Biogeosciences Discuss., 12, 3145–3176, 2015
www.biogeosciences-discuss.net/12/3145/2015/
doi:10.5194/bgd-12-3145-2015

Biogeosciences
Discussions
Open Access

Identifying climatic drivers of tropical forest dynamics

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Received: 25 November 2014 – Accepted: 19 January 2015 – Published: 11 February 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

In the context of climate changes, identifying and then predicting the impacts of climatic drivers on tropical forest dynamics is becoming a matter of urgency. We used a coupled model of tropical tree growth and mortality, calibrated with forest dynamic data from the 20 year study site of Paracou, French Guiana, in order to introduce and test a set of climatic variables. Three major climatic drivers were identified through the variable selection procedure: drought, water saturation and temperature. Drought decreased annual growth and mortality rates, high precipitation increased mortality rates and high temperature decreased growth. Interactions between key functional traits, stature and climatic variables were investigated, showing best resistance to drought for trees with high wood density and for trees with small current diameters. Our results highlighted strong long-term impacts of climate variables on tropical forest dynamics, suggesting potential deep impacts of climate changes during the next century.

1 Introduction

In French Guianan forests, the intra-annual climate variability is strongly structured by the occurrence of the dry seasons: a long dry season from mid-August to mid-November, and a short one in March. Such a seasonality is typical in many tropical forest areas, and implies various changes of the availability of resources, such as water and light, necessary to tree development and to forest functioning. The seasonality of tree growth and tree mortality is consequently highly studied in tropical forests, with demonstrable success in the past (Wagner et al., 2012; Grogan and Schulze, 2012; Brando et al., 2010). Tree growth is mainly related to water availability, resulting in growth during the wet months and static or even contracted states during the dry season months (Grogan and Schulze, 2012). The use of a convenient water availability estimator like the relative extractable water (REW) (Wagner et al., 2011) shows that low levels of REW rather than lack of rainfall per se are the key drivers of the decrease in growth rate, or even of the stop, at a seasonal time step. (Wagner et al., 2012). At another time scale, long-term forest dynamic changes may also be related to exceptional climate events. Effects of unusual dry periods on tree growth and mortality may enlighten us about the long-term processes linking water availability and tree dynamics. After the intense 2005 drought in Amazonia, the forest suffered an additional mortality, leading to a huge loss of alive tree biomass (Phillips et al., 2009). A consensus about higher mortality due to severe drought events has recently emerged (Choat et al., 2012; Allen et al., 2010). Experimental droughts in Brazil provide results in line with this consensus (Nepstad et al., 2007; da Costa et al., 2010; Brando et al., 2008). Besides exceptional events and the intra-annual seasonal rhythmicity, there is a gap in our research knowledge on an inter-annual scale investigating the potential links between inter-annual climate variations and forest dynamics from a long-term perspective. This gap is partly due to the weak magnitude of variation of the demographic rates when compared to what is observed from a seasonal point of view or from some spectacular events. This gap is also due to the lack of sites in tropical forests where annual regular inventories of tree growth and death are performed and where climatic data on the same time-scale are available. Convenient tools are needed to process these data. A modelling approach may help to tackle these questions (Zuidema et al., 2013) because models can mechanistically link climate conditions, resource acquisition, allocation, and functional plant traits to tree growth and survival. Functional traits have been recently used to include functional diversity in models of tree growth (Hérault et al., 2011; Rüger et al., 2012; Wagner et al., 2014) and tree mortality (Aubry-Kientz et al., 2013). Such models need to start from potential underlying physiological processes, helping to articulate hypotheses that will serve as the basis for building the models.

Some climatic variables are expected to play a role in forest dynamics regarding the tree's physiological processes. Water stress due to drought is well documented (Phillips et al., 2009; Allen et al., 2010). Water insufficiency leads generally to higher mortality rates and lower growth (Choat et al., 2012). Water stress needs to be estimated, and diverse estimators may be found in the literature (Wagner et al., 2011; Toledo et al., 2011; Aragão et al., 2007; Malhi et al., 2009). The length of the dry season seems to be the simplest estimator. The REW described in the study of Wagner et al. (2011) was computed using the daily rainfall and gave an estimate of the quantity of water available for tree development. This indicator is already related to intra-annual forest dynamics in Wagner et al. (2012). Although water availability is expected to reduce growth and increase mortality, these impacts have to be investigated on an inter-annual time-scale.

Rain may also be responsible for water saturation, a phenomenon that is far less studied but that can have an effect on tree mortality or growth. For instance, Ferry et al. (2010) underlined a higher mortality rate in waterlogged areas. Inter-annual variations of rain quantities can lead to more or less waterlogged soils, independent of their topographical location, implying instability that can cause cascading tree-falls.

The effects of temperature are less consensual; some studies suggested that tropical forests can be near a high temperature threshold and that these systems may be more vulnerable to climate change than previously believed (Clark et al., 2003). For instance, Clark et al. (2003) showed a negative correlation between 16 year diameter increments and annual means of daily minimal temperature in La Selva, Costa Rica, while Toledo et al. (2011) found a positive correlation between annual diameter growth and temperature in Bolivia. An explanation for such apparently conflicting results was proposed by Dong et al. (2012), that the effects of variability in solar radiation and daily minimum temperature on tree growth appear to be largely independent.

