Pan-Tropical Analysis of Climate Effects on Seasonal Tree Growth

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Abstract

Climate models predict a range of changes in tropical forest regions, including increased average temperatures, decreased total precipitation, reduced soil moisture and alterations in seasonal climate variations. These changes are directly related to the increase in anthropogenic greenhouse gas concentrations, primarily CO2. Assessing seasonal forest growth responses to climate is of utmost importance because woody tissues, produced by photosynthesis from atmospheric CO2, water and light, constitute the main component of carbon sequestration in the forest ecosystem. In this paper, we combine intra-annual tree growth measurements from published tree growth data and the corresponding monthly climate data for 25 pan-tropical forest sites. This meta-analysis is designed to find the shared climate drivers of tree growth and their relative importance across pan-tropical forests in order to improve uptake models in a global change context. Tree growth reveals significant intra-annual seasonality at seasonally dry sites or in wet tropical forests. Of the overall variation in tree growth, 28.7% was explained by the site effect, i.e. the tree growth average per site. The best predictive model included four climate variables: precipitation, solar radiation (estimated with extrasolar radiation reaching the atmosphere), temperature amplitude and relative soil water content. This model explained more than 50% of the tree growth variations across tropical forests. Precipitation and solar radiation are the main seasonal drivers of tree growth, causing 19.8% and 16.3% of the tree growth variations. Both have a significant positive association with tree growth. These findings suggest that forest productivity due to tropical tree growth will be reduced in the future if climate extremes, such as droughts, become more frequent.

Introduction

Tropical forests are being threatened on an unprecedented scale by global changes. Temperatures across tropical forest regions are currently increasing [1] and are expected to continue to increase with a concomitant decrease in precipitation over the next decades [2–4]. Climate models predict a range of changes in tropical forest regions, including increased frequency of extreme climatic events, increased average temperatures, increased atmospheric CO2 and changes in seasonal distribution and interannual variability of rainfall [5–9]. Tropical forests play an important role in the mitigation of anthropogenic atmospheric CO2 emissions by constituting a major reservoir of terrestrial carbon and a large and persistent carbon sink [10–12]. Feedback between tropical forests and the local and regional climate has also been demonstrated [4,13].

Tree growth is linked with atmospheric CO2 through photosynthesis. The last 20 years have seen a substantial increase in the number of publications focusing on the effects of climate on tropical tree growth. A search performed on Web of Science in March 2013 using the keywords 'climate', 'tropical forest', 'growth' and 'trees' returned fewer than 15 articles per year before 2000 and more than 60 articles in 2012, for a total of 541 articles focusing on the effect of climate on tropical tree growth. Long-term variations in tree growth have been reported on long-term forest plots, but the determinants of these variations are still being discussed [14–19]. Due to the annual or multi-annual census frequency of long-term forest plots, most studies focus on the annual or multi-annual variation in tree growth even though most tropical forests undergo an intrannual seasonality in climate [1,6,20–22]. In single-site-based studies, seasonal rhythms of tree
growth have been linked to seasonal variations in water availability, rainfall, temperature and solar radiation (Table 1). Rain or lack of rain is often implicitly viewed as the main drivers of forest dynamics [23], as annual net primary production (NPP) positively correlates with the annual sum of precipitation at large scales [24] and rainfall seasonality plays a key role in the forest’s response to climate variability [25]. The relation between the amount of rainfall and water availability for trees is not straightforward and is determined by various soil and plant characteristics (i.e. permanent wilting point, field capacity, root distribution). Consequently, water stresses are increasingly estimated using soil water balance models [26,27], including some that are explicitly designed for tropical forests [28]. Irradiance is directly linked to plant photosynthetic capacity, which in turn drives carbon uptake and plant growth [29]. The occurrence of dry periods linked to cloud-cover reduction was found to enhance canopy photosynthetic capacity by 25% throughout Amazonia [30]. The effects of rising temperatures on the physiology of tropical trees are currently debated within the scientific community [21,32]. Some studies suggest that reductions in photosynthetic rates at temperatures above 30°C are driven by reductions in stomatal conductance in response to higher leaf-to-air vapour pressure deficits [31] or by a direct down-regulation of biochemical processes during CO₂ fixation [33,33]. Recent studies, however, suggest that tropical tree mortality may increase significantly with increasing night-time temperatures, while tree growth appears surprisingly sensitive to variations in mean annual night-time temperatures of 1–2°C [35].

Table 1. Expected tropical tree growth response to climate variables.

| variable | predicted effect | references | process |
|----------|-----------------|------------|---------|
| Relative extractable water (REW) | + | [28,62] | photosynthesis, xylem tension, stomatal closure, leaf flush |
| Rainfall | + | [19, 23, 24, 35, 58, 59, 61, 97–90] | photosynthesis, xylem tension, stomatal closure, leaf flush |
| Temperature mean (Tmean) | – | [31–33,92,93] | photosynthesis kinetic, stomatal closure |
| Temperature min (Tmin) | – | [14,17,35,66] | photosynthesis kinetic, stomatal closure |
| Temperature max (Tmax) | – | [19,31,33] | photosynthesis kinetic, stomatal closure |
| Vapour pressure deficit (VPD) | no | [94,95] | stomatal closure, transpiration |
| Irradiance | + | [17,21,29,30,64,70,74] | photosynthesis, phenology |
| Friction velocity (U*) | no | [94,95] | photosynthesis, transpiration |

*: expected growth response to the climate variable: (+) trees are expected to grow faster with high values of the climate variable, (−) trees are expected to grow slower with high values of the climate variable. #: biological processes involve in the tree growth response to a given climate variation. VPD is vapour pressure deficit, and Friction velocity (U*) is a climate variable provided by eddy flux data, which is correlated with wind speed. Relative extractable water (REW), is a daily value between 0 and 1; when $REW = 1$, the amount of extractable water by the tree is at its maximum and when $REW = 0$, no water is available for the trees [28].

