et al.*, 2000] have consistently reported that short-term tropical droughts increase tree mortality. By temporarily raising mortality rates over large areas, relatively small local impacts of droughts can scale to have significant impacts on the carbon cycle, of the order of  $\approx 1$  Pg C at the scale of the Amazon Basin, mostly via longer-term committed atmospheric releases from necromass as a result of temporarily elevated mortality [Phillips *et al.*, 2009], and with potentially long lasting impacts on the forest canopy [Saatchi *et al.*, 2013].

While plot-based studies have characterized the effect of natural tropical forest drought on tree mortality, they have failed to detect a clear impact on tree growth rates [Doughty *et al.*, 2015; Phillips *et al.*, 2009], suggesting that any such impacts are either minor or not easily detected in nature due to problems of small sample sizes, inadequate temporal resolution, or measurement precision. Furthermore, the effect of repeated droughts at the basin level on mortality and growth remains unknown. The occurrence in 2010 of a second major Amazon Basin-wide drought after a 5 year interval, and the 2007 drought over a large area of southeastern Amazonia, combined with the increasing sampling intensity of the RAINFOR plot network, provided a unique opportunity to now address these questions.

Here we present the first basin-scale, ground-based evaluation of the impact of the 2010 drought and repeat droughts on Amazon forest biomass dynamics using a set of measurements of biomass, growth, and mortality. Specifically, we test whether, (H1) the net effect of drought alters stand level biomass, (H2) drought affects tree mortality and growth, and (H3) previous droughts (or the plot drought history) affect the response of the forest to the 2010 event.

To address these questions, we first quantify the magnitude of the climatological drought for each plot based on previously used [Aragão *et al.*, 2007; Phillips *et al.*, 2009] and alternative metrics of drought stress. We then estimate the impact of the 2010 event on plots by calculating the change in biomass loss



**Figure 1.** Spatial patterns in the 2010 biomass anomaly ( $\Delta B$ ) for plot clusters, including mean (a) net change, (b) productivity (recruitment + growth), and (c) mortality (all in  $\text{Mg ha}^{-1} \text{ yr}^{-1}$ ). Up (down) arrows indicate an increase (decrease) in values compared to the mean baseline 1998 to pre-2010. The background indicates the drought  $\delta W$  Z-scores.

(through tree mortality) and productivity (defined as the growth gains of stems plus recruitment) during the drought interval against the long-term (pre-2010) baseline of mortality and productivity for these plots (i.e., mortality and productivity anomalies). Finally, we evaluate whether plots undergoing single, repeat, or no drought differ in biomass dynamics in 2010, evaluating changes for each of the nearly 100 plots (mean size = 1.2 ha) distributed across 38 geographically distinct South American tropical forest locations (supporting information Table S2). Using a subset of plots with short census intervals that span the 2010 drought, we evaluate results in the context of a long-term baseline in forest biomass dynamics in South American mature forests with a net positive biomass sink that has gradually declined over time [Brienen *et al.*, 2015].

## 2. Methods

### 2.1. Forest Census Data

Forests had been sampled using established plot recensus protocols, over multiple census intervals across the Amazon Basin over three decades as part of the RAINFOR plot network, [Phillips *et al.*, 2010a] (Figure 1). In brief, all live tree stems with diameter ( $D$ )  $\geq 10$  cm were measured at 1.3 m height or above buttresses and deformities. "Emergency" postdrought recensus campaigns were conducted across the basin to evaluate the effect of both the 2005 and 2010 droughts. For 2010, a total of 97 plots were selected for recensus that provided a maximum census length of  $< 3.5$  years and spanned the 2010 event. The mean (median) plot area was 1.2 (1.0) ha and mean (median) census length 2.3 (2.1) years. This census interval is similar to that used for the 2005 drought analysis (mean = 2.0 years) [Phillips *et al.*, 2009]. Data are curated within the ForestPlots.net



web application and database [Lopez-Gonzalez *et al.*, 2011, 2009]. For treatment of changes in the diameter point of measurement, we follow the recommendations of Talbot *et al.* [2014], as used in the recent pan-Amazonian study of Brienen *et al.* [2015] (supporting information).

## 2.2. Biomass Dynamics and Anomaly

Aboveground biomass ( $B$ ) was estimated for each tree stem for all plots and summed per hectare (Mg/ha) from queries within ForestPlots.net based on a pantropical moist forest equation [Chave *et al.*, 2005]:

$$B = 0.0509 \times \rho D^2 H \quad (1)$$

where  $D$  is tree bole diameter in cm,  $\rho$  wood specific gravity ( $\text{g cm}^{-3}$ ), and  $H$  tree height in m. Individual tree  $\rho$  was assigned based on taxonomy from values compiled in a global wood density database [Chave *et al.*, 2009; Zanne *et al.*, 2009]. In the absence of taxonomic information for a tree, the mean  $\rho$  from all stems in the plot was applied. Additional details of level of taxonomic determination and protocols are included in the supporting information. Tree  $H$  for a given  $D$  varies among geographic region and with environment [Banin *et al.*, 2012; Feldpausch *et al.*, 2011] and was included in all estimates of  $B$ . Tree height was estimated with South America region level Weibull models of the form

$$H = a(1 - \exp(-bD^c)) \quad (2)$$

with coefficients and regions from Feldpausch *et al.* [2012]. These regions have been chosen based on substrate geological age [Fittkau, 1971]. The net change in  $B$  (and thus carbon) per hectare was estimated as the sum of biomass gained by recruitment of individuals into the 10 cm  $D$  class plus the gain in  $B$  of surviving trees, minus the  $B$  loss due to mortality. Biomass values were converted to carbon estimates using the fraction 0.5.

Long-term plot measurements used as the pre-2010 baseline data were previously reported in detail [e.g., Brienen *et al.*, 2015; Phillips *et al.*, 2009]. Censuses corresponding to the 2010 event were defined as those spanning the dry season of 2010 with <3.5 years in total census length. The year 1998 was chosen as the start of the reference period for the practical reason that it represents the start of precipitation data availability from the Tropical Rainfall Monitoring Mission (TRMM). The scale of the sampling and funding limitations makes it impossible to synchronize all measurements or conduct annual census work everywhere. Therefore, census start and end dates vary, as do census lengths.

To evaluate the effect of drought(s) on biomass dynamics, we used absolute values of net change, mortality, and gains in biomass ( $B$ ) between the various census intervals and also calculated the anomalies in net change, mortality, and gains (using notation: Delta,  $\Delta$ ) from a baseline mean value for 1998–2010. For instance, the net biomass change anomaly ( $\Delta B$ ) was calculated for each plot as the net change  $B$  during the drought census minus the plot mean baseline net  $B$  change since 1998 to pre-2010, excluding the 2010 plot census interval. To gain insights in the drivers of change in biomass, we also analyzed data on plot level changes in wood density ( $\text{g cm}^{-3}$ ), number of trees dying ( $\text{ha}^{-1}$ ), and tree basal area ( $\text{m}^2 \text{ha}^{-1}$ ). These metrics were compared between 2010 and the mean of all previous measurements for a plot. Since we specifically focus on drought impacts, and need plots that allow comparisons predrought and postdrought having census intervals that bracket the 2010 drought, our data set is substantially smaller than that used in the recent Brienen *et al.* [2015] analysis ( $n = 321$  plots). That data set includes plots that have longer census intervals that may span drought and nondrought periods and multiple droughts for a single census. The Brienen *et al.* [2015] data set is more appropriate for basin-wide estimates of biomass dynamics over long periods, while our data selection is tailored to capture 2010 drought-specific effects.

## 2.3. Precipitation Anomalies and Drought

Precipitation time series data from 1998 to 2012 were sourced from the Tropical Rainfall Monitoring Mission (TRMM) product 3B43 version 7 [NASA, 2012] derived mainly from satellite and some ground values. Monthly precipitation ( $P$ ) estimates, calculated from hourly average precipitation rates of  $0.5^\circ \times 0.5^\circ$  longitude by latitude grid cells, were extracted for each plot location.

We classified drought stress for each plot based on the maximum census climatological water deficit ( $W$ ) modified from Aragão *et al.* [2007]. In addition, we evaluated two alternative drought indices, the Standard Precipitation Index ( $SPI$ ) and the Standard Precipitation Evapotranspiration Index ( $SPEI$ ) [Vicente-Serrano *et al.*, 2010] (supporting information).  $SPI$  and  $SPEI$  are multiscalar drought indices that measure drought

**Table 1.** Total Biomass Change and  $\Delta B$  Change (Including 95% Bootstrap Confidence Intervals) During the 2010 Drought Interval (2.3 Years) by Region for the Amazon Basin for  $\delta W < -1.6$

Region	Forest Area <sup>a</sup> (10 <sup>6</sup> ha)	Area Droughted <sup>b</sup>	Fraction Area Droughted <sup>b</sup>	N Plots	Total Sample Area (ha)	Mean $\Delta B$ (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	(0.025–0.975)	Mean Change B Net (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	(0.025–0.975)	Total Change C in Sink <sup>c</sup> (Pg)	(0.025–0.975)	Estimated C Sink <sup>c</sup> (Pg)	(0.025–0.975)
1. Northwest	125.6	66.2	0.53	25	21.7	-1.59	-3.49	0.10	-1.71	1.63	-0.18	0.02	-0.19
2. Guiana Shield	153.3	50.7	0.33	12	30.5	-1.42	-3.57	0.83	-0.47	2.26	-0.12	0.08	-0.04
3. Central east Amazon	110.3	47.6	0.43	12	20	-2.67	-4.99	-0.06	-3.65	-0.15	-0.21	-0.15	-0.29
4. South west Amazon	87.2	53.9	0.62	34	37.5	-2.00	-3.18	-0.84	-2.00	-0.02	-0.18	-0.09	-0.18
5. Brazilian Shield	158.8	97.0	0.61	14	14	-2.30	-4.02	-0.73	-1.60	1.02	-0.38	-0.02	-0.26
Whole Basin	635.2	315.5	0.50	97	123.64	-1.95	-2.77	-1.18	-1.13	0.18	-1.07	-0.16	-0.97
Pg C yr <sup>-1</sup>													

<sup>a</sup>Forest cover area calculated by region [Feldpausch et al., 2012] using Global Land Cover 2000 data [Bartholomé et al., 2002].

<sup>b</sup> $\delta W < -1.6$ .