In this study, we first explore the potential relationships existing between climate variables computed on two-year time step and forest dynamics. We identify independent variable responsible for the inter-annual variation of growth and mortality rates. These variables are then included in a coupled growth-mortality model to test their multivariate effects. Finally, we include in the model some interactions between functional traits and the climate predictors to test for a potential differentiated response depending on the individual functional identity.

2 Materials and methods

2.1 Data collection

Three datasets were used in this study. The study site is located in Paracou, French Guiana (5°18′N, 52°55′W). The forest is typical of Guianan rain forests and the dominant tree families are *Fabaceae, Chrysobalanaceae, Lecythidaceae,* and *Sapotaceae*. More than 700 species of trees ≥ 10 cm DBH (diameter at breas height) have been described at the site.

Mean annual precipitation averages 2980 mm (30 year period), and the site receives nearly two-thirds of its annual precipitation during the long rainy season between mid-March and mid-June, and less than 50 mm per month in September and October (Wagner et al., 2011).

2.1.1 Tree dynamic

The first data set is an inventory of trees > 10 cm DBH in the six natural forest plots of 6.25 ha in Paracou. Mortality and diameter growth have been censused every two years between 1991 and 2011. DBH was calculated from circumference measures made to a precision of 0.5 cm. We excluded individuals with buttresses or other problems that required an increase in measurement because we were unsure about the height of the initial points of measurement for these trees. The data set contained 20 340 trees. For each tree and every two years, we know the location, DBH, vernacular name, status (dead or alive), and the mode of death for dead trees (tree-fall or standing death). Vernacular names are the common names used by local tree spotters. As botanical identification of the trees species was completed in 2012, a large part of the trees that died during the study period (1991–2011) have only a vernacular name and no botanical determination. The method of Aubry-Kientz et al. (2013) is used to handle this uncertainty and to integrate the information on botanical determination contained in the vernacular names of trees that were not identified.

2.1.2 Functional traits

The second data set was a collection of five functional traits of 335 Guianan tree species that occur at the Paracou site (see Table 1). Traits are related to leaf economics, stem economics and life history and are extracted from a large database (Baraloto et al., 2010a, b).

The leaf economics reflects a trade-off between investments in productive leaves with rapid turnover vs. costly physical leaf structure with a longer playback. The stem economics defines a similar trade-off at the stem level: dense wood vs. high wood water content and thick bark (Baraloto et al., 2010b). Life-history strategies describe how trees allocate resources to different organs and how these allocation translate into a species' ability to compete for resources and finally to grow, survive, reproduce and disperse (Rüger et al., 2012).

2.1.3 Climate

The third data set consists of climate data. Six variables were provided by the Climatic Research Unit (CRU) at the University of East Anglia (Mitchell and Jones, 2005), consisting in month-by-month variations in climate over the last century calculated on high-resolution grids ($0.5^\circ \times 0.5^\circ$) (Mitchell and Jones, 2005). We used the aggregated variables (mean or sum, depending of the nature of the observed process) for two years, from July to July, to include the dry season (mid-August to mid-November). Selected variables that may have an impact on forest dynamics are the cloud cover (Cld), the potential evapo-transpiration (Pet), the precipitation (Pre), the daily mean temperature (Tmp), the vapour pressure (Vap) and the wet day frequency (Wet).

Three other climate variables are computed using the relative extractable water (REW) computed with a water balance model developed by Wagner et al. (2011) calibrated at our study site and taking the daily precipitation from the CRU into account; this REW index takes values between 0 and 1 at our study site, corresponding to the available water for trees. This REW index is used to compute $\mathrm{Nb}_{\mathrm{under}}$, the number of days under a REW threshold of 0.4, which is the threshold recommended in Wagner et al. (2011); A_{under}, the area over the REW curve and under the threshold of 0.4; and A_{over}, the area situated under the REW curve and over the threshold of 0.95. Nb_{under} and A_{under} are built to be indicators of drought, while A_{over} is related to soil water saturation. All climate variables are centred to allow an easier interpretation of the results.

2.2 Model

The model used in this study consists of a model coupling growth and mortality processes at the whole community scale. The likelihood is computed using the distribution probability of mortality (Eqs. 1 and 2) and the computed growth rate (Eq. 3), as detailed in the Appendix. A vigour index is added into the mortality process, taking the past growth into account. We added the climate variables into the two processes to highlight the links between some climate drivers and one particular process.

$$p_{i,s,t} = \text{logit}^{-1}\left(\gamma_1 \times \text{clim}_1 + \theta_1 \times \text{Vigour}_{i,s,t} + \theta_2 \times \frac{\text{DBH}_{i,s,t-1}}{\text{DBHmax}_s} + \theta_3 \times \left(\frac{\text{DBH}_{i,s,t-1}}{\text{DBHmax}_s}\right)^2 \right.$$
$$\left. + \theta_4 \times \text{Hmax}_s + \theta_5 \times \text{WD}_s + \theta_6 \times \text{Tough}_s\right) \tag{1}$$

with

$$\text{Vigour}_{i,s,t} = \log\left(\frac{\text{AGR}_{i,s,t-1}+1}{\widehat{\text{AGR}}_{i,s,t-1}+1}\right), \tag{2}$$