Table 2. Climate datasets used to model seasonal tropical tree growth at a pantropical scale.

| climate variable | full name | unit | origin |
|------------------|-----------|------|--------|
| pre | precipitation | mm | CRU-TS3.10.01 |
| sol* | Extraterrestrial solar radiation | mm/month as equivalent of evaporation | CGIAR-CSI |
| cld | cloud cover | % | CRU-TS3.1 |
| Pre | Potential Evapotranspiration | mm | CRU-TS3.1 |
| swc | relative soil water content | unit less | CGIAR-CSI |
| tmp | mean temperature | °C | CRU-TS3.1 |
| tmin | minimal temperature | °C | CRU-TS3.1 |
| tmx | maximal temperature | °C | CRU-TS3.1 |
| vap | vapour pressure | hPa | CRU-TS3.1 |
| dtr | temperature amplitude | °C | CRU-TS3.1 |

*: sol per day (mm/day equivalent) is calculated using the methodology presented in [39] specifically for the 15th day of each month to describe averages per month. Total sol per month (mm/month equivalent) is calculated by multiplying the value of sol for the 15th day of the month by the number of days in the month, 1 mm.day⁻¹ equivalent of evaporation = 2.45 MJ.m⁻².day⁻¹.

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| reference | country       | site                | Long. | Lat.  | method                  | time scale | No. of trees | Type a | duration (mm/yyyy) | dbh growth mean ± SD (mm/month) |
|-----------|---------------|---------------------|-------|-------|-------------------------|------------|--------------|--------|-------------------|---------------------------------|
| [78]      | Ghana         | Tinte Bepo         | −2.10 | 7.07  | dendrometer band         | monthly    | 42           | 2      | 11/1997–3/1999    | 0.32 ± 0.28                     |
| [43]      | Costa Rica    | Guanacaste          | −85.50| 10.75 | dendrometer band         | daily      | 19           | 3      | 2/1978–1/1979     | 0.27 ± 0.33                     |
| [100]     | Ecuador       | RBSF                | −79.07| −3.97 | electronic point dendrometer | daily    | 5            | 3      | 4/2006–2/2009     | 0.27 ± 0.38                     |
| [101]     | Brazil        | Rio Cachoera        | −49.71| −25.25| dendrometer band         | weekly     | 120          | 2      | 11/2007–9/2008    | 1.11 ± 0.97                     |
| [33]      | Costa Rica    | La Selva             | −84.00| 10.43 | dendrometer band         | monthly    | 28           | 1      | 6/2006–11/2008    | 0.3 ± 0.09                      |
| [44]      | DRC           | Luki forest         | 13.18 | −5.58 | graduated tape          | monthly    | 30           | 2      | 5/2006–7/2007     | 0.19 ± 0.59                     |
| [102]     | Brazil        | ZF-2                | −60.12| −2.59 | dendrometer band         | Monthly    | 272          | 1      | 1/2000–12/2000    | 0.15 ± 0.05                     |
| [103]     | Costa Rica    | Guanacaste          | −85.50| 10.75 | dendrometer band         | weekly     | 40           | 3      | 8/1969–7/1970     | 0.39 ± 0.37                     |
| [104]     | French Guiana | Paracou             | −52.91| 5.28  | dendrometer band         | weekly     | 9            | 3      | 10/1979–6/1982    | 0.64 ± 0.23                     |
| [105]     | Ivory Coast   | Lamto               | −5.03 | 6.22  | dendrometer band         | daily      | 6            | 3      | 2/1973–7/1981     | 0.28 ± 0.2                      |
| [106]     | Brazil        | Tapajos             | −54.97| −2.85 | dendrometer band         | monthly    | 734          | 3      | 12/2001–12/2005   | 0.31 ± 0.14                     |
| [107]     | Uganda        | Budongo             | 31.54 | 1.73  | dendrometer band         | monthly    | 318          | 3      | 7/2003–12/2009    | 0.1 ± 0.05                     |
| [19]      | Kenya         | Kakamega            | 34.86 | 0.35  | dendrometer band         | monthly    | 770          | 3      | 7/2003–12/2009    | 0.19 ± 0.03                     |
| [90]      | Brazil        | Marajopa            | −50.27| −7.83 | dendrometer band         | monthly    | 67           | 2      | 2/1997–11/2001   | 0.5 ± 0.55                     |
| [90]      | Brazil        | Marajopa            | −50.27| −7.83 | dendrometer band         | monthly    | 40           | 3      | 1/1997–10/2001   | 0.51 ± 0.55                     |
| [80]      | Ethiopia      | Munessa-Shashamene Forest | 38.87 | 7.43  | electronic point dendrometer | daily    | 4            | 3      | 4/2008–8/2009    | 0.45 ± 0.39                     |
| [108]     | Ghana         | Pinkwae             | −0.13 | 5.75  | dendrometer band         | weekly     | 79           | 2      | 2/1978–4/1979    | −0.2 ± 0.78                     |
| [108]     | Ghana         | Pinkwae             | −0.13 | 5.75  | dendrometer band         | weekly     | 2            | 3      | 3/1978–4/1979    | −0.24 ± 0.79                    |
| [109]     | Brazil        | Ibiacu              | −47.72| −22.78| dendrometer band         | monthly    | 5            | 3      | 3/1999–4/2006    | 0.34 ± 0.47                     |
| [110]     | Mexico        | El Palmar           | −104.47| 19.13| dendrometer band         | monthly    | 23           | 2      | 9/2002–8/2003    | 0.24 ± 0.36                     |
| [110]     | Mexico        | La Barcinesa        | −104.42| 19.15| dendrometer band         | monthly    | 14           | 2      | 9/2002–8/2003    | 0.09 ± 0.29                     |
| [61]      | Brazil        | Tapajos             | −54.97| −2.85 | dendrometer band         | monthly    | 450          | 2      | 11/1999–5/2001   | 0.21 ± 0.06                     |
| [111]     | Malaysia      | Selangor plantation | 101.52| 3.51  | dendrometer band         | weekly     | 6            | 3      | 1/1993–12/1995   | 0.55 ± 0.32                     |
| [112]     | Thailand      | SERS                | 101.93| 14.50 | dendrometer band         | weekly     | 6            | 3      | 4/2004–2/2006    | 0.04 ± 0.04                     |
| [113]     | Brazil        | CPM                 | −50.50| −29.00| tree ring analysis       | monthly    | 12           | 1      | 5/2005–5/2006    | 0.08 ± 0.08                     |
| [114]     | India         | Attapadi            | 76.45 | 11.08 | dendrometer band         | monthly    | 101          | 3      | 3/1980–10/1983   | 0.19 ± 0.12                     |
| [79]      | French Guiana | Paracou             | −52.91| 5.28  | dendrometer band         | weekly     | 161          | 3      | 6/2007–1/2009    | 0.14 ± 0.06                     |
| [115]     | Indonesia     | Muara Bungo         | 102.21| −1.49 | meter                   | monthly    | 40           | 3      | 4/2004–4/2006    | 0.84 ± 0.23                     |
| [116]     | Ecuador       | RBSF                | −79.07| −3.97 | electronic point dendrometer | daily    | 1            | 3      | 4/2006–8/2009    | 0.23 ± 0.38                     |
| [117]     | Venezuela     | RFC                 | −70.75| 7.50  | dendrometer band         | monthly     | 6            | 3      | 4/1978–4/1982    | 0.75 ± 0.52                     |
A pantropical analysis of the effects of climate seasonality on tropical tree growth is still missing in the literature. Most of our knowledge comes from single-site-based studies that often suffer from collinearity problems between climate drivers. In this paper, we ran a meta-analysis of monthly tropical tree growth at the pantropical scale in which multiple gradients of climate variables allowed us to disentangle the effect of each climate driver on tropical tree growth. We focused on the seasonal effect of climate on tree growth in tropical forests by using data from papers reporting tree growth measurements with a high periodicity (from daily to monthly censuses) and global climate datasets. We gathered 30 datasets in which growth measurements have been recorded for 3412 individual trees from 25 pantropical forest sites.

