Introduction

Tropical forests are being threatened at an unprecedented scale by global change. The Amazonian region has already experienced severe droughts recently, such as in 1998 and 2005. Temperatures across Amazonia are currently increasing [1] and are expected to continue to increase with a concomitant decrease in precipitation over the next decades [2,3]. For instance, the HadCM3 model under updated emissions scenarios predicts severe drying events over Amazonia for the XXIe century [4,5]. Climate changes in the tropics have become an increasing concern for their potential impacts on the global carbon cycle. Indeed, tropical forests represent a major reservoir of terrestrial carbon, accounting for half of the estimated 558 Pg of carbon stored in vegetation [6] with 86 Pg for the Amazon basin alone [7]. Improving our knowledge on the climate drivers of forest dynamic will enhance our ability to assess the impact of climate change on carbon cycle [8]. Most current studies performed in tropical rain forests have highlighted three major climate drivers of forest dynamics: soil water content, solar irradiance and air temperature.

Rain or lack of rain is often implicitly viewed as the main driver of forest dynamics [9], as annual NPP generally positively correlates with annual amount of precipitation [10] and that rainfall seasonality plays a key role in the forest response to climate variability [11], table 1. When rainfall is less than evapotranspiration, soil moisture is gradually depleted, increasing tensions in the xylem sap that can eventually trigger stomatal closure and other physiological responses [12]. A lack of water availability or rain could limit tree growth. The relation between the amount of rainfall and water availability for trees is not straightforward and is determined by various soil and plant characteristics (permanent wilting point, field capacity, root distribution). Consequently, water stresses are increasingly estimated using Soil Water Balance Models [13], among which are now available some models explicitly designed for tropical forests [14].

Irradiance is obviously directly linked to the plant photosynthetic ability through the Photosynthetic Photon Flux Density (PPFD), in turn driving carbon uptake and plant growth, [15], table 1. All over Amazonia, the occurrence of dry periods, through cloud cover reduction, was found to enhance canopy photosynthetic capacity by 25% [16]. But as high levels of irradiance occurred in dry season, we may not rule out the possibility that irradiance have a negative effect on tree growth [17].

The effects of rising temperature on the physiology of tropical forest trees are actively debated through the scientific community. Some works suggest that although reductions in photosynthetic rate at temperature above 30°C may occur, these are driven by reductions in stomatal conductance in response to higher leaf-to-
Table 1. Expected tree growth response to climate variables.

| variable    | predicted effect | references | process | references |
|-------------|------------------|------------|---------|------------|
| REW         | +                | [31]       | 26.6cm photosynthesis, xylem tension, stomatal closure, leaf flush |
| rainfall    | +                | [9,10,12,19,66-68] | 26.6cm photosynthesis, xylem tension, stomatal closure, leaf flush |
| T mean      | –                | [18,52,70-72]   | photosynthesis kinetic, stomatal closure |
| T min       | –                | [19,54,73]      | photosynthesis kinetic, stomatal closure |
| T max       | –                | [18,71]        | photosynthesis kinetic, stomatal closure |
| VPD         | no               | [74,75]       | stomatal closure, transpiration |
| irradiance  | +                | [22,23]       | photosynthesis, phenology |
| –           | –                | [17]          |          |
| –           | no               | [23,73,78]     |          |
| U*          | +                | [24]          | 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.

Materials and Methods

Study Site

The study site is located in Paracou, French Guiana (5°18’N, 52°23’W), a lowland tropical rain forest near Sinnamary [27]. This site is part of a private domain owned by the CNES (Centre National d’Études Spatiales), and is granted to the CIRAD (Centre de Coopération Internationale en Recherche Agronomique pour le Développement) through an agreement which dedicated the area for forest research activities. The site receives about 2/3 of the annual 3160 mm±161 of precipitation between mid-March and mid-June, and is subject to a 2–3 months dry season around October [14] during which rainfall is less than 50 mm.month\(^{-1}\) [28]. The most common soils in Paracou are the shallow ferralitic soils limited in depth by a more or less transformed loamy saprolith [27]. The site is located approximately 40 m above sea level [27] and is made up of a succession of small hills. The forest is typical of Guianan rainforests [29,30]. More than 550 woody species attaining 2 cm DBH (Diameter at Breast Height, i.e. 130 cm) have been described at the site, with an estimated 160–180 species of trees >10 cm DBH per hectare. The annual DBH increment averages 0.12±0.01 cm.yr\(^{-1}\) and the gain of biomass due to tree growth averages 4.31±0.164 Mg.ha\(^{-1}\).yr\(^{-1}\) [30,31].
The dominant families at the site include Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae and Burseraceae. No specific permits were required for the following described field studies and this study did not involve endangered or protected species.

