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Vulnerability of Commercial Tree Species to Water Stress in Logged Forests of the Guiana Shield

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Abstract: The future of tropical managed forests is threatened by climate change. In anticipation of the increase in the frequency of drought episodes predicted by climatic models for intertropical regions, it is essential to study commercial trees' resilience and vulnerability to water stress by identifying potential interaction effects between selective logging and stress due to a lack of water. Focusing on 14 species representing a potential or acknowledged commercial interest for wood production in the Guiana Shield, a joint model coupling growth and mortality for each species was parametrized, including a climatic variable related to water stress and the quantity of aboveground biomass lost after logging. For the vast majority of the species, water stress had a negative impact on growth rate, while the impact of logging was positive. The opposite results were observed for the mortality. Combining results from growth and mortality models, we generate vulnerability profiles and ranking from species apparently quite resistant to water stress (*Chrysophyllum* spp., *Goupia glabra* Aubl., *Qualea rosea* Aubl.), even under logging pressure, to highly vulnerable species (*Sterculia* spp.). In light of our results, forest managers in the Guiana Shield may want to conduct (i) a conservation strategy of the most vulnerable species and (ii) a diversification of the logged species. Conservation of the already-adapted species may also be considered as the most certain way to protect the tropical forests under future climates.

Keywords: climate change; growth rates; mortality rates; Paracou; selective logging

1. Introduction

Undergoing climate changes will have serious impacts on tropical forests [1,2], particularly in the Amazon Basin [3], resulting from changes in rainfall patterns and increased water stress [4]. A consensus has emerged on the lengthening and strengthening of the drought periods regarding precipitation predicted by models of the Intergovernmental Panel on Climate Change (IPCC) [5]. Moreover, the variability of the dry season length in Amazonia [6] has been underestimated in the climate models used for the IPCC 5th assessment report so that the projected changes of the dry-season length are likely to be the lower bound of the ongoing changes [7]. Recent studies have tried to understand the potential impact of this increase in water stress on tropical forests [8–12].

A consensus about higher mortality due to high drought has emerged, thanks to the large number of studies on the effect of the intense droughts of 2005 and 2010 in Amazonia [13,14] and to results of experimental droughts in Brazil [15,16]. Recently, [17] showed that the response of wood production to anthropogenic climate change not only depends on the physiological responses of individual trees, but is also highly contingent on whether forests adjust in composition and structure. Indeed, some studies have shown that mortality results from interactions between climate and competition on an individual scale [18], but competition is hard to estimate [19,20] and is consequently seldom included in models of forest response to climate change.

Half of standing tropical forests, up to 400 million hectares, is designated by national forest services for timber production [21]. In this context, clarifying the role of tree harvesting in forest management under future climates is essential. Selective logging has been recognized as one of the less disturbing land-use changes [22]. As a result, sustainable logging through reduced-impact rules is often promoted as the best way to both develop local economy and to preserve large rainforest areas. However, this "middle-way" between deforestation and integral conservation is politically charged, and sustainability remains poorly defined [23]. Indeed, logging unavoidably causes carbon loss for decades [24,25], while logging impacts on biodiversity are more difficult to quantify [26]. Additionally, it may also be expected that selective logging reduces water competition for residual trees, so that the simultaneous effect of increased water stress and logging activities could interplay to shape the response of production forests to undergoing climate changes [2,27–29]. Two theoretical hypotheses are debated in the current literature. (i) Logging is known to modify the floristic composition of the forest, for example in logging gaps where the installation of pioneer species is highly favored [30]. Logging could, as a result, have a negative effect on the global ecosystem resistance to water stress because these pioneer species, which allocate their resources for a fast growth, are less resistant to water stress [31]. (ii) Logging activities create canopy openings that expose understorey trees to sunlight of increased duration and intensity [32]. As a consequence, resource competition, especially for light and water, between surviving trees strongly decreases immediately after logging, and this promotes rapid growth of residual trees [28,33,34]. In this way, logging would have a beneficial impact on the resilience of tropical rainforests to water stress by reducing the competition for resources and, thereby, reducing: (i) water-stress induced mortality; and (ii) water-stress-induced growth slowing.

Presently, the extension of areas devoted to forest production is particularly rapid in the neotropics, even in the most sparsely-populated forests, such as in the Guiana Shield [35]. For example, in Suriname, production areas have increased from 2.5 M–4.0 M ha in the last twenty years when timber production has doubled from 200,000–400,000 m^3 in the last three years. In French Guiana, forests areas managed for production also increased by 2.2 M ha in the last twenty years, but mean annual timber production is still limited to about 75,000 m^3, with a very low logging rate of one to six trees ha^{-1} [36]. It is expected that the timber demand will increase, as demographic projections forecast a doubling of the Guianan population before 2030. In both countries, timber selection is concentrated on a few species: *Dicorynia guianensis* Amsh. (common name: Angélique) and *Qualea rosea* (Gongolo Rose) constitute 60% of the wood logged in French Guiana and 35% of the wood logged in Suriname.

Studies about the possible interactions between climate and logging on forest dynamics are hampered by data availability [18]. The intervals between censuses are often long [37], and climatic variables need to be aggregated over these long periods, erasing exceptionally wet or dry seasons' effects. In this study, we took advantage of a 75-ha forest dynamic dataset from a long-term logging experiment, where all trees with DBH > 10 cm were censused every two years over a 20-year post-logging period. Fourteen forest species (Table 1) were identified, together with forest managers, as potentially interesting for the Guianan timber industry using criteria, including natural abundance [38], current level of exploitation or future logging potential.

We tackle two questions: (i) How will these commercial species respond, in terms of demographic rates, to the increase in water stress induced by climate change? (ii) Will logging and water stress interact, making some species more vulnerable than others?

Table 1. List of the commercial species taken into account in the study. Reported are the number of trees, the range in diameter and the percentage of biomass (before logging) in the 12 plots of the study site in Paracou, French Guiana. The current exploitation level was calculated as the relative percentage of extracted timber volumes during the last 25 years in French Guiana.

Common Name	Taxonomic Identification	Number of Trees	DBH Range (cm)	% Biomass	Exploitation Level
Angélique	*Dicorynia guianensis* Amsh.	647	(10.00–99.63)	2.40	41.63%
Balata Franc	*Manilkara bidentata* (A.DC.) Chevalier	138	(10.00–102.50)	0.77	2.28%
Balata Pomme	*Chrysophyllum* spp.	205	(10.00–59.36)	1.62	0.04%
Boco	*Bocoa prouacensis* Aubl.	1135	(10.00–68.75)	2.51	0.01%
Carapa	*Carapa surinamensis* Miq.	702	(10.00–63.66)	0.70	0.04%
Gonfolo Gris	*Ruizterania albiflora* (Warm.) Marcano-Berti	73	(10.00–81.01)	0.59	1.43%
Gonfolo Rose	*Qualea rosea* Aubl.	669	(10.00–105.99)	4.50	21.12%
Goupi	*Goupia glabra* Aubl.	291	(10.00–95.49)	1.29	1.89%
Grignon Franc	*Sextonia rubra* (Mez) van der Werff	188	(10.00–126.68)	1.23	8.94%
Kobe	*Sterculia* spp.	460	(10.00–73.68)	0.73	0.0003%
Manil Marécage	*Symphonia* spp.	69	(10.00–75.28)	2.30	0.0003%
Wacapou	*Vouacapoua americana* Aubl.	874	(10.00–106.31)	3.44	1.29%
Wapa	*Eperua falcata* Aubl.	2628	(10.00–103.13)	10.17	0.49%
Yayamadou Montagne	*Virola michelii* Heckel	344	(10.00–61.27)	0.27	0.26%

2. Materials and Methods

2.1. Site Characteristics

The study was conducted using data from the Paracou experimental site (5°18′ N, 52°55′ W), a lowland tropical rain forest near Sinnamary, French Guiana. It is typical of Northern Guianan *terra firme* rain forests [39,40], with a high species diversity (more than 500 woody species attaining 10 cm diameter at breast height (DBH) found at the site) and dominant tree families including *Fabaceae*, *Chrysobalanaceae*, *Lecythidaceae*, *Sapotaceae* and *Burseraceae*. Nearly two-thirds of the annual 3040 mm of precipitation are between mid-March and mid-June, followed by a long dry season from mid-August to mid-November [41]. Most common soils in Paracou are acrisol, limited in depth by a transformed loamy saprolite ($\leq$1 m deep), which has a low permeability and leads to lateral drainage during heavy rains [42].

