Research Article

Are Commonly Measured Functional Traits Involved in Tropical Tree Responses to Climate?

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Climate models predict significant rainfall reduction in Amazonia, reducing water availability for trees. We present how functional traits modulate the tree growth response to climate. We used data from 3 years of bimestrial growth measurements for 204 trees of 53 species in the forest of Paracou, French Guiana. We integrated climate variables from an eddy covariance tower and functional trait values describing life history, leaf, and stem economics. Our results indicated that the measured functional traits are to some extent linked to the response of trees to climate but they are poor predictors of the tree climate-induced growth variation. Tree growth was affected by water availability for most of the species with different species growth strategies in drought conditions. These strategies were linked to some functional traits, especially maximum height and wood density. These results suggest that (i) trees seem adapted to the dry season at Paracou but they show different growth responses to drought, (ii) drought response is linked to growth strategy and is partly explained by functional traits, and (iii) the limited part of the variation of tree growth explained by functional traits may be a strong limiting factor for the prediction of tree growth response to climate.

1. Introduction

Lower tree growth rates have been reported from all tropical regions in extreme El Niño events, when temperatures reach absolute records and severe droughts occur in many areas [1–3]. Over Amazonia, temperature increases have already been observed [4] and climate models predict drying for the 21st century [5–7].

The response of tropical forests to fine climate variations or to particular climatic events has received increasing attention during recent years [1, 8–10], highlighting the sensitivity of tropical forest ecosystems to the climatic variables for which a change is expected, especially temperature and precipitation. But understanding the diversity of responses to climate variations is needed to predict long-term changes in forest dynamics and community structure. Investigating such a research question is challenging because of the high diversity of tree species in most tropical tree communities, often above 100 species·ha^{-1}.

Functional trait-based approaches offer a promising way to bypass species when modeling dynamics of highly-diverse communities [11, 12]. Recently, Herault et al. [13] showed that the growth of 50 neotropical tree species can be accurately predicted by four functional traits. Crossing from species to functional traits has several advantages, including (i) strongly decreasing the number of model parameters and (ii) allowing biological and ecological interpretations of the growth trajectory. Handling species by their shared morphological, physiological, and phenological characteristics is the central theme of this approach. Several functional traits, known as

the Leaf-Height-Seed strategy framework, have been proposed to reflect important functional axes that drive plant performance [14, 15]. An important recent breakthrough was the description of a leaf economics spectrum (LES) which reflects a tradeoff between investments in productive leaves with rapid turnover versus costly physical leaf structure with a longer payback [16]. However, recently Osnas et al. [17] showed that the LES is an artifact of normalization by leaf mass per area (LMA). The normalization independent LES turns out to be very weak. Height reflects the final plant stature and its vertical position in the vegetation, and, thus, its access to light [18]. Seed mass, although not physiologically related to adult plant growth, is an important indicator of the overall species life-history strategy, with fast-growing pioneers tending to have smaller seeds [19]. Baraloto et al. [20] have recently pointed out that wood density is decoupled from leaf traits and they propose a stem economics axis of trait variation. In the following, we detailed the interactions between climate and functional traits expected to affect tree growth. We focused on the trait/climate growth rate interactions in adult trees only, because the role of functional traits in tree growth may change during ontogeny [21].

Among life-history traits, maximum height reflects the adult place in the vertical profile of the canopy, a proxy of light availability [22]. Poorter et al. [23] suggested that tall trees, that is, having crowns in the forest canopy, are exposed to drier conditions more than understorey species. In other words, tall trees often fail to maintain their evaporative demand in dry periods. Granier et al. [24], using sapflow measurements, observed that big trees, that is, trees having large DBH and/or DBH_{max}, have higher water demands. For some dominant trees, total tree sapflow reached values as high as $30\,kg{\cdot}h^{-1}$ (250–$300\,kg{\cdot}day^{-1}$). Nepstad et al. [25] used an experimental drought (reduction of 60% of incoming rainfall) to show that, after 3.2 years, the treatment resulted in a 38% increase in mortality rates. Mortality rates increased 4.5-fold among large trees (DBH > 30 cm) and 2-fold among medium trees (10–30 cm dbh). Even if Nepstad et al. [25] did not focus on tree growth, a diminution of tree growth preceding death is often observed [26, 27]. In this paper, we hypothesize that species with high diameter max and height max as well as the biggest individual trees would be much more sensitive to drought events and that drought would negatively affect their growth. Seed mass, even if not directly related to adult plant performance, is an important index of life-history strategy of species, and fast-growing species tend to have small seeds [19, 28]. We hypothesize that species with small seeds could be more sensitive to drought conditions because of their tendency to be fast-growing species, that is, a less conservative resource strategy.