Growth Data
Seasonal changes in trunk circumference were monitored in 205 trees from 54 species using homemade steel dendrometer bands [32]. These trees were located in the footprint area of the Guyaflux tower. Tree growth was censused every 40 days from January 2007 to December 2010 (mean = 39 days, sd = 19.8). We defined a categorical variable, period, corresponding to each time step between two successive DBH measures. We use diameter growth in the following analysis rather than biomass increment because the distribution of our sampled trees is not representative of the structure of the forest.

Meteorological Data
In 2003, a 55 m high self-supporting metallic tower, Guyaflux, was built in the Paracou forest in a natural 100 m² gap [28] in order to measure greenhouse gas exchange between the ecosystem and the atmosphere using the eddy covariance methodology. The top of the tower is about 20 m higher than the overall canopy, and meteorological and eddy flux sensors are mounted 2 m above the tower [28]. A large panel of climate variables was recorded at a half-hourly time-step (details in Table 2). Most climate variables exhibited strong seasonal changes, highlighting the north/south movements of the Inter-Tropical Convergence Zone (Fig. 1).

Finally, we used a soil water balance model, developed and validated for tropical forests [14], in order to estimate water availability for trees. The model computes daily water fluxes (tree transpiration, understory evapotranspiration, rainfall interception and drainage), soil water content at different layers and relative extractable water for trees for the entire soil (REW). 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 trees. Stricto sensu REW is an environmental variable but, as soil properties and root distribution do not affect the value of REW in the Paracou forest [31], REW was computed at the forest level and considered as a climate variable in this study.

In a preliminary study, we investigated the association between climate variables through a principle component analysis (PCA) on the normalized climate dataset to describe how the variance of the dataset was structured by the climatic variables and to select representative variables based on correlations between them in order to lower multicollinearity problems in the subsequent analyses.

Including Climate Variables in Growth Models
We modelled the link between tree growth and climate with a linear regression framework. We first included a factorial variable tree in the growth model to take into account the individual behaviours of tree growth. This individual tree effect was not further analysed here as the main objective of this study was to analyse the global population pattern rather than the individual tree one; we just took it into account in order to avoid any statistical bias in our results. Next we included the factorial variable period, which estimates a model parameter for each period. This reference model, called $m_0$, was explicitly built to estimate the maximum part of variance that can be imputable to climatic variation, the period effect. An arising problem was that periods include different numbers of days, i.e. they did not exactly have the same length. We thus built a seasonal growth model:

$$DBH_{i,d+1} - DBH_{i,d} = tree_i + day_d + \varepsilon_{i,d} \quad \text{with } \varepsilon_{i,d} \sim N(0, \sigma^2) \quad (1)$$

where $DBH_{i,d}$ is the diameter of tree $i$ on the day $d$, $tree_i$ is the individual effect of tree on daily growth for the tree $i$, $day_d$ is the effect of the day $d$ on growth of all the trees and $\varepsilon_{i,d}$ is the error of the model assumed normal. The growth for the tree $i$ over the period $j$ starting the day $d$ and during $nd_j$ days was provided by summing $nd_j$ times equations (1):

$$DBH_{i,d+nd_j} - DBH_{i,d} = nd_j \times tree_i + \frac{day_d + \ldots + day_{d+nd_j-1}}{nd_j} + \frac{\varepsilon_{i,d} + \ldots + \varepsilon_{i,d+nd_j-1}}{nd_j}$$

The equation (2) simplified:

$$Gr_{i,j} = nd_j \times tree_i + \text{period}_j + \varepsilon_{i,j} \quad \text{with } \varepsilon_{i,j} \sim N(0, nd_j \sigma^2) \quad (3)$$

where $Gr_{i,j}$ is the growth of tree $i$ over the period $j$, $\text{period}_j$ is the effect period for period $j$, $nd_j$ is the number of days of period $j$ and $\varepsilon_{i,j}$

| Variable | Daily computation | Description | Mean   | SD     | Unit             |
|----------|------------------|-------------|--------|--------|------------------|
| iradiance| mean             | global irradiance | 590.34 | 170.17 | MJ.m⁻².d⁻¹       |
| T min    | minimum          | temperature minimum | 23.43  | 0.82   | celsius degree   |
| T max    | maximum          | temperature maximum | 28.37  | 1.35   | celsius degree   |
| REW      | -                | relative extractable water | 0.77   | 0.28   | -                |
| VPD      | mean             | vapor pressure deficit | 6.05   | 1.68   | kPa              |
| rainfall | sum              | precipitation | 9.03   | 17.21  | mm               |
| $U^*$    | mean             | friction velocity | 0.37   | 0.11   | m.s⁻¹            |

Table 2. Descriptive statistics of the climate variables from 2007 to 2010.