This paper has three specific objectives: (i) to find the climate drivers of tree growth across tropical forests; (ii) to quantify tree growth variations in response to climate among tropical forests; and (iii) to give a modeling framework to improve the model predictions of seasonal carbon uptake by tropical tree growth in a global change context.

Materials and Methods

Climate datasets

We used climate datasets from two sources (Table 2): the Climate Research Unit (CRU) at the University of East Anglia [36] and the Consortium for Spatial Information website (CGIAR-CSI, http://www.cgiar-csi.org). From the CRU, we used variables from the CRU-TS3.1 and CRU-TS3.10.01 monthly climate global datasets available at 0.5° resolution from 1901–2009: 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). pet was calculated using the grass reference evapotranspiration equation [37,38], which is a variant of the Penman-Monteith method using the gridded tmp, tmn, tmx, vap and cld. pre was square-root transformed prior to data modeling to address heteroscedasticity. From the CGIAR-CSI, we used the monthly average of extraterrestrial solar radiation as well as the Global Soil-Water Balance [27]. The first dataset defines the solar radiation reaching the top of the Earth’s atmosphere (sol) and is a function of Earth-sun geometry and time of year. sol per day (mm/day equivalent) is calculated using the methodology presented in [39] specifically for the 15th day of each month to describe averages per month. Total sol per month (mm/month equivalent) is calculated by multiplying the value of sol for the 15th day of the month by the number of days in the month, 1 mm.day⁻¹ equivalent of evaporation = 2.45 MJ.m⁻².day⁻¹. The latter dataset provides hydrological raster data (ESRI Grid format) describing actual evapo-transpiration and soil water content for a monthly time-series from period 1901–2009 using CRU-TS3.1 as the primary climate data input.

Tree growth data

A search performed on Web of Science in March 2013 using the keywords 'climate', 'tropical forest', 'growth' and 'trees' returned 541 articles focusing on effect of climate on tropical tree growth. Among these publications, our analysis used only the publications with seasonal tree growth data (from daily to monthly censuses) available in the article graphics, available in an online repository.
or provided by the authors. The tree growth data were extracted from the article graphics using WebPlotDigitizer 2.5 (http://arohatgi.info/WebPlotDigitizer/, Table 3). Three types of data were found: (i) single observations by tree and time step at a given site (see [43]); (ii) mean and standard deviation (SD) by species at a given site for each time step (see [44]); and (iii) only the mean and SD of all trees at a site for each time step [35]. In addition, these data may come from measurements with dendrometer bands, electronic point surveys, tree ring analyses or graduated tapes. The minimum diameter at breast height (DBH) used in the articles is 10 cm. Among sites, Selangor and Muara Bungo are forest plantations. Finally, they have different time step between measurements: monthly, weekly or daily. We converted these primary datasets by making a linear approximation of the growing trajectory in order to obtain a mean and a standard deviation by month and dataset for each available calendar year. Datasets from the same site were assumed to be samples from the same population and were not analyzed separately. This could affect the value of the whole population mean growth, but here we are only interested in the monthly variations of tree growth (site effect is considered as a random effect). The final dataset is comprised of 30 datasets of 25 pantropical forest sites, for a total of 3412 individual trees (Figure 1, Table 3). The data, monthly tree growth mean and SD, are freely available upon request to the corresponding author. No specific permits were required for the described field studies and this study did not involve endangered or protected species.

Preliminary analysis

First, we investigated the association between climate variables on a monthly time scale through a principal component analysis (PCA) on the normalized climate dataset, i.e. climate variables were centred and scaled, to describe how the variance of the climate dataset was structured. Next, to measure spatial autocorrelation in tree growth observations between sites, we computed the Moran’s Index statistics of the mean monthly growth by sites [45]. This index range from -1, strong negative spatial autocorrelation, to +1, strong positive spatial autocorrelation. The significance of Moran’s I is evaluated by using a Z score and p-value generated by random permutation [46]. The null hypothesis states that there is no spatial autocorrelation for the variable within the geographic area. The interannual and intra-annual variability climate variable was described by computing the coefficient of variation (CV) for each variable (i.e. standard deviation × 100 divided by the mean) of the annual mean and monthly values of the climate time series over the period of the CRU data (1901–2009). To detect, estimate and test seasonal patterns in the tree growth time series, we used temporal regression models from the R package season [47]. The model was fitted using a sine and cosine term that together described the sinusoid. These parameters were added to a generalized linear model to explain tree growth data and test the existence of a seasonal pattern. The existence of a seasonal pattern was determined by the zero-test based on Snedecor’s F statistic. This method is known as the cosinor test.

