

Identifying climatic drivers of tropical forest dynamics

M. Aubry-Kientz¹, V. Rossi^{2,3,4}, F. Wagner^{2,5}, and B. Hérault²

¹Université des Antilles et de la Guyane, UMR ‘Ecologie des Forêts de Guyane’, Campus agronomique de Kourou, France.

²CIRAD, UMR ‘Ecologie des Forêts de Guyane’, Campus agronomique de Kourou, France.

³CIRAD, UPR Bsef, Montpellier, France.

⁴Université de Yaoundé I, UMMISCO (UMI 209), BP337, Yaoundé, Cameroun.

⁵Remote sensing division, National Institute for Space Research-INPE, São José dos Campos, SP, Brazil.

Correspondence to: B. Hérault
(bruno.herault@cirad.fr)

Abstract. In the context of climate change, identifying and then predicting the impacts of climatic drivers on tropical forest dynamics is becoming a matter of urgency. To look at these climate impacts, 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.

sonal tree demography to climate seasonality (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 proxy 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). Similar major mortality events were observed in Panama (Condit, 1995), in chinese rainforests (Tan et al., 2013) or in South-East Asia (Slik, 2004). Water exclusion experiments in Brazil provide results in line with a deep impact of drought on tree mortality (Nepstad et al., 2007; da Costa et al., 2010; Brando et al., 2008). Between the time scale of exceptional events and the time-scale of intra-annual seasonal rhythmicity, there is a gap in our knowledge on the inter-annual scale. 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 to 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 precise climatic data on the same time-scale are available. Moreover, the potential links between inter-annual

1 Introduction

Tropical forests are characterized by high annual precipitation and high evapotranspiration. Nevertheless, strong seasonal variations in rainfall inputs, partly driven by atmospheric movements related to the monsoon or latitudinal changes in the inter-tropical convergence zone, occur in most tropical regions around the world (Feng et al., 2013). Such seasonality 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 increasingly studied in tropical forests, with some studies having succeeded in linking sea-

climate variations and tropical forest dynamics should be studied from a multi-decadal long-term perspective in order to be representative of the climatic variability and of the variability of forest dynamic responses (Clark et al., 2010).

Some climatic variables (mainly water stress, water saturation and temperature) 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 relative extractable water (REW) described in the study of Wagner et al. (2011) estimates the quantity of water available for tree development and has been proved to be highly performant to predict 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 use a modelling approach in order to mechanistically link climate conditions and functional plant traits to tree growth and survival (Zuidema et al., 2013). 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). We first question 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 (wood density and tree size) and climate predictors to test for a potential differentiated response depending on the individual functional identity. First, tree species having high wood density have been reported to better resist drought events as compared to lower density ones (Phillips et al., 2010). Part of these differences is related to differences in hydraulic failure, as wood density is linked to xylem structure. Second, the current tree size also influence resistance to drought events or other climatic perturbations (Nepstad et al., 2007; Condit et al., 2004). Two main hypotheses are debated. 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 water from tree roots to a higher altitude in the forest canopy.

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 breast 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 (Wagner et al., 2011), and less than 100 mm per month from August to November (Figure 11).

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 height because we were unsure about the height of the initial points of measurement for these trees. The data set contained 20,340 trees from 642 species. 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 220
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
(Table 11). These 335 species represent 79% of the total
number of individual trees included in this study. We used
the procedure described in Aubry-Kientz et al. (2013) to as- 230
sign functional trait values to trees for which (i) the species
is known but trait values were not available, (ii) the species
was not determined at the species level and (iii) the tree was
dead before being identified. Traits are related to leaf eco-
nomics, stem economics and life history and are extracted 235
from a large database (Baraloto et al., 2010a, b).

The leaf economics reflects a trade-off between investments
in productive leaves with rapid turnover versus costly phys-
ical leaf structure with a longer payback. The stem economics
defines a similar trade-off at the stem level: dense wood ver- 240
sus high wood water content and thick bark (Baraloto et al.,
2010b). Life-history strategies describe how trees allocate re-
sources 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). 245
Some of these functional traits are accurate proxies of growth
trajectories (Héroult et al., 2010; Héroult et al., 2011) and
mortality rates (Aubry-Kientz et al., 2013).