and

$$\log(\widehat{\text{AGR}}_{i,s,t-1}+1) =$$
$$(\gamma_2 \times \text{clim}_2 + \theta_7 \times \text{DBHmax}_s + \theta_8 \times \text{WD}_s + \theta_9 \times \text{Hmax}_s + \theta_{10} \times \delta 13\text{C}_s)$$

$$\times \exp\left(-\frac{1}{2}\left(\frac{\log\left(\frac{\mathrm{DBH}_{i,t-2}}{\theta_{11}\times \mathrm{DBHmax}_s}\right)}{\theta_{12}\times \mathrm{WD}_s}\right)^2\right), \tag{3}$$

and

$$\log(\mathrm{AGR}_{i,s,t-1}+1)=\log(\widehat{\mathrm{AGR}}_{i,s,t-1}+1)+\varepsilon_i, \tag{4}$$

with

$$\varepsilon_i \sim \mathcal{N}(0,\theta_{13}). \tag{5}$$

where $p_{i,s,t}$ is the probability of dying of tree i of species s between time $t-1$ and t; $\widehat{\mathrm{AGR}}_{i,s,t-1}$ is the predicted growth between time $t-2$ and time $t-1$. $\mathrm{AGR}_{i,s,t-1}$ is the observed growth between time $t-2$ and time $t-1$; DBHmax_s, Hmax_s, WD_s, Tough_s and $\delta 13\mathrm{C}_s$ are functional traits of species s to which tree i belongs (see Table 1); $\theta_1,\theta_2,\cdots\theta_{13}$ are parameters to be estimated, and ε_i is an individual error term following a normal distribution; γ_1 and γ_2 are the parameter vectors linking the climate predictors with the processes of mortality and growth respectively; clim_1 and clim_2 are the vectors of climate predictors included in the processes of mortality and growth, respectively.

2.3 Variable selection

To identify the different axes of variation of our climate data set and avoid including collinear variables in the model, we realized a principal component analysis (PCA) on the climate variables.

We included all climate variables one by one in each process of the model and computed the partial likelihood for each sub-model of growth or mortality we obtained. This provides a first result about the importance of each climate variable. Depending on these results and on their degree of collinearity from the PCA, we selected some climate variables and included them in the growth model and in the logit function of mortality.

2.4 Model inference

We implemented a MCMC algorithm to estimate the model parameters (Robert and Casella, 2004). A random walk was used as a proposal distribution to sample new values of parameters that were or were not selected, using the ratio of Metropolis–Hasting. Only SD was sampled in an inverse-gamma posterior distribution with a Gibbs sampler. All the algorithms and statistical treatments were implemented with R software (R core Team, 2014).

2.5 Functional trait and forest dynamic responses

Wood density and DBH of each individual tree are often expected to play roles in the tree water budget (see Table 4). Thus, we included in the model an interaction between wood density and the drought estimator A_{under}, an interaction between DBH and A_{under}, and an interaction between DBH and precipitation Pre.

The current tree diameter may also influence resistance drought events or other climatic perturbations (Nepstad et al., 2007; Condit et al., 2004). Two main hypotheses may be tested. First, small, young trees that are not well established and that do not have deep roots may be more sensitive and may suffer under stressful water conditions. Second, large, older trees may feel water stress because they must maintain their photosynthesis activities and carry sap to a higher altitude. We tested these two hypotheses using interaction effects (see Table 4).

Species vary over one order of magnitude in their wood density (WD), ranging from 0.08 to 1.39 g cm^3 (Iida et al., 2012), and the encountered range of wood density is particularly large in species-rich tropical rainforests (Chave et al., 2006, 2009). Wood density is a key functional trait because of its importance for mechanical stability, defence against herbivores, hydraulic conductivity, photosynthetic carbon gain and diameter growth rates of plants (Poorter et al., 2008). High wood density implies thin and short xylem vessels with small pit-pores, which decrease the risk of embolism and cavitation. Trees with high wood density are then expected to be less sensitive to drought.

The term A_{under} multiplied by $\mathrm{WD}_{\mathrm{max}} - WD$ accounts for the effect of drought on trees with low wood density. This term is added in growth and mortality to test this effect (see Table 4).

3 Results

3.1 Variable selection

The variable selection was realised using the literature, the PCA results, and the results of the univariate analysis.

3.1.1 PCA

The PCA underlines one principal axis, explaining 48 % of the inertia and strongly negatively correlating with variables Tmp and Pet. The variables Wet and Cld are positively correlated with this axis, while Vap, A_{under} and $\mathrm{Nb}_{\mathrm{under}}$ are negatively correlated with this axis (see Fig. 1). The second axis is strongly negatively correlated with Pre and $\mathrm{Area}_{\mathrm{over}}$. The third axis is essentially negatively correlated with A_{under}.

3.1.2 Univariate analyses

When the climate variables are included one by one in each model, all variables but precipitation (Pre) had an effect in the growth process, while only few had an effect in the mortality process (see Table 3). The climates variables associated with the mortality process are Pre, $\mathrm{Nb}_{\mathrm{under}}$ and A_{under}. In the growth model, A_{under} is the best predictor according to the likelihood. In the mortality process, the best value of likelihood is obtained when N_{under} is included.