2.2. Data

Twelve plots of 6.25 ha each were established in 1984 for a complete annual inventory of all trees $\geq$10 cm of diameter at breast height (DBH). These plots underwent 3 different logging treatments between October 1986 and May 1987, with 3 plots assigned as controls. An average of 10 trees $\geq$50 cm DBH (Treatment 1), 40 trees $\geq$40 cm DBH (Treatment 2) and 45 trees $\geq$40 cm DBH (Treatment 3) were removed per hectare. Forest inventories have been conducted since 1984 (Table 2). Censuses of mortality, recruitment and diameter growth were conducted every year until 1995 and every 2 years thereafter. DBH was calculated from circumference measures made to a precision of 0.5 cm. We used data from 1991–2011 (Figure 1). For each tree, we know the location, DBH, name and status (dead or alive).

2.3. Quantifying Water Stress

Quantifying water stress for trees is a delicate issue. The relation between the amount of rainfall and water availability for trees is not linear and is determined by various soil and plant or ecosystem characteristics (permanent wilting point, field capacity, root distribution). Consequently, water stresses are increasingly estimated using soil water balance models [43], among which some models explicitly designed for tropical forests are now available [41]. We chose, as the water stress indicator, an estimator derived from the daily relative extractable water index (REW), estimated with a soil water balance model calibrated for the Paracou forest at the stand level [41]. The daily REW was calculated from

soil water content as the ratio of the daily extractable water (EW) over the maximum extractable water (EWmax). EW is defined as the difference in soil water content between field capacity (soil water matricpotential of −0.03 MPa) and wilting point (soil water matric potential of −1.6 MPa) in the entire root zone up to a 2-m depth [43]. The −1.6 MPa permanent wilting point value was chosen following [44] who used it to assess the effect of the 2003 drought event on carbon dynamics in European forests. We used soil water retention curves obtained at different depths in the soil to get field capacity and wilting point water content. We then computed the daily REW values for the complete soil profile over the entire studied period [45]. Our water stress index was computed as the area over the REW curve and under the theoretical threshold of 40% defined as the limit below which trees experience major physiological stress [45]. The index was computed using daily rainfall data over two-year periods corresponding to forest census intervals. Because no major change in the index behavior was detectable among topographical levels and among soil types in the Paracou forest [41], a single model was used for all plots.

Table 2. Forestry treatments implemented on the Paracou plots in 1986–1987. The percentage of biomass loss (% AGB loss) is defined as the difference between the pre-logging aboveground forest biomass and its minimum value reached during the 4 years after the logging operations.

Treatments	Plot Numbers	Timber Logging	Fuelwood Logging	Thinning	% AGB Loss
Control	P1, P6, P11	-	-	-	-
T1	P2, P7, P9	DBH $\geq$ 50 cm, mean of 10 trees/ha	-	-	(12%–33%)
T2	P3, P5, P10	DBH $\geq$ 50 cm, mean of 10 trees/ha	-	DBH $\geq$ 40 cm, all non-valuable species, mean of 30 trees/ha	(33%–56%)
T3	P4, P8, P12	DBH $\geq$ 50 cm, mean of 10 trees/ha	40 cm $\leq$ DBH $\leq$ 50 cm, all non-valuable species, mean of 20 trees/ha	DBH $\geq$ 40 cm, all non-valuable species, mean of 15 trees/ha	(35%–66%)

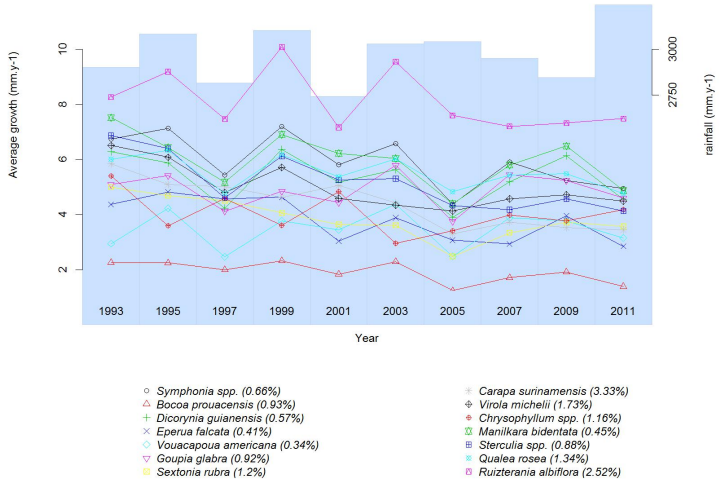


Figure 1. Annual precipitation and growth trajectories of the 14 studied commercial species over the studied period. Annual mortality rates are reported in bracket.

2.4. Model

The joint growth-mortality model used is based on 2 sub-models. The first one is a non-linear hump-shaped growth model (Equation (1) and (2)) successfully developed by [46] in which the growth trajectory depends on 3 parameters: G_{max} (the maximum growth rate), D_{opt} (the diameter at

maximum growth) and K (the kurtosis of the curve defining the shape of the ontogenetic variation in the growth rate).

$$\begin{aligned} log(\widehat{AGR}_{i,t-1}+1) = (&\theta_7 + \theta_8 \times Water_{t-1} + \theta_9 \times AGBL_i \\ &+ \theta_{10} \times Water_{t-1} \times AGBL_i) \\ &\times exp\left(-\frac{1}{2}\left(\frac{log\left(\frac{D_{i,t-2}}{\theta_{11}}\right)}{\theta_{12}}\right)^2\right) \end{aligned} \quad (1)$$

$$log(AGR_{i,t-1}+1) = log(\widehat{AGR}_{i,t-1}+1) + \varepsilon \quad (2)$$

where:

$\varepsilon \sim N(0, \theta_{13})$;
θ are all unknown parameters that we will infer;
ε is an error term following a normal distribution.

$Water_t$ is here a covariate related to the water stress undergone by trees at time t. To include the logging impact in the model, we quantified it by the above-ground biomass (AGB ha^{-1}) loss measured, at the 6.25-ha plot level, right after the logging. This value varies from 0–225 t ha^{-1}, which is the covariate indicated by $AGBL_i$ in the equation. To compare, mean above-ground biomass loss (AGBL) in current harvested blocks in French Guiana is estimated between 20% and 35% that correspond to 70–100 tMS ha^{-1} [36]. An interaction between the water stress and the logging effect ($Water_{t-1} \times AGBL_i$) is also included.