The raw data, excepted REW, are registered at a half-hourly time-step.

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is the error of the model assumed normal. The model (3) was not suited to classical linear regression because the variance \( \sigma^2 \) of the error terms changed over the periods \( j \). We normalized the equation (3) to reach residual error variance equality, which led to the reference model \( m_0 \):

\[
\frac{G_{ij}}{\sqrt{n_d}} = \sqrt{n_d} \times \text{tree}_i + \frac{\text{period}_j}{\sqrt{n_d}} + e_{ij} \quad \text{with} \quad e_{ij} \sim \mathcal{N}(0, \sigma^2)
\]

(4)

where \( e_{ij} = \bar{e}_{ij} / \sqrt{n_d} \) and \( \text{Var}(e_{ij}) = \text{Var}(\bar{e}_{ij}) / n_d = \sigma^2 \).

Figure 1. Variation of the climate variables during a 4-year study period in French Guiana. Note that the climate is affected by the north/south movements of the Inter-Tropical Convergence Zone and the site receives nearly two-thirds of its annual 3041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month during the 3-months dry season.

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Ranking Climate Variables According to their Effect on Tree Growth

We first assessed the ability of the registered climate variables (details in Table 2) to explain the between-periods variance by substituting them to the period effect in the reference model \( m_0 \). In a first step, we performed univariate analyses for each climate variable by fitting the models \( m_{varclim} \) for \( varclim = \text{REW}, U^*, T_{\text{min}}, T_{\text{max}}, \text{irradiance}, \text{VPD}, \text{Patm}, \text{HR} \) or rainfall, defined by:

\[
\frac{G_{ij}}{\sqrt{n_d}} = \sqrt{n_d} \times \text{tree}_i + \beta_{\text{varclim}} \times \frac{\text{varclim}}{\sqrt{n_d}} + e_{ij}
\]

(5)
In a second step, we adopted a multivariate approach and included all the climate variables into a single model, for which we looked for the best model according to the Bayesian Information Criterion (BIC), mBIC (eq.6).

$$\frac{Gr_{ij}}{\text{nd}_j} = \sqrt{\text{nd}_j} \times \text{tree}_i + \beta_{\text{REW}} \frac{REW_j}{\text{nd}_j} + \beta_{U^*} \frac{U^*_j}{\text{nd}_j} + \beta_{\text{irradiance}} \frac{\text{irradiance}_{ij}}{\text{nd}_j} + e_{ij}$$

(6)

The model mBIC was obtained after an exhaustive screening of the candidate models using the package gMvulti [33]. We used this package in order (i) to find the best variable linear combination that contains the maximum of information to link growth and climate variables according to the BIC criterion, and (ii) to lower the multicollinearity problem by dropping some climate variables that are highly correlated with each other (Fig. 2). We used BIC, instead of the classically used AIC, to avoid over-parameterization as this criterion is consistent and parsimonious for model selection with respect to large datasets [34].

Finally, we compared the fitted models mBIC, mvarclim and mBIC through their percentage of variance explained and their predictive quality. The later was assessed by computing the root mean square errors of predictions, RMSEP:

$$\text{RMSEP} = \sqrt{\frac{1}{\text{N}_\text{tree} \times \text{N}_\text{period}} \sum_{i=1}^{\text{N}_\text{tree}} \sum_{j=1}^{\text{N}_\text{period}} (G_{ij} - \hat{G}_{ij})^2}$$

(7)

where $G_{ij}$ is the observed values of growth and $\hat{G}_{ij}$ is the model predictions of growth.

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

**Results**

**Selection of Climate Variables**

All climate variables were correlated with at least one other climate variable (Fig. 2). Minimum temperature and $U^*$ were intimately linked to each other but moderately with the other climate variables. Maximal temperature was positively correlated with irradiance and negatively with rainfall, relative extractable water and air relative humidity. The correlation circle of the PCA (Fig. 2) highlighted these patterns of correlation, which are mainly due to the strong seasonality of the climate in French Guiana [14,28,32]. In order to limit critical correlations between climate variables, we kept in the following analysis the variable for which we have a strong physiological assumption of their effect on tree growth, $U^*$, REW, irradiance, $T_{\text{max}}$ and $\text{VPD}$. We also kept rainfall to compare its predictive power with REW and minimum temperature due to the previous results of its effect on tree growth [19].