3.1.3 Variable selection

The Pet and temperature are indicators of the energy that the system receives and are expected to play a role in tree growth (Clark et al., 2003; Dong et al., 2012). These variables are strongly correlated together ($r = 0.8$) and negatively correlated with the first axis of the PCA (Pet, $C = -0.45$ and Tmp, $C = -0.44$). This is not surprising, as Pet is computed using the temperature (Allen et al., 1998). As these two variables are strongly correlated, we finally included the temperature, which had a better likelihood score than Pet when it is included in the growth model. Neither Pet nor the temperature had an effect if included in the mortality process.

The second axis of the PCA is related to water saturation and is correlated with Pre ($C = -0.68$) and A_{over} ($C = -0.61$); only A_{over} had an effect when included in the growth process, but the likelihood is the worst score obtained, which is why we did not include this variable in the final model. Concerning mortality, Pre had an effect and is thus included in both the final growth and mortality model.

The third axis of the PCA is strongly correlated with the drought estimator A_{under}, which is the better climate driver of growth regarding the likelihood. A_{under} also had an effect on the mortality process, and is finally included in the two processes in the final model.

3.2 Full model inference

The growth trajectory was adjusted by a size-dependent diameter growth model. Parameters linking the maximal growth to the functional traits DBHmax, WD, Hmax and δ13C have have similar values to (Hérault et al., 2011) (see Table 5), i.e., maximum growth rates increase with increasing DBHmax, and decreasing WD, Hmax and δ13C. Diameter at maximum growth is attained for 0.794DBHmax. The parameters linking the probability of mortality to Hmax, WD and Tough converged around negative values, meaning that the probability of dying is lower when the tree is high, has a high wood density and/or high laminar toughness.

The drought estimator (A_{under}) converged to negative values in the growth and mortality processes; thus growth and mortality computed at our biannual time-scale are lower when the drought estimator A_{under} is higher. The parameter linking mortality with precipitation (Pre) is positive. This finding implies that mortality rate is higher during two-year time-scale with high precipitation. The parameter linking temperature (tmp) and growth takes negative values; thus growth values are lower during the warmest periods.

3.3 Functional variability of responses

In the growth process, interaction between $\text{WD}_{\text{max}} - \text{WD}$ and drought is negative (Table 4), implying that trees with lower WD are more sensitive to drought and reduce their growth more. Moreover, interactions linking the current diameter and drought are also negative; thus larger trees are more sensitive to drought and reduce their growth more compared to smaller trees. None of the interaction terms included in the mortality process had an effect (Table 4).

4 Discussion

We highlighted the climate drivers of forest dynamics in the Guianan tropical forest by using a community growth-mortality modeling framework. The Bayesian algorithms used to infer the model and select the best predictors allow us great flexibility. The vigour index is negatively related to mortality, i.e., trees that grow more than expected have a lower probability of dying, and trees with lower-than-expected growth have a higher probability of dying. A limited number of interactions between climate variables and functional traits was tested because of our a priori selection of three climate predictors. One can argue that some climatic variables that were disregarded in the first step would increase the likelihood if included in interactions with a functional trait. This pathological case is very improbable (Wagner et al., 2014) and will necessitate an impractical amount of computational time to be tested. One can also note that few climate variables had an effect when included in the mortality process, while almost all had an effect in the growth process. However, the magnitude of the impact of climate variables is stronger in the mortality process (observed mortality rate varying between 1.6 and 2.5 % of mortality/2 years, while observed growth rates vary between 1.9 and 2.5 mm/2 years, Fig. 4).

4.1 Water stress

The water stress during the dry season, estimated with A_{under}, negatively impacts the growth and mortality processes. Trees will thus grow less quickly and have a lower probability of dying during two-year periods with the most intense dry seasons. The reduction of growth is expected, and has many ecophysiological causes. Indeed, water is essential for sap fluxes and for photosynthesis efficiency. The reduction of growth is furthermore linked with the current DBH and the species' wood density (Table 4). Big trees are more sensitive to water stress than small trees. This was expected in light of the results obtained after rainfall exclusion (da Costa et al., 2010). Indeed, maintenance costs are higher for big trees, making these trees more vulnerable to the driest periods. Regarding the wood density, species with high values are more resistant to drought. This is consistent with our hypothesis that high wood density implies thin and short xylem vessels and thus decreases the risk of embolism and cavitation. As the ability of trees to recover from periods of sustained drought is strongly related to their embolism resistance (Choat et al., 2012), a tree with high wood density will be more able to maintain growth during dry years. For similar reasons, we expected a positive impact of A_{under} on mortality, as long-time drought may increase mortality rates. Results showed the inverse pattern, but this may be explained by some field observations. After experimental trough-fall exclusions, high mortality rates were observed in Tapajos and Caxiuaña, and our results seemed to be contradictory. The real intensity of the drought during the driest seasons in our dataset is, by far, less stressful than the 50 % rainfall exclusion performed during the experiment (Nepstad, 2002). Moreover, our time-scale of two years and our framework prevented us from seeing long-term effects induced by repeated drought events. When plotting tree mode of death against drought estimator (A_{under}), no evidence was observed for a potential trend (Fig. 2), suggesting that standing death is not more frequent during the driest periods. To conclude, our results confirmed that the relationship between drought and mortality may be challenging to estimate and to link with their underlying causes at an inter-annual time scale.