<sup>c</sup>Including aboveground B ( $\geq 10$  cm D) and the unmeasured components ( $< 10$  cm D, lianas, and roots).

severity according to intensity and duration and can distinguish the start and end of drought episodes; SPEI, unlike SPI, accounts for variation in potential evapotranspiration.  $W$  is based on the approximation that moist tropical forest canopy transpires  $\sim 100$  mm/month, the mean evapotranspiration value ( $E$ ) obtained from ground measurements over different seasons and for different regions of Amazonia [da Rocha et al., 2004; Shuttleworth, 1988; von Randow et al., 2004]. When  $P$  is  $< 100$  mm, the forest enters into water deficit. In calculating  $W$  on a plot-by-plot basis, the following rules were applied for each month ( $n$ ):

$$\text{If } W_{n-1} - E + P_n < 0; \quad (3)$$

$$\text{then } W_n = W_{n-1} - E + P_n; \quad (4)$$

$$\text{else } W_n = 0 \quad (5)$$

where  $E$  is evapotranspiration (100 mm),  $P$  is precipitation in a given month, and  $W_n$  is  $\leq 0$ . The annual maximum climatological water deficit (annual  $W$ ) was obtained for each forest plot as the most negative value of the climatological water deficit among all the months in each year, with year being based on the start of the rainy season (October) to the end of the dry season (September). Since we mostly lack annual recensus data, taking the mean annual  $W$  across multiyear census intervals [Phillips et al., 2009] would have obscured the drought for 2010. Preliminary tests showed that there was no significant relationship between the mean annual  $W$  as computed in Phillips et al. [2009] and forest change dynamics during the 2010 event. We therefore also calculated and used in the analysis the absolute maximum census  $W$  for each plot for a given census interval that may span several years. As a reference baseline, the long-term mean  $W$  was calculated for each plot from all historic census data from 1998 to the most recent census (but excluding the 2005 and 2010 drought). To quantify the intensity and duration of drought during a given census period relative to long-term mean values, water stress was calculated as the difference ( $\Delta$ ) of the census interval maximum climatological water deficit ( $W_t$ ) from the long-term mean from 1998 to 2012 (excluding 2005 and 2010) ( $\bar{W}_{1998-2012}$ ). Plots were first classified as “droughted” during a census interval if the difference  $\Delta W < -25$  mm, for comparison with Phillips et al. [2009]. In addition, we used a second threshold based on Z-scores,  $\delta W$ , by classifying plots as droughted when  $\Delta W / \sigma_{1998-2012}$  was  $< -1.6$ , where  $\sigma_{1998-2012}$  is the standard deviation of  $W$  from 1998 to 2012 (excluding 2005 and 2010). This latter threshold takes into account the background variability in  $W$  that the forest experiences, with  $-1.6 \sigma$

corresponding to a 90% confidence interval. To evaluate the effect of repeated droughts (e.g., 2005, 2007, and 2010) on vegetation dynamics in 2010, the time since last drought was calculated for each plot as the census interval from the last time instance when  $\delta W < -1.6$  to the date of the recensus that spanned the 2010 drought. An evaluation of errors associated with TRMM estimates of precipitation indicates that TRMM data provide accurate estimates for areas with precipitation  $< 300 \text{ mm month}^{-1}$  but may overestimate rainfall for the most extreme water deficits (e.g.,  $< -300 \text{ mm}$ ) [Aragão *et al.*, 2007]. This indicates that estimates of water deficits using TRMM are likely to be conservative.

#### 2.4. Scaling Drought Effects to the Basin

The Amazon forest area was estimated based on the evergreen and closed deciduous classes of the Global Cover 2000 data [Bartholomé *et al.*, 2002]. These data were updated for Brazil using the deforestation data through 2010 obtained from the INPE Assessment of Deforestation in Brazilian Amazonia project (PRODES) (<http://www.inpe.br/>) (Table 1). To estimate the total basin-wide effect of the 2010 drought in these forest areas, we scaled  $\Delta B$  values to the Amazon Basin as follows. The  $\Delta B$  mean and 95% bootstrapped confidence intervals were multiplied by the area considered as having been exposed to precipitation anomalies ( $\delta W < -1.6$ ; SI:  $\Delta W < -25 \text{ mm}$ , as in Phillips *et al.* [2009]) and multiplied by the mean census period spanning the 2010 drought, 2.29 years, to estimate the change during the census interval. To estimate the effect on unmeasured  $B$ , we used several ratios of aboveground  $B$  to liana  $B$ , small tree  $B$ , and belowground  $B$ . We applied 0.099 as the estimated ratio of trees  $< 10 \text{ cm } D$  and lianas  $> 1 \text{ cm } D$  to trees  $> 10 \text{ cm } D$  in Amazonia, and for the belowground  $B$  applied the ratio 0.37 for  $B$  belowground to  $B$  aboveground [Phillips *et al.*, 2008], and summed all  $B$  converted to carbon (0.5) by Amazon region [Feldpausch *et al.*, 2012].

#### 2.5. Statistical Analysis

Plot census level changes in  $B$  dynamics, including net change, growth, and mortality, were examined for the predrought and postdrought census intervals and in comparison to the long-term mean ( $\Delta B$  values: difference from the long-term mean) as using two- and one-sample Wilcoxon signed rank tests and Welch two-sample weighted  $t$  tests. Bootstrapped 95% confidence intervals were estimated by resampling the data 1000 times. The relationship between  $\Delta B$  and  $\Delta W$  was examined using weighted linear regression and rank estimation [Kloke and McKean, 2013]. Tests were conducted at the unweighted plot level and weighted cluster level. Clusters represent plots in close proximity ( $< 100 \text{ km}$ ) with similar climatic conditions. Weighting follows Brienen *et al.* [2015] with weights calculated as the square root of the plot or total cluster area times the census interval length. Regression analysis at the cluster level also uses these same weights (i.e., procedure of weighted means for clusters and weighted mean regression, whereby a large plot monitored for many years would contribute more to a given cluster mean). Processing of TRMM data and forestplots.net vegetation data and all statistical analyses and maps were conducted with the R Statistical Platform [R Development Core Team, 2013] version 3.1.0. TRMM netCDF files were manipulated with the “raster” package [Hijmans and van Etten, 2013]. The “Rfit” package was used for rank estimation for linear models [Kloke and McKean, 2013].

### 3. Results

#### 3.1. Drought Spatial Patterns

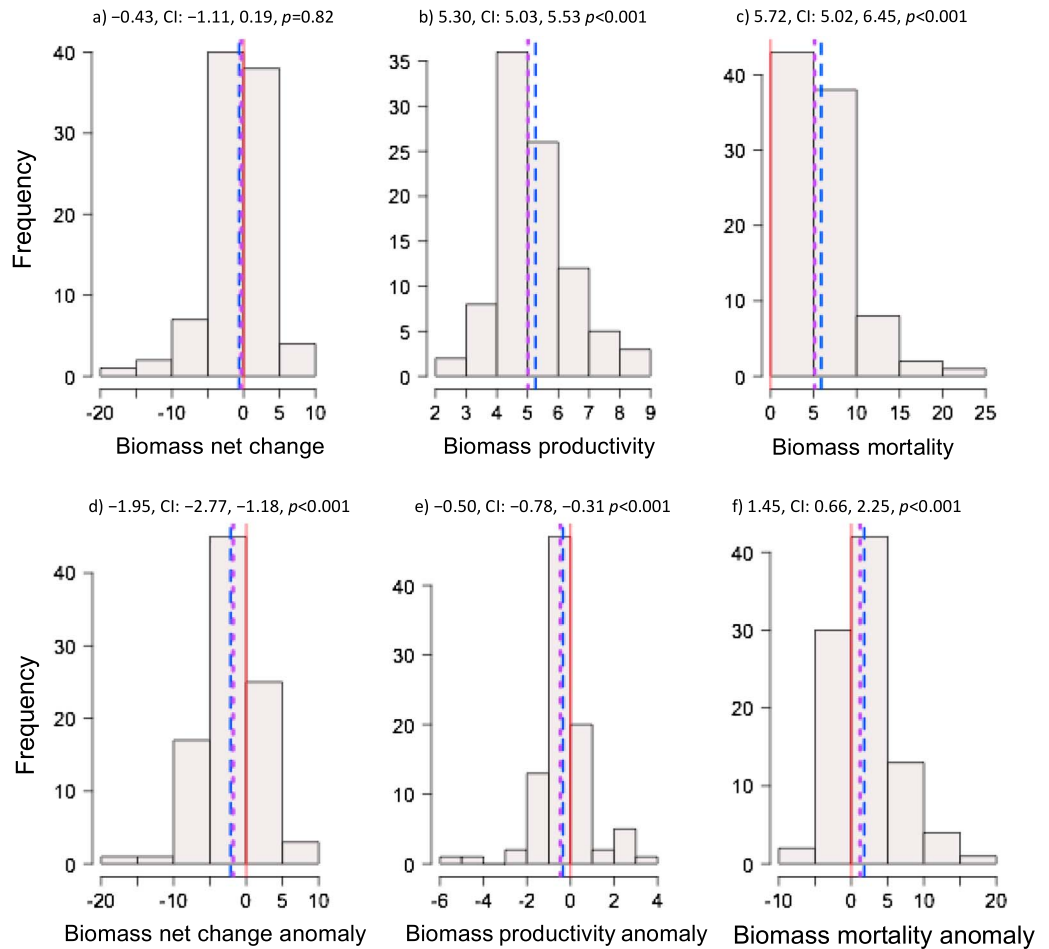
For the 2010 event, approximately 30–60% of each of the five Amazon regions was classified as being drought affected according to the criterion  $\delta W \leq -1.6$  (Table 1). A total of 3.16 million  $\text{km}^2$  (~50%) of the entire Amazon Basin experienced water deficits of  $\delta W \leq -1.6$  (Figure 1). As a consequence, 65 of the 97 plots sampled were estimated as having experienced cumulative water deficits,  $\Delta W$ , more severe than the long-term mean.