Modeling seasonal tree growth

We modeled the link between tree growth, site and climate variables in a mixed linear model framework at a monthly time step. Here, we assumed that each growth measurement was independent and that our multiple-site design enabled us to deal with the collinearity of climate variable present in each site. We set the climate variables as fixed effects and the site as a random effect. We set the site effect as a random effect in order to avoid any statistical bias in our results. This site effect was not further analyzed as the main objective of the study was to understand seasonal variations of tree growth. In order to rank the climate effects, we considered various growth models:

• \( m_0 \), the reference model:

\[
Inc_{ij} = \beta_0 + \zeta_i + \epsilon_{ij}
\]  

(1)

• \( m_{varclim} \), for each climate variable \( varclim \), an univariate model:

\[
Inc_{ij} = \beta_0 + \zeta_i + \beta_{varclim} \times varclim + \epsilon_{ij}
\]  

(2)

• \( m_{BIC} \), the model with the best combination of climate variables, \( Comb_{BIC} \), according to the Bayesian Information Criterion (BIC):

\[
Inc_{ij} = \beta_0 + \zeta_i + \sum_{varclim Comb_{BIC}} \beta_{varclim} \times varclim + \epsilon_{ij}
\]  

(3)

Where \( Inc_{ij} \) is the average tree diameter growth for the site \( i \) for the month \( j \), \( \zeta_i \) is the random site effect assumed to follow a normal distribution \( N(0, \sigma^2_{\zeta}) \) and \( \epsilon_{ij} \) is the residual error assumed
Table 4. Descriptive statistics of climate variables.

| site              | GES* | pre | tmn | tmp | tmx | dtr | swc | vap | cld | sol |
|-------------------|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| Attapadi          | TAr  | 2158 | 1498.3 | 214 | 25.7 | 30.2 | 8.8 | 0.8 | 24.7 | 50.5 |
| Budongo           | TAr  | 1322 | 1363.8 | 17.5 | 23.4 | 29.3 | 11.9 | 0.8 | 20.5 | 59.9 |
| CPM               | SCf  | 1741 | 935.1 | 12.1 | 16.5 | 21 | 9.4 | 1 | 15.3 | 65.8 |
| El Palmar         | TAw  | 1076 | 1414.3 | 17.7 | 24.6 | 31.6 | 11.4 | 0.9 | 28.2 | 4745 |
| FLONA SFP         | SCf  | 1643 | 888.7 | 11.6 | 26.8 | 32.5 | 11.4 | 0.9 | 18.2 | 47291 |
| Guanacaste        | TAwb | 1749 | 1606.9 | 21.1 | 26.8 | 32.5 | 11.4 | 0.9 | 18.2 | 47291 |
| Ibi catu          | TM   | 1518 | 1097.7 | 16.1 | 21.3 | 28.8 | 14.9 | 0.9 | 15.5 | 5220.8 |
| La Barcinera      | TAw  | 1709 | 1414.3 | 17.7 | 24.6 | 31.6 | 11.4 | 0.9 | 15.5 | 5220.8 |
| La Selva          | TAr  | 3948 | 1358.2 | 17.9 | 23.1 | 28.3 | 10.4 | 1 | 23.5 | 529.2 |
| Laimto            | TAr  | 1321 | 1122.5 | 21.8 | 26.5 | 31.2 | 9.4 | 0.9 | 27.3 | 5282.3 |
| Luki forest       | TAr  | 1069 | 9478.7 | 20.8 | 24.6 | 28.6 | 7.8 | 0.8 | 24.8 | 5310.6 |
| Marajoara         | TAr  | 1873 | 1068.4 | 19.5 | 25.6 | 31.8 | 12.3 | 0.8 | 28.5 | 5310.6 |
| Muara Bungo       | TAr  | 2686 | 1260.5 | 22.9 | 27.2 | 31.6 | 8.7 | 1 | 29.9 | 5310.6 |
| Munessa-Shashamene | TM  | 1192 | 1358.2 | 10.1 | 23.8 | 13.7 | 0.8 | 10.2 | 5268.6 |
| Paracou           | TAr  | 3035 | 12462.2 | 22.5 | 26.3 | 30.1 | 7.6 | 0.9 | 29.5 | 5291.3 |
| Pinkwae           | TAwb | 998 | 1222.6 | 24.1 | 27.5 | 30.9 | 6.8 | 0.7 | 27.7 | 5310.6 |
| RSBSF             | TM   | 973 | 1439.9 | 47. | 31.3 | 12.8 | 7.8 | 0.5 | 15.5 | 5311.6 |
| RCF               | TAwb | 1696 | 1184.6 | 22.3 | 27.3 | 32.4 | 10.1 | 0.9 | 27.6 | 5268.5 |
| Rio Cachoeira     | SCf  | 1526 | 931.3 | 126. | 18.1 | 23.7 | 11.1 | 1.3 | 16.5 | 5304.8 |
| Selangor plantation | TAr | 2840 | 1065.9 | 20.3 | 24.7 | 29.1 | 8.7 | 1 | 27.4 | 5310.6 |
| SERS              | TAr  | 1558 | 1268.1 | 21.6 | 26.7 | 31.9 | 10.2 | 0.7 | 26.9 | 5310.6 |
| Tapajos           | TAr  | 1958 | 1126.8 | 21.8 | 26.5 | 31.2 | 9.4 | 0.9 | 29.7 | 5310.6 |
| Tinte Bepo        | TAr  | 1246 | 1123 | 21.8 | 26.5 | 31.3 | 9.5 | 0.8 | 25.1 | 5310.6 |
| ZF-2              | TAr  | 223 | 1161.1 | 23.2 | 27.4 | 31.6 | 8.4 | 0.9 | 30.3 | 5316.5 |

Descriptive statistics of climate variables: Annual mean; coefficient of variation of annual means (CV, inter) and coefficient of variation of monthly values (CV, intra) of precipitation (pre); potential evapotranspiration (pet); minimal, mean and maximal temperatures (respectively tmn, tmp and tmx); daily temperature amplitude (dtr); soil water content (swc); vapour pressure (vap); cloud cover (clc); and extraterrestrial solar radiation (sol). Coefficients of variations (standard deviation divided by the mean of the variable) of monthly climate time series are computed over the period of the CRU data (1991–2008). ^4 Globale Ecological Zone defined by FAO (55); TAr: Tropical rainforest; TAw: Tropical moist deciduous forest; TAwb: Tropical dry forest; TM: Tropical mountain system; and SCf: Subtropical humid forest.