4.2 Water saturation

Water saturation had a strong effect on mortality; mortality rate varied between 1.5 and 2 % per 2 years with increasing total precipitation. This is consistent with the hypothesis that trees are more vulnerable when the soil is saturated. When looking at the cause of tree death, about half of tree deaths are due to standing death and half to tree-fall. This ratio is strongly correlated with precipitation, and when the precipitation increased, the mode of death is mostly tree-fall (Fig. 2). This confirms the observation of Ferry et al. (2010) and the hypothesis that waterlogged soils in space or in time are risky for trees. Moreover, during the rainy season, strong rainfall events often come with strong winds that may accelerate this process (Toledo et al., 2011). Studies observing a relationship between tree mortality and excess of water in the soil primarily focus on geographical variation (Ferry et al., 2010; de Toledo et al., 2012) and conclude that excess water in the soil restricts root establishment because productivity of fine roots and rooting depth are generally low in sandy soils and soils with high moisture content. Our results highlight that the time dimension is also very important and should be reassessed.

4.3 Temperature

Temperature is identified as predictor of trees' decreasing growth. As the temperature rises, the velocity of reacting molecules increases, leading to more rapid reaction rates but also to damage of the tertiary structures of the enzymes and reduced enzyme activity and reaction rates (Fitter and Hay, 2001; Lloyd and Farquhar, 2008). These two processes are responsible for a bell-shaped curve of growth response to temperature (Fitter and Hay, 2001). Temperature can affect photosynthesis through modulation of the rates of activity of photosynthetic enzymes and the electron transport chain, and in a more indirect manner, through leaf-temperatures defining the magnitude of the leaf-to-air vapour pressure difference, a key factor influencing stomatal conductances (Lloyd and Farquhar, 2008). In tropical forests, as temperatures are already high, rising temperatures may imply lower growth, consistent with results from Clark et al. (2003). This temperature effect may become the most problematic for forest dynamics, considering the rising temperatures that are predicted, with a great degree of certainty, by climate models for the next century (Stocker et al., 2013). As no consensus has been reached yet, additional studies using regular inventories are urgently needed (Reed et al., 2012; Corlett, 2011) to explain the conflicting patterns found in the extant literature (Dong et al., 2012).

5 Conclusions

Our study highlights the complex link between the various components of the climate and tropical forest dynamics. Our modelling framework allows us to study inter-annual variations of climatic variables and identify which of these climatic variables are the drivers of tree dynamics in the study site of Paracou, French Guiana. Drought, precipitation and temperature were highlighted as strong drivers of tree growth and/or mortality. Drought is expected to become longer and stronger in the future; precipitation is expected to be drastically reduced, and the temperature will rise drastically during the next century. Thus, in light of our results, raising awareness of the potential impacts of climate changes on tropical forest dynamics is urgent.

Appendix A: Growth-mortality model

Growth and mortality processes were linked through tree vigour and are parametrized simultaneously. If tree i stays alive, it grows at a growth rate $\mathrm{AGR}_{i,s,t}$, and its diameter $D_{i,t-1}$ becomes $D_{i,t}$. The joint model likelihood is then

$$\prod_{t=1}^{n} f(D_{i,t}|D_{i,t-1}) \cdot (1 - p_{i,s,t}) \tag{A1}$$

if tree i stays alive during the length of the studied period,

$$p_{i,s,k} \cdot \prod_{t=1}^{k-1} \left(f(D_{i,t}|D_{i,t-1}) \cdot (1 - p_{i,s,t}) \right) \tag{A2}$$

if tree i dies between time $k-1$ and time k, where

- $f(D_{i,t}|D_{i,t-1})$ is the probability density for a tree with diameter $D_{i,t-1}$ at time $t-1$ to have a diameter $D_{i,t}$ at time t; this quantity is used to compute the vigour estimator.
- $p_{i,s,t}$ is the probability of dying between time $t-1$ and time t, which depends on the vigour estimator, added in the model by multiplying the vigour estimator by β_0.

The model computes a mortality probability $p_{i,s,t}$ and a predicted growth rate $\widehat{\mathrm{AGR}}_{i,s,t}$.

Appendix B: Growth and mortality simulations for Oxandra and Hevea

Simulations presented in Fig. 3 are realized using median values for tree functional traits. These median values do not have any ecological meaning, and the figure was realized only to show how climatic drivers impact the tree growth and mortality in reality

(Fig. 4) and in our model (Fig. 3). To show more realistic simulations, the same patterns are plotted for two species that differ in their ecological strategies in Fig. 5. The first column shows the simulated dynamics of *Oxandra asbeckii*, a relatively small tree. The second column shows the simulated dynamics of *Hevea guianensis*, which is a canopy tree reaching heights of 50 m and which has a low wood density. These two strongly contrasting species show two different growth and mortality rates, although the effects of climatic drivers stay the same.

Acknowledgements. Funding came from the Climfor Project (Fondation pour la Recherche sur la Biodiversité) and from the Guyasim Project (European structural funding, PO-feder). The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript. This work also benefited from an "Investissement d'Avenir" grant managed by the Agence Nationale de la Recherche (CEBA, ref ANR-10-LABX-0025) and from a grant from the Centre de Coopération Internationale en Recherche Agronomique pour le Développement.

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Table 1. The five functional traits used in the growth-mortality model. Descriptions of the traits, abbreviations used in this study and ranges observed in our data set.