#### 3.2. Biomass Changes Over Droughted and Nondroughted Periods

##### 3.2.1. Absolute Biomass Change

During both the 2010 (Figure 2) and 2005 events (Table 2), plots on average did not gain aboveground biomass, regardless of whether they experienced precipitation anomalies. These results were in contrast to the same plots having positive net change in biomass (i.e., a net sink) during the designated full pre-2010 drought baseline period, and for the period between 2004 and pre-2010, and for the period following the





**Figure 2.** Plot level biomass change in 2010 (mean, 95% bootstrapped confidence intervals) for (a) net change, (b) productivity, (c) mortality, and mean  $\Delta B$  (2010 – (mean pre-2010 to 1998)) and for anomalies in (d) net change, (e) productivity, and (f) mortality. The dashed blue and purple lines represent the mean and median, and the solid red line is centered at zero ( $n = 97$ ). Units:  $\text{Mg ha}^{-1} \text{yr}^{-1}$ .

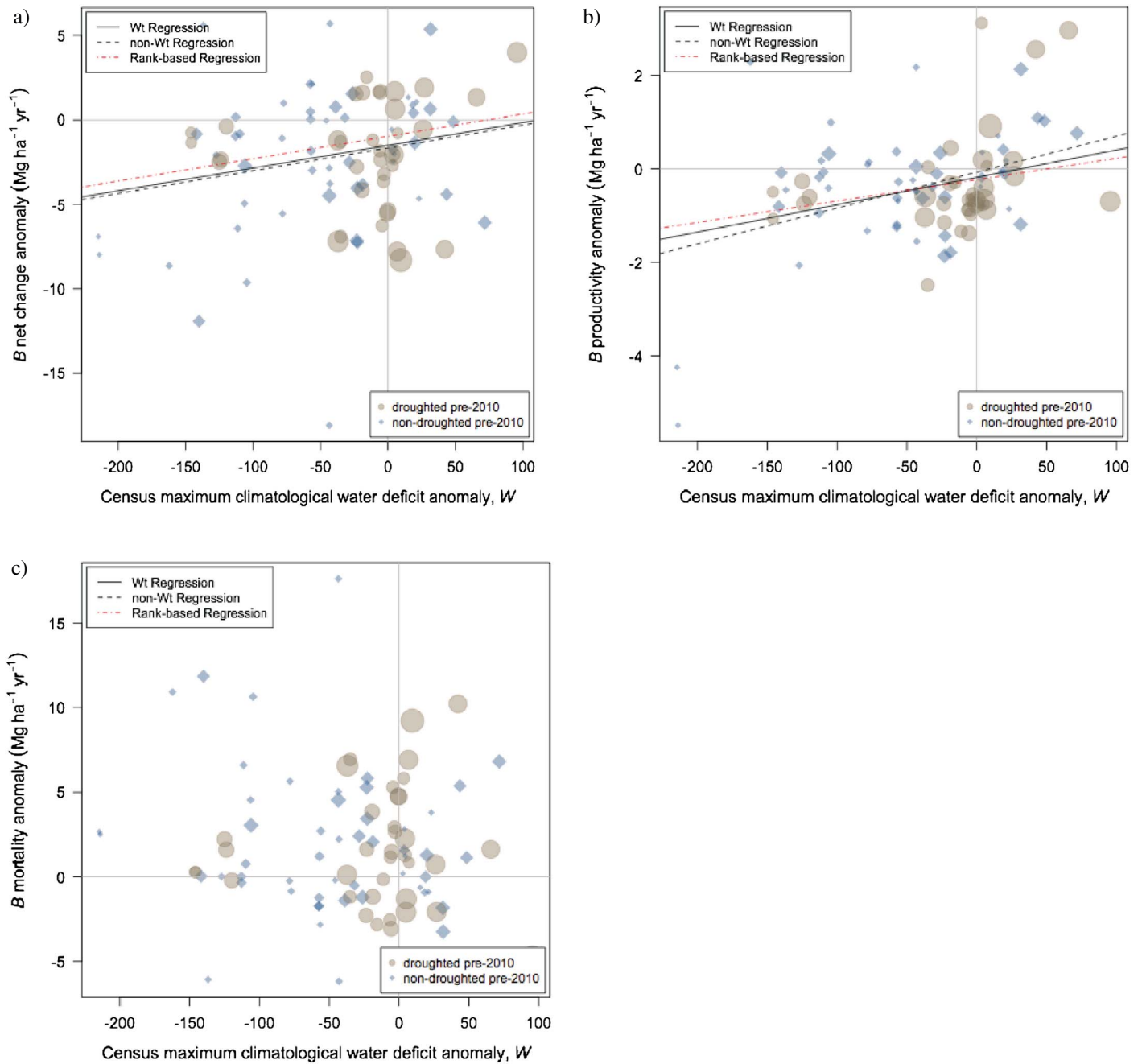
2005 drought and prior to the 2010 drought (2007 to pre-2010), and for the period that spanned both the 2005 and the 2010 droughts (2003 to post-2010).

### 3.2.2. Biomass Change Anomaly

Independent of drought classification, the mean net biomass change anomaly,  $\Delta B$  (i.e., 2010 minus long-term mean), was strongly and significantly negative during the 2010 census interval, confirming that biomass change was much lower in 2010 compared to the long-term mean of positive biomass change (Figure 2d). In terms of underlying biomass fluxes, the 2010 drought interval also showed significantly lower total tree

**Table 2.** Net Change in Biomass (Nonweighted Mean,  $\text{Mg ha}^{-1} \text{yr}^{-1}$ ) During, Before, and Spanning the 2010 Event, and During the 2005 Event (2004–2007), Including 95% Bootstrap Confidence Intervals and Results of the  $t$  Test

Period	Net Biomass Change	CI	$n$	$p$ Value
2010 event	-0.43	-1.11, 0.19	97	0.26
2005 event	0.91	-0.002, 1.81	45	0.07
Baseline: 1998 to pre-2010	1.33	0.90, 1.74	97	<0.01
2004 to pre-2010	1.11	0.70, 1.46	89	0.01
2007 to pre-2010	1.36	0.50, 2.19	61	<0.05
2003 to post-2010	0.82	0.04, 1.60	63	<0.05

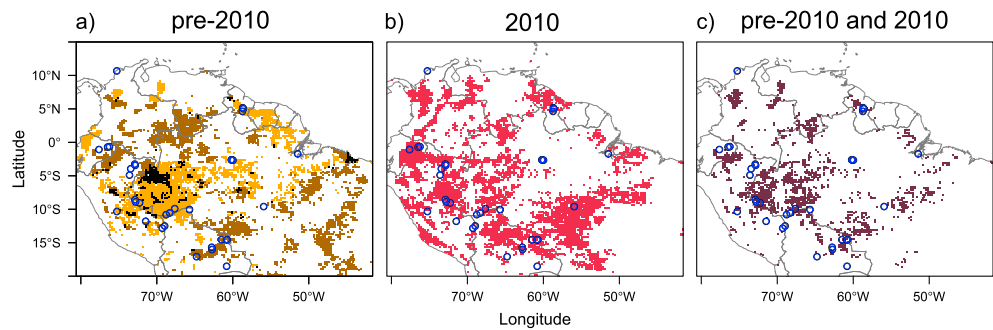


**Figure 3.** Plot level vegetation dynamics during the 2010 drought: (a)  $\Delta B$  net change ( $p = 0.026$  weighted regression,  $p = 0.044$  nonweighted regression,  $p = 0.036$  rank-based regression), (b)  $\Delta B$  productivity (growth + recruitment) ( $p = 0.002$  weighted regression,  $p < 0.001$  nonweighted regression,  $p = 0.015$  rank-based regression), (c)  $\Delta B$  mortality (all in  $\text{Mg ha}^{-1} \text{yr}^{-1}$ ) versus the  $\Delta W$  (absolute  $W$  in 2010 census – mean of census absolute  $W$  values) for the pre-2010 to 1998 baseline. Symbol size is proportional to the intensity of the last pre-2010  $\delta W$ , showing plots droughted (brown circles) and nondroughted from 2000 to pre-2010 ( $\delta W$  Z-score  $< -1.6$ ) (blue diamonds).

productivity (i.e., growth plus recruitment) (Figure 2e) and greater biomass losses due to mortality (Figure 2f) compared to the long-term mean.

### 3.3. Biomass Change and Drought Intensity

Our data suggest that (H1) the magnitudes of anomalies ( $\Delta B$ ) in net biomass change and productivity for the 2010 event were significantly related to the severity of the drought (measured as the change in  $W$



**Figure 4.** Areas droughted based on  $\delta W$  Z-score  $< -1.6$  for (a) pre-2010 (2005, orange or 2007, brown), (b) 2010 (red), and (c) pre-2010 (2005 or 2007) and 2010. A small percentage of the basin was droughted in both 2005 and 2007 (black in Figure 4a). Blue circles show plot locations.

during the drought period). Thus, forests more heavily droughted in 2010 gained less biomass in 2010 (Figure 3a) and (H2) trees on average grew less (Figure 3b) compared to the pre-2010 baseline that spanned multiple droughts.

In contrast, (H2) anomalies in mortality during 2010 did not covary with the severity of the drought (Figure 3c). The intercepts for net  $\Delta B$  change were negative when  $\Delta W$  was zero (Figure 3) indicating that even for plots that were not considered to be anomalously dry in 2010, net  $\Delta B$  was lower than during the baseline period (1998 to pre-2010). The results for the anomalies in net biomass change and mortality were consistent (while anomalies in productivity were not) with results with  $\Delta W$  when using an alternative metric, SPI, to quantify drought anomalies (supporting information Figure S3).