2.1.3 Climate

The third data set consists of climate data (Table 12). 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 250
(0.5*0.5 degree) (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). Se-
lected variables that may have an impact on forest dynamics
are the cloud cover (*Clid*), the potential evapo-transpiration
(*Pet*), the precipitation (*Pre*), the daily mean temperature
(*Tmp*), the vapour pressure (*Vap*) and the wet day frequency 255
(*Wet*).

Three other climate variables were computed using the re-
lative extractable water (REW) computed with a water bal-
ance 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 Nb_{under} , the 260

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 indi-
cators of drought, while A_{over} is related to soil water sat-
uration. 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 model is build taking advantage of two prelimi-
nary studies where the growth (Héroult et al., 2011) and the
mortality (Aubry-Kientz et al., 2013) sub-models were de-
veloped. The likelihood is computed using the distribution
probability of mortality (equations 3 and 4) and the computed
growth rate (equations 5 and 6). A vigour index is added into
the mortality process, taking the past growth of the two previ-
ous year into account (Aubry-Kientz et al., 2015). We added
the climate variables into the two processes to highlight the
links between some climate drivers and one particular pro-
cess. Because the final forest dynamic model was not linear,
we build a MCMC algorithm under a bayesian framework
to infer the parameter posterior distributions. Growth and
mortality processes were linked through tree vigour and are
parametrized simultaneously. If tree i stays alive, it grows at
a growth rate $AGR_{i,s,t}$, and its diameter $DBH_{i,t-1}$ becomes
 $DBH_{i,t}$. The joint model likelihood is then

$$\prod_{t=1}^n f(DBH_{i,t}|DBH_{i,t-1}) * (1 - p_{i,s,t}) \quad (1)$$

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

$$p_{i,s,k} * \prod_{t=1}^{k-1} (f(DBH_{i,t}|DBH_{i,t-1}) * (1 - p_{i,s,t})) \quad (2)$$

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

- $f(DBH_{i,t}|DBH_{i,t-1})$ is the probability density for a
tree with diameter $DBH_{i,t-1}$ at time $t - 1$ to have a
diameter $DBH_{i,t}$ at time t ; this quantity is used to com-
pute 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 θ_1 .

The model computes a mortality probability $p_{i,s,t}$ and a pre-
dicted growth rate $\widehat{AGR}_{i,s,t-1}$.

$$p_{i,s,t} = \text{logit}^{-1} \left(\gamma_1 \times \text{clim}_1 + \theta_1 \times \text{Vigour}_{i,s,t} \right. \\ \left. + \theta_2 \times \frac{\text{DBH}_{i,s,t-1}}{\text{DBHmax}_s} + \theta_3 \times \left(\frac{\text{DBH}_{i,s,t-1}}{\text{DBHmax}_s} \right)^2 \right. \\ \left. + \theta_4 \times \text{Hmax}_s + \theta_5 \times \text{WD}_s + \theta_6 \times \text{Tough}_s \right) \quad (3)$$

with

$$\text{Vigour}_{i,s,t} = \log \left(\frac{\text{AGR}_{i,s,t-1} + 1}{\widehat{\text{AGR}}_{i,s,t-1} + 1} \right), \quad (4)$$

and

$$\log(\widehat{\text{AGR}}_{i,s,t-1} + 1) = (\gamma_2 \times \text{clim}_2 + \theta_7 \times \text{DBHmax}_s + \theta_8 \times \text{WD}_s + \theta_9 \times \text{Hmax}_s + \theta_{10} \times \delta 13C_s) * \\ \exp \left(-\frac{1}{2} \left(\frac{\log \left(\frac{\text{DBH}_{i,t-2}}{\theta_{11} \times \text{DBHmax}_s} \right)}{\theta_{12} \times \text{WD}_s} \right)^2 \right), \quad (5)$$

and

$$\log(\text{AGR}_{i,s,t-1} + 1) = \log(\widehat{\text{AGR}}_{i,s,t-1} + 1) + \varepsilon_i, \quad (6)$$