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to follow a normal distribution $N(0, N_{obs} \times \sigma^2)$ weighted by $1/N_{obs}$, which is the inverse of the number of observation periods by site. The mixed model parameters were estimated with the algorithms of the R package lme4 [48]. To estimate the parameter confidence intervals with a probability of 95%, we generated 10000 parameter samples from the posterior distribution of the fitted model parameters using the Markov Chain Monte Carlo methods [48]. Then, the confidence intervals for the parameters (Highest Posterior Density [HPD] intervals) were constructed from the empirical posterior distribution of the 10000 samples as the intervals containing the parameters with the nominal probability [48].

Evaluation of the model performance was made by computing goodness-of-fit-measures with the R package lmmfit [49–52]. To find the best variable linear combination that contains the maximum of information to link growth and climate variables (the model $m_{BIC}$), we ran an exhaustive screening of the candidate models using a stepwise procedure based on the Bayesian information criterion, BIC [53]. We used BIC, instead of the classically used AIC, to avoid over-parameterization and multicollinearity problems, as this criterion is consistent and parsimonious for model selection with respect to large datasets [54]. We made a residual analysis to verify if the error of the model $m_{BIC}$ had a bias for any of the selected variables in this model. That is, we computed the Pearson’s product-moment correlation coefficient $(r)$ between the residual of the model $m_{BIC}$ and the variables of this model and tested if this coefficient was statistically different from zero.

The predictive quality of the fitted models was assessed by computing the root mean square errors of predictions, RMSEP.

$$\text{RMSEP} = \sqrt{\frac{\sum_{i=1}^{N_{site}} \sum_{j=1}^{N_{month}} (\text{Inc}_{ij} - \hat{\text{Inc}}_{ij})^2}{N_{site} \times N_{month}}}$$ (4)

where $\text{Inc}_{ij}$ is the observed values of tree growth for the site $i$ and for the month $j$, and $\hat{\text{Inc}}_{ij}$ are the model predictions of growth.

All analyses were performed using the R-project software (http://www.r-project.org/).

**Results**

**Climate gradients**

The 25 sites represent a large sample of tropical forests under different tropical climates corresponding to five global ecological tropical zones [55](Table 4). The gradient of the annual mean of precipitation ranges from 973.9 mm (RBSF, Ecuador) per year to 3948.1 mm (La Selva, Costa Rica). The coefficient of variation (CV) of interannual precipitation ranges from 12.5% (SERS, Thailand) to 35.2% (RBSF, Ecuador). Intra-annual CV of monthly precipitation distribution precipitation ranges from 13% (CPM, Brazil) to 116.9% (El Palmar and La Barcinera, Mexico). The sites undergo a large variability in the distribution of precipitations throughout the year, from zero months (La Selva)
Table 5. Seasonality of mean monthly tree growth with cosinor analysis for the studied sites.

| Site                        | Amplitude | Phase   | Low phase | p value |
|-----------------------------|-----------|---------|-----------|---------|
| Attapadi                    | 0.129     | Month = 7.6 | Month = 1.6 | <0.05   |
| Budongo                     | 0.031     | Month = 7.3 | Month = 1.3 | <0.05   |
| CPM                         | 0.104     | Month = 12.2 | Month = 6.2 | <0.05   |
| El Palmar                   | 0.437     | Month = 7.7 | Month = 1.7 | <0.05   |
| FLONA SFP                   | 0.213     | Month = 1.1 | Month = 7.1 | <0.05   |
| Guanacaste                  | 0.396     | Month = 7.3 | Month = 1.3 | <0.05   |
| Ibicatu                     | 0.470     | Month = 1.5 | Month = 7.5 | <0.05   |
| Kakamega                    | 0.019     | Month = 7.5 | Month = 1.5 | <0.05   |
| La Barcinera                | 0.361     | Month = 6.8 | Month = 12.8 | <0.05   |
| La Selva                    | 0.092     | Month = 9  | Month = 3  | <0.05   |
| Lamto                       | 0.067     | Month = 6.9 | Month = 12.9 | <0.05   |
| Luki forest                 | 0.535     | Month = 1.4 | Month = 7.4 | <0.05   |
| Marajoara                   | 0.684     | Month = 12.6 | Month = 6.6 | <0.05   |
| Muara Bungo                 | 0.211     | Month = 8.6 | Month = 2.6 | <0.05   |
| Munessa-Shashamene Forest   | 0.380     | Month = 6.4 | Month = 12.4 | <0.05   |
| Paracou                     | 0.091     | Month = 2.6 | Month = 8.6 | <0.05   |
| Pinkwae                     | 1.033     | Month = 7  | Month = 13 | <0.05   |
| RBSF                        | 0.361     | Month = 2.2 | Month = 8.2 | <0.05   |
| RFC                         | 0.645     | Month = 7.6 | Month = 1.6 | <0.05   |
| Rio Cachoeira               | 1.235     | Month = 1.3 | Month = 7.3 | <0.05   |
| Selangor plantation         | 0.380     | Month = 6.7 | Month = 12.7 | <0.05   |
| SERS                        | 0.033     | Month = 7.4 | Month = 1.4 | <0.05   |
| Tapajos                     | 0.089     | Month = 1.9 | Month = 7.9 | <0.05   |
| Tinte Bepo                  | 0.223     | Month = 6.9 | Month = 12.9 | <0.05   |
| ZF-2                        | 0.066     | Month = 1.1 | Month = 7.1 | <0.05   |

Month = 1 corresponds to January. The amplitude is the difference between the higher and lower points in mm/month of the sinusoid fitted in the cosinor analysis. The phase and the low phase are, respectively, the month with the highest/lowest tree growth value according to the sinusoid fitted in the cosinor analysis. A p value <0.05 indicates that the statistically significant existence of a seasonal pattern cannot be rejected.