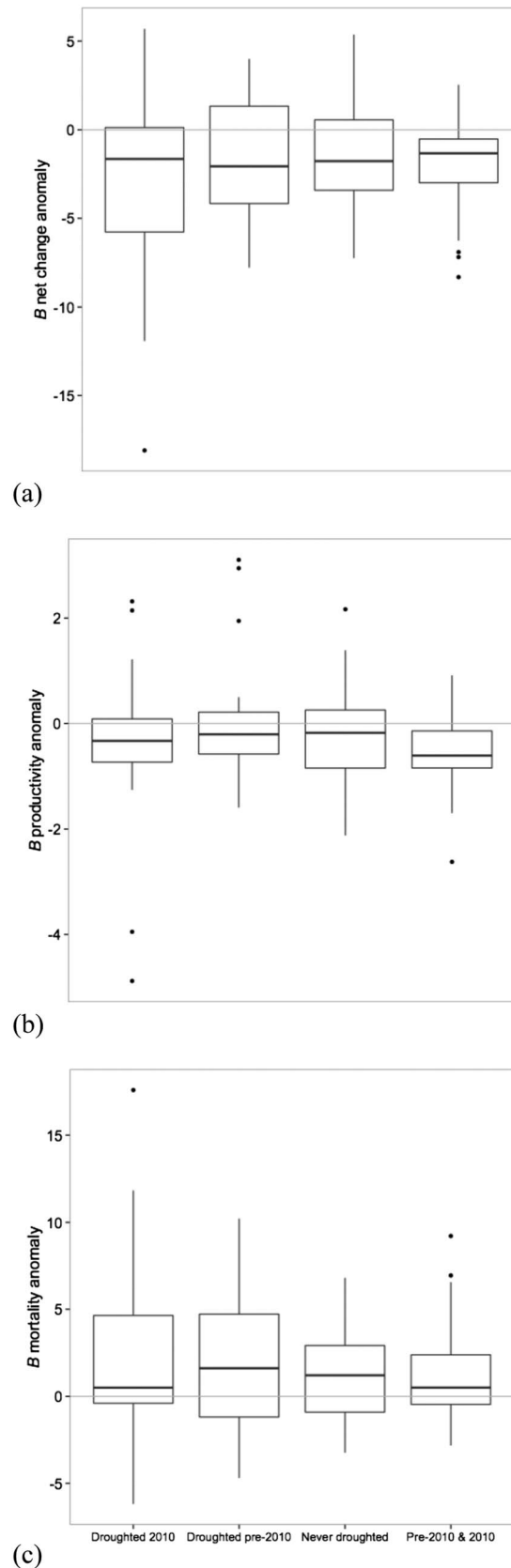
### 3.4. Wood Density, Number, and Size of Trees Dying

We detected weak impacts of the 2010 drought in terms of traits of those trees which died. On average, there was a weak but significant tendency in the more strongly droughted plots for lighter wood density taxa to be more at risk of death (supporting information Figure S4a). There was, however, no indication that the size of trees that died was related to the drought intensity (supporting information Figure S4b). For plots undergoing the greatest precipitation anomalies ( $\delta W < -1.6$ ) ( $n = 48$ ), the number of stems dying per year increased by 30% during the 2010 event compared to the pre-2010 mean (mean number of trees dying increased from 10.1 to 13.2 ( $p < 0.001$ )) (supporting information Table S1).

### 3.5. Effect of Repeated Drought

The TRMM-based analysis indicates that parts of Amazonia experienced anomalously high water stress anomalies over the past decade in addition to the 2010 event (e.g., during 2005 and 2007) (supporting information Figure S1,  $\delta W$  annual time series). The total combined area classified as droughted in 2005 or 2007 covered large areas of the Amazon Basin based on  $\delta W$  Z-scores  $\leq -1.6$  (Figure 4a). The 2005 event most affected an area in western, central, and northeastern Amazonia, while the most severe  $\delta W$  anomalies in 2007 were more dispersed throughout Amazonia. The 2010 event, having affected a much larger area than either 2005 or 2007 (Figure 4b), spanned areas droughted in 2005 or in 2007 but rarely in both (Figure 4a). Thus, a large part of western and southern Amazonia that was droughted in 2010 was also droughted in either 2005 or 2007 (Figure 4c).

Interestingly, we found (H3) no significant difference in net change, productivity, or mortality during the 2010 event between plots that experienced droughts before or plots that were never droughted (Figure 5). However, there were patterns that highlight the 2010 drought effect and indicate a potential lag in effects from previous droughts. For example, on average, stands that had the most negative  $\Delta B$  productivity anomaly were classified as droughted in pre-2010 and 2010, suggesting an interaction between pre-2010 and the 2010 drought. Plots classified as never droughted during the study period also had negative  $\Delta B$  net change, negative productivity, and positive mortality anomalies. Mortality was extremely “noisy” in 2010, having high standard deviation in plots (Figure 5).



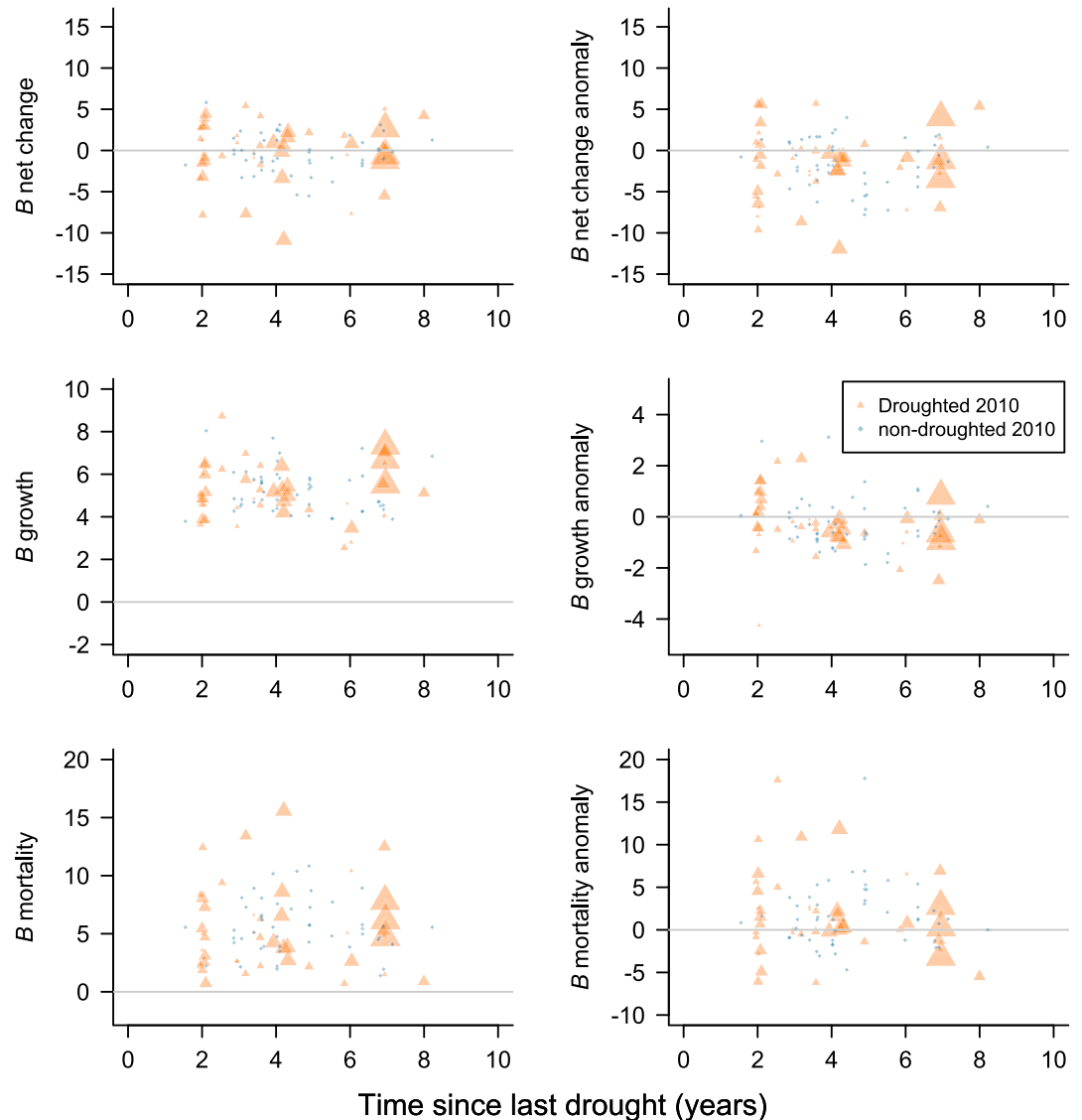
The time since last drought (the interval from the last  $\delta W$  Z-score  $< -1.6$  to the current interval) failed to explain any differences in  $\Delta B$ ,  $B$  net change, or  $B$  gains due to growth or loss due to mortality in 2010. This was the case whether all continuous time since last drought data were combined (Figure 6) or when examining discrete periods corresponding to the time since the 2007, 2005, and pre-2005 droughts (supporting information Figure S6).

### 3.6. Regional Patterns and Basin-Wide Scaling

Our data show that intact forests during the 2010 drought lost biomass in three of the five regions and that forests in none of the regions, on average, gained biomass (Table 1). Furthermore, those plots performing poorly in 2010 compared to the long-term mean (negative  $\Delta B$  changes in plot dynamics) were not confined to a single region (Figure 1). Plots having the most negative  $\Delta B$  net change values and largest  $\Delta B$  loss due to mortality in 2010 corresponded to regions with the greatest  $\delta W$  anomaly, which was the southern half of Amazonia. The northwest and Guiana Shield had  $\Delta B$  net change values that did not differ significantly from the long-term mean.

Scaling field measurements by region from intact nonanthropogenically degraded plots and the unmeasured aboveground and belowground components for forest census spanning the 2010 event, we estimated that the basin was carbon neutral during 2010 ( $-0.07$  confidence interval (CI):  $-0.42, 0.23 \text{ Pg C yr}^{-1}$ ) (Table 1). This represents a reversal of the long-term carbon sink, with an estimated net reduction in carbon uptake ( $\Delta C$  net change) in 2010 of  $-0.47 \text{ Pg C yr}^{-1}$  (or  $-1.1 \text{ Pg C}$  during the average 2.3 year 2010 census interval). Approximately 30% of the reduction in C uptake in 2010 was caused by a reduction in productivity ( $-0.14 \text{ Pg C yr}^{-1}$  (CI:  $-0.27, -0.03$ )), while the remainder is due to increased tree mortality and subsequent dead wood decomposition which is not immediately released to the atmosphere.

**Figure 5.** In 2010, biomass change anomaly ( $\Delta B$ ) (a) net change, (b) growth, and (c) mortality for plots undergoing or not undergoing drought in 2010 and in pre-2010 (2000 to <2010). All values are in  $\text{Mg ha}^{-1} \text{yr}^{-1}$ . Plots with census  $\delta W$  Z-scores  $< -1.6$  were classified as droughted. None of the classes were significantly different (Tukey HSD  $p > 0.05$ ).