with

$$\varepsilon_i \sim \mathcal{N}(0, \theta_{13}). \quad (7)$$

where $p_{i,s,t}$ is the probability of dying of tree i of species s between time $t-1$ and t ; $\widehat{\text{AGR}}_{i,s,t-1}$ is the predicted growth between time $t-2$ and time $t-1$. $\text{AGR}_{i,s,t-1}$ is the observed growth between time $t-2$ and time $t-1$; DBHmax_s , Hmax_s , WD_s , Tough_s and $\delta 13C_s$ are functional traits of species s to which tree i belongs (Table 11); $\theta_1, \theta_2, \dots, \theta_{13}$ 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 Markov Chain Monte Carlo 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 standard deviation was sampled in an inverse-gamma posterior distribution with a Gibbs sampler. The functional traits used as demographical predictors were uncertain because botanical determination was incomplete for the older censuses, and not all values of functional traits were available for all species. We used the method developed in Aubry-Kientz et al. (2013) to handle these uncertainties. All the algorithms and statistical treatments were implemented with R software (core Team, 2014).

2.5 Functional trait and forest dynamic responses

Functional traits were introduced in the final model with an interaction term by multiplying a climatic variable with a functional trait. We did not test all possible interactions but, based on results from a literature survey, we investigated biological-meaningful interactions only (Table 13). 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 .

Species vary over one order of magnitude in their wood density (WD), ranging from 0.08 to 1.39 g.cm³ (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 $(WD_{max} - WD)$ accounts for the effect of drought on trees with low wood density. This term is added in growth and mortality to test this effect (Table 13).

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 46% of the inertia and strongly negatively correlating with variables

350 *Tmp* and *Pet*. The variables *Wet* and *Cld* are positively 400
correlated with this axis, while *Vap*, A_{under} and Nb_{under}
are negatively correlated with this axis (Figure 12). The
second axis (20%) is strongly negatively correlated with *Pre*
and $Area_{over}$. The third axis (12%) is essentially negatively
355 correlated with A_{under} . 405

3.1.2 Univariate analyses

When the climate variables are included one by one in each 410
model, all climate variables but precipitation (*Pre*) had an 415
effect in the growth process, while only few had an effect
in the mortality process (Table 14). The climate variables
associated with the mortality process are *Pre*, Nb_{under} and
 A_{under} . In the growth model, A_{under} is the best predictor
according to the likelihood. In the mortality process, the best
365 value of likelihood is obtained when Nb_{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 420
tree growth (Clark et al., 2003; Dong et al., 2012). These
variables are strongly correlated ($r=0.8$) and negatively
370 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 only 425
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} ($C=-0.61$).
380 A_{over} only had an effect when included in the growth
process. However, both the effect size and the likelihood 430
(Table 14) were the worst score obtained so that we did
not include this variable in the final model. Concerning
385 mortality, *Pre* had a clear effect (Figure 13) and is thus
included as a proxy of water saturation in the final mortality
model. 435

The third axis of the PCA is strongly correlated with the
drought estimator A_{under} , which is the better climate
390 driver of growth regarding the likelihood and the effect
size. A_{under} also had an effect on the mortality process,
and is finally included in the two processes in the final model. 440

3.2 Full model inference

395 The growth trajectory was adjusted by a size-dependent di- 445
ameter growth model (Figure 14). Parameters linking the
maximal growth to the functional traits DBH_{max} , WD ,
 H_{max} and $\delta^{13}C$ have similar values and interpreta-
tions to Hérault et al. (2011), *i.e.* maximum growth rates

increase with increasing DBH_{max} , and decreasing WD ,
 H_{max} and $\delta^{13}C$ (Table 15). Maximum growth rate is at-
tained for a tree diameter equal to $0.794 * DBH_{max}$. The pa-
rameters linking the probability of mortality to H_{max} , 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 mor-
tality computed at our biannual time-scale are lower when
the drought estimator A_{under} is higher. The parameter link-
ing mortality with precipitation (*Pre*) is positive. This find-
ing implies that mortality rate is higher during two-year time-
scale with high precipitation. In our dataset, the highest to-
tal precipitation was, albeit non-significantly, rather related
to the highest proportion tree-fall deaths (Figure 15). The pa-
rameter linking temperature (*tmp*) and growth takes negative
values; thus growth values are lower during the warmest pe-
riods.