The second sub-model is a mortality model (Equation (3)) developed by [47], computing the individual probability of dying at each time step.

$$\begin{aligned} p_{i,t} = logit^{-1}(&\theta_1 \times log\left(\frac{AGR_{i,t-1}+1}{\widehat{AGR}_{i,t-1}+1}\right) + \theta_2 \times D_{i,t-1} \\ &+ \theta_3 \times (D_{i,t-1})^2 + \theta_4 \times Water_t + \theta_5 \times AGBL_i \\ &+ \theta_6 \times Water_t \times AGBL_i) \end{aligned} \quad (3)$$

We expect θ_2 to be negative and θ_3 to be positive in the probability of dying, leading to a U-shape mortality curve. This means that a tree has higher risks of dying when it is young and small or large and old, than when it has an intermediate DBH, a phenomenon that we can explain by intense competition among the youngest and by senescence for the oldest [47].

These 2 processes are interdependent, insofar as past tree growth has an impact on the individual probability of dying [48,49], and similar ecological predictors can be simultaneously implied in the two processes. To address the delicate issue of coupling both processes, we used the methodology developed in [50] to link growth and mortality through the individual tree vigor. Tree vigor is estimated with $log\left(\frac{AGR_{i,t}+1}{\widehat{AGR}_{i,t}+1}\right)$, where $AGR_{i,t}$ is the observed absolute growth rate between time $t-1$ and time t for individual tree i, and $\widehat{AGR}_{i,t}$ is the predicted absolute growth rate between time $t-1$ and time t for individual tree i using the growth sub-model. At each time step, an individual tree i may die with probability $p_{i,t}$. If tree i stays alive, it grows at a growth rate $AGR_{i,t}$, and its diameter $D_{i,t-1}$ becomes $D_{i,t}$. The joint model likelihood is then computed using Equation (4) or (5):
if tree i stays alive during the length of the studied period:

$$\prod_{t=1}^{n} f(D_{i,t}|D_{i,t-1}) \times (1 - p_{i,s,t}) \quad (4)$$

if tree i dies between time $k-1$ and time k:

$$p_{i,s,k} \times \prod_{t=1}^{k-1} (f(D_{i,t}|D_{i,t-1}) \times (1 - p_{i,s,t})) \quad (5)$$

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 grow to diameter $D_{i,t}$ at time t computed with Equation (1) and (2);
$p_{i,t}$ is the probability of dying between time $t-1$ and time t computed with Equation (3).

2.5. Inference and Selection Method

A Bayesian Monte-Carlo Markov chain (MCMC) method was implemented to estimate the parameters [51]. A random walk was used as the proposed distribution to sample new values of parameters that were or were not selected, using the ratio of Metropolis–Hastings. The only parameter that was not sampled this way was the standard deviation of the growth model θ_7, for which an inverse-gamma posterior distribution with a Gibbs sampler was used because the θ_7 *a posteriori* law was mathematically tractable.

Since values of vigor change as predicted growth changes, growth and mortality processes were parametrized simultaneously. The growth model is taken into account through the vigor estimate when mortality parameters are estimated. All parameters are sampled one by one at each step, and the global likelihood is computed. For each commercial species, we realized 1000 iterations of the Metropolis–Hastings algorithm in order to achieve convergence of 10 parallel MCMC chains. Then, we reduced the variance of the proposition laws and reran the algorithm. A satisfying staying rate was achieved after 3000 iterations. We then used a burning of 1000 iterations and a thinning of 10 to achieve a satisfying auto-correlation. All of the algorithms and statistical treatments were implemented using R software [52]. We used the selection method proposed by Kuo-Mallick [53] to determine whether it was significant to include an interaction between climate and water stress in the growth model or in the mortality model. The method consists of multiplying each interaction term we want to test by an indicator, whose value will be either 1 (term included in the model) or 0 (term not included). A Gibbs algorithm was used to attribute either 1 or 0 to the indicator, and a Metropolis–Hastings within Gibbs algorithm was used to estimate the value of the parameters. We decided to include the interaction effect when the expectation of the indicator given by the Kuo-Mallick method was above 0.8.

2.6. Quantifying Vulnerability

The water stress effect, represented by the covariate ($Water_t$), has the same range for all of the species. The parametrization of the joint model for each species gives us the values of parameters θ_4 and θ_8 multiplying $Water_t$ in the 2 sub-models. In order to quantify a standardized (*i.e.*, comparable between species) impact of water stress on both (growth and mortality) demographic processes, further calculations were necessary.

For the growth process, we considered a value of water stress of 1 and a value of above-ground biomass loss (AGBL) corresponding to the logging Treatment 3, and we calculated the impact on growth using Equation (6):

$$Impact\ on\ growth = \frac{\theta_8 \times Water_t + \theta_{10} \times AGBL}{\theta_7} \quad (6)$$

This index describes the proportional decrease of growth rates observed with water stress. No impact of water stress on the growth of the tree species considered corresponds to a value of

0. If an interaction between water stress and logging is selected by the step-wise procedure for a given species, then θ_{10} is not null.

For the mortality process, the calculations used were more complicated due to the logit function in Equation (3). We calculated a basal signal (Equation (7)) relating the ontogeny of the tree with the probability of dying and included a water stress effect:

$$basal\ signal = \theta_2 \times median(DBH) + \theta_3 \times (median(DBH))^2 \quad (7)$$

The probabilities of dying with (Equation (8)) and without (Equation (9)) water stress were then calculated:

$$proba_{\text{with water stress}} = logit^{-1}(basal\ signal + \theta_4 \times Water_t + \theta_6 \times AGBL) \quad (8)$$

$$proba_{\text{without water stress}} = logit^{-1}(basal\ signal) \quad (9)$$

We considered again a standard value of water stress of 1. The impact was quantified using Equation (10):

$$Impact\ on\ mortality = \frac{proba_{\text{with water stress}}}{proba_{\text{without water stress}}} \quad (10)$$

This index reflects the increase in probability of dying observed with water stress. No impact of water stress on the mortality of the tree species considered corresponds to a value of 1.

3. Results

Parameters of the growth process converged slower than parameters of the mortality process. This reflects the weight of each process in the total likelihood. The growth process influenced the two terms of the likelihood, while the mortality process influenced only the term linked with the probability of dying. The growth model performed very well for predicted values between 0.5 and 3. Below 0.5 (1.6% of data), observed values were under-predicted, and above three (0.09% of data), observed values were over-predicted (Figure 2). Predicted mortality probabilities were significantly higher for trees that died in the time period (Figure 3).

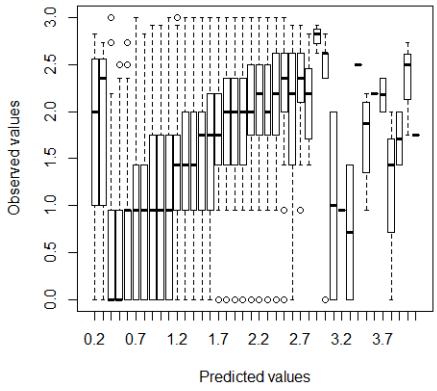


Figure 2. Performance of the DBH growth model. Observed values (without the unit due to the logarithmic transformation) are plotted against predicted values. The model performed well for predicted values between 0.5 and three. Below 0.5 (1.6% of data), observed values are under-predicted, and above three (0.09% of data), observed values are over-predicted. These biases are thus due to the very low number of observations on the ends of the prediction range.

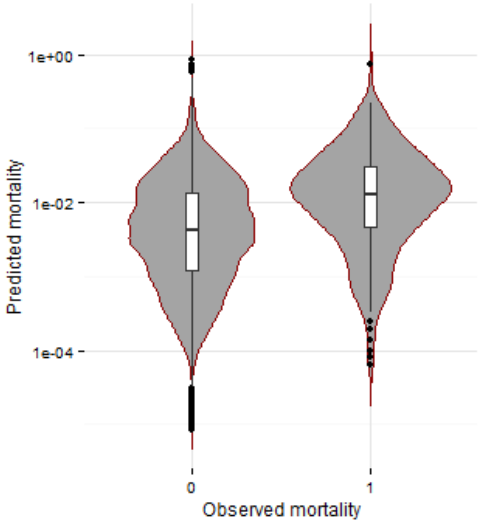


Figure 3. Performance of the mortality model assessed with violin plots as a combination of a box plot and a kernel density plot in grey. Predicted mortality probabilities are higher for trees that died in the time period.