**Figure 6.** Tree growth and mortality dynamics in 2010 for plots droughted and nondroughted in 2010 versus time since last pre-2010 precipitation anomaly,  $\delta W < -1.6$ : (top row)  $B$  net change and  $B$  net change anomaly ( $\Delta B$ ), (middle row)  $B$  growth and  $B$  growth anomaly, and (bottom row)  $B$  mortality and  $B$  mortality anomaly, all in  $\text{Mg ha}^{-1} \text{yr}^{-1}$ . Symbol size is proportional to the intensity of the  $\delta W$  Z-score in 2010, and symbol color and shape correspond to plots classified as droughted ( $\delta W < -1.6$ ) or nondroughted in 2010. None of the relationships were significant ( $p > 0.05$ ).

#### 4. Discussion

We have analyzed tree growth and mortality across the Amazon using forests censuses which cover the 2010 drought period. Similar to the 2005 event, we found (H1) an effect of precipitation anomalies on the net biomass change of the forests. In contrast to 2005, in 2010 we detected (H2) the first clear evidence for a widespread reduction in forest productivity (growth) in the Amazon due to drought. Mortality was (H2) also elevated in 2010, but not related to estimated precipitation anomalies. We found (H3) no evidence for the hypothesis that repeated droughts led to an enhanced impact.

##### 4.1. Net Change in Biomass

The 2010 drought was one of the most geographically extensive of the last few decades. On average, our plots did not gain biomass in 2010, regardless of drought classification (Figure 2). The lack of net biomass gain was widespread and not confined to one region (Figure 1). This reversal was in contrast to the same plots



previously acting as a carbon sink [Baker *et al.*, 2004; Phillips *et al.*, 2009]. Our results are consistent with reported long-term decline of the Amazon forest carbon sink [Brienen *et al.*, 2015], which has been most marked during the last decade.

#### 4.2. Growth and Mortality Impacts

In contrast to the 2005 event, which only saw elevated mortality [Phillips *et al.*, 2009], we now find that the net reduction in carbon uptake during the 2010 event was caused by a combination of both higher mortality and slower tree growth (Figure 2). The significantly elevated mortality rates during the 2010 drought interval indicate that drought is only partially responsible for the earlier reported long-term increase in mortality rates found by Brienen *et al.* [2015]. In addition, we show that significant reductions in growth contributed a further 30% to a weakening of the sink capacity of the basin during the 2010 drought. However, because the slow-down in growth and the increase in mortality began well before the 2005 event, additional processes may contribute to the long-term sink decline [cf. Brienen *et al.*, 2015].

We found that changes in growth or recruitment (but not mortality) relate to the intensity of the drought (Figure 3 and supporting information Figure S3). While the effects of the drought on net biomass changes are broadly in line with results from the 2005 event [Phillips *et al.*, 2009], we find two important differences: (i) on average, trees in plots more intensely droughted grew less in 2010 compared to the long-term mean and (ii) there was no relation between biomass losses due to mortality and drought severity in 2010. And, related to this, there was no difference in biomass net change between plots classified as droughted or nondroughted [Phillips *et al.*, 2009]. Thus, even plots that were not droughted showed elevated mortality during the 2010 event.

Experimental rainfall exclusion has been shown to cause a reduction in growth. Drying of Amazonian forest under throughfall exclusion experiments (TFEs) indicated that wood productivity can decline substantially with a sustained precipitation reduction [Brando *et al.*, 2008; da Costa *et al.*, 2010; Nepstad *et al.*, 2007; Rowland *et al.*, 2015]. The multiyear TFE experiments and natural drought are not directly comparable, since artificial droughts induce different artificially induced soil deficits, and lack the pattern of lower atmospheric humidity typical of natural droughts. Despite these differences, results from the two TFE experiments, both in eastern Amazonia, appear broadly in line with our observations of plots across the Amazon Basin. For example, not only were net biomass change anomalies for basin-wide plots similar during the 2005 and 2010 events, but also, the basin-wide plots now exhibited a clear reduction in growth due to drought, as has been seen in the TFE. Further, plots lost biomass and had growth reductions in response to drought throughout the Amazon Basin (Figure 1), despite large difference in precipitation, soil texture, depth, and drainage in plots and despite basin-scale fertility gradients [Quesada *et al.*, 2011]. The TFE experiments also showed that drought-related tree mortality can take several years to occur, so that basin-wide forest inventories following the 2010 event may only capture part of the mortality.

Fast-growing trees with low wood density may be most sensitive to drought [McDowell *et al.*, 2008; Phillips *et al.*, 2009]. In line with predictions, during the 2010 event trees with lower wood density were most affected by the greatest water deficits (Figure S4a). However, in contrast to the results from the TFE [da Costa *et al.*, 2010] and from the 2005 event [Phillips *et al.*, 2009], we did not find strong evidence that the size of trees that died in plots with most severe water deficit anomalies during the 2010 event was on average larger than in previous intervals. This may suggest different mortality mechanism for the largest trees during the 2010 event.

The lack of a significant relationship between mortality and our measured drought intensity in our study contrasts with results from the 2005 drought [Phillips *et al.*, 2009] and the TFE experiments [Brando *et al.*, 2008; da Costa *et al.*, 2010; Nepstad *et al.*, 2007]. The TFE experiments found that mortality rates under experimental drought were higher than those observed in plots undergoing natural droughts of lower intensity. Stem mortality rates in the TFE peaked in the year with the greatest water deficit (2005) for all stem size classes, indicating that drought effects on mortality can be detected within the year of severe water deficits [da Costa *et al.*, 2010]. Following the peak, mortality may continue to be elevated for some size classes (e.g., >40 cm in da Costa *et al.* [2010]). A lack of a relationship between mortality and drought intensity in 2010 may be partially explained by several factors: (1) by predrought conditions and limitations of the metric *W*. For example, the drought mortality relationship may be partially obscured by the record precipitation in 2009; (2) there may be a lag in tree mortality until water deficits become extreme [da Costa *et al.*, 2010]; and

(3) the metric  $W$  is insufficient to capture the drought stress experienced by trees growing on widely varying soils and under varying climatic conditions. However, using two other drought metrics that account for additional climate variables, we similarly failed to detect an effect on mortality during this time period (supporting information). This is both mechanistically and ecologically interesting, suggesting that other factors may also be affecting mortality in our plots.

Nevertheless, mortality was on average generally higher in our Amazon plots in 2010 (Figure 2), and higher mortality during drought years has been reported for other biomes and may have longer-term impacts such as species compositional change via the selection of more drought-adapted species. For example, forests in parts of western and central Africa have recently changed compositionally in response to drought [Fauset *et al.*, 2012; Ouédraogo *et al.*, 2013]. Increased mortality due to drought is not restricted to tropical forests [e.g., Allen *et al.*, 2010; van Mantgem *et al.*, 2009]. Boreal forests of Canada, for example, have undergone an increase of  $4.7\% \text{ yr}^{-1}$  in mortality over the last 40 years, with this increase attributed to regional decline in precipitation [Peng *et al.*, 2011].

### 4.3. Repeated Drought Impacts

Our analysis is the first ground-based Amazon Basin-wide study to examine effects due to the 2010 drought and interactive effects of repeat drought. Our results show that variation in precipitation significantly affects the carbon balance of intact tropical forest in the Amazon Basin. However, we find (H3) no evidence for the hypothesis that repeated droughts lead to enhanced impact, suggesting that drought effects in 2010 were largely independent from previous droughts. While mortality increased significantly in 2010, we find that drought effects are not substantially compounded in 2010 for those forests undergoing pre-2010 droughts. Thus, net change in biomass during the 2010 event was approximately the same and independent as to whether a plot was or was not considered as having been droughted in recent history, prior to 2010 (Figure 5). Thus, the hypothesis that earlier drought impacts may have simply weeded out trees destined to die (i.e., pre-2010 droughts advanced mortality events, thereby “inoculating” forests to later droughts) is not validated by our results. Overall, there was neither an additional effect (degradation) nor was there interfering effect (inoculation) of repeated droughts. Variable census length and 2010 following an anomalously wet year are two factors that may limit the ability to detect either effect; therefore, these are cautious interpretations. That the Amazon trees proved sensitive to two major droughts in 5 years suggests that these forests will continue to exhibit reduced growth and enhanced mortality rates in response to any future periods of drought severity similar to the 2005, 2007, and 2010 events studied here. Finally, Amazonian forests appear to have a degree of forest level resilience in terms of their demonstrated ability to return to be a net above-ground carbon sink. Thus, results from experimentally droughted forests [Brando *et al.*, 2008; da Costa *et al.*, 2010] and from our natural drought observations showing that plots returned to acting as net sinks following the 2005 event (Table 1) both suggest that the reduction in growth following drought may be short term.

The effects of precipitation anomalies can also be interpreted through the mortality spiral proposed by Franklin *et al.* [1987]. For example, drought-stressed trees may undergo a series of stress events such as hydraulic fatigue [Rowland *et al.*, 2015] and nonstructural carbohydrate depletion [Doughty *et al.*, 2014] leading to death, with reductions in growth one proximate cause of death. Trees may also shift their allocation of carbon in response to drought. A recent study found that during and after drought, trees adapt carbon allocation strategies by shifting allocation between wood, canopy, and roots and reducing autotrophic respiration [Doughty *et al.*, 2015, 2014]. Our results of a consistent and drought-associated reduction in growth during the 2010 event contrast with the report of Doughty *et al.* [2015] that productivity remained constant. This contrast may be due to differences in the number of plots sampled and spatial and temporal differences between the two studies. Doughty *et al.* [2015] focused on intensive 1–3 month measurements in 13 plots representing dry and humid forests and had 1 year of pre-2010 baseline data, while the current study mobilizes two decades of baseline data. Understanding regional variation and how response plasticity may allow some trees to better respond to repeated droughts will help to understand factors that delay or accelerate the onset of death. There is also a need to improve understanding of the interaction between recent anomalously hot dry seasons [Jiménez-Muñoz *et al.*, 2013] and precipitation anomalies.

### 4.4. Stand- and Basin-Scale Effects

Our ground-based measurements permit evaluation of space-, airborne-, and flux tower-based observations of drought. Based on analysis of TRMM and gauge-based precipitation data [Lewis *et al.*, 2011; Marengo

*et al.*, 2011], the 2010 drought was reported to have extended across a much larger area than the 2005 drought. Our ground-based measurements confirm that forests in these regions lost biomass compared to the long-term mean; however, the mechanisms by which forests lost biomass due to drought differ from 2005. Satellite data have suggested that some areas affected by the drought in 2005 had persistent changes in tree canopies up to several years after the drought that were attributed to changes in structure and water content of the forest upper canopy [Saatchi *et al.*, 2013]. Our plots lack the synoptic coverage that remote sensing permits, and so long-term impacts in some parts of the Amazon may not be inconsistent with our analysis. Nevertheless, our direct measurements of forest dynamics show that the carbon balance impacts of Amazon previous droughts have been rather short lived, since after the losses of the 2005 event, forests quickly returned, on average, to carbon sink status. In addition, we did not observe any evidence for an inoculation effect nor for an additive effect of previous droughts on the effect of the 2010 drought.