Along the stem economic spectrum, bark thickness may have no direct link with the climate response as this trait is mainly linked to the tree defence strategy [29]. But bark thickness is indirectly linked to diameter increment due to the shrinkage of stems during dry seasons [30]. Trees with the highest bark water contents and thicknesses displayed the strongest decreases in girth during the dry season as well as the highest increases at the start of the wet season [31].

Santiago et al. [32] demonstrated that wood density is well linked to hydraulic efficiency, in turn positively correlated to the photosynthetic potential. The ecological strategy "many narrow conduits" versus "fewer wider conduits" highlights the tradeoff between the hydraulic efficiency of wide conduits and the cavitation resistance of narrow conduits [33]. This cavitation resistance is a potentially great asset to the growth of species with high wood densities when the available soil water content starts to decline at the end of the wet season. This is because species with low densities are known to be more sensitive to water availability and to have a less conservative resource strategy [34]. In this paper, we hypothesize that species with high wood density would be less sensitive to drought events and that drought would negatively affect the growth of softwood species.

Along the leaf economic spectrum, specific leaf area (SLA) indicates the leaf efficiency for light capture per unit biomass invested [35]. SLA is weakly or not related to the growth of large-sized trees [23] for which leaf area and light interception are largely determined by branching patterns, the number of meristems, and tree architecture [36]. Species with high SLA tend to have (i) short-lived leaves with high N and P mass contents [16, 37], (ii) high mass-based maximum photosynthetic rates [38] and are usually found at the fast payback end of the leaf economic spectrum [20]. This combination of traits is usually found in species with fast growth rates [28]. At the opposite end, leaf traits associated with low SLA (thick leaf blade; small, thick-walled cells) have often been interpreted as ecological adaptations to drought, that is, allowing, at least in evergreen species, continued leaf function (or at least postponing leaf death) under very dry conditions [16, 39]. A tight correlation amongst leaf K and leaf N or P concentrations was highlighted among neotropical trees [20]. Leaf K concentration is associated with stomatal control. K^+ concentration when stomata are open is nearly ten times larger than the K^+ concentration when stomata are closed [40]. Potassium limitation has been shown to have a negative effect on the ability of plants to control stomata, often leading to a reduction in water-use efficiency [41, 42]. It may be expected that species with low values of K might be more sensitive to drought as they have less flexibility to control stomata apertures, and, thus, less flexibility to limit the loss of water. Finally, $^{\delta 13}C$ can provide a direct estimate of a tree's water use efficiency, WUE [43]. Leaf $^{\delta 13}C$ is often thought to be an integrative indicator of stomatal response to atmospheric dryness [44, 45] and is strongly correlated with SLA. Species with low water use efficiency have been found to have small SLA [20, 37, 46]. This trait has not been directly used by the existing coupled vegetation/climate models but would allow assignment of a key parameter for drought adaptation [47]. Here, soft traits referred to traits that are relatively easy and quick to quantify, often good correlates of hard traits, which may be more accurate indicators of plant functions responsible for responses or effects at the ecosystem or biome scale, but which are difficult to quantify for large numbers of species in many regions of the world [38, 48]. In this paper, we hypothesize that drought conditions could first affect species with a high SLA (high water use efficiency, soft leaf trait).

Hard leaf traits such as leaf water potential at turgor loss (π_{tlp}) and leaf water potential at full turgor (π_0) are known to give an explanation of species tolerance to drought across biomes at the worldwide scale [49]. Here, we focus on tropical rainforests and make a first analysis of the link between soft traits and tree growth response to drought, that is, the plant performance.