3.1. Variable Selection

The Kuo-Mallick procedure showed clear results, bringing out four species for which an interaction had to be included to improve the model likelihood (Figure 4). The final growth model included, as a result, an interaction term for three species: Carapa, Manil Marécage and Wapa. The selection rate was above 99% for all selected species. Regarding the mortality model, an interaction term was only selected for the Grignon Franc, with a selection rate of 86%.

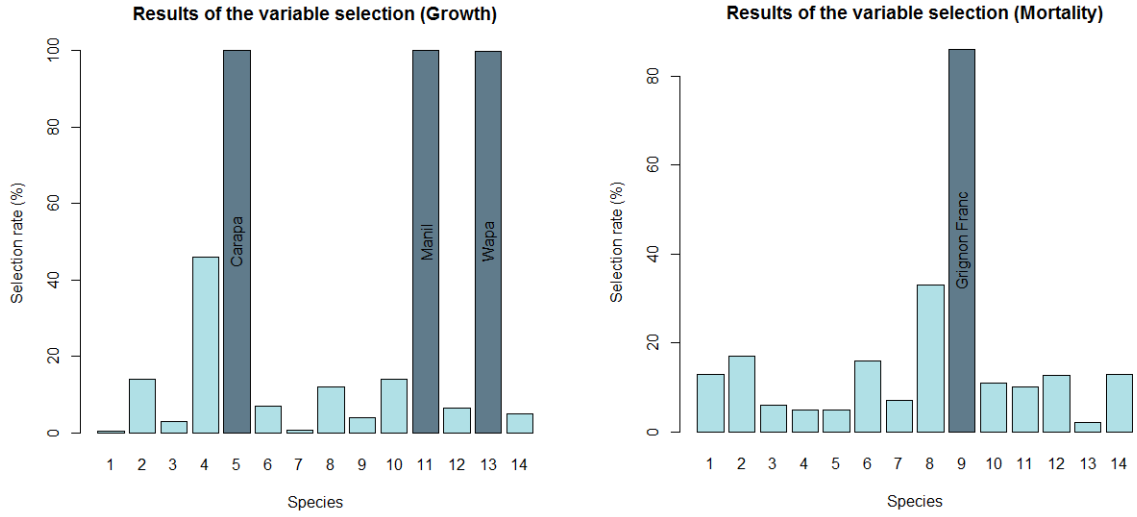


Figure 4. Selection rates of the interaction term $Water_t \times AGBL_i$ in the growth (left) and mortality (right) models resulting from the Kuo-Mallick selection method. Three species revealed an interaction effect in the growth model, whereas only the Grignon Franc showed an interaction effect in the mortality model.

3.2. Response to the Combined Effects of Logging and Water Stress

3.2.1. Growth

A general signal was common to all species (Figure 5a). The growth rate was lower when the tree was exposed to an increased water stress, but logging had an opposite effect insofar as it decreased competition among trees for common resources, such as light and water in the soil. Besides this common pattern, differences between species can be pointed out (Figure A1). All of the species were distributed along a gradient, as illustrated in Figure 5. Some of them were well resistant to water stress (like the Balata Pomme) and showed nearly horizontal isoclines. Other tree species appeared more affected by the lack of water, though exploitation plays an offsetting role (Angélique). For the later species, the isoclines were more vertical. Finally, the Manil Marécage illustrates how the interaction between logging and water stress can twist the curves and lead to a lower-than-expected growth rate when the water stress becomes too significant, even with logging.

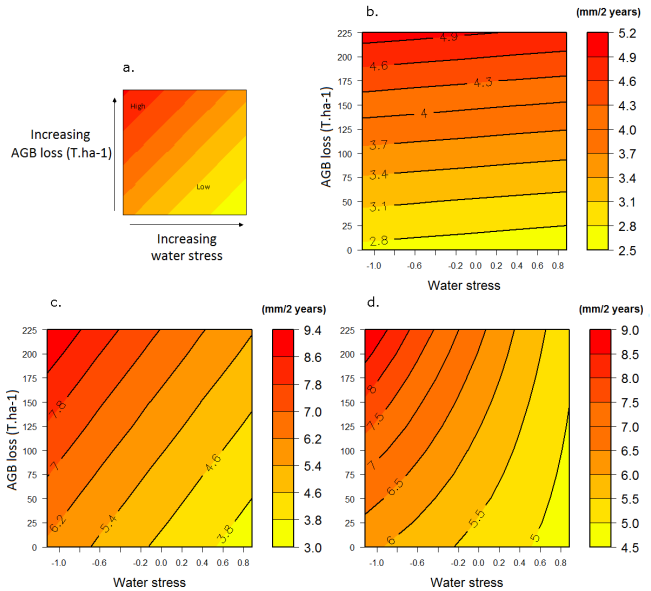


Figure 5. The expected pattern (**a**) and simulation of DBH growth rates under different water stress and logging for the Balata Pomme (**b**); the Angélique (**c**) and the Manil Marécage (**d**). These three species illustrate the gradient along which all species are distributed. Some are well resistant to water stress (like the Balata Pomme), others are more affected by the exploitation (Angélique), and finally, the Manil Marécage illustrates how the interaction between logging and water stress can twist the curves and lead to a low growth rate when the water stress becomes too significant, even with logging.

3.2.2. Mortality

Most species (12 out of 14) showed a common tendency: the probability of dying is higher when the tree was exposed to an increased water stress; however, exploitation had an opposite effect by decreasing competition, and exploitation reduced mortality rates in the medium term (Figure 6). All of the species sharing this tendency (*i.e.*, all except Grignon Franc and Yayamadou) were distributed along a gradient illustrated in Figure 6.

Some of them were resistant to water stress (Wacapou). Many other tree species (Boco, but also Goupi or Gonfolo Gris) appeared less resistant to the lack of water, though exploitation could play an offsetting role to a certain extent. Some species had isoclines that tend to be vertical, conveying a deep impact of water stress on the probability of dying (Kobe, Carapa). A completely different profile was observed for Yayamadou for which the combination of high water stress and intense logging is the most beneficial, leading to a peculiar pattern (Figure A2).