Our “bottom-up” basin-wide results are in line with “top-down” estimates based on regional atmospheric inversion using airborne measurements of gas concentrations. Thus, after taking into account carbon losses due to forest loss and fire in 2010, the Amazon Basin vegetation was estimated to be carbon neutral ( $0.03 \pm 0.22 \text{ Pg C yr}^{-1}$ ) [Gatti *et al.*, 2014] or a sink ( $0.1$  to  $0.2 \text{ Pg C yr}^{-1}$ ) [Laan-Luijkx *et al.*, 2015] (note that our sign convention for carbon sinks and sources differs from Gatti *et al.*, 2014 and Laan-Luijkx *et al.*, 2015. In our convention, carbon uptake by the land vegetation is considered to be a flux with a positive sign while carbon release is a negative flux). This compares to a ground-based estimate from this study including estimates of aboveground and belowground commitments that the basin was biomass carbon neutral during 2010 ( $-0.07 \text{ Pg C yr}^{-1}$  CI:  $-0.42$ ,  $0.23$ ) (Table 1). This represents a marked reduction in carbon uptake when compared to either pre-2005 ground-based estimates ( $0.39 \pm 0.10 \text{ Pg C yr}^{-1}$ ) [Phillips *et al.*, 2009] or to atmospheric inversion estimates for 2011 ( $0.25 \pm 0.14 \text{ Pg C yr}^{-1}$ ) [Gatti *et al.*, 2014]. It is important to note that estimates by different techniques are not fully comparable in process or in time—ground plots “see” the response of aboveground forest biomass, while atmospheric measurements of carbon dioxide emissions are also affected by autotrophic and heterotrophic respiration, and decay of necromass produced by drought-induced mortality will not be seen immediately. Scaling vegetation response to the 2010 event is also limited by uncertainty in total carbon storage in roots and uncertainty in shifts in carbon allocation during and following the event [Doughty *et al.*, 2015]. Notwithstanding these caveats, it is remarkable how closely the bottom-up and top-down estimates compare for the 2010 carbon balance.

#### 4.5. Challenges in Evaluating Drought Response: Alternative Drivers and Limitations

There are a number of challenges in evaluating response for the Amazon Basin to the 2010 drought including, and not limited to the following (i) vegetation dynamics show long-term (decadal-scale) changes [Brienen *et al.*, 2015], and separating specific changes during the 2010 drought from such long-term changes is challenging; (ii) the 2010 drought was bracketed by some of the wettest years on record, and there are interactions among several factors; and (iii) some, but not all, of drought versus climate relationships observed for the 2005 drought apply to the 2010 event.

There are long-term changes occurring in Amazonian forests, with increasing levels of turnover, even before the 2005 drought [Brienen *et al.*, 2015; Phillips and Gentry, 1994]. This long-term increase in mortality may be due to other drivers in addition to drought, such as faster growth leading to shorter tree lifespans [Bigler and Veblen, 2009; Di Filippo *et al.*, 2015], increasing liana abundance [Phillips *et al.*, 2002] leading to increased tree death [van der Heijden *et al.*, 2015], and increasing climate variability other than droughts [Gloor *et al.*, 2013; Jiménez-Muñoz *et al.*, 2013]. The reduction in the rate that Amazon forests are gaining carbon over the last three decades [Brienen *et al.*, 2015] results in a challenge in evaluating drought responses, since the baseline itself is changing (i.e., increasing mortality and decreasing net change). In this study we used the baseline 1998 to pre-2010, which corresponds to the TRMM time window. As expected, since the rate of carbon gain has declined [Brienen *et al.*, 2015], when we run the same analysis using all available pre-2010 baseline data back to the 1980s, the biomass loss due to the 2010 drought ( $\Delta B$  net change) was greater still as the net biomass gains in the baseline back to the 1980s were greater (values not reported).

Furthermore, the exceptional wet years both preceding and following the 2010 drought represent an underlying intensification of the Amazon climate system, with annual precipitation on average increasing [Gloor *et al.*, 2013]. The 2010 drought may have been less intense compared to previous droughts due to the effect of the higher than average precipitation in 2009 [Chen *et al.*, 2013]. The changes required different approaches in analyzing the 2010 drought compared to the 2005 drought. These wet years may have

dampened the drought effect on trees, with soil moisture being on average higher prior to onset of the drought, and soils rapidly rewetting following the drought. Because the 2010 drought was preceded by record rainfall in 2009, it was necessary to use the *maximum W* for a given census interval that may span several years, rather than the mean [e.g., Aragão *et al.*, 2007; Phillips *et al.*, 2010b, 2009]. Site-specific estimates of precipitation and soil moisture would also improve understanding of drought response. Our finding of different drivers of change in net biomass (reduction in productivity) in the 2010 event than the 2005 event suggests that attempts to use results from one drought (e.g., 2005) to extrapolate to another using TRMM rather tree census data [e.g., Lewis *et al.*, 2011] may not accurately represent pathways and responses. We found consistent relationships for some but not all of the changes in vegetation dynamics anomalies versus water deficits using alternative metrics (e.g., SPI, supporting information). Ultimately, these impacts can be best understood by directly measuring them on the ground and not simply by extrapolation from previous drought responses.

#### 4.6. Future Considerations

Our findings have a number of implications. Amazonian forests appear to have a moderate level of resilience to repeated droughts, with fast postdrought returns to net carbon gains; however, the decline in productivity in 2010 shows a new response that was not recorded in the previous drought. Forests responded in a similar way across a large precipitation gradient (Figure 1). If trends in climate over the past few decades continue, the future climate of the Amazon Basin is liable to be one with greater extremes [Gloor *et al.*, 2013], including greater dry season water deficits [Fu *et al.*, 2013]. It is unclear how these dual extremes may affect forests. Our results, and those from Phillips *et al.* [2009] for the 2005 drought, show that forest responses per unit area are usually rather small, but that the extent over which they can act is vast, so that they have notable carbon cycle implications at regional and global scales. Finally, our finding of a reduction in productivity due to drought has important implications for estimating the longevity of the Amazon carbon sink [Brienen *et al.*, 2015].

Based on these results, it is possible to make a number of recommendations:

1. *Suite of physiological, carbon cycling, and composition measurements.* The presence of a large, extensive plot network with long-term plot-based data has allowed us to partition drought response into growth and mortality. However, more work is needed to understand the underlying tree physiological responses involved and potential shifts in species composition.
2. *Soil effects.* Additional studies are required to understand interaction between drought and soil (e.g., supporting information), since variation in soils affects structure and productivity [Aragão *et al.*, 2009; Quesada *et al.*, 2012].
3. *Reducing uncertainty.* Assessing changes in belowground processes due to water deficits remains a major challenge and source of uncertainty. A lack of relationship between changes in aboveground *B* and drought metrics derived from TRMM suggests a need for better weather data collected at each plot.
4. *Interaction among multiple factors.* Alternative water deficit metrics evaluated in this study (supporting information) such as the SPEI include indirect effects of temperature via the Penman-Monteith equation to estimate evapotranspiration. However, the interaction between multiple factors such as temperature and water deficits requires greater attention.
5. *Spatial representativeness.* The network of permanent forest plots has grown steadily and is dispersed across the basin, yet important regions are still underrepresented. There is a clear need for ground-based assessments of tree growth and dynamics to fill key spatial gaps (both standard census and “intensive” plots) and thus also improve the prospects for validating large-scale observations of forest canopy properties made remotely from space. Droughts over the last two decades have tended to focus on the southern Amazon border; these forests may serve as critical indicators of potential forest dieback due to future droughts.

Greater, coordinated effort in both ground-based and air/space-borne observations will help better determine the stand level processes and tree level mechanisms involved in forest responses to drought. Plot-based observations will help interpret and refine Earth observation techniques [e.g., Samanta *et al.*, 2010], improve dynamic vegetation models [Galbraith *et al.*, 2010], constrain estimates of carbon emissions [Gatti *et al.*, 2014; Phillips *et al.*, 2009], and validate predictions of the fate of Amazonian forests [Cox *et al.*, 2004; Huntingford *et al.*, 2013].



## 5. Conclusions

Drought negatively impacts neotropical forest carbon storage, and our study shows for the first time that it can cause a large-scale reduction in tropical forest productivity. Our results suggest further that Amazon forest response is to some extent predictable, being of similar magnitude to the 2005 drought, but that pathways differ between events, with different results found for mortality and productivity in 2010 compared to 2005. Our estimates of basin-wide vegetation being carbon neutral in 2010 closely match estimates independently derived from a regional-scale inversion using airborne measurements of greenhouse gases [Gatti *et al.*, 2014]. Despite drought being a natural feature of the Amazonian climate regime, there is large uncertainty regarding changes in the frequency, intensity, and impact of these events in the future [Huntingford *et al.*, 2013]. However, the intensities of future droughts are likely exacerbated by elevated temperatures, and it is therefore crucial that we improve understanding of forest response to drought events. Forests were not “inoculated” against a second major drought in 5 years, suggesting that should there be a future climate regime characterized by ever greater dry season soil water deficits as predicted by some models [Fu *et al.*, 2013], then declining productivity and increasing mortality may begin to degrade forests.