In this paper, we addressed three specific questions which are as follows. (i) Are functional traits involved in tropical tree growth response to seasonal variation of climate? (ii) Which traits are linked to resistance to drought? (iii) Finally, how far can functional traits help in predicting the future of tropical forests in terms of composition toward expected changes of climate? We hypothesize that life-history traits and stem economic spectrum traits, more so than leaf traits, could explain the growth response to drought, that is, the capacity or not to maintain diameter growth during drought periods. Furthermore, we suspect that the tree growth response to climate is associated with the growth strategies of tropical trees, fast growing species being more affected by fast changes of climate conditions in terms of growth.

2. Methods

2.1. Site. The study site is located in Paracou, French Guiana (5°18′N, 52°23′W), a lowland tropical rainforest near Sinnamary [50]. The climate is affected by the north/south movements of the Intertropical Convergence Zone and the site receives nearly two-thirds of its annual 3041 mm of precipitation between mid-March and mid-June, and less than 50 mm per month in September and October. The most common soils in Paracou are the shallow ferralitic soils limited in depth by a more or less transformed loamy saprolite [50]. The site is located approximately 40 m above sea level [50] and is made up of a succession of small hills. The forest is typical to Guianan rainforests [51]. More than 550 woody species attaining 2 cm DBH (diameter at Breast Height, i.e., 130 cm) have been described at the site, with an estimated 160 species of trees > 10 cm DBH per hectare [52]. The dominant families at the site include Leguminosae, Chrysobalanaceae, Lecythidaceae, Sapotaceae, and Burseraceae.

2.2. Data. Seasonal changes in trunk circumference were monitored in 204 trees from 53 species using home-made steel dendrometer bands [31]. Tree growth was censused every c. 40 days from 2007 to 2010 (mean = 39, sd = 19.8). Information on 13 key functional traits (related to leaf economics, stem economics, and life-history) measured on mature trees (DBH > 10 cm) of the 53 focal species was extracted from a trait database of French Guianan tree species [53] (see Table S1.1 in Supplementary Material available online at http://dx.doi.org/10.1155/2014/389409). The values of functional traits used in this study are mean-species values for French Guiana and Paracou is amongst the sites used for functional trait measurements in this database. Details of sample collection and trait measurements are available in Baraloto et al. [20] for the leaf and stem economic traits and in the study by Herault et al. [22] for the life-history traits.

The 95th percentile diameters were used as estimates of DBH_{max} to minimize the weight of outliers [54]. These traits represent complementary axes of tree ecological strategies in tropical forests (Table 1) and have been proposed to be important for tree performance through ontogeny [14, 23, 55] and for growth responses to climate variations [20, 33, 45]. Due to a strong correlation between bark thickness and $^{\delta 13}C$ on one hand and current tree size on the other [29], bark thickness and $^{\delta 13}C$ were corrected with the method given in Baraloto et al. [20].

2.3. Meteorological Data. In 2003, a 55 m self-supporting metallic eddy covariance flux tower, Guyaflux, was built in the Paracou forest in a natural 100 m^2 gap, with minimal disturbance to the upper canopy. This location covers a range of more than 1 km of forest in the direction of the prevailing winds. The top of the tower is about 20 m higher than the overall canopy. Meteorological and eddy flux sensors (full details in Bonal et al. [56]) were mounted 3 m above the tower. A large set of climatic variables were recorded at a daily time step (supporting information, Table S2.1). Most climatic variables exhibited strong seasonal changes, highlighting the north/south movements of the Intertropical Convergence Zone (supporting information, Figure S2.1).

We used a water balance model explicitly designed for tropical forests [57] to estimate water availability for trees. The model computes daily water fluxes (tree transpiration, understorey evapotranspiration, rainfall interception, and drainage), soil water content at different layers, and relative extractable water for trees for the entire soil (REW). REW is a daily value between 0 and 1; when REW = 1, the amount of extractable water by the tree is at its maximum, and when REW = 0, no water is available for trees. We created with REW a variable of water stress, SWD for soil water deficit, SWD = 1 − REW.