Functional traits	Abbreviation	Range
Maximum diameter (m)	DBHmax	[0.13;1.11]
Maximum height (dm)	Hmax	[0.8;5.6]
Trunk xylem density (g cm^{-3})	WD	[0.28;0.91]
Laminar toughness (N)	Tough	[0.22;11.4]
Foliar δ13C composition (%)	δ13C	[–3.61;–2.62]

Table 2. The climate variables included in the growth-mortality model. Descriptions of the climate variables, abbreviations used in this study, ranges observed in our data set, and sources used to compute the variables: CRU means that the variable is provided by the Climate Research Unit (Mitchell and Jones, 2005), and REW means that the variable is computed from the water balance model of Wagner et al. (2011).

Variable	Abbreviation	Range	Source
Cloud cover (%)	Cld	[56.85417;60.70833]	CRU
Potential evapo-transpiration (mm)	Pet	[80.4;84.4]	CRU
Precipitation (mm)	Pre	[5486.3;6207.3]	CRU
Daily mean temperature (°C)	Tmp	[26.12917;26.91667]	CRU
Vapour pressure (HPA)	Vap	[705.7;724.7]	CRU
Wet day frequency (days)	Wet	[385.23;432.12]	CRU
Number of days with REW < 0.4	$\mathrm{Nb}_{\mathrm{under}}$	[89;170]	REW
Area over REW and < 0.4	A_{under}	[9.05203;32.96535]	REW
Area under REW and > 0.95	A_{over}	[8.274586;12.485895]	REW

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Table 3. Results of the estimation process for each parameter associated with the climate variables. The variables were added in the growth process or in the mortality process in an univariate way, i.e., one by one, and all parameters were estimated using a Metroplis-Hastings algorithm. Only significant results are represented.

	Growth		Mortality	
Variable	Estimator	95 % credibility interval	Estimator	95 % credibility interval
Cld	0.027	[0.025;0.029]	–	–
Pet	−0.033	[−0.035;−0.031]	–	–
Pre	–	–	0.00035	[0.00022;0.00048]
Tmp	−0.17	[−0.25;−0.06]	–	–
Vap	−0.0048	[−0.0052;−0.0043]	–	–
Wet	0.0010	[0.0006;0.0014]	–	–
$\mathrm{Nb}_{\mathrm{under}}$	−0.0017	[−0.0023;−0.0011]	−0.0026	[−0.0035;−0.0018]
A_{under}	−0.0060	[−0.0076;−0.0042]	−0.0075	[−0.0113;−0.0039]
A_{over}	−0.013	[−0.015;−0.011]	–	–

Table 4. Functional variability of responses to climate variables. The functional variability is included in the model with an interaction term, i.e., multiplying a climatic variable with a given tree feature. Most hypotheses were not verified, but two significant effects are highlighted: large trees reduce their growth more during dry years, and trees with high wood density reduce their growth less during dry years.

Process	Climatic variable	Tree feature	Expected effect	Reference	Result
growth	A_{under}	DBH	Big trees reduce their growth more during drought	Condit et al. (2004)	as expected
	A_{under}	DBH$_{\text{max}}$-DBH	Small trees reduce their growth more during drought	Hanson et al. (2001)	no result
	A_{under}	WDmax-WD	Trees with high wood density reduce their growth less during drought	Markesteijn (2010)	as expected
mortality	A_{under}	DBH	Big trees have a higher probability of dying during drought	Nepstad et al. (2007)	no result
	A_{under}	DBH$_{\text{max}}$-DBH	Small trees have a higher probability of dying during drought	Hanson et al. (2001)	no result
	A_{under}	WDmax-WD	Trees with high wood density better resist drought	Phillips et al. (2009)	no result
	Pre	DBH	Big trees have higher probability of falling during high precipitation	Ferry et al. (2010)	no result

Table 5. Result of the estimation process for the final model. The Metropolis-Hastings algorithm ran with 2000 iterations, burning of 1000 iterations, thinning of 10 iterations.

Process	Variable	Parameter	Estimator	95 % credibility interval
mortality	vigour	θ_1	−0.52	[−0.56;−0.49]
	DBH/DBHmax	θ_2	−0.61	[−1.03;−0.30]
	$(\text{DBH}/\text{DBHmax})^2$	θ_3	0.48	[0.30;0.77]
	Hmax	θ_4	−0.40	[−0.44;−0.36]
	WD	θ_5	−2.8	[−3.0;−2.5]
	Tough	θ_6	−0.36	[−0.41;−0.30]
	Pre	γ_1	0.00032	[0.00021;0.00044]
	A_{under}	γ_1	−0.0053	[−0.0087;−0.0023]
growth	DBHmax	θ_7	1.81	[1.78;1.84]
	WD	θ_8	−0.40	[−0.44;−0.35]
	Hmax	θ_9	−0.063	[−0.070;−0.057]
	δ13C	θ_{10}	−0.21	[−0.22;−0.20]
	Dopt DBHmax	θ_{11}	0.80	[0.76;0.84]
	K WD	θ_{12}	2.36	[2.27;2.44]
	tmp	γ_2	−0.067	[−0.093;−0.045]
	A_{under}	γ_2	−0.0049	[−0.0054;−0.0044]
	ε	γ_{13}	0.579	[0.576;0.583]