**Model Selection**

More than 26% of the observed variation in tree growth may be imputable to the individual tree behavior (models mBIC, Table 3) while the period effect explained 9% of the variance of tree growth. This means that climate variables alone can explain up to 9% of the variance of tree growth. From the univariate analyses (models mvarclim), REW explained the largest part of the period effect on tree growth (60%, see Fig. 3). $U^*$, Rainfall or minimum temperature alone explained between 38 and 54% of this period effect. Maximum temperature, $\text{VPD}$ and irradiance explained less than 26% of the period effect. REW was thus, by far, the main predictor of individual tree growth. During the dry season when REW decreased below 0.4, the averaged population diameter growths were the smallest within the year and sometimes stopped, Fig. 4. At the beginning of the rainy season, REW and tree growth quickly increased simultaneously. However, at the end of the dry season, tree growth and REW did not exhibit the same pattern, i.e. the averaged individual tree growth began to decline before the REW itself diminished.

The selection procedure using the BIC criterion kept 3 climate variables in the final multivariate model mBIC: REW, minimum temperature and irradiance, Table 4. The proportion of variance imputable to each climate variable as well as the values of the model parameters were hard to interpret in the mBIC model because climate variables were highly correlated. However, from the univariate analyses, we determined that all climate variables have positive parameters indicating a positive effects on tree growth (Table 4). All in all, the variance of the period effect on individual tree growth is well-explained by the final model mBIC, with 79.0% of variance of the period effect, i.e. 7.1% of the tree growth variance, explained by the combination of these three climate factors (Fig. 3).

**Model Predictions**

The model mBIC did not completely succeed in accurately predicting the seasonal growth. Indeed, the obtained RMSEP was slightly above the mean value of growth (mean growth $= 0.026 \text{ mm.d}^{-1}$, RMSEP $= 0.035 \text{ mm.d}^{-1}$). In general, the model overestimated the individual growth under 0.05 mm.d$^{-1}$ and underestimated the growth above 0.1 mm.d$^{-1}$ (Fig. 5).

**Discussion**

In this study, we showed that 9% of the observed variation in individual tree growth was attributable to fine-scale climate variations and demonstrated that water availability was the main...
driver of tree growth in a neotropical forest. The individual behaviour of each tree explained 26% of growth variation and a substantial fraction of variation in growth remained unexplained with our model. Tree growth is obviously influenced by several additional environmental variables, such as competition for light and nutrients [35–37]. Their effects were included in the model through the individual effect $tree_i$ and we assumed that they were constant over the study period. We also did not consider the ontogenetic trajectory that depends on complex environmental changes that may have occurred during the 4-year census period [38]. The remaining unexplained 65% of tree growth variance could be linked (i) to complex changes in environmental conditions during the experiment, such as change in light availability created by a new forest gap, or (ii) to complex biological properties, such as the inherent rhythm of leaves and flowers phenology or changes in ontogenetic growth trajectory. In this study, we made the strong assumption that each growth measurement was independent of others. For instance, a single heavy rain in dry season does not have the same effect than a single heavy rain in wet season. Further research should improve these components of the model to take better account of seasonal change of tree growth. For example, future predictions of the