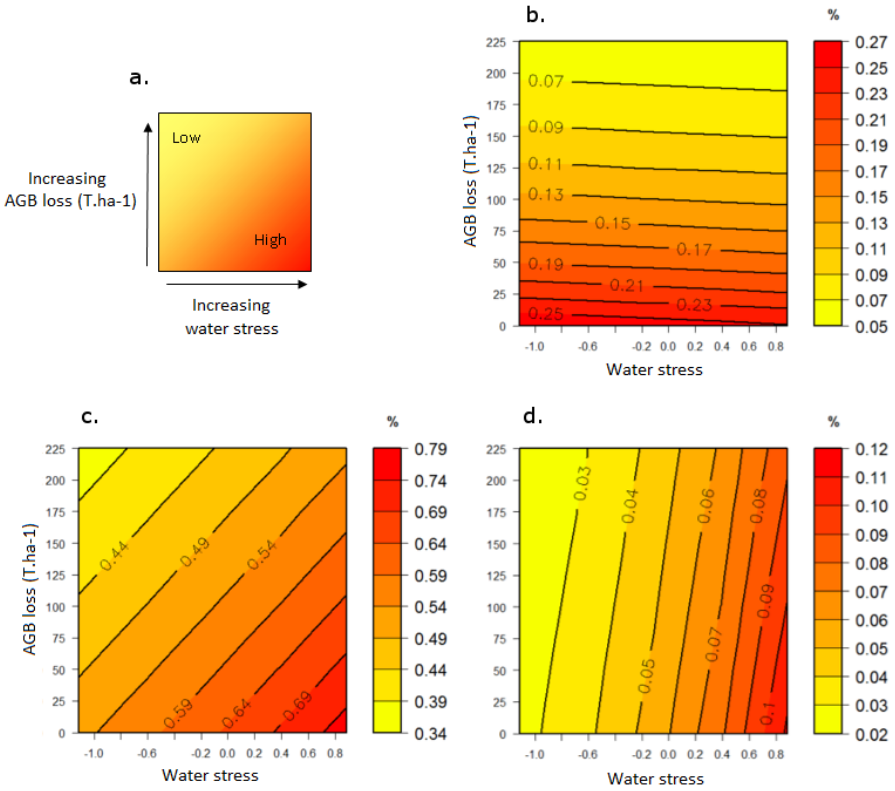


Figure 6. The expected pattern (**a**) and the simulation of the probabilities of dying under different water stress and exploitation intensity for the Wacapou (**b**), the Boco (**c**) and the Kobe (**d**). These three species illustrate the gradient along which the majority of tree species are distributed, though some species differ notably. The Wacapou (b) is quite resistant to water stress, while other species are more affected. The majority of them have the same profile as the Boco (c), which means that for them, logging plays an offsetting role; however, for species like the Kobe (d) or the Carapa, water stress is the dominant factor of mortality, and exploitation cannot change the tendency.

3.3. Response Profiles

Growth and mortality were used to generate vulnerability profiles (Figure 7). A common pattern emerges, as the majority of species appear to be in the right lower panel limited by the two 'no impact' dashed lines. For most species in this study, water stress has a negative effect on growth rates and increases the probability of dying.

Three groups of species may be delineated. Some species were quite resistant to water stress (green circle). The Balata Pomme was representative of this profile, where water stress only slightly increased the probability of dying, and the decrease in growth rate appeared limited compared to other species. Some were affected by water stress (orange circle), with a gradient of differing responses, from: (i) species that managed to reduce their growth in order to resist water stress, maintaining a probability of dying close to the norm (e.g., Boco); to (ii) species in which no significant growth reduction was observed, but water stress led to a significant increase in mortality rates (e.g., Gonfolo Gris). Finally, the last species (Kobe) appeared highly vulnerable to water stress. Its probability of dying indeed increased with water stress, and its growth rate was also significantly reduced.

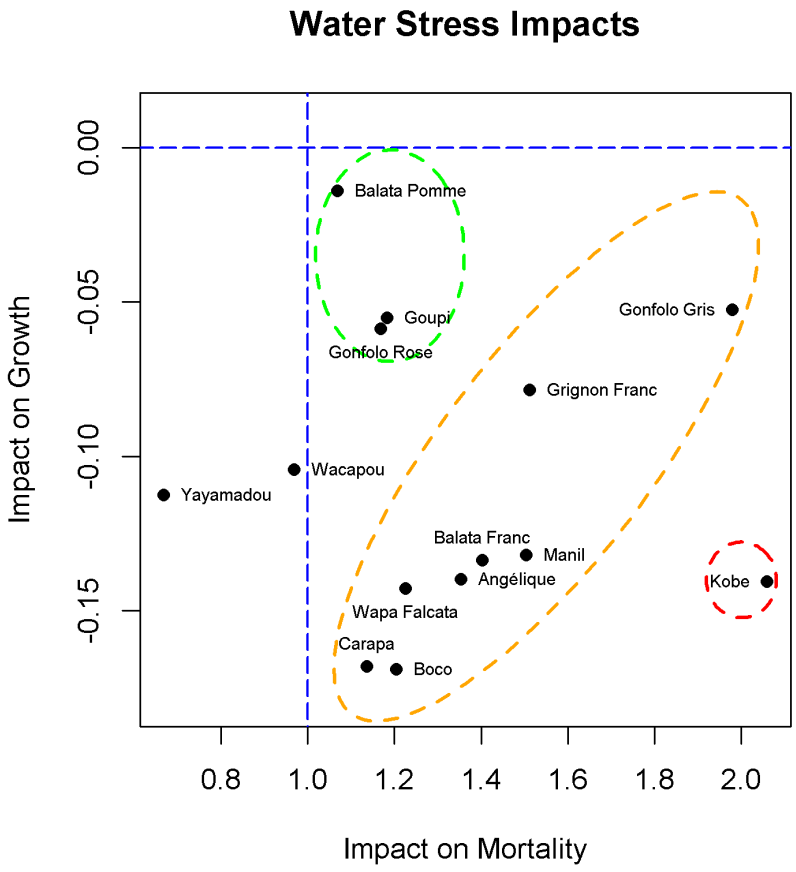


Figure 7. Water stress impacts on growth and mortality. No impact is represented by the horizontal (growth) or vertical (mortality) blue dashed lines. The higher the water stress impacts, the more negative the values for growth and the more positive the values for mortality. Three vulnerability groups of species were made and are represented with green (low vulnerability), orange (medium vulnerability) and red (high vulnerability) dashed lines.

4. Discussion

Using a joint growth-mortality modeling framework, we show that water stress had a negative impact on growth rate, while the impact of logging was positive for the majority of the commercial species from the Guiana Shield. The opposite results were observed for the mortality, *i.e.*, water stress increases while logging decreases mortality rates. However, we did not see strong interaction effects between logging and water stress. The quality of the fit of our models was similar to other models developed to (i) assess the effect of logging [32], (ii) analyze neighborhood influence [54] or (iii) investigate soil influences on tropical forest dynamics [55]. A substantial fraction of individual variation remains unexplained (Figures 2 and 3). Forest dynamics is influenced by several non-investigated environmental variables (topography, light availability, *etc.*) and also by the unique individual tree vigor [50].

4.1. Growing under Water Stress

Tree growth performance under drought is a well-documented issue [9,10,13]. Water stress leads to a drop in soil water potential, resulting in a decrease of the leaf water potential [56]. This triggers a reduction in stomatal conductance, enabling the tree to reduce excessive transpiration, but at the same time limiting the carbon assimilation. In the case of prolonged drought, this reduction in stomatal conductance may lead to a continued decline of assimilation and, thus, a noticeable growth reduction. Tree species in tropical forests are not equal with respect to the value of leaf water potential at turgor

loss π_{tlp} [57]. We still do not know whether this π_{tlp} could be a good predictor of the decrease of tree performance under water stress [58]. If so, foresters would benefit from an easy-to-measure leaf functional trait in order to rapidly spot the most vulnerable commercial species in the field [59].

4.2. Staying Alive under Water Stress

The physiological causes of tree death under extreme drought events are mainly related to hydraulic properties of wood. Again, commercial trees do not have the same ability to resist embolism. In a water stress period, an increased number of xylem vessels run the risk of cavitation, because water transported through the xylem is under negative pressure [10]. The resultant air embolism blocks xylem conduits and reduces the tree's ability to move water from soil to sites of photosynthesis, with vessels becoming completely dysfunctional. A series of events, such as the loss of tree hydraulic conductivity, stomatal closure and, finally, the abscission of leaves, shoots and branches, will ultimately lead to death [10,60]. If water became insufficient, the competition for these resource will increase, and the most adapted trees will be favored [13]. Our results would suggest that the commercial species the most resistant to embolism are Balata Pomme, Wacapou or Yayamadou, while the most vulnerable could be Kobe or Gonfolo Gris (Figure 7). These results based on demographic data only should be confirmed by hydraulic conductance measurement in the lab.