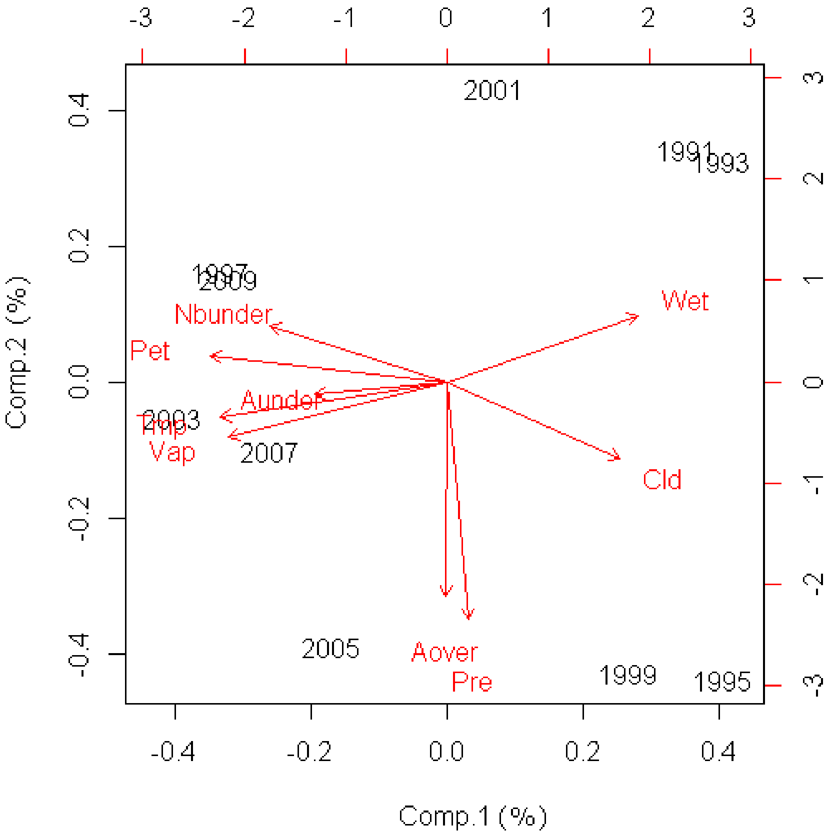

Figure 1. Results of the principal component analysis performed on climatic variables. The first axis (46 % of variance) is mainly driven by the variables Pet (potential evapo-transpiration) and tmp (temperature). The second axis (20 % of variance) is mainly driven by A_{over} (area over REW and < 0.4) and Pre (precipitation) and may be interpreted as an axis representing the excess of water. The third axis (not represented here, 13 % of variance), is mainly driven by A_{under} (area under REW and > 0.95), which is an indicator of water stress.

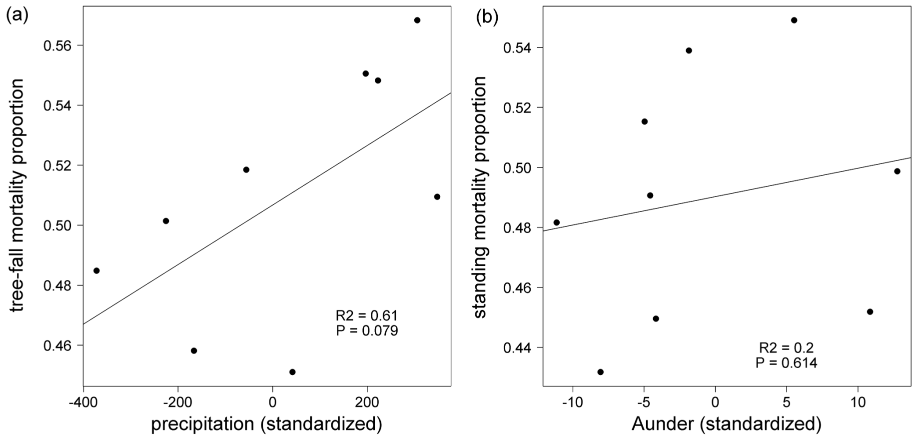

Figure 2. Proportion of dead trees caused by tree-fall plotted against the climate variable Pre **(a)** and proportion of dead trees caused by standing death plotted against the climate variable A_{under} **(b)**. About 50 % of tree deaths are tree-fall; this proportion is higher during 2 years periods with high precipitation. No significant correlation between the mode of death and the drought intensity A_{under} was noted.

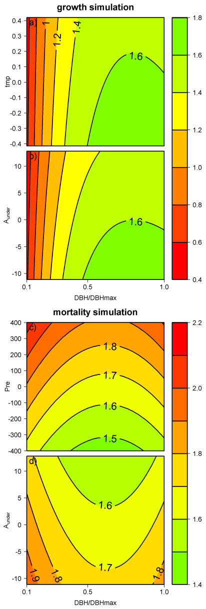

Figure 3. Climatic drivers of tree dynamics. Simulations are made using median values for tree functional traits. Growth (in mm/2 years) is computed with varying temperature **(a)** and with varying water stress **(b)** and is plotted against the ontogeny (DBH/DBHmax). Growth rises with reduced temperature and reduced water stress. This is more noticeable for large values of DBH/DBHmax, which means for large, old trees. Mortality (% per 2 years) is computed with varying precipitation **(c)** and with varying water stress **(d)** and is plotted against the ontogeny (DBH/DBHmax). Mortality rate rises with rising precipitation and reduced water stress. This illustration clearly shows the effects of climate variables and ontogeny on tree growth and mortality, but the median functional traits used do not represent a real "mean" tree. To evaluate more precisely the dynamics for two different species, we plotted the same curves for *Oxandra Asbeckii* and *Hevea guianensis* in Appendix B.