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Three major climate gradients are represented in the Principal component analysis (PCA)(Figure 2). The first axis (x-axis in Figure 2a) represents a gradient of increasing temperature, that is highly correlated with vapour pressure. Sites close to the equator that are located at high altitudes are on the left of this axis, with sites far from the equator experiencing a cold season (Figure 2c). The second axis (y-axis in Figure 2a) has a strong contribution from variables that reflect water availability. The third axis (y-axis in Figure 2b) appears to be related to solar radiation. Ordination of the continental location of the studied sites on the PCA axis (Figure 2d) revealed that sites in Asia were slightly warmer and had higher vapour pressures than those in America and Africa. Ordination of the studied countries on the PCA axis (Figure 2c) reveals that some countries are separated from others because of climate: from cold (Ecuador) to warm (Indonesia) and from dry tropical (Mexico) to wet tropical (Malaysia)(Figure 2e). In the following analysis, we kept all the climate variables as we have a strong physiological assumption of their effect on tree growth (Table 1).

Tree growth descriptive analysis

We cannot reject the null hypothesis that there is no spatial autocorrelation present in mean tree growth observations between sites at alpha = 0.05 (Moran’s I observed = 0.0102, expected = −0.042, SD 0.123, p.value = 0.672). Tree diameter growth shows a significant intra-annual seasonality at all the studied sites, even sites with mean annual precipitation rates close to 4000 mm (La Selva, Costa Rica)(Table 5 and Figure 3).

Climate effects on tree growth

More than 28.69% of the observed seasonal variation in tree growth may be imputable to the site effect (reference model m0, Table 6), while climate variables alone explain a maximum of 19.92% (squared root monthly precipitation). The variables sol, cld, vap, dtr, tmn and swc explained between 9.65 and 16.30% of the climate effect, while imp, pet and tmx explained less than 2.13%. The selection procedure, which used the BIC criterion, kept four climatic variables ($\sqrt{\text{PRE}}, \text{sol}, \text{dtr}, \text{swc}$) in the final multivariate model.
These four climate variables together explained 29.79% of the total observed monthly tree growth variation. The parameter values for the fixed effect in the univariate analysis indicate the direction of the relation between the climate variables and tree growth (Table 6). Among the four selected variables, pre (0.03), swc (0.58) and sol (0.09) have a positive link with tree growth and dtr (20.08) has a negative link (Table 6).

The obtained root mean squared error of prediction (RMSEP) was slightly below the mean value of observed monthly growth (mean growth = 0.325 mm.month$^{-1}$, RMSEP = 0.279 mm.month$^{-1}$). In general, the model underestimated growth when it was above 1 mm.month$^{-1}$ (Figure 4). There was no significant correlation between the selected variable and the residuals of the model $m_{\text{BIC}}$ ($r_{\text{pre}} = -0.46 \times 10^{-6}$, p-value > 0.99; $r_{\text{swc}} = 1.8 \times 10^{-7}$, p-value > 0.99; $r_{\text{sol}} = 1.9 \times 10^{-7}$, p-value > 0.99; $r_{\text{dtr}} = 6.1 \times 10^{-1}$, p-value > 0.99). Tree growth values increase linearly with extrasolar radiations (Figure 5), and a strong increase in tree growth occurred between 0 and 200 mm.month$^{-1}$ of precipitation; above these values, the increase in tree growth was less pronounced and had a linear shape.

Figure 3. Evolution of mean monthly tree growth values and standard deviation for the studied forest sites. The red line represents a cubic smoothing spline. doi:10.1371/journal.pone.0092337.g003
Table 6. Model parameters, standard errors, t values and posterior densities of the univariate (m_arclim) and complete (m_BIC) analyses.