4.3. Reducing the Competition to Improve the Water Budget

Reducing the general level of competition by logging may have different impacts not only on the water, but also on the soil nutrients and light budget for the remaining trees, allowing them to grow faster and to decrease the probability of dying due to self-thinning [61]. Positive effects of logging *per se* last more than eight years [62] and may be increased by the use of silvicultural treatments [63,64]. The latter is of particular importance considering the productivity of the remaining big trees [65]. Although reducing the competition through logging may counterbalance the impacts of water stress by increasing the average amount of water available per tree, our results show that interaction terms (θ_6 and θ_{10}) are rarely retained in the final models for the 14 studied commercial species. This means that logging and water stress did not deeply interact on the tree demographic responses. In other words, the increase of growth or survival in logged forests is similar in dry or wet years with no interaction or 'synergistic' effect, positive or negative, for droughts affecting logged forests. This is surprising because it is sometimes assumed that the reduction of competition is an effective way to fight against drought. This was very clearly observed in temperate zones where the gain can last several decades [27]. All things being equal, we know that drought suffered by the trees is mainly due to evapotranspiration of mature tree leaves [41]. Our result can then be explained by the relatively rapid return (a few years) after logging of the leaf area index to levels similar to non-logged forests in the Amazon [66]. This would mean that our ability to change the competition to help the forest to endure periods of water stress is relatively limited. However, we need to acknowledge that we lack long-term experience in manipulating both tree competition and water stress *in situ* to validate these results [67].

4.4. Guidelines for Forest Management

Maintaining a high species diversity in time will ensure the tree population adaptability to new environmental conditions. In this way, a conservation strategy of the most vulnerable species is arguable. As three species (Carapa, Manil Marécage and Wapa) are particularly vulnerable to water stress under logging (negative θ_{10}), the exploitation of these species should be avoided. It is also noticeable that the Angélique, the first tree species logged in French Guiana, appears vulnerable to water stress. Logging companies should thus reduce logging intensities on Angélique while diversifying the logged species. This diversification should lead to a preferential exploitation of species, like the Balata Pomme, the Goupi or the Gonfolo Rose, which are more resilient to water stress. It also appears necessary to alleviate the pressure on species like the Kobe, the Gonfolo Gris or the

Boco, as they were revealed vulnerable to water stress by our study. With minimal logging pressure on the most vulnerable species, a larger genetic pool will be conserved, thus maximizing the species adaptive potential to drier conditions by natural selection of the most resistant genomes. Moreover, the diversification of logged species has other benefits; Putz *et al* [23] showed that a prolonged harvest strategy on a single species will drastically drop the original timber stock to population levels that will not allow the second logging rotation.

5. Conclusions

Our results allowed a commercial-species-centered interpretation of the influence of logging and drought on growth and mortality, the fundamental processes of post-logging forest dynamics. We point out some global trends on the response of the commercial species studied for each demographic process: (i) growth rates increase with logging and decrease with water stress; while (ii) probabilities of dying have the exact opposite pattern. Resistant species were identified (e.g., Balata Pomme), and on the contrary, the Kobe or the Angélique stood out as more vulnerable. Forest plots are sometimes dominated by one species, and the commercial tree population is rarely homogeneous in space. This is the case for the Angélique, which is extremely abundant in some areas of the Guiana Shield. Some future studies need to address these particular areas, to study the potential amplification feedback effects. Indeed, as the Angélique appears vulnerable to water stress, increased mortality of areas dominated by this species will likely experience a drastic loss of biomass and other changes for the remaining trees. As earlier suggested [17], the forests structure will potentially condition the response to climate changes. Even if our studied species are somewhat representative of the major commercial species of the Amazon [40], studying forests that are under different climatic conditions is urgent for climate-sustainable forestry in the neotropics.

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Author Contributions: Study conception and design: H.F., M.A.-K., B.H. Acquisition of data: M.A.-K., O.B., L.D., S.G., V.R. Analysis and interpretation of data: H.F., M.A.-K., R.G., B.H. Drafting of manuscript: H.F., B.H. Critical revision: L.D., S.G.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A.

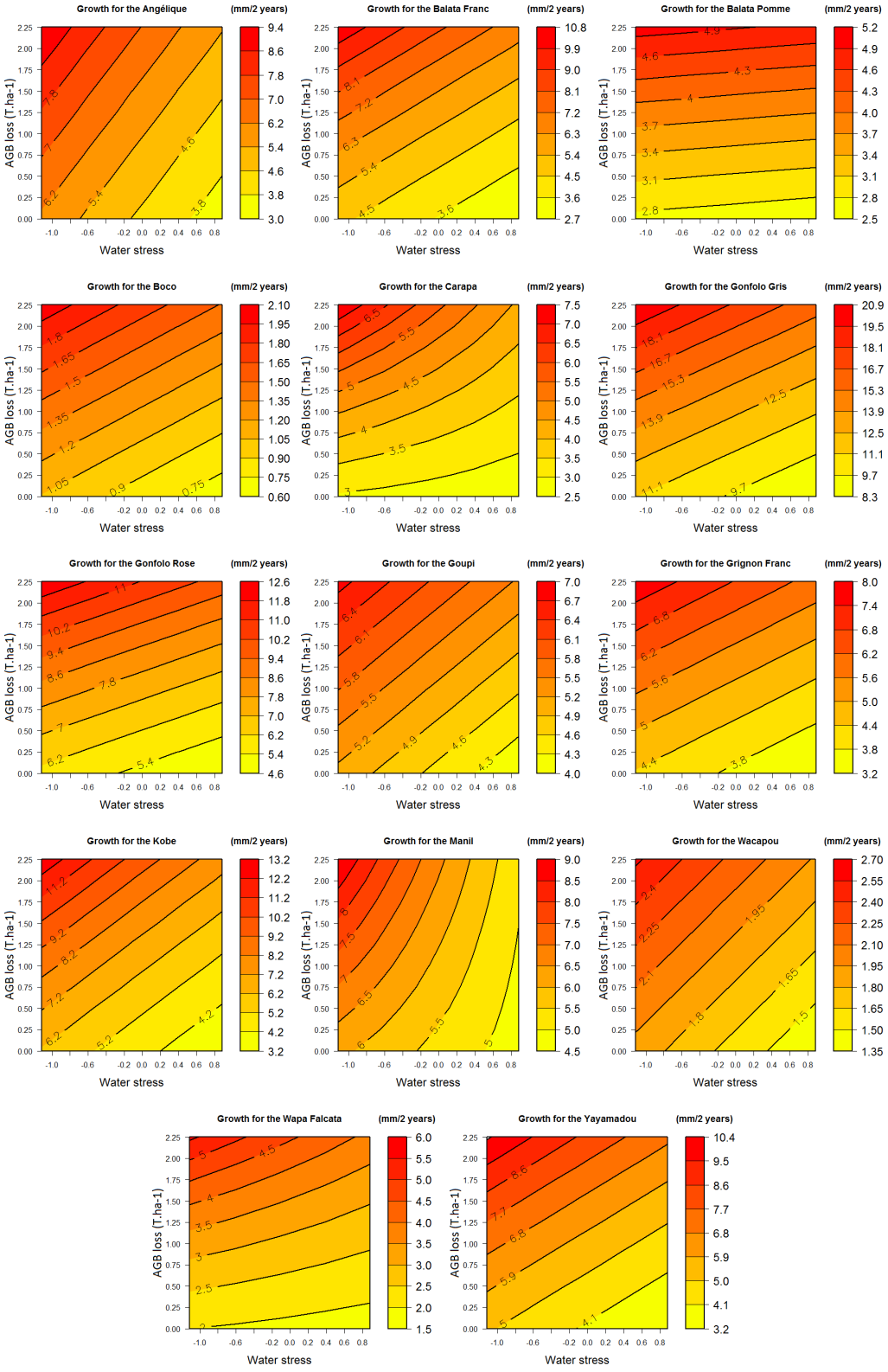


Figure A1. Simulation of growth under different water stress and exploitation intensities for the 14 studied commercial species from French Guiana.