### Acknowledgments

Forest inventory data are curated in the ForestPlots database, <https://www.forestplots.net>. This paper is a product of the RAINFOR network, supported by Natural Environment Research Council (NERC) Urgency, Standard, and Consortium grants Assessing the impacts of the 2010 drought at the Amazon forest-savanna zone of tension (NE/I02982X/1), Niche Evolution of South American Trees (NE/I028122/1), AMAZONICA (NE/F005806/1), and TROBIT (NE/D005590/1), the European Union's Seventh Framework Programme project 282664, AMAZALERT, **CNPq/PELD (403725/2012-7)**, a Gordon and Betty Moore Foundation grant, and ERC grant “Tropical Forests in the Changing Earth System.” Additional data were included from the Tropical Ecology Assessment and Monitoring (TEAM) Network, a collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution, and the Wildlife Conservation Society, and partly funded by these institutions, the Gordon and Betty Moore Foundation, and other donors. T.R.F. was supported by a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Brazil, grant (177/2012). O.L.P. was supported by a European Research Council Advanced Grant and a Royal Society Wolfson Research Merit Award. J.C. and M.R.M. were supported by Investissement d'Avenir grants of the ANR (CEBA: ANR-10-LABX-25-01 and TULIP: ANR-10-LABX-0041) and from CNES funds (TOSCA). This is paper number 694 in the Biological Dynamics of Forest Fragments project. We thank I. Amaral, A. Araujo-Murakami, O.S. Bánki, J. Barichivich, P. C. Barros, P. Brando, L. Blanc, C. Doughty, T. Gaudi, N. Higuchi, T.J. Killeen, E. Lenza, P.S. Morandi, A. Parada, M.C. Peñuela-Mora, N.C.A. Pitman, Z. Restrepo, A. Roopsind, C. Roth, D. Sasaki, A. Sota, J. Talbot, M. Toledo, R. K. Umetsu, and R. Zagt for their assistance with collection or sharing data and two anonymous referees for their helpful suggestions to improve the manuscript. T.R.F. performed analyses and wrote the paper with major input from O.L.P., R.B., J.L., and E.G. O.L.P., J.L., and Y.M. conceived the RAINFOR forest census plot network program, and E.G., T.R.B., T.R.F., and R.B. contributed to its development. O.L.P., T.R.F., J.L., Y.M., and E.G. conceived the study and received funding. O.L.P., T.R.F., R.J.W.B., and A.M.M. coordinated data collection with the help of most coauthors. T.R.F., R.B., A.M.M., O.L.P., and G.L.G. performed quality control on the data with the help of most coauthors. All remaining authors contributed data. All authors commented on the analysis, presentation of the data, and manuscript.

### References

- Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Venetier, T. Kitzberger, A. Rigling, D. D. Breshears, and E. Hogg (2010), A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests, *For. Ecol. Manage.*, **259**, 660–684.
- Anderegg, W. R. L., L. D. L. Anderegg, J. A. Berry, and C. B. Field (2014), Loss of whole-tree hydraulic conductance during severe drought and multi-year forest die-off, *Oecologia*, **175**, 11–23.
- Aragão, L. E. O. C., Y. Malhi, R. M. Roman-Cuesta, S. Saatchi, L. O. Anderson, and Y. E. Shimabukuro (2007), Spatial patterns and fire response of recent Amazonian droughts, *Geophys. Res. Lett.*, **34**, L07701, doi:10.1029/2006GL028946.
- Aragão, L. E. O. C., et al. (2009), Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils, *Biogeosciences*, **6**(12), 2759–2778.
- Baker, T. R., et al. (2004), Increasing biomass in Amazonian forest plots, *Philos. Trans. R. Soc. London B Biol. Sci.*, **359**(1443), 353–365.
- Banin, L., et al. (2012), What controls tropical forest architecture? Testing environmental, structural and floristic drivers, *Global Ecol. Biogeogr.*, **21**(12), 1179–1190.
- Bartholomé, E., A. S. Belward, F. Achard, S. Bartalev, C. Carmona-Moreno, H. Eva, S. Fritz, J.-M. Grégoire, P. Mayaux, and H.-J. Stibig (2002), GLC 2000: Global Land Cover Mapping for the year 2000—Project Status November 2002, *Rep.*
- Bigler, C., and T. T. Veblen (2009), Increased early growth rates decrease longevity of conifers in subalpine forests, *Oikos*, **118**(8), 1130–1138.
- Brando, P. M., D. C. Nepstad, E. A. Davidson, S. E. Trumbore, D. Ray, and P. Camargo (2008), Drought effects on litterfall, wood production and belowground carbon cycling in an Amazon forest: Results of a throughfall reduction experiment, *Philos. Trans. R. Soc. London B Biol. Sci.*, **363**(1498), 1839–1848.
- Brienen, R. J. W., et al. (2015), Long-term decline of the Amazon carbon sink, *Nature*, **519**(7543), 344–348.
- Chave, J., et al. (2005), Tree allometry and improved estimation of carbon stocks and balance in tropical forests, *Oecologia*, **145**(1), 87–99.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne (2009), Towards a worldwide wood economics spectrum, *Ecol. Lett.*, **12**(4), 351–366.
- Chen, Y., I. Velicogna, J. S. Famiglietti, and J. T. Randerson (2013), Satellite observations of terrestrial water storage provide early warning information about drought and fire season severity in the Amazon, *J. Geophys. Res. Biogeosci.*, **118**, 495–504, doi:10.1002/jgrg.20046.
- Chou, C., J. C. Chiang, C.-W. Lan, C.-H. Chung, Y.-C. Liao, and C.-J. Lee (2013), Increase in the range between wet and dry season precipitation, *Nat. Geosci.*, **6**(4), 263–267.
- Clark, D. B., D. A. Clark, and S. F. Oberbauer (2010), Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO<sub>2</sub>, *Global Chang. Biol.*, **16**(2), 747–759.
- Coelho, C. A. S., I. A. F. Cavalcanti, S. M. S. Costa, S. R. Freitas, E. R. Ito, G. Luz, A. F. Santos, C. A. Nobre, J. A. Marengo, and A. B. Pezza (2012), Climate diagnostics of three major drought events in the Amazon and illustrations of their seasonal precipitation predictions, *Meteorol. Appl.*, **19**(2), 237–255.
- Condit, R. (1995), Research in large, long-term tropical forest plots, *Trends Ecol. Evol.*, **10**(1), 18–22.
- Cox, P. M., R. A. Betts, M. Collins, P. P. Harris, C. Huntingford, and C. D. Jones (2004), Amazonian forest dieback under climate-carbon cycle projections for the 21st century, *Theor. Appl. Climatol.*, **78**, 137–156.
- Cox, P. M., P. P. Harris, C. Huntingford, R. A. Betts, M. Collins, C. D. Jones, T. E. Jupp, J. A. Marengo, and C. A. Nobre (2008), Increasing risk of Amazonian drought due to decreasing aerosol pollution, *Nature*, **453**(7192), 212–215.
- da Costa, A. C., et al. (2010), Effect of 7 yr of experimental drought on vegetation dynamics and biomass storage of an eastern Amazonian rainforest, *New Phytol.*, **187**(3), 579–591.
- da Rocha, H. R., M. L. Goulden, S. D. Miller, M. C. Menton, L. D. V. O. Pinto, H. C. de Freitas, and A. M. e Silva Figueira (2004), Seasonality of water and heat fluxes over a tropical forest in eastern Amazonia, *Ecol. Appl.*, **14**(sp4), 22–32.
- Di Filippo, A., N. Pederson, M. Baliva, M. Brunetti, A. Dinella, K. Kitamura, H. D. Knapp, B. Schirone, and G. Piovesan (2015), The longevity of broadleaf deciduous trees in Northern Hemisphere temperate forests: Insights from tree-ring series, *Front. Ecol. Evol.*, **3**, 46.
- Doughty, C. E., et al. (2014), Allocation trade-offs dominate the response of tropical forest growth to seasonal and interannual drought, *Ecology*, **95**(8), 2192–2201.
- Doughty, C. E., et al. (2015), Drought impact on forest carbon dynamics and fluxes in Amazonia, *Nature*, **519**(7541), 78–82.
- Espinoza, J. C., J. Ronchail, J. L. Guyot, C. Junquas, P. Vauchel, W. Lavado, G. Drapeau, and R. Pombosa (2011), Climate variability and extreme drought in the upper Solimões River (western Amazon Basin): Understanding the exceptional 2010 drought, *Geophys. Res. Lett.*, **38**, L13406, doi:10.1029/2011GL047862.