**Table 3. Variance decomposition of the univariate analysis.**

| model  | components | Df   | Sum Sq | Mean Sq | % of variance | F value | P value |
|--------|------------|------|--------|---------|---------------|---------|---------|
| $M_0$  | tree       | 204  | 2.9130 | 0.01427 | 26.197        | 11.472  | <0.001  |
|        | period     | 35   | 0.9970 | 0.02848 | 8.966375      | 22.885  | <0.001  |
|        | residuals  | 5792 | 7.2095 | 0.00124 | 64.33643      |         |         |
| $M_{REW}$ | tree     | 204  | 2.9130 | 0.01428 | 26.197        | 10.934  | <0.001  |
|         | $REW$     | 1    | 0.5983 | 0.59833 | 5.380854      | 458.170 | <0.001  |
|         | residuals | 5826 | 7.6082 | 0.00131  | 68.42195      |         |         |
| $M_{rain}$ | tree    | 204  | 2.9130 | 0.01428 | 26.197        | 10.685  | <0.001  |
|         | $rain$    | 1    | 0.4206 | 0.42064 | 3.782924      | 314.758 | <0.001  |
|         | residuals | 5826 | 7.7859 | 0.00134  | 70.01988      |         |         |
| $M_{T_{min}}$ | tree | 204  | 2.9130 | 0.01427 | 26.197        | 10.627  | <0.001  |
|         | $T_{min}$ | 1    | 0.3781 | 0.37809 | 3.400231      | 281.378 | <0.001  |
|         | residuals | 5826 | 7.9499 | 0.00136  | 71.49485      |         |         |
| $M_{T_{max}}$ | tree | 204  | 2.9130 | 0.01427 | 26.197        | 10.464  | <0.001  |
|         | $T_{max}$ | 1    | 0.2566 | 0.25663 | 2.307954      | 188.071 | <0.001  |
|         | residuals | 5826 | 7.8285 | 0.00134  | 70.40257      |         |         |
| $M_{VPD}$ | tree    | 204  | 2.9130 | 0.01427 | 26.197        | 10.207  | <0.001  |
|         | $VPD$    | 1    | 0.0559 | 0.05586 | 0.5025887     | 39.946  | <0.001  |
|         | residuals | 5826 | 8.1507 | 0.00139  | 73.30021      |         |         |
| $M_{irr}$ | tree     | 204  | 2.9130 | 0.01427 | 26.197        | 10.184  | <0.001  |
|         | $irradiance$ | 1  | 0.0380 | 0.03804 | 0.3421205     | 27.133  | <0.001  |
|         | residuals | 5826 | 8.1685 | 0.00140  | 73.46068      |         |         |
| $M_{U^*}$ | tree     | 204  | 2.9130 | 0.01427 | 26.197        | 10.184  | <0.001  |
|         | $U^*$     | 1    | 0.5325 | 0.53248 | 4.7886        | 404.247 | <0.001  |
|         | residuals | 5826 | 7.6741 | 0.00132  | 69.01414      |         |         |
| $M_{BIC}$ | tree     | 204  | 2.9130 | 0.01427 | 26.197        | 10.184  | <0.001  |
|         | $REW$     | 1    | 0.5983 | 0.59833 | 5.380854      | 469.699 | <0.001  |
|         | $T_{min}$ | 1    | 0.0154 | 0.01781 | 0.1387580     | 12.112  | <0.001  |
|         | $irradiance$ | 1  | 0.1739 | 0.17388 | 1.563707      | 136.497 | <0.001  |
|         | residuals | 5823 | 7.4189 | 0.00127  | 66.71948      |         |         |

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effects of precipitation variability on carbon assimilation and on tree growth could be improved by the use of tree hydrodynamic models that mechanistically relate tree transpiration and stomatal conductance to soil moisture, through resolving water stresses in the tree system [39,40].

Soil Water Availability
Soil water availability strongly impacts productivity as directly observed in seasonal tropical forests [41,42] and as deduced from experimental forest droughts [12,43]. In our study where tree growth was linked to soil water availability at a seasonal time step, we were able to go further than earlier studies performed at an annual scale [10,44]. Indeed, our methodological approach allowed us to rank the effects of the different climate variables tested here on tree growth. We showed that low levels of \(REW\), rather than lack of rainfall, are the key driver of the decrease, or even the stop, of diameter increment. This result thus points to the main influence of soil water availability on the biological processes (i.e. cell division in cambial tissues) associated with secondary growth of tropical rainforest species. However, Stahl et al. [32] even highlighted a shrinkage of the circumference of some trees during dry seasons at the same site and concluded that seasonal variations in tree circumference partly reflect variation in trunk biophysical properties. Deciphering the relative importance of stem shrinkage and/or decrease in diameter growth in dry seasons was beyond the scope of this work and supplementary in situ experiments are needed. Nevertheless, the Paracou forest experienced strong dry seasons during the study period with even several months with precipitation <50 mm.month\(^{-1}\) (0–4 month\(\times\)year\(^{-1}\)). During these events, the amount of rainfall was always below the potential evapotranspiration, which never falls below 100 mm.month\(^{-1}\) in Paracou [45]. This water limitation may solely explain the slowdown of girth increment, as reported in many seasonal tropical forests [42]. However, even under strong water limitation, most trees seem to be able to maintain their baseline functioning [46] and the decrease in gross ecosystem productivity under severe dry conditions did not exceed 20% of wet season values at the Paracou site [28]. The apparent discrepancy between high ecosystem-level gross productivity and low community secondary growth at our site can be explained by a large proportion of the photosynthate products stocked into reserve pools under soil drought conditions [47].