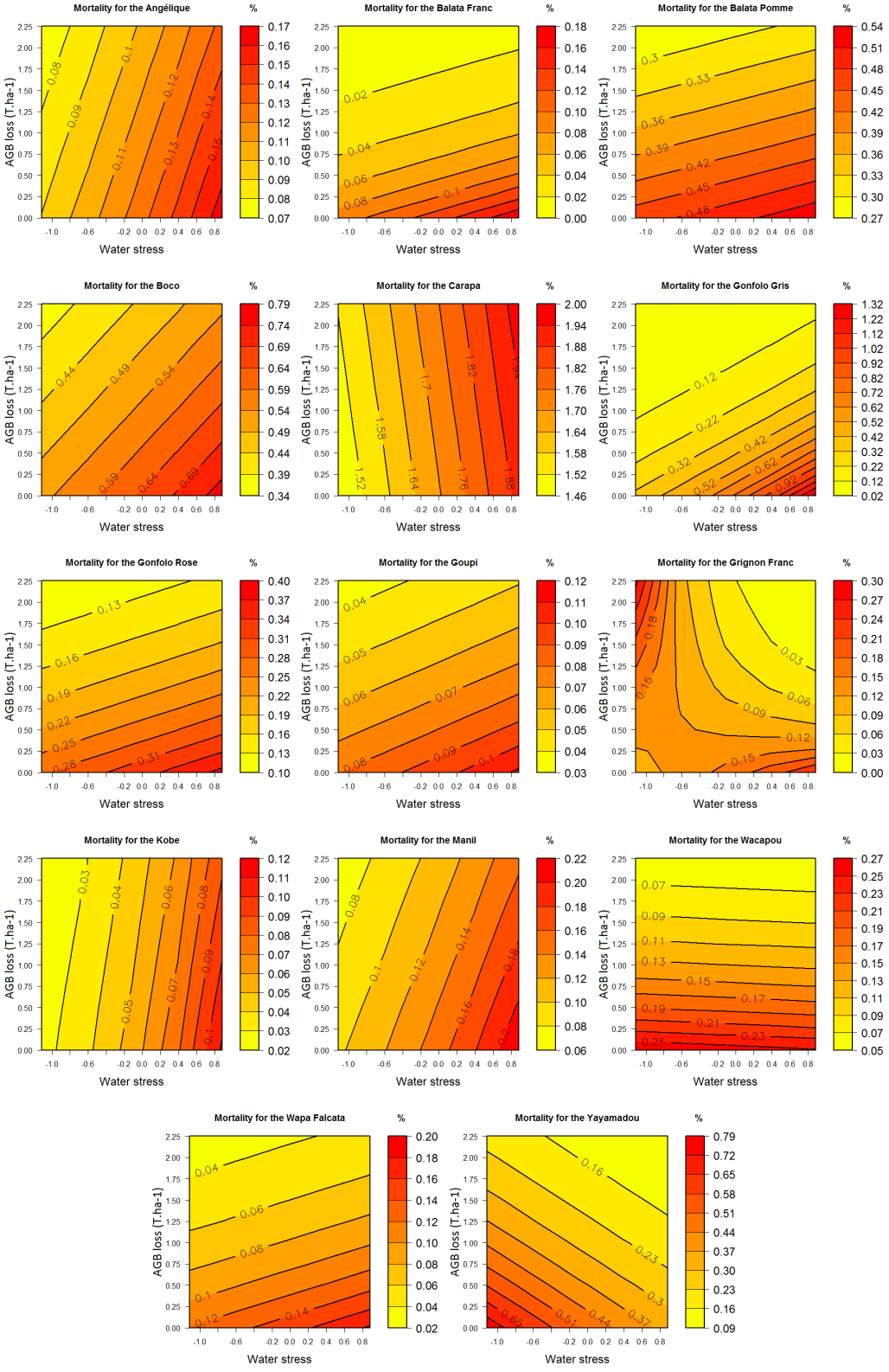


Figure A2. Simulation of probabilities of dying under different water stress and exploitation intensities for the 14 studied commercial species from French Guiana.

Table A1. Values of the model parameters for the 14 studied commercial species.

Species	Parameter	Median	0.05	0.95	Species	Parameter	Median	0.05	0.95
Angélique	θ_1	−0.534	−0.855	−0.162	Balata	θ_1	−0.291	−1.44	0.561
	θ_2	−3.14	−3.43	−2.87	Franc	θ_2	−2.98	−4.11	−2.40
	θ_3	0.320	0.288	0.355		θ_3	0.251	0.105	0.366
	θ_4	0.308	−0.037	0.619		θ_4	0.312	−0.517	1.09
	θ_5	−0.111	−0.461	0.207		θ_5	−1.17	−2.68	−0.103
	θ_6	-	-	-		θ_6	-	-	-
	θ_7	1.69	1.65	1.73		θ_7	1.63	1.57	1.71
	θ_8	−0.24	−0.26	−0.21		θ_8	−0.219	−0.272	−0.164
	θ_9	0.17	0.14	0.20		θ_9	0.339	0.285	0.399
	θ_{10}	-	-	-		θ_{10}	-	-	-
	θ_{11}	29.7	29.1	30.4		θ_{11}	46.6	40.7	61.5
	θ_{12}	0.879	0.843	0.915		θ_{12}	1.23	1.07	1.52
	θ_{13}	0.601	0.577	0.621		θ_{13}	0.490	0.455	0.536
Balata Pomme	θ_1	−0.452	−0.958	−0.0182	Boco	θ_1	−0.520	−0.733	−0.277
	θ_2	−3.45	−3.86	−3.09		θ_2	−3.37	−3.53	−3.24
	θ_3	0.542	0.468	0.624		θ_3	0.519	0.488	0.555
	θ_4	0.0848	−0.402	0.498		θ_4	0.188	0.0113	0.393
	θ_5	−0.240	−0.640	0.107		θ_5	−0.164	−0.351	−0.00925
	θ_6	-	-	-		θ_6	-	-	-
	θ_7	1.30	1.25	1.38		θ_7	0.600	0.582	0.622
	θ_8	−0.0167	−0.0720	0.0302		θ_8	−0.102	−0.118	−0.0842
	θ_9	0.212	0.175	0.253		θ_9	0.179	0.164	0.193
	θ_{10}	-	-	-		θ_{10}	-	-	-
	θ_{11}	25.7	24.7	26.6		θ_{11}	28.3	25.1	39.4
	θ_{12}	0.663	0.617	0.729		θ_{12}	1.45	1.18	2.33
	θ_{13}	0.667	0.632	0.713		θ_{13}	0.494	0.438	0.506
Carapa	θ_1	−0.559	−0.736	−0.386	Gonfolo Gris	θ_1	−0.256	−0.804	0.356
	θ_2	−2.94	−3.13	−2.71		θ_2	−2.05	−2.69	−1.57
	θ_3	0.515	0.459	0.568		θ_3	0.205	0.138	0.291
	θ_4	0.131	−0.0625	0.329		θ_4	0.691	0.143	1.22
	θ_5	0.0152	−0.157	0.163		θ_5	−1.18	−2.29	−0.15
	θ_6	-	-	-		θ_6	-	-	-
	θ_7	1.33	1.30	1.37		θ_7	2.35	2.27	2.45
	θ_8	−0.0353	−0.0796	0.00127		θ_8	−0.128	−0.200	−0.0593
	θ_9	0.248	0.228	0.270		θ_9	0.266	0.193	0.347
	θ_{10}	−0.0845	−0.115	−0.0577		θ_{10}	-	-	-
	θ_{11}	25.7	24.1	28.7		θ_{11}	40.2	37.6	43.5
	θ_{12}	1.20	1.03	1.55		θ_{12}	1.07	0.965	1.21
	θ_{13}	0.636	0.614	0.659		θ_{13}	0.483	0.441	0.533
Gonfolo Rose	θ_1	−0.983	−1.23	−0.720	Goupi	θ_1	−0.960	−1.56	−0.385
	θ_2	−2.36	−2.55	−2.21		θ_2	−3.01	−3.32	−2.66
	θ_3	0.231	0.212	0.252		θ_3	0.280	0.237	0.325
	θ_4	0.175	−0.0849	0.423		θ_4	0.166	−0.297	0.608
	θ_5	−0.432	−0.678	−0.161		θ_5	−0.364	−0.899	0.111
	θ_6	-	-	-		θ_6	-	-	-
	θ_7	1.83	1.78	1.87		θ_7	1.73	1.67	1.82
	θ_8	−0.107	−0.145	−0.0763		θ_8	−0.0960	−0.148	−0.0499
	θ_9	0.289	0.262	0.314		θ_9	0.105	0.0611	0.150
	θ_{10}	-	-	-		θ_{10}	-	-	-
	θ_{11}	35.0	34.1	36.1		θ_{11}	29.0	28.0	30.3
	θ_{12}	0.960	0.921	0.999		θ_{12}	0.878	0.805	0.957
	θ_{13}	0.755	0.725	0.778		θ_{13}	0.760	0.726	0.805