- Fauset, S., T. R. Baker, S. L. Lewis, T. R. Feldpausch, K. Affum-Baffoe, E. G. Foli, K. C. Hamer, and M. D. Swaine (2012), Drought-induced shifts in the floristic and functional composition of tropical forests in Ghana, *Ecol. Lett.*, *15*(10), 1120–1129.
- Feldpausch, T. R., et al. (2011), Height-diameter allometry of tropical forest trees, *Biogeosciences*, *8*(5), 1081–1106.
- Feldpausch, T. R., et al. (2012), Tree height integrated into pantropical forest biomass estimates, *Biogeosciences*, *9*(8), 3381–3403.
- Fittkau, E. J. (1971), Esboço de uma divisão ecológica da região amazônica, paper presented at Proc. Symp. Biol. Trop. Amaz., Florencia y Leticia.
- Franklin, J. F., H. Shugart, and M. E. Harmon (1987), Tree death as an ecological process, *BioScience*, *36*, 550–556.
- Fu, R., et al. (2013), Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection, *Proc. Nat. Acad. Sci.*, *110*(45), 18110–5, doi:10.1073/pnas.1302584110.
- Galbraith, D., P. E. Levy, S. Sitch, C. Huntingford, P. Cox, M. Williams, and P. Meir (2010), Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change, *New Phytol.*, *187*(3), 647–665.
- Gatti, L. V., et al. (2014), Drought sensitivity of Amazonian carbon balance revealed by atmospheric measurements, *Nature*, *506*(7486), 76–80.
- Gloor, M., R. J. W. Brienen, D. Galbraith, T. R. Feldpausch, J. Schöngart, J. L. Guyot, J. C. Espinoza, J. Lloyd, and O. L. Phillips (2013), Intensification of the Amazon hydrological cycle over the last two decades, *Geophys. Res. Lett.*, *40*, 1729–1733, doi:10.1002/grl.50377.
- Hijmans, R. J., and J. van Etten (2013), Raster: Geographic data analysis and modeling, R package version 2, *Rep.*, pp. 1–25. [Available at <http://CRAN.R-project.org/package=raster>.]
- Huntingford, C., P. Zelazowski, D. Galbraith, L. M. Mercado, S. Sitch, R. Fisher, M. Lomas, A. P. Walker, C. D. Jones, and B. B. Booth (2013), Simulated resilience of tropical rainforests to CO<sub>2</sub>-induced climate change, *Nat. Geosci.*, *6*(4), 268–273.
- Jiménez-Muñoz, J. C., J. A. Sobrino, C. Mattar, and Y. Malhi (2013), Spatial and temporal patterns of the recent warming of the Amazon forest, *J. Geophys. Res. Atmos.*, *118*, 5204–5215, doi:10.1002/jgrd.50456.
- Kitoh, A., H. Endo, K. Krishna Kumar, I. F. A. Cavalcanti, P. Goswami, and T. Zhou (2013), Monsoons in a changing world: A regional perspective in a global context, *J. Geophys. Res. Atmos.*, *118*, 3053–3065, doi:10.1002/jgrd.50258.
- Kloke, J., and J. McKean (2013), Rfit: Rank estimation for linear models. [Available at <http://CRAN.R-project.org/package=Rfit>.]
- Laan-Luijckx, I., I. Velde, M. Krol, L. Gatti, L. Domingues, C. Correia, J. Miller, M. Gloor, T. Leeuwen, and J. Kaiser (2015), Response of the Amazon carbon balance to the 2010 drought derived with CarbonTracker South America, *Global Biogeochem. Cycles*, *29*, 1092–1108, doi:10.1002/2014GB005082.
- Lewis, S. L., P. M. Brando, O. L. Phillips, G. M. van der Heijden, and D. Nepstad (2011), The 2010 Amazon drought, *Science*, *331*(6017), 554.
- Lopez-Gonzalez, G., S. L. Lewis, M. Burkitt, B. T.R. and O. L. Phillips (2009), ForestPlots.net Database, edited.
- Lopez-Gonzalez, G., S. L. Lewis, M. Burkitt, and O. L. Phillips (2011), ForestPlots.net: A web application and research tool to manage and analyse tropical forest plot data, *J. Veg. Sci.*, *22*(4), 610–613.
- Malhi, Y., L. E. O. C. Aragão, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, C. McSweeney, and P. Meir (2009), Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest, *Proc. Nat. Acad. Sci.*, *106*(49), 20,610–20,615.
- Marengo, J. A., C. A. Nobre, J. Tomasella, M. F. Cardoso, and M. D. Oyama (2008), Hydro-climate and ecological behaviour of the drought of Amazonia in 2005, *Philos. Trans. R. Soc. London B Biol. Sci.*, *363*(1498), 1773–1778.
- Marengo, J. A., J. Tomasella, L. M. Alves, W. R. Soares, and D. A. Rodriguez (2011), The drought of 2010 in the context of historical droughts in the Amazon region, *Geophys. Res. Lett.*, *38*, L12703, doi:10.1029/2011GL047436.
- McDowell, N., et al. (2008), Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought?, *New Phytol.*, *178*(4), 719–739.
- McDowell, N. G., D. J. Beerling, D. D. Breshears, R. A. Fisher, K. F. Raffa, and M. Stitt (2011), The interdependence of mechanisms underlying climate-driven vegetation mortality, *Trends Ecol. Evol.*, *26*(10), 523–532.
- NASA (2012), TRMM 3B43(7): Monthly 0.25 x 0.25 degree merged TRMM and other sources estimates, edited, NASA Distrib. Active Arch. Cent., Goddard Space Flight Cent. Earth Sci., Greenbelt, Md. [Available at [http://disc.sci.gsfc.nasa.gov/precipitation/documentation/TRMM\\_README/TRMM\\_3B43\\_readme.shtml](http://disc.sci.gsfc.nasa.gov/precipitation/documentation/TRMM_README/TRMM_3B43_readme.shtml).]
- Nepstad, D. C., I. M. Tohver, D. Ray, P. Moutinho, and G. Cardinot (2007), Mortality of large trees and lianas following experimental drought in an Amazon forest, *Ecology*, *88*(9), 2259–2269.
- O'Brien, M. J., S. Leuzinger, C. D. Philipson, J. Tay, and A. Hector (2014), Drought survival of tropical tree seedlings enhanced by non-structural carbohydrate levels, *Nature Clim. Change*, *4*(8), 710–714, doi:10.1038/nclimate2281.
- Ouédraogo, D.-Y., F. Mortier, S. Gourlet-Fleury, V. Freycon, N. Picard, and M. Turnbull (2013), Slow-growing species cope best with drought: evidence from long-term measurements in a tropical semi-deciduous moist forest of Central Africa, *J. Ecol.*, *101*(6), 1459–1470.
- Parker, J., and R. L. Patton (1975), Effects of drought and defoliation on some metabolites in roots of black oak seedlings, *Can. J. For. Res.*, *5*(3), 457–463.
- Peng, C., Z. Ma, X. Lei, Q. Zhu, H. Chen, W. Wang, S. Liu, W. Li, X. Fang, and X. Zhou (2011), A drought-induced pervasive increase in tree mortality across Canada's boreal forests, *Nat. Clim. Change*, *1*(9), 467–471.
- Phillips, O. L., and A. H. Gentry (1994), Increasing turnover through time in tropical forests, *Science*, *263*(5149), 954–958.
- Phillips, O. L., et al. (2002), Increasing dominance of large lianas in Amazonian forests, *Nature*, *418*(6899), 770–774.
- Phillips, O. L., S. L. Lewis, T. R. Baker, K. J. Chao, and N. Higuchi (2008), The changing Amazon forest, *Philos. Trans. R. Soc. London B Biol. Sci.*, *363*(1498), 1819–1827.
- Phillips, O. L., et al. (2009), Drought sensitivity of the Amazon rainforest, *Science*, *323*(5919), 1344–1347.
- Phillips, O. L., T. R. Baker, R. Brienen, and T. R. Feldpausch (2010a), Field manual for plot establishment and remeasurement. [Available at <http://www.geog.leeds.ac.uk/projects/rainfor/>, Accessed date 02-2012.]
- Phillips, O. L., et al. (2010b), Drought-mortality relationships for tropical forests, *New Phytol.*, *187*(3), 631–646.
- Potter, C., S. Klooster, C. Hiatt, V. Genovese, and J. C. Castilla-Rubio (2011), Changes in the carbon cycle of Amazon ecosystems during the 2010 drought, *Environ. Res. Lett.*, *6*(3), 034024.
- Quesada, C. A., J. Lloyd, L. O. Anderson, N. M. Fyllas, M. Schwarz, and C. I. Czimczik (2011), Soils of Amazonia with particular reference to the RAINFOR sites, *Biogeosciences*, *8*(6), 1415–1440.
- Quesada, C. A., et al. (2012), Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate, *Biogeosciences*, *9*(6), 2203–2246.
- R Development Core Team (2013), R: A language and environment for statistical computing, R Foundation for Statistical Computing, *Rep.*, Vienna, Austria, [Available at <http://www.R-project.org/>.]
- Rowland, L., et al. (2015), Death from drought in tropical forests is triggered by hydraulics not carbon starvation, *Nature*, *528*(7580), 119–122.
- Saatchi, S., S. Asefi-Najafabady, Y. Malhi, L. E. Aragao, L. O. Anderson, R. B. Myneni, and R. Nemani (2013), Persistent effects of a severe drought on Amazonian forest canopy, *Proc. Natl. Acad. Sci. U.S.A.*, *110*(2), 565–570.

- Sala, A., F. Piper, and G. Hoch (2010), Physiological mechanisms of drought-induced tree mortality are far from being resolved, *New Phytol.*, *186*(2), 274–281.
- Samanta, A., S. Ganguly, H. Hashimoto, S. Devadiga, E. Vermote, Y. Knyazikhin, R. R. Nemani, and R. B. Myneni (2010), Amazon forests did not green-up during the 2005 drought, *Geophys. Res. Lett.*, *37*, L05401, doi:10.1029/2009GL042154.
- Shuttleworth, W. J. (1988), Evaporation from Amazonian rainforest, *Philos. Trans. R. Soc. London B Biol. Sci.*, *233*(1272), 321–346.
- Talbot, J., et al. (2014), Methods to estimate aboveground wood productivity from long-term forest inventory plots, *For. Ecol. Manage.*, *320*, 30–38.
- van der Heijden, G. M. F., J. S. Powers, and S. A. Schnitzer (2015), Lianas reduce carbon accumulation and storage in tropical forests, *Proc. Natl. Acad. Sci. U.S.A.*, *112*(43), 13,267–13,271.
- van Mantgem, P. J., et al. (2009), Widespread increase of tree mortality rates in the western United States, *Science*, *323*(5913), 521–524.
- Vicente-Serrano, S. M., S. Beguería, J. I. López-Moreno, M. Angulo, and A. El Kenawy (2010), A new global 0.5° gridded dataset (1901–2006) of a Multiscalar Drought Index: Comparison with Current Drought Index Datasets based on the Palmer Drought Severity Index, *J. Hydrometeorol.*, *11*(4), 1033–1043.
- Vlam, M., P. J. Baker, S. Bunyavejchewin, and P. A. Zuidema (2014), Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees, *Oecologia*, *174*(4), 1449–1461.
- von Randow, C., et al. (2004), Comparative measurements and seasonal variations in energy and carbon exchange over forest and pasture in South West Amazonia, *Theor. Appl. Climatol.*, *78*(1–3), 5–26.
- Wang, W. F., C. H. Peng, D. D. Kneeshaw, G. R. Larocque, and Z. B. Luo (2012), Drought-induced tree mortality: Ecological consequences, causes, and modeling, *Environ. Rev.*, *20*(2), 109–121.
- Williams, E., A. Dall'Antonia, V. Dall'Antonia, J. M. d. Almeida, F. Suarez, B. Liebmann, and A. C. M. Malhado (2005), The drought of the century in the Amazon Basin: An analysis of the regional variation of rainfall in South America in 1926, *Acta Amazonica*, *35*, 231–238.
- Williamson, G. B., W. F. Laurance, A. A. Oliveira, P. Delamonica, C. Gascon, T. E. Lovejoy, and L. Pohl (2000), Amazonian tree mortality during the 1997 El Niño drought, *Conserv. Biol.*, *14*(5), 1538–1542.
- Zanne, A. E., G. Lopez-Gonzalez, D. A. Coomes, J. Ilic, S. Jansen, S. L. Lewis, R. B. Miller, N. G. Swenson, M. C. Wiemann, and J. Chave (2009), Data from: Towards a worldwide wood economics spectrum, *Dryad Data Repos.*, doi:10.5061/dryad.234.

## Erratum

In the originally published version of this article, in the second paragraph of the section titled “Stand- and Basin-Scale Effects”, there was an error in the values for Gatti et al., 2014 and Lann-Luijckx et al., 2015. This error has since been corrected, and this version may be considered the authoritative version of record.