| Model  | Parameter Effect | Estimates Std. Error | t value Variance Std. Dev. MCMC mean HPD95 lower HPD95 upper pMCMC Pr(|t|) | RMSEP BIC R2 fixed R2 |
|--------|-----------------|----------------------|-----------------|------------------------|------------------------|------------------------|------------------------|------------------------|
| m_BIC  | site.names random | 0.0355 0.1885 0.1577 0.1599 0.1184 0.2038 0.2787 412.4698 29.79 50.25 |
|        | Residual random | 0.0800 0.2829 0.2845 0.2846 0.2713 0.2975 |
|        | (Intercept) fixed | -0.7247 0.1635 -4.4336 -0.7492 -1.0585 -0.4339 0.0001 0.0000 |
|        | (pre -0.5) fixed | 0.0118 0.0027 4.4017 0.0120 0.0067 0.0171 0.0001 0.0000 |
|        | sol_m fixed | 0.0024 0.0002 10.3592 0.0024 0.0019 0.0028 0.0001 0.0000 |
|        | dtr fixed | -0.0300 0.0078 -3.8291 -0.0283 -0.0430 -0.0139 0.0002 0.0001 |
|        | swc fixed | 0.2462 0.0674 3.5999 0.2492 0.1196 0.3817 0.0002 0.0003 |
| m pre | site.names random | 0.0346 0.1861 0.1588 0.1608 0.1192 0.2057 0.2983 515.5249 19.82 42.99 |
|        | Residual random | 0.0914 0.3023 0.3038 0.3040 0.2901 0.3184 |
|        | (Intercept) fixed | -0.0158 0.0394 -0.4006 -0.0157 -0.0860 0.0562 0.6666 0.6888 |
|        | (pre -0.5) fixed | 0.0303 0.0202 15.1909 0.0303 0.0264 0.0343 0.0001 0.0000 |
| m sol | site.names random | 0.0414 0.2034 0.1695 0.1715 0.1296 0.2177 0.3043 556.2737 16.30 40.67 |
|        | Residual random | 0.0951 0.3084 0.3103 0.3104 0.2956 0.3245 |
|        | (Intercept) fixed | -1.0027 0.1042 -9.6261 -0.9997 -1.1959 -0.7884 0.0001 0.0000 |
|        | sol_m fixed | 0.0030 0.0002 13.4849 0.0030 0.0026 0.0035 0.0001 0.0000 |
| m cld | site.names random | 0.0333 0.1825 0.1576 0.1594 0.1183 0.2040 0.3065 563.8953 15.56 39.81 |
|        | Residual random | 0.0965 0.3106 0.3120 0.3122 0.2975 0.3264 |
|        | (Intercept) fixed | -0.4837 0.0691 -6.9952 -0.4766 -0.6100 -0.3444 0.0001 0.0000 |
|        | cld fixed | 0.0115 0.0009 13.1090 0.0114 0.0097 0.0132 0.0001 0.0000 |
| M pre | site.names random | 0.0345 0.1856 0.1601 0.1621 0.1193 0.2073 0.3078 571.9796 14.82 39.34 |
|        | Residual random | 0.0972 0.3118 0.3133 0.3135 0.2992 0.3284 |
|        | (Intercept) fixed | 0.1542 0.0352 4.3855 0.1542 0.0933 0.2184 0.0001 0.0000 |
| m vap | site.names random | 0.0111 0.0001 12.7430 0.0111 0.0009 0.0132 0.0001 0.0000 |
|        | Residual random | 0.0962 0.3102 0.3134 0.3136 0.2998 0.3290 |
|        | (Intercept) fixed | 1.2160 0.0842 14.4368 1.1559 0.9919 1.3130 0.0001 0.0000 |
|        | vap fixed | 0.0931 0.0048 12.3119 0.0472 0.0368 0.0579 0.0001 0.0000 |
| m swc | site.names random | 0.0319 0.1785 0.1564 0.1582 0.1146 0.2039 0.3174 625.9566 9.77 35.49 |
|        | Residual random | 0.1034 0.3215 0.3229 0.3230 0.3082 0.3382 |
|        | (Intercept) fixed | -0.1696 0.0580 -2.9216 -0.1715 -0.2826 -0.0609 0.038 0.0036 |
| Model | Parameter | Effect | Estimates | Std. Error | t value | Variance | Std. Dev. | MCMC median | MCMC mean | HPD95 lower | HPD95 upper | pMCMC | Pr(>|t|) | RMSEP | BIC | R2 fixed | R2 |
|-------|-----------|--------|-----------|------------|----------|----------|-----------|-------------|-----------|-------------|-------------|-------|--------|--------|-----|---------|-----|
| swc   | fixed     | 0.5807 | 0.0578    | 10.0435    | 0.5837   | 0.4723   | 0.7025    | 0.0001      | 0.0000    |             |             |       |        |       |     |         |     |
| m    | site.names | random | 0.0944    | 0.3072    | 10.0435  | 0.5837   | 0.4723   | 0.7025    | 0.0001      | 0.0000    |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0944 | 0.3072    | 10.0435    | 0.5837   | 0.4723   | 0.7025    | 0.0001      | 0.0000    |             |             |       |        |       |     |         |     |
| m    | Intercept | fixed  | 0.0685    | 0.1291    | -6.7262  | 0.3231   | 0.3085   | 0.3387    |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0685 | 0.1291    | -6.7262    | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0685 | 0.1291    | -6.7262    | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Intercept | fixed  | 0.0396    | 0.1989    | 10.0435  | 0.3231   | 0.3085   | 0.3387    |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0396 | 0.1989    | 10.0435    | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0396 | 0.1989    | 10.0435    | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Intercept | fixed  | 0.0329    | 0.1814    | 10.0435  | 0.3231   | 0.3085   | 0.3387    |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0329 | 0.1814    | 10.0435    | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0329 | 0.1814    | 10.0435    | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Intercept | fixed  | 0.0523    | 0.0724    | 7.6338   | 0.3231   | 0.3085   | 0.3387    |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0523 | 0.0724    | 7.6338     | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0523 | 0.0724    | 7.6338     | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Intercept | fixed  | 0.0400    | 0.2000    | 17.17    | 0.3231   | 0.3085   | 0.3387    |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0400 | 0.2000    | 17.17      | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0400 | 0.2000    | 17.17      | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Intercept | fixed  | 0.4356    | 0.1755    | 2.4825   | 0.3231   | 0.3085   | 0.3387    |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.4356 | 0.1755    | 2.4825     | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.4356 | 0.1755    | 2.4825     | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Intercept | fixed  | 0.0385    | 0.1962    | 16.96    | 0.3231   | 0.3085   | 0.3387    |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0385 | 0.1962    | 16.96      | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Random    | 0.0385 | 0.1962    | 16.96      | 0.3231   | 0.3085   | 0.3387    |             |             |             |             |       |        |       |     |         |     |
| m    | Intercept | fixed  | 0.3184    | 0.0347    | 9.1815   | 0.3231   | 0.3085   | 0.3387    |             |             |             |       |        |       |     |         |     |

Table 6. Model parameters, standard errors and t-values. The parameter values of posterior parameters densities (MCMC median and MCMC mean) and their 95% confidence intervals (Highest posterior density at 95% [HPD95] lower and upper) and associated p-value are estimated from a distribution of 10000 parameter samples computed with Monte Carlo Markov Chains from the model parameters. Goodness-of-fit criterion of the growth models are root mean square error of prediction (RMSEP), Bayesian Information Criterion (BIC), $R^2$ of the fixed part of the model ($R^2_{fixed}$) and $R^2$ of the complete model (fixed plus random part). doi:10.1371/journal.pone.0092337.t006
Discussion

Our meta-analysis provides the first overview of climate effects on tree growth variations at a seasonal time scale for tropical forest areas. Tree growth reveals a strong intra-annual seasonality at all sites (Table 5), including seasonally dry sites and wet tropical forests. We found a common climatic signal explaining 29.79% of the observed seasonality in forest growth (Table 6). Precipitation (19.82%) and extraterrestrial solar radiation (16.30%) were the major climate drivers. The tree growth average per site (i.e. the random site effect) explained 28.69% of overall growth variation, and a substantial fraction of variation (50%) in growth remained unexplained with our modeling framework. We have to acknowledge that our sample of 3412 trees could not be used to fully reproduce the complete behavior of all the tropical forests, however our analysis demonstrated that a common signal in the climate determinism of tree growth seasonality is observed at the pan-tropical scale.