2.4. Data Analysis. As an initial exploration of the covariation among functional traits, we investigated their associations through a principle component analysis (PCA) on the normalized traits dataset. We conducted this analysis to support the interpretation of functional traits implication in tree growth response to climate. We modelled the link between tree growth and the functional traits/climate interactions in a linear regression framework. The model was built at a daily time step. We first included a discrete variable tree in the model to account for an individual tree effect in tree growth so as not to bias our result. Next we included the discrete variable period which estimates a model parameter for each census period. This variable captured the variance due to the climatic effect common to all individuals from all species. Tree and period are treated as fixed factors and estimated in the model. We then explored the interaction between functional traits and climatic variables one by one. The interaction between the current DBH and climate variables was also investigated to test the hypothesis of a size-mediated response to climate stress. All interactions were successively tested in univariate models to lower multicollinearity problems associated with multivariate models. Prior to the analysis, functional traits were scaled, that is, each value was divided by the trait

Table 1: Functional traits used in the study, their role in tree functional strategy [20], the range of values represented by the 53 species in this study, the range of values for tree species of French Guiana [20], and associations between functional traits and expected growth response to water availability reported in the literature.

	Roles	Units	Sample range[a]	FG range[b]	WET[c]	DRY[d]	References
Life-history							
DBH_{max}	Architecture and structure	mm	190–980	10–1254	+*	–*	Granier et al. [24]; Nepstad et al. [25, 70]; Monserud [26]; Wyckoff and Clark [27]
$Height_{max}$	Architecture and structure	m	18–50	8–56	+	–	Poorter et al. [23]; Herault et al. [13]
Seed mass	Reproductive investment	g	<0.01–>20	<0.01–>20	–	+	Moles et al. [19]; Poorter and Bongers [28]
Stem economic spectrum							
Wood density	Transport structure defense	$g \cdot cm^{-3}$	0.38–0.84	0.28–0.88	–	+	Santiago et al. [32]; Chave et al. [33]; Markesteijn et al. [34]
Bark thickness	Defense	mm	(−4.7)–13	(−6.2)–13.4		+	Stahl et al. [31]; Baker et al. [30]
Leaf economic spectrum							
SLA	Resource capture, defense	$cm^2 \cdot g^{-1}$	5.41–16	4.02–24.78	+	–	Poorter et al. [23, 35]; Sterck and Bongers [36]; Wright et al. [16]; Fyllas et al. [37]; Cornelissen et al. [38]; Poorter and Bongers [28]
K	Resource capture	$g \cdot g^{-1}$	$2 \times 10^{-3} - 2 \times 10^{-2}$	$1.2 \times 10^{-3} - 2.2 \times 10^{-2}$	+	–	Roelfsema and Hedrich [40]; Marschner [41]; Santiago and Wright [42]
N	Resource capture	$g \cdot g^{-1}$	$1 \times 10^{-2} - 4 \times 10^{-2}$	$1 \times 10^{-2} - 4.5 \times 10^{-2}$	+	–	Baraloto et al. [20]; Poorter and Bongers [28]
P	Resource capture	$g \cdot g^{-1}$	$3 \times 10^{-4} - 2 \times 10^{-3}$	$2.9 \times 10^{-4} - 2.15 \times 10^{-3}$	+	–	Baraloto et al. [20]; Poorter and Bongers [28]
C/N	Resource capture, defense	$g \cdot g^{-1}$	13–34	11–47	–	+	Baraloto et al. [20]; Poorter and Bongers [28]
LTD	Resource capture, defense	$g \cdot cm^{-3}$	$2.5 \times 10^{-5} - 5.6 \times 10^{-5}$	$2.1 \times 10^{-5} - 1.45 \times 10^{-4}$	–	+	Wright et al. [16]; Donovan et al. [39]
Chlorophyll	Resource capture	$\mu g \cdot mm^{-2}$	48–100	21–150	–	+	Wright et al. [16]; Baraloto et al. [20]; Cornelissen et al. [38]
Toughness	Defense	N	0.85–3.4	0.2–11.4	–	+	Wright et al. [16]; Donovan et al. [39]
$\delta^{13}C$	Resource capture	‰	(−1.7)–2.5	(−2.9)–4.8	+	–	Farquhar et al. [43]; Prentice et al. [44]; Lamont et al. [46]; Fyllas et al. [37]; Baraloto et al. [20]

[a] Range of traits values of the Paracou sample, [b] range of traits values of French Guiana (FG) extract from the BRIDGE database [20], [c] expected growth response to wet conditions, [d] expected growth response to drought conditions, * (+) trees with high values of a given functional trait are expected to grow faster, and (−) trees with high values of a given functional trait are expected to grow slower.