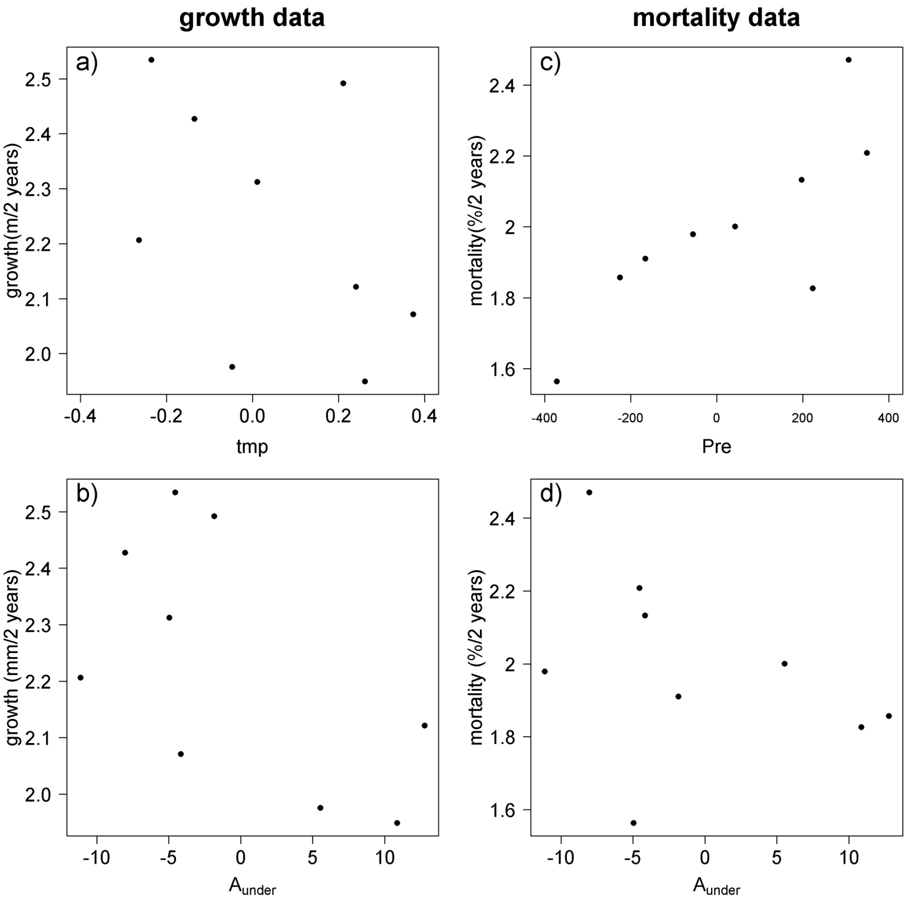

Figure 4. Climatic drivers of tree dynamics. Observed mean growth (mm/2 years) is plotted against temperature **(a)** and against the water stress **(b)**. Observed mortality rate (proportion / 2 years) is plotted in abscissa against precipitation **(c)** and against the water stress **(d)**.

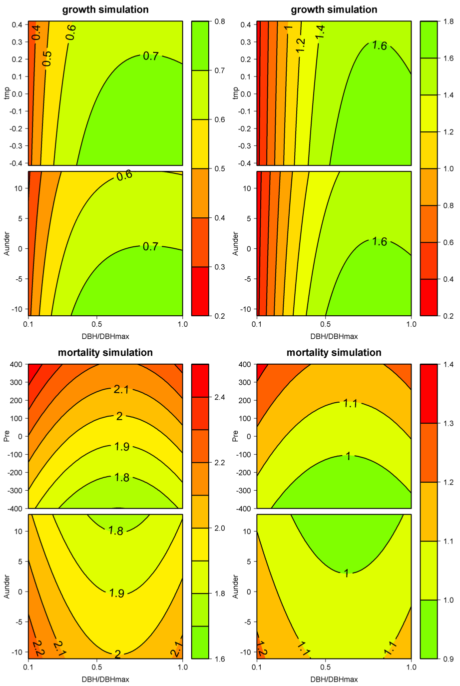

Figure 5. Predictions of growth and mortality depending of climatic drivers for *Oxandra asbeckii* and *Hevea guianensis*. Simulations are made using the functional traits values of the species *Oxandra asbeckii* (left) and *Hevea guianensis* (right). Growth (in mm/2 years) is computed with varying temperature (first line) and with varying water stress (second line), and is plotted against the ontogeny (DBH/DBHmax). Growth rises with reduced temperature and reduced water stress. This is more noticeable for large values of DBH/DBHmax, which means large, old trees. Mortality (% per 2 years) is computed with varying precipitation (third line) and with varying water stress (fourth line) and is plotted against the ontogeny (DBH/DBHmax). Mortality rate rises with rising precipitation and reduced water stress.