Climate effect on tree growth

In this study, precipitation was found to be the major seasonal driver of tree growth. Precipitation strongly impacts tree growth, as directly observed in seasonal and unseasonal tropical climates [19,35,56-59] and as deduced from experimental forest droughts [60,61]. The prominence of precipitation as a predictor of forest growth is slightly different from previous studies [62]; in French Guiana, we found that soil water availability was the main determinant of diameter growth, i.e. better than rainfall. Of course, both variables are strongly correlated (Figure 2), but this difference could be explained by some sites where relative soil water availability \(swc\) was at its maximum throughout the year despite marked precipitation seasonality (e.g. La Selva, CPM, Muara Bungo, Rio Cachoeira and Schangor). At the same time, the importance of solar radiation, \(sol\), in the complete model \((m_{bic})\) reflects the obvious role of light in shaping tree growth (Figure 5).

Solar radiation is directly linked to PPFD (Photosynthetic Photon Flux Density), which in turn drives carbon uptake and plant growth [29]. Some authors support the hypothesis that increasing surface solar radiation contributes to the increasing forest growth rate over the Amazon [63,64]. It must be noted that the extraterrestrial solar radiation we used has a value above the real solar radiation value reaching the forest surface. Indeed, \(sol\) was computed as a monthly mean over 50 years and does not account for local cloud cover or aerosol radiation absorption.

Investigating the effects of temperature on the physiology of tropical forest trees [31,65] is of primary importance today given the temperature increases expected over the next century [5,7]. Some authors suggest that tropical trees are more sensitive to temperatures than other trees because (i) they live at or close to the highest annual average temperatures on Earth, and (ii) tropical species naturally encounter limited variation in temperatures (< 4°C over 20° of latitude) [32]. Our results suggest that temperature variations are of secondary importance in shaping tropical tree seasonal growth; nevertheless, they do play a role. Minimal temperature was slightly positively correlated with tree growth, whereas maximal temperature had no effect. This positive relation between tree growth and temperature is not consistent with previous observations in Costa Rica [35,66], where an increase in night-time temperatures had a negative effect on tree growth, and in East Africa [19], where maximum temperatures had a negative effect on tree growth. Such patterns were not found at our global working scale.

Tree growth variability in time and space

Our results suggest that most tropical trees experience seasonal cycling growth even in extremely wet environments, as already reported at la Selva [35]. On a pantropical scale, we showed that secondary growth was higher during the wet season; tree growth increased with precipitation and relative soil water content (Table 6). This result is not consistent with other studies that...
have shown that tropical forests are able to maintain or even to increase their productivity during the dry season [67–70]. This suggests different uses of carbohydrates. Some studies have reported that evergreen species in seasonally dry environments accumulate carbohydrates during the dry season because photosynthesis continues while wood production ceases [71] and that deciduous species accumulate carbohydrates at the onset of the dry season to support respiration costs when they are leafless [72,73]. Some studies relied on the Enhanced Vegetation Index (EVI, an index of canopy photosynthetic capacity [30]) to highlight changes in forest phenology driven by the solar cycle [74,75]. In the same way, a variation in the EVI has been observed for the entire Amazon region [30], and the link between phenology and the solar cycle has also been reported for Terra Firme forests [76]. The variability in tree growth at a seasonal scale is likely driven by climate seasonality and dependent on the seasonal allocation of carbohydrates to processes other than tree diameter growth, such as leaf and root production or respiration.

Stem shrinkage during dry periods may be an important limitation of this work [77–79], e.g. the negative value of mean annual tree growth at Pinkwae. Other negative monthly growth values exist at almost all the study sites. 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 [80]. These authors concluded that water scarcity during the long dry season induced cambial dormancy. Furthermore, after the onset of the rainy season, (i) bark swelling started quite synchronously among trees; (ii) bark swelling was maximum after few rainy days; and (iii) evergreen trees were able to quickly initiate wood formation. Recently at the Paracou forest site, some authors have showed that biomass increments were highly correlated between the first and the last quantile of trunk bark thickness and between the first and the last quantile of trunk bark density, suggesting that secondary growth is driven by cambial activity [75].

In this study, we focused on seasonal variation of tree growth, but the inter-site variance must be studied to build a full predictive model. At our pantropical working scale, there was no evident spatial auto-correlation. The site effect, i.e. the average growth of trees at a given site, is likely shaped by several additional environmental variables, such as soil fertility, forest floristic composition and competition for light and nutrients [81–83]. These effects were included in the model through the random site effect $\gamma_i$, and we assumed that these effects were constant over the study period. We also did not consider the different ontogenetic stages of trees and the ontogenetic growth trajectory that depends on complex environmental changes that may have occurred during the census period [84]. Recently, a study using LiDAR and a four-year diameter growth census demonstrated that variation in canopy metrics appeared to be essential to predict biomass growth [85]. Clearly, remotely-sensing methods, whether radar, LiDAR or optical [86], can help us to derive stand variables, especially canopy height, and therefore can be used as valuable additional predictors to monitor forest growth over large tropical areas.

Tropical tree growth under climate change

Globally, current IPCC scenarios predict an intensification of the dry season in tropical areas during the 21st century [7]. Amongst climate variables, our results highlighted the predominant role of precipitation in shaping seasonal forest growth. If a global rainfall reduction is confirmed in the future, it can be expected that tree growth will be affected (Figure 5). Climate change is not the only possible cause for reductions in precipitation; deforestation could lead to reductions in precipitation as the air passages over forests increase tropical rainfall intensity [4]. Solar radiation appeared almost as important as rainfall. Cloud reduction due to drier dry seasons, may subsequently improve tree growth. Our results suggest that, with the global changes observed, forest productivity due to tropical tree growth will encounter modifications due to change in climate seasonality.

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Author Contributions

Conceived and designed the experiments: FW VR BH. Analyzed the data: FW. Contributed reagents/materials/analysis tools: FW VR BH MA DB HD RG CS AT. Wrote the paper: FW VR BH MA DB HD RG CS AT.

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