TABLE 2: Functional traits mediate tropical tree responses to climate variations among 53 neotropical species. Shown are percentages of tree growth variance explained by the interaction of traits and climate factors in univariate analysis. Only significant interactions are shown based on the difference between BIC values of the model and BIC_{ref}. *** denote a difference >10, ** >2 and * between 0 and 2. (+) trees with high values of a given functional trait grew significantly faster when a given climate variable was high. (−) trees with high values of a given functional trait grew significantly slower when a given climate variable was high.

	DBH	$Height_{max}$	WdDens	N	CN	LTD	Chlo	Tough
REW^a						0.19*** (+)	0.12** (+)	
Rain	0.24*** (+)					0.34*** (+)	0.13** (+)	
SWD^b	0.38*** (−)	0.11** (−)	0.08** (+)	0.15** (−)	0.13** (+)	0.08* (−)		0.15** (+)
Irradiance	0.12** (−)		0.11** (+)	0.08* (−)				0.12** (+)
T_{max}				0.08* (−)				
T_{min}				0.08* (−)				
Wind.speed				0.09* (−)		0.09* (+)	0.08* (+)	
VPD^c	0.08* (−)			0.09* (−)	0.08* (+)			

^{a}Relative extractable water, ^{b}soil water deficit (1-REW), and ^{c}vapour pressure deficit.

standard error. The growth model was fitted with weighted least squares, with weights calculated to correct the facts that (i) growth, climatic, and traits data were summed over different period lengths and (ii) the number of studied trees varied among species. Consider:

$$
\begin{aligned}
Gr_{i,j} &= nd_j \times tree_i + nd_j \times period_j \\
&\quad + nd_j \times \theta \times (var_{trait} \times var_{clim}) + \epsilon_{i,j}, \\
\epsilon_{i,j} &\sim \mathcal{N}\left(0, weight \times \sigma^2\right), \\
weight &= nd_j \times n_{indSp},
\end{aligned} \tag{1}
$$

where $Gr_{i,j}$ is the growth in diameter and in mm of the tree i over the period j, $tree_i$ is the individual daily tree effect, $period_j$ is the daily period effect, θ quantifies the effect of the interaction between the trait value var_{trait} and the climate variable var_{clim}, and nd_j is the number of days of the period j. The weight is the product of the number of days of the period, nd_j, with the number of individuals from each species in the data, n_{indSp}.

To test the significance of each trait/climate interaction, we computed for each univariate model the Bayesian information criterion, BIC [58]. We compared this BIC to the Bayesian information criterion value of the model that includes the fixed trait variable and the fixed climate variable but that omits their interaction, BIC_{ref}. A BIC lower than BIC_{ref} means that the information carried by the interaction improved the model even if it added a parameter.

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

3. Results

The first axis of the principal component analysis (Figure 1) explained 31.15% of the variance in the trait dataset and was positively correlated with N, P, SLA, K, $^{\delta13}$C, and negatively correlated to C/N, toughness, LTD, and wood density. The second axis explained 12.63% of variance and was positively correlated with bark thickness, toughness, and K.
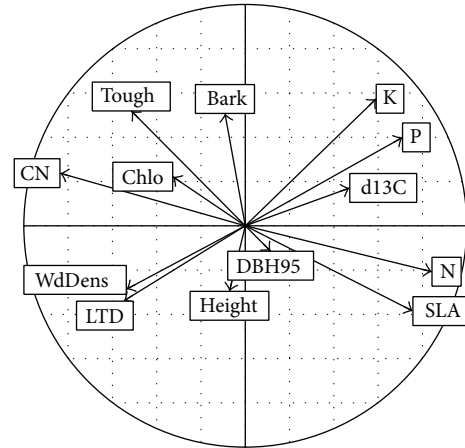

FIGURE 1: Correlation circle of the functional traits principal component analysis.