Table A1. *Cont.*

Species	Parameter	Median	0.05	0.95	Species	Parameter	Median	0.05	0.95
Grignon Franc	θ_1	−0.813	−1.34	−0.322	Kobe	θ_1	−0.0742	−0.671	0.833
	θ_2	−2.54	−2.88	−2.24		θ_2	−4.36	−4.90	−3.55
	θ_3	0.210	0.182	0.236		θ_3	0.581	0.466	0.654
	θ_4	0.396	−0.0195	0.930		θ_4	0.755	−0.192	1.42
	θ_5	−0.682	−1.289	−0.0567		θ_5	−0.0818	−0.798	0.604
	θ_6	−0.994	−1.682	−0.319		θ_6	-	-	-
	θ_7	1.61	1.53	1.68		θ_7	1.79	1.71	1.86
	θ_8	−0.123	−0.179	−0.0727		θ_8	−0.253	−0.315	−0.190
	θ_9	0.238	0.189	0.287		θ_9	0.315	0.262	0.365
	θ_{10}	-	-	-		θ_{10}	-	-	-
	θ_{11}	46.1	43.3	50.7		θ_{11}	37.7	35.3	40.9
	θ_{12}	0.887	0.825	0.979		θ_{12}	0.958	0.865	1.07
	θ_{13}	0.726	0.685	0.773		θ_{13}	0.804	0.762	0.856
Manil Marécage	θ_1	−1.06	−1.45	−0.605	Wacapou	θ_1	−0.443	−0.748	−0.171
	θ_2	−4.62	−5.09	−4.20		θ_2	−2.81	−2.97	−2.63
	θ_3	0.791	0.709	0.885		θ_3	0.296	0.267	0.320
	θ_4	0.404	−0.0364	0.882		θ_4	−0.0224	−0.330	0.257
	θ_5	−0.142	−0.567	0.276		θ_5	−0.666	−1.07	−0.367
	θ_6	-	-	-		θ_6	-	-	-
	θ_7	1.85	1.81	1.88		θ_7	1.04	1.01	1.07
	θ_8	−0.106	−0.131	−0.076		θ_8	−0.108	−0.132	-0.0869
	θ_9	0.0816	0.0610	0.1005		θ_9	0.103	0.0821	0.123
	θ_{10}	−0.0610	−0.0841	−0.0365		θ_{10}	-	-	-
	θ_{11}	24.9	24.1	25.5		θ_{11}	17.4	14.0	19.7
	θ_{12}	0.920	0.865	0.997		θ_{12}	1.46	1.25	1.79
	θ_{13}	0.481	0.465	0.498		θ_{13}	0.729	0.709	0.748
Wapa	θ_1	−0.648	−0.821	−0.460	Yayamadou Montagne	θ_1	−1.64	2.01	−1.16
	θ_2	−3.08	−3.23	−2.97		θ_2	−4.18	−4.61	−3.61
	θ_3	0.314	0.299	0.334		θ_3	0.817	0.677	0.914
	θ_4	0.196	0.0535	0.356		θ_4	−0.436	−1.07	−0.0885
	θ_5	−0.613	−0.831	−0.378		θ_5	−0.589	−0.976	−0.0941
	θ_6	-	-	-		θ_6	-	-	-
	θ_7	1.06	1.04	1.07		θ_7	1.61	1.54	1.70
	θ_8	−0.0388	−0.0531	−0.0228		θ_8	−0.180	−0.231	−0.135
	θ_9	0.294	0.282	0.306		θ_9	0.280	0.238	0.323
	θ_{10}	−0.0497	−0.0531	−0.0228		θ_{10}	-	-	-
	θ_{11}	31.3	30.4	32.3		θ_{11}	26.4	25.7	27.4
	θ_{12}	1.16	1.11	1.22		θ_{12}	0.677	0.631	0.750
	θ_{13}	0.648	0.639	0.658		θ_{13}	0.682	0.641	0.727

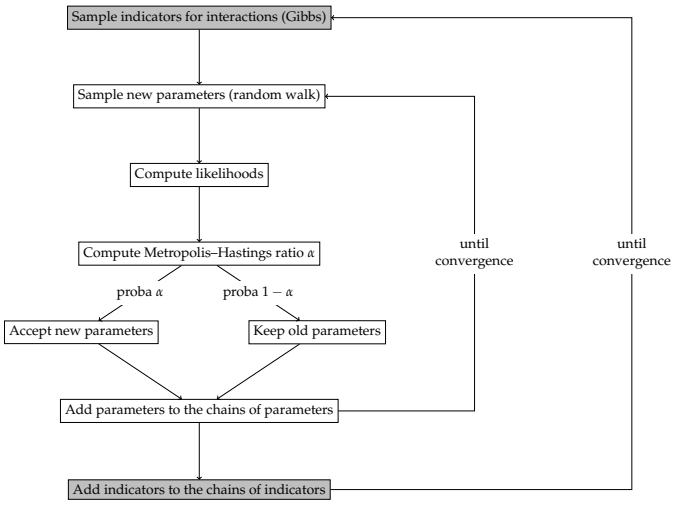


Figure A3. Flow chart of the parameter estimation method. A Bayesian Monte-Carlo Markov chain (MCMC) method was implemented to estimate the parameters. A random walk was used as the proposed distribution to sample new values of parameters that were or were not selected, using the ratio of Metropolis–Hastings. We used the Kuo-Mallick selection method to determine whether it was significant to include an interaction between climate and water stress. A Gibbs algorithm was used to attribute either one or zero to the indicator, and a Metropolis–Hastings within Gibbs algorithm was used to estimate the value of the parameters. We decided to include the interaction effect when the expectation of the indicator given by the Kuo-Mallick method was above 0.8.

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