Figure 3. Ranking climate variables according to their effects on diameter growth of 205 trees from 54 neotropical species. The period effect represent 9% of the variance of tree growth. Note that (i) the model BIC catches more than 80% of the period effect and (ii) the water availability \((REW)\) alone captures 60% of the period effect, respectively 7.1 and 5.4% of the variance of tree growth. doi:10.1371/journal.pone.0034074.g003

Figure 4. Averaged diameter growth of 205 trees from 54 neotropical species during 4 consecutive years plotted against the evolution of water availability \((REW, \text{dashed line})\). Note that the highest increments occur in the first weeks of the wet season, regardless of the intensity of these early rainfall events. doi:10.1371/journal.pone.0034074.g004
growth increments occurred (see Fig. 5) during the early wet season. The same pattern has already been observed at La Selva leading Clark et al. [19] to conclude a strong link between growth and rainfall. However, a direct effect of rain on biological processes leading to secondary growth is rather hypothetical, and other processes are involved to explain this relationship. In a tropical forest of Ethiopia with a strong seasonality, high-resolution electronic dendrometers have been combined to wood anatomy investigation to describe cambial growth dynamics [48]. These authors have observed that lack of water availability 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 a few rainy days and (iii) evergreen trees were able to quickly initiate wood formation. Namely, we still do not know whether this increment is due to cambial activity, sapwood or bark swelling or, more probably, a combination of these [32]. A flush of nutrient availability at the start of the rain season may also explain this swift diameter increment as the first rainfall events make available a large pool of nutrients accumulated during the dry season [49].

Table 4. Model parameters, standard errors and t values of the univariate (\(m_{\text{varclim}}\)) and final multivariate (\(m_{\text{BIC}}\)) analyses.

| model   | climate variable | estimate | Std. Error | t value | P value |
|---------|------------------|----------|------------|---------|---------|
| \(m_{\text{varclim}}\) | \(REW\)         | \(4.658 \times 10^{-3}\) | \(2.176 \times 10^{-3}\) | 21.405 | <0.001  |
|         | rainfall         | \(2.015 \times 10^{-4}\) | \(1.136 \times 10^{-3}\) | 17.741 | <0.001  |
|         | \(T_{\text{min}}\) | \(2.209 \times 10^{-4}\) | \(1.317 \times 10^{-3}\) | 16.774 | <0.001  |
|         | \(T_{\text{max}}\) | \(1.532 \times 10^{-4}\) | \(1.117 \times 10^{-3}\) | 13.714 | <0.001  |
|         | VPD              | \(3.028 \times 10^{-5}\) | \(4.791 \times 10^{-6}\) | 6.320  | <0.001  |
|         | irradiance       | \(2.255 \times 10^{-6}\) | \(4.330 \times 10^{-7}\) | 5.209  | <0.001  |
|         | \(U^*\)          | \(1.241 \times 10^{-2}\) | \(6.175 \times 10^{-3}\) | 20.106 | <0.001  |
| \(m_{\text{BIC}}\) | \(REW\)         | \(1.628 \times 10^{-3}\) | \(3.542 \times 10^{-3}\) | 4.596  | <0.001  |
|         | \(T_{\text{min}}\) | \(4.471 \times 10^{-4}\) | \(3.739 \times 10^{-3}\) | 11.959 | <0.001  |
|         | irradiance       | \(-1.107 \times 10^{-2}\) | \(9.474 \times 10^{-7}\) | -11.683| <0.001  |

Models \(m_{\text{varclim}}\) were separately fit for each climate variable.

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Temperature

Investigating the effects of temperature on the physiology of tropical forest trees [18,50] is, today, of primary importance, given increases expected over the next century [25,51]. Some authors suggest that tropical trees are, more than others, sensitive to temperature increases because (i) they live at or close to the highest annual average temperatures on Earth and (ii) tropical species naturally encounter limited variation in temperature (<4°C over 20° of latitude) [52]. In French Guiana, the increase in average temperature follows the general trend of Amazonia, 0.25±0.05°C per decade [1,53]. This increase in average temperature is mainly

Figure 5. Predicted versus observed diameter growth under the model \(m_{\text{BIC}}\). The white dashed line is the identity line \(y=x\). Note that the model overestimated the individual growth under 0.05 mm.d\(^{-1}\) and underestimated the growth above 0.1 mm.d\(^{-1}\).

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driven, in French Guiana, by the minimum daily temperatures over the last 50 years (unpublished data). We found that temperature variations were of secondary importance for tree growth at a seasonal time step. Nevertheless, minimal temperature was slightly positively correlated with tree growth (Fig. 3), whereas maximal temperature had no effect. The interpretation of this significant correlation is rather biologically difficult, as minimal daily temperature still remain rather high at our site (never less than 21°C) and seasonal variations in these temperatures remain rather low. At La Selva [19], annual growth was found to be sensitive to variations in mean annual night-time temperature of 1–2°C. However, we argue that the climate at La Selva is near aseasonal with no strong dry periods and tree diameter increment never really stops. Thus, the observed relationship at La Selva may have arisen because night-time temperature is a proxy of drought events, as the census with the strongest dry season was the census with the highest mean annual night-time temperature [19,54].