3.3 Functional variability of responses

In the growth process, interaction between ($WD_{max} - WD$)
and drought is negative (Table 13), implying that trees with
lower WD are more sensitive to drought and reduce their
growth more. Moreover, interactions linking the current di-
ameter and drought are also negative; thus larger trees are
more sensitive to drought and reduce their growth more com-
pared to smaller trees. None of the interaction terms included
in the mortality process had an effect (Table 13).

4 Discussion

In this study, we questioned the importance of the climate
drivers of tropical forest dynamics by using a community
growth-mortality modeling framework. First, one can note
that few climate variables had an univariate effect when
included in the mortality process, while almost all had
an univariate 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, Figure
13). Next, we developed bayesian algorithms to infer the
multivariate nonlinear model and select the best predictors
with a great flexibility. We found that drought decreased an-
nual growth and mortality rates, high precipitation through
soil water saturation increased mortality rates and high
temperature decreased growth (Figure 14). We confirmed
that 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. Moreover, the posterior values
for obtained the functional trait parameters are coherent

with results of H erault et al. (2011) and Aubry-Kientz et al. (2013), increasing our confidence in (i) the developed algorithm and (ii) the biological determinisms of the ecological processes we want to model. This confirms that the functional trait-based approach could be successfully used to predict climate-induced tree dynamics in highly diverse tropical forests for which taxonomic data may be lacking but functional trait data are available. A limited number of interactions between climate variables and functional traits was tested because of our selection of three climate predictors. One can argue that some climatic variables that were disregarded in the first selection 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.

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 13). 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 rates. Experimental trough-fall exclusions conducted in Tapajos and Caxiua na indeed demonstrated that 50% rainfall exclusion led to very high mortality rates (Nepstad, 2002). Our results show no positive effect of drought intensity on mortality rates (Table 14) and look contradictory to Nepstad (2002). However, the natural variability of the drought intensity (total rainfall from 5486 to 6207 mm) in our dataset is hardly comparable to the experimental 50% reduction in total rainfall. Moreover, our modeling framework prevented us from seeing long-term effects induced by repeated drought events because the drought variable values depend only on the last 2-year climate. One may also expect that standing death is more

frequent during the driest periods but, when plotting tree mode of death against drought estimator (A_{under}), no evidence was observed for a potential trend (Figure 15). 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 Pre 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 water saturated. In the Paracou forest, about half of tree deaths are due to standing death and half to tree-fall. This ratio looks, albeit non-significantly ($R^2=0.61$, $P=0.08$) because of the low number of observations ($n=9$), linked with total precipitation. The highest total precipitation led to the highest proportion tree-fall deaths (Figure 15). 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 variation in soil water saturation 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 tropical forest dynamics, considering the rising tempera-

555 tures that are predicted, with a great degree of certainty, by
climate models for the next century (Stocker et al., 2013). 605
Indeed, as temperature was identified as a strong predictor
of growth, all else being equal, averaged community growth
and forest productivity may consequently decrease in time.
560 This decline in productivity in time is perhaps what we are
starting to see throughout the Amazon (Brienen et al., 2015).
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 of
565 the temperature effect found in the extant literature (Dong
et al., 2012). Finally, we need to acknowledge that we do
not know much about how forest dynamics will behave in
the next century under temperature conditions that will be
so different from what is actually observed. In this context,
570 manipulative warming experiments are increasingly vital to
better predict the future of tropical forest dynamics (Cavaleri
et al., in press).

5 Conclusions

Global climate models converge to simulate, at least for the
Amazonian region, a change in precipitation regime and tem-
575 perature conditions over the coming decades (Malhi et al.,
2009). Drought is expected to become longer and stronger in
the future (Joetzjer et al., 2013) and the temperature will con-
tinue rising drastically during the next century (Stocker et al.,
2013). Our modelling framework allows us to study inter-
580 annual variations of climatic variables and identify which of
these climatic variables are the key drivers of tropical for-
est dynamics. Drought, precipitation and temperature were
highlighted as strong drivers of tree growth and/or mortality.
Drought decreased annual growth and mortality rates, high
585 temperature decreased growth and high precipitation events
increased mortality rates. Moreover, we demonstrated best
resistance to drought for trees with high wood density and
for trees with small current diameters, giving us some possi-
ble indications on the future composition of a tropical forest
590 where droughts are becoming more frequent. In light of these
results, raising awareness of the current impacts of climate
changes on tropical forest dynamics is urgent.