More than 33.5% of the observed variation in tree growth could be attributed to individual tree behaviour, with the period effect explaining 15.0% of the tree growth variance. This means that climate variables alone could explain up to 15% of the variance of tree growth. The interaction term between a single trait and a single climate variable captured a maximum of 0.38% of the variance (Table 2). The BIC selection procedure retained 24 trait/climate interactions (Table 2). With the exception of relative air humidity and atmospheric pressure, all climate variables showed interactions with traits for predicting tree growth. Six of the 13 functional traits DBH_{max}, Bark, SLA, K, P, and $^{\delta13}$C were not associated to any climate variables for predicting tree growth.

3.1. Life-History. Tree species with a high $Height_{max}$ grew more slowly when the soil water deficit was high, and larger trees also grew more slowly in drought conditions (high SWD and high irradiance) and when vapour pressure was high. Furthermore, trees with large DBH grew faster during the wet period.

3.2. Stem Economics.

Trees with high wood densities grew more rapidly during drought events (high SWD and high irradiance).

3.3. Leaf Economics.

Trees with high foliar N (and low CN ratio) grew more slowly during drought events (high SWD and high irradiance), or when vapour pressure was high and temperatures and wind speed were maximum. Trees with high leaf tissue densities had higher growths in wet seasons (high REW and high precipitation), when wind speed is high, and lower growths were observed when soil water deficit was high. Trees with high leaf chlorophyll content had a higher growth in wet conditions (high REW and high precipitation) and when wind speed was high. Finally, trees with high leaf toughness had a higher growth in drought conditions (high SWD and high irradiance).

4. Discussion

We observed direct links between functional traits and growth response to climate variations, an important step to improve global vegetation models in predicting tropical forest responses to global change [45, 59]. However, we found that the interaction term between a single trait and a single climate variable captured a significant but very thin part of the variance of tree growth, Table 2. Effects of functional traits may be noticeable throughout the whole year, as found for leaf tissue density (LTD) or current diameter (DBH) for which interactions were significant both in wet and in dry seasons (Table 2). However, most of the effects we detected were seasonal. Positive interactions with REW and/or rain indicated that a high value of a given trait was correlated with more rapid growth in wet seasons while positive interactions with irradiance, soil water, deficit and/or vapour pressure deficit highlighted better growth in dry periods. Overall, water (REW, SWD, and rain) and light (irradiance) shaped the functional trait responses. Wind speed and VPD are proxies of water and light, respectively (supporting information, Figure S2.1). Wind speed reaches its maximum value at the start of the rain season and VPD is strongly correlated to irradiance and soil water deficit (supporting information, Table S3.1). Contrary to the results of Clark et al. [1], temperature variations captured a negligible proportion of growth variance. We propose two related explanations. First, in French Guiana, temperatures are very stable throughout the year unlike other climate variables (supporting information, Figure S2.1). Second, photosynthesis requires light and water directly, whereas temperature only changes the kinetics of the reaction. As a result, within the relatively narrow range of average minimum and maximum temperatures of our study (23.4–28.4 °C), only a minor change in photosynthesis kinetics can be expected [9].

4.1. Life-History Traits.

Big trees (DBH) in our study were clearly more affected by drought events than smaller ones. Big trees have higher water demands, are more exposed to light irradiance, and have their crowns in drier environments than the forest understorey [25]. Our results are therefore consistent with general trends from 18 mortality studies in Amazonia, 12 of which have demonstrated higher mortality rates for larger trees during drought events, three found no size-related effect, and three indicated higher mortality for smaller trees [60]. We also found that taller species ($Height_{max}$) were more affected by drought than smaller-statured species. However, species of larger girth (DBH_{max}) did not exhibit this pattern. This highlights the fact that most of the individual trees in our study were closer to their maximum height than to their maximum diameter due to the power relationship between height and DBH. This also explains why DBH_{max} is a better index than $Height_{max}$ for placing a tree along its ontogenetic trajectory [13]. Considering this result we suggest that individual tree DBH, and to a lesser extent the species $Height_{max}$, can be used as an index of tree growth response to water stress.