Irradiance

Surprisingly, amongst the climate variables that were significantly correlated with seasonal growth variation, irradiance had the smallest effect on tree growth (Fig. 3). Gross primary production is limited by irradiance in the Paracou forest, but the critical level where irradiance becomes limiting is rarely attained [28]. In the final model selected by BIC, irradiance had a surprising negative effect on growth. In fact, the model used irradiance to lower tree growth during the strongest dry seasons. These extreme slowdowns of tree growth could be linked to the leaf fall phenology mediated by high irradiance events as previously observed in Tapajos forest [46,55]. Irradiance has been previously reported to be the main determinant of leaf fall timing in aseasonal [56] as well as in seasonal rainforests [57,58]. However, in Paracou, litter production remains high all over the year [28,59] and a peak is observed around September [28,60], i.e. when irradiance is the highest. This could lead us to conclude that the massive loss of leaves in September led to a decrease in the whole-ecosystem photosynthetic capacity, in turn driving the growth slowdown. However, enhanced vegetation index (EVI, a proxy of chlorophyll activity) is also highest during this period due to the establishment of newly formed leaves [60]. In this context, the negative link between irradiance and tree growth should be cautiously interpreted and we suggest that future work should be carried out to test this phenology effect on tree growth.

Conclusions

Globally, current IPCC scenarios predict an intensification of the dry period for the Guiana shield [25] during the XXIst century. Amongst climate variables, our results highlight the predominant role of water availability in determining tree growth. If rainfall reduction was confirmed in the future, it may be expected that tree growth will be affected. 91% of the variance in stem increment unresolved may be due to neotropical trees acclimation to quick changing environmental conditions at Paracou or more likely to the limitations of our modeling approach that does not account for biological lags. While photosynthesis or gross primary production often adjusts immediately to environmental conditions, structural growth may be correlated with environmental conditions occurring weeks to years earlier [60–65]. Indeed, dry periods lead to an effective decrease in stem diameter growth but their actual intensity hardly affects the global annual tree growth that appears more dependent on the increment at the onset of the rain seasons than on the duration of the dry seasons. In other words, six or nine months of rain season seems to be equivalent as the highest increments occur in the first weeks of the wet season, regardless of the intensity of these early rainfall events (Fig. 4). In this context, it seems necessary to explicitly include the effect of water stress on tree growth in forest simulators to test, in silico, the impact of different climate scenarios on the future dynamics of the rainforest.