Appendix A: Growth and mortality simulations for Oxandra an Hevea

595 Simulations presented in Figure 14 are realized using me-
dian 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 (Figure 13) and in our model (Fig-
600 ure 14). To show more realistic simulations, the same pat-
terns are plotted for two species that differ in their ecologi-
cal strategies in Figure 16. The first column shows the sim-
ulated 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 me-
ters 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.

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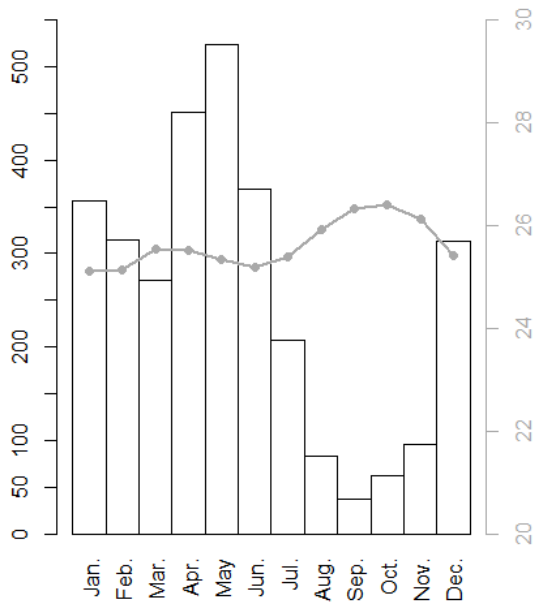


Figure 11. Ombrothermic diagram of the Paracou forest, data from the 2001-2014 time period (precipitation in m) on the left, temperature in °C on the right

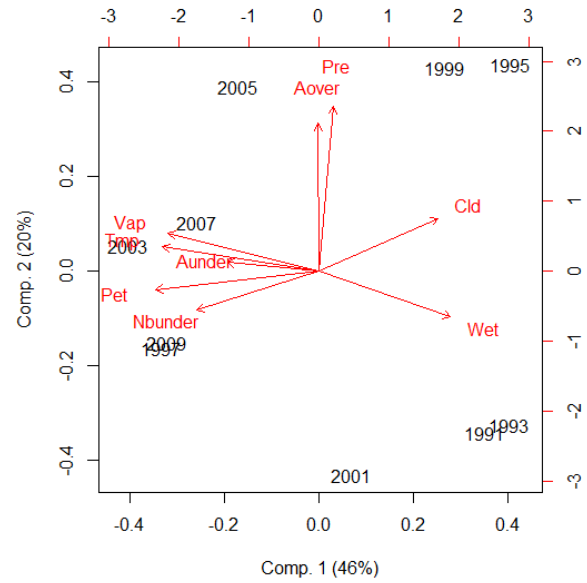


Figure 12. Results of the principal component analysis performed on climatic variables (red arrows) where census years are plotted to see the interannual climate variability in the Paracou dataset. The first axis (46% of variance) is mainly driven by the variables *Pet* (potential evapo-transpiration) 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 soil water saturation. 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.

Table 11. 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.

Biological spectrum	Functional traits	Abbreviation	Range
Life-history	Maximum diameter (m)	<i>DBH_{max}</i>	[0.13;1.11]
Life-history	Maximum height (dm)	<i>H_{max}</i>	[0.8;5.6]
Wood economics	Trunk xylem density (g.cm ⁻³)	<i>WD</i>	[0.28;0.91]
Leaf economics	Laminar toughness (N)	<i>Tough</i>	[0.22;11.4]
Leaf economics	Foliar $\delta^{13}C$ composition (‰)	$\delta^{13}C$	[-3.61;-2.62]

Table 12. The climate variables included in the growth-mortality model. Descriptions of the climate variables, abbreviations used in this study, ranges observed over two years 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 over 2 years	Source
Cloud cover (%)	<i>Cld</i>	[56.8 ; 60.7]	CRU
Potential evapo-transpiration (mm)	<i>Pet</i>	[80.4 ; 84.4]	CRU
Precipitation (mm)	<i>Pre</i>	[5486.3 ; 6207.3]	CRU
Daily mean temperature (°C)	<i>Tmp</i>	[26.1 ; 26.9]	CRU
Vapour pressure (HPA)	<i>Vap</i>	[705.7 ; 724.7]	CRU
Wet day frequency (days)	<i>Wet</i>	[385.2 ; 432.1]	CRU
Number of days with REW <0.4	<i>N_{under}</i>	[89 ; 170]	REW
Area over REW and <0.4	<i>A_{under}</i>	[9.1 ; 32.9]	REW
Area under REW and >0.95	<i>A_{over}</i>	[8.3 ; 12.5]	REW

Table 13. Functional variability of expected responses to climate variables based on the literature. 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 based on literature	Reference	Result from this study
growth	<i>A_{under}</i>	DBH	Big trees reduce their growth more during drought	Condit et al. (2004)	as expected
	<i>A_{under}</i>	<i>DBH_{max}</i> -DBH	Small trees reduce their growth more during drought	Hanson et al. (2001)	no result
	<i>A_{under}</i>	WD _{max} -WD	Trees with high wood density reduce their growth less during drought	Markestijn (2010)	as expected
mortality	<i>A_{under}</i>	DBH	Big trees have a higher probability of dying during drought	Nepstad et al. (2007)	no result
	<i>A_{under}</i>	<i>DBH_{max}</i> -DBH	Small trees have a higher probability of dying during drought	Hanson et al. (2001)	no result
	<i>A_{under}</i>	WD _{max} -WD	Trees with high wood density better resist drought	Phillips et al. (2009)	no result
	<i>Pre</i>	DBH	Big trees have higher probability of falling during high precipitation	Ferry et al. (2010)	no result

Table 14. Results of the estimation process for each demographic 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 Metropolis-Hastings algorithm. Effect sizes were estimated by multiplying the amplitude of the observed variable to the absolute value of the estimator. Only significant results are represented.

Variable	Growth			Mortality		
	Estimator	95% CI	Effect size	Estimator	95% CI	Effect size
<i>Cld</i>	0.027	[0.025;0.029]	0.10	-	-	-
<i>Pet</i>	-0.033	[-0.035;-0.031]	0.13	-	-	-
<i>Pre</i>	-	-	-	0.00035	[0.00022;0.00048]	0.25
<i>Tmp</i>	-0.17	[-0.25;-0.06]	0.13	-	-	-
<i>Vap</i>	-0.0048	[-0.0052;-0.0043]	0.09	-	-	-
<i>Wet</i>	0.0010	[0.0006;0.0014]	0.05	-	-	-
<i>Nb_{under}</i>	-0.0017	[-0.0023;-0.0011]	0.14	-0.0026	[-0.0035;-0.0018]	0.21
<i>A_{under}</i>	-0.0060	[-0.0076;-0.0042]	0.14	-0.0075	[-0.0113;-0.0039]	0.18
<i>A_{over}</i>	-0.013	[-0.015;-0.011]	0.05	-	-	-

Table 15. 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. In the growth process, variables with * are included in the exponential kernel.

Process	Variable	Parameter	Estimator	95% credibility interval
mortality	vigour	θ_1	-0.52	[-0.56;-0.49]
	DBH/DBH _{max}	θ_2	-0.61	[-1.03;-0.30]
	(DBH/DBH _{max}) ²	θ_3	0.48	[0.30;0.77]
	H _{max}	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]
	<i>Pre</i>	γ_1	0.00032	[0.00021;0.00044]
	<i>A_{under}</i>	γ_1	-0.0053	[-0.0087;-0.0023]
growth	DBH _{max}	θ_7	1.81	[1.78;1.84]
	WD	θ_8	-0.40	[-0.44;-0.35]
	H _{max}	θ_9	-0.063	[-0.070;-0.057]
	$\delta^{13}C$	θ_{10}	-0.21	[-0.22;-0.20]
	DBH _{max} *	θ_{11}	0.80	[0.76;0.84]
	WD*	θ_{12}	2.36	[2.27;2.44]
	<i>tmp</i>	γ_2	-0.067	[-0.093;-0.045]
	<i>A_{under}</i>	γ_2	-0.0049	[-0.0054;-0.0044]
	ϵ	γ_{13}	0.579	[0.576;0.583]