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Author Contributions

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

References

1. Malhi Y, Wright J (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 359: 311–329.
2. Solomon S, Plattner GK, Knutti R, Friedlingstein P (2009) Irreversible climate change due to carbon dioxide emissions. Proceedings of the National Academy of Sciences of the United States of America 106: 1704–1709.
3. Harrin PP, Huntingford C, Cox PM (2008) Amazon basin climate under global warming: the role of the sea surface temperature. Philosophical Transactions of the Royal Society B-Biological Sciences 363: 1753–1759.
4. Burke EJ, Brown SJ, Christidis N (2006) Modeling the recent evolution of global drought and projections for the twenty-first century with the hadley centre climate model. Journal of Hydrometeorology 7: 1113–1125.
5. Johns T, Gregory J, Ingram W, Johnson C, Jones A, et al. (2003) Anthropogenic climate change for 1860 to 2100 simulated with the HadCM3 model under updated emissions scenarios. Climate Dynamics 20: 503–612.
6. Houghton RA (2005) Aboveground forest biomass and the global carbon balance. Global Change Biology 11: 945–958.
7. Saatchi SS, Houghton RA, Alvra C, Soares JV, Yu V (2007) Distribution of aboveground live biomass in the amazon basin. Global Change Biology 13: 816–837.
8. Nepstad D, Moutinho P, Dias M, Davidson E, Cardinot G, et al. (2002) The effects of partial throughfall exclusion on canopy processes, aboveground production, and biogeochemistry of an Amazon forest. Journal of Geophysical Research-Atmospheres.
9. Granier A, Breda N, Binon P, Viller S (1999) Aumped water balance model to evaluate duration and intensity of drought constraints in forest stands. Ecological Modelling 116: 269–283.
10. Wagner F, Herault B, Stahl C, Bonal D, Rosal V (2011) Modeling water availability for trees in tropical forests. Agricultural and Forest Meteorology 151: 1202–1213.
11. Graham EA, Malley SK, Kinajina K, Phillips NG, Wright SJ (2003) Cloud cover limits net CO2 uptake and growth of a rainforest tree during tropical rainy seasons. Proceedings of the National Academy of Sciences of the United States of America 100: 572–576.
12. Huete AR, Didan K, Shimabukuro YE, Ratana P, Saleska SR, et al. (2006) Amazon rainforests grow-in with sunlight in dry season. Geophysical Research Letters 33.
13. Xiao X, Hagen S, Zhang Q, Keller M, Moore B III (2006) Detecting leaf phenology of seasonally moist tropical forests in South America with multi-temporal MODIS images. Remote Sensing of Environment 103: 465–473.
19. Clark DB, Clark DA, Oberbauer SF (2010) Annual wood production in a tropical forest in NE Costa Rica linked to climatic variation but not to increasing CO2. Global Change Biology 16: 747–759.
20. Granier A, Huc R, Colin F (1992) Transpiration and stomatal conductance of two arbor fabric species growing in plantations (sinamor aramoa and geopha glabra) in french guyana. Annals of Forest Science 49: 17–24.
21. Meiner F, Goldstein G, Holbrook N, Jackson P, Gavelier J (1993) Stomatol and environmentalcontrol of transpiration in a lowland tropical forest tree. Plant Cell and Environment 16: 429–436.
22. Brando PM, Goetz SJ, Baccini A, Nepstad DC, Beck PSA, et al. (2010) Seasonal and interannual variability of climate and vegetation indices across the Amazon. Proceedings of the National Academy of Sciences of the United States of America 107: 14603–14609.
23. Franks PJ, Farquhar GD (1999) A relationship between humidity response,growth form and photosynthetic operating point in c3-plants a 3722-2008. Plant Cell and Environment 22: 1337–1349.
24. Reichstein M, Tornhuanen J, Roupsord O, Ouurcial J, Rambal S, et al. (2002) Ecosystem respiration in two Mediterranean evergreen oak forests:drought effects and decomposition dynamics. Functional Ecology 16: 27–39.
25. Solomon S, Qiu D, Manning M, Marquis M, Areyt K, et al. (2007) Climate Change 2007, the Fourth Assessment Report (AR4). Intergovernmental Panel on Climate Change, 103 p.
26. Clark D, Clark D (1999) Assessing the growth of tropical rain forest trees: Issues for forest modelling and management. Ecological Applications 9: 961–997.
27. Gourlet-Fleury S, Geih JM, Laroussinie O (2004) Ecology and management of a neotropical rainforest - lessons drawn from Paracou, a long-term experimental research site in French Guiana. Elsevier.
28. Bidal D, Bosc A, Ponton S, Geroj YT, Burban B, et al. (2008) Impact of severe dry season on new ecosystem exchange in the Neotropical rainforest of French Guiana. Global Change Biology 14: 1917–1933.
29. ter Steege H, Pitman NCA, Phillips OL, Chave J, Sabatier D, et al. (2006) Continental-scale patterns of canopy tree composition and function across Amazon. Nature 443: 444–447.
30. Ruthsathias E, Wagner F, Herault B, Nicolinia EA, BLanc L (2010) Contrasting above-ground biomass balance in a Neotropical rain forest. Journal of Vegetation Science 21: 672–682.
31. Wagner F, Ruthsathias E, BLanc L, Herault B (2010) Effects of plot size and census interval on descriptors of forest structure and dynamics. Biotropica 42: 664–671.
32. Stahl C, Burban B, Borpy F, Jolin ZB, Sermalia J, et al. (2010) Seasonal variation in atmospheric relative humidity contributes to explaining seasonal variation in trunk circumference of tropical rain-forest trees in French Guiana. Journal of Tropical Ecology 26: 395–405.
33. Calvagno D, de Mazancourt C (2010) 2010: a water for Easy Automated Model Selection with (Generalized) Linear Models. Journal of Statistical Software 34: 1–29.
34. Burnham K, Anderson D (2004) Multimodel inference - understanding AIC and the new statistics. Journal of Wildlife Management 68: 1105–1117.
35. Uriarte M, Canham C, Thompson J, Zimmerman J (2004) A neighborhood dimensional model of water flow in soil-plant systems based on plant Water Availability Drives Tree Growth
75. Enquist B, Leffler A (2001) Long-term tree ring chronologies from sympatric tropical dry-forest trees: individualistic responses to climatic variation. Journal of Tropical Ecology 17: 41–60.

76. Laurance SGW, Laurance WF, Nascimento HEM, Andrade A, Fearnside PM, et al. (2009) Long-term variation in Amazon forest dynamics. Journal of Vegetation Science 20: 323–333.

77. Arias PA, Fu R, Hoyos CD, Li W, Zhou L (2011) Changes in cloudiness over the Amazon rainforests during the last two decades: diagnostic and potential causes. Climate Dynamics 37: 1151–1164.

78. Nemani R, Keeling C, Hashimoto H, Jolly W, Piper S, et al. (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300: 1560–1563.