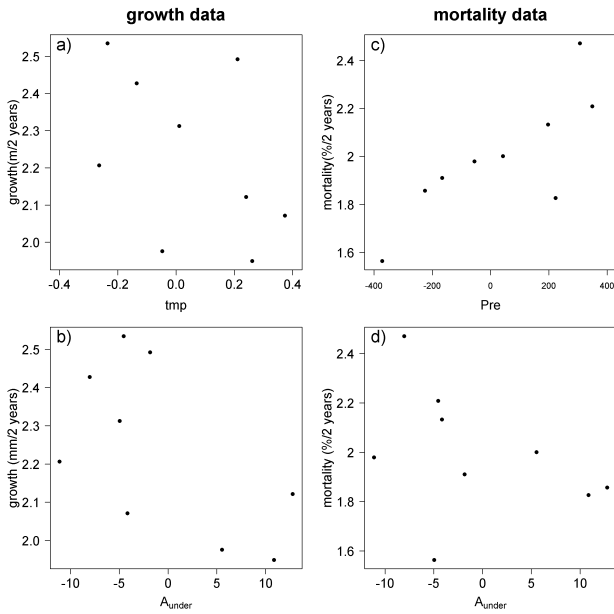


Figure 13. Climatic drivers of tree dynamics. Observed mean growth (mm / 2 years) is plotted against temperature (a) and against the water stress (b). Observed mortality rate (proportion / 2 years) is plotted in abscissa against precipitation (c) and against the water stress (d).

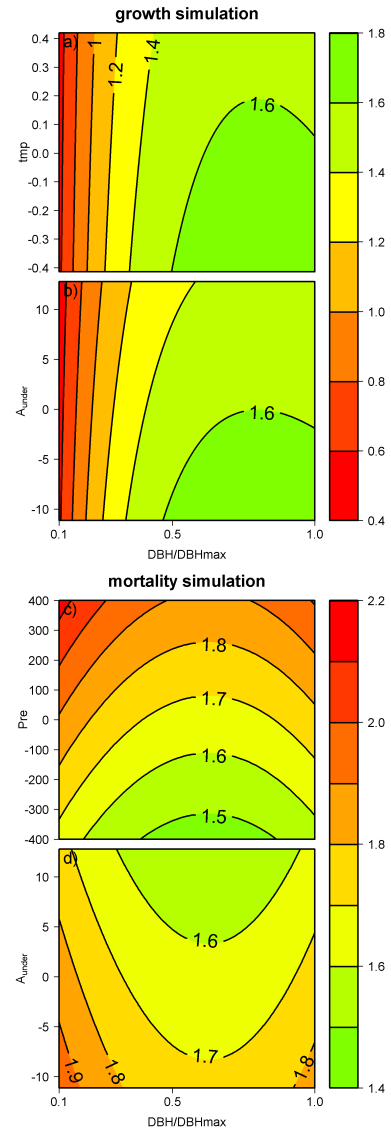


Figure 14. Climatic drivers of tree dynamics. Simulations are made using median values for tree functional traits. Growth (in mm / 2 years) is computed with varying temperature (a) and with varying water stress (b) and is plotted against the ontogeny (DBH/DBHmax). Growth rises with reduced temperature 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 A.

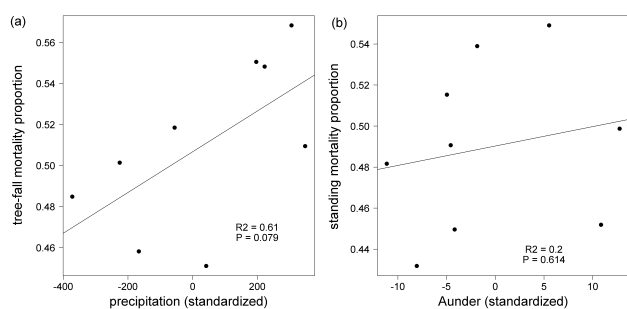


Figure 15. Proportion of dead trees caused by tree-fall plotted against the climate variable Pre (a) and proportion of dead trees caused by standing death plotted against the climate variable A_{under} (b). About 50% of tree deaths are tree-fall; this proportion is quite higher but not significant (F-statistic test, $P=0.079$) during 2-yr periods with high precipitation. No significant correlation (F-statistic test, $P=0.814$) between the mode of death and the drought intensity A_{under} was noted.

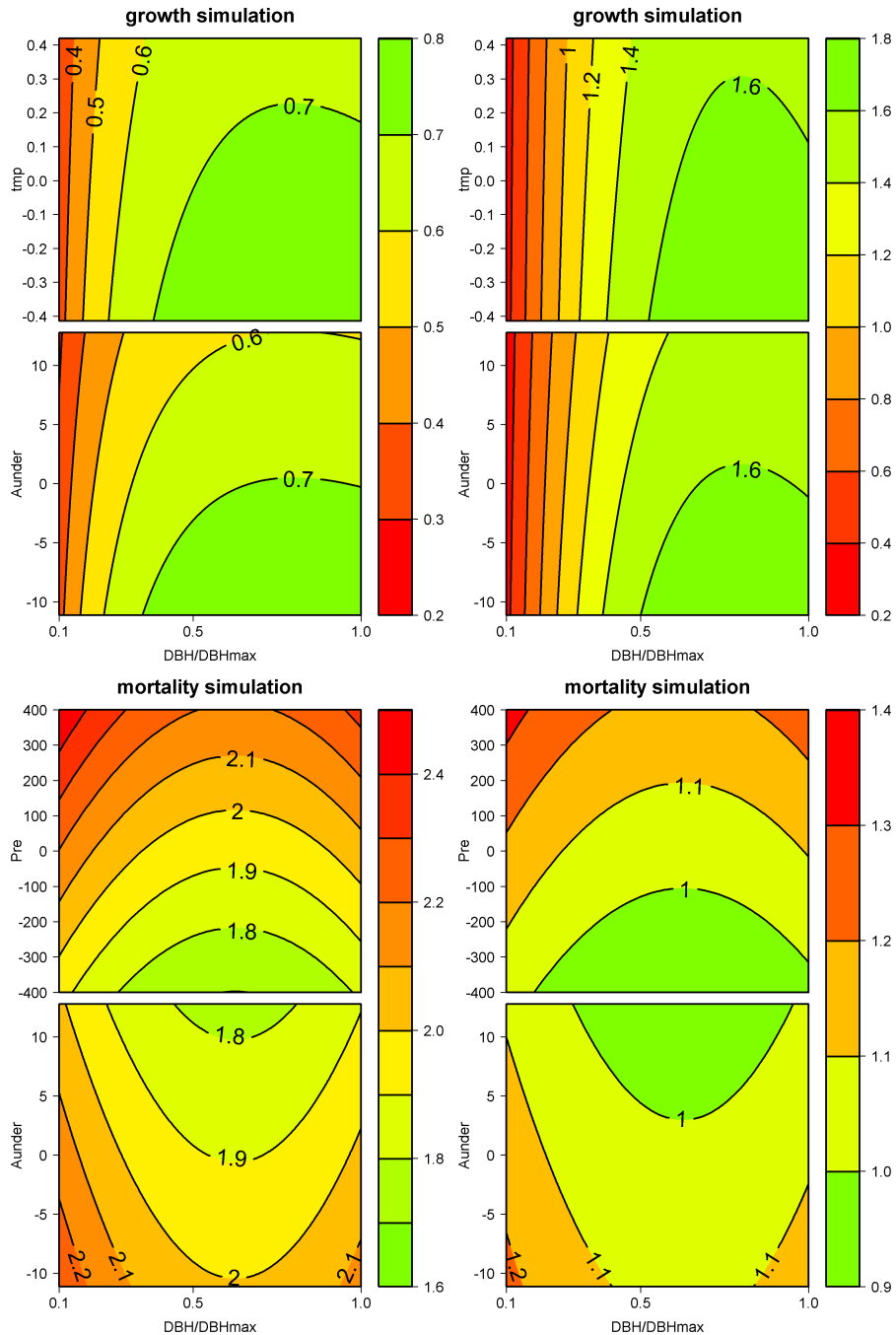


Figure 16. Predictions of growth and mortality depending of climatic drivers for *Oxandra asbeckii* and *Hevea guianensis*. Simulations are made using the functional traits values of the species *Oxandra asbeckii* (left) and *Hevea guianensis* (right). Growth (in mm / 2 years) is computed with varying 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.