4.2. Stem Economics.

Consistent with the assumption that dense-wood species have smaller vessels that prevent them from embolism and that allow them to maintain baseline growth under drought conditions [33, 34], we found that trees with the densest wood were the least affected by drought. In contrast, fast-growing species with large vessels and lighter wood appeared to be more sensitive to drought. And we should keep in mind that this growth response to drought may be coupled with a buckling resistance and a biomechanic strength due to more fibres that constitute themselves as important survival attributes for the trees with the densest wood. We found no relationship between bark thickness and tree growth response. Even if this trait did not mediate the tree response to drought, bark thickness is well known as a good proxy for resistance to fire [29] which may increase under future climate-change scenarios for the Amazon basin [61].

4.3. Leaf Economics.

Recent studies have suggested that leaf traits do not explain differential growth of adult trees in tropical forests [13, 23]. However, our results showed that some leaf traits could be implicated in tree growth response to climate (N, CN, LTD, Chlo, and Tough). Species with high nutrient concentrations are usually found at the fast payback end of the "economic spectrum" [16]. On the other hand, leaf traits associated with low SLA (thick leaf blade; small, thick-walled cells) have often been interpreted as adaptations that allow continued leaf functioning (or at least postponing leaf death) under very dry conditions [16, 39]. Our results are not consistent with this hypothesis. In our dataset, N leaf concentration was more discriminating than SLA for tree growth response to drought. At a global scale, there is a strong negative correlation between leaf N content and leaf lifespan [16, 39]. It may be expected that trees with long-lived leaves suffer less from regular drought events while trees with short-lived leaves senesce their leaves when stressed and, consequently, stop their secondary growth (Table 2) [62]. Leaf toughness, chlorophyll content, and leaf tissue density are intimately correlated (Table 1) but their effect seems to be associated with different seasons. In the wet season, species with high chlorophyll content and high leaf tissue densities have more rapid growth (Table 2). This could be linked to the capacity

of species with high value of chlorophyll to have better capacity to use the lower light levels of the wet season. Leaf toughness traits are uncorrelated with relative growth rates but correlated positively with leaf lifespan [63, 64]. Furthermore, leaf toughness is negatively correlated with other leaf traits favouring fast growth [20]. Species with a high toughness could have a higher growth in drought conditions, that is, higher temperatures and irradiance, due to their position on the leaf economic spectrum, as opposed to fast growing species. δ^{13}C was not correlated with growth response to climate. Foliar δ^{13}C is an indicator of leaf-level water-use efficiency reflecting a tradeoff between photosynthetic rates and stomatal conductance [65]. With the complete French Guianan tree functional trait database (668 species), Baraloto et al. [20] have found that foliar δ^{13}C was weakly correlated with LES and SES, when corrected for stature. They conclude that the sensitivity of this measure to microhabitat variation may preclude its utility as a plant functional trait at the community scale in systems with a complex vertical structure such as tropical forests.

4.4. Rethinking the Tree Growth Response. We present a unique dataset integrating climatic variables and tree growth records with trait values at high resolution. Yet at best our model explains 48.9% of the variance of tree growth. Surprisingly, the interactions between traits and climate, even if some were significant and followed the general frame of the expected results, explained only a limited part of the variation in tree growth, no more than 0.4% each. This may be a strong limiting factor for use of a functional trait modeling framework to predict future growth in a climate change context. Further research will be needed to explore the functional link between traits and tree growth response to climate, including the integration of some hard traits that are not typically included in functional trait screenings, including leaf and stem anatomies and leaf turgor pressure [49, 66, 67]. During the 3 years of the study, climatic conditions have followed the classical pattern of wet season and dry season successions. Even the dry season can be considered as particularly dry for tropical forest with 3-4 months with less than 50 mm; no extreme changes in climate were observed on the period of the study. The dry period could be usual for the investigated trees, and they may not have used extreme strategies of growth which are assumed to be mediated by some functional traits. The majority of trees stopped their growth in the dry season. But some species are able to maintain their growth more days than others (Figure 2) and we point out in this study that fast growing species growth rates could be more impacted than slow growing species due to their less conservative resource-use strategy. Anyway, it might be interesting to add memory in modelling annual growth. Indeed, our results suggest that growth is at its maximum at the beginning of the rainy season, when water and light are available, and the leaves are new. Similar climatic conditions are frequent during the long rainy season (January to June) but the leaves age [68] and secondary growth decreases symmetrically (Figure 2). A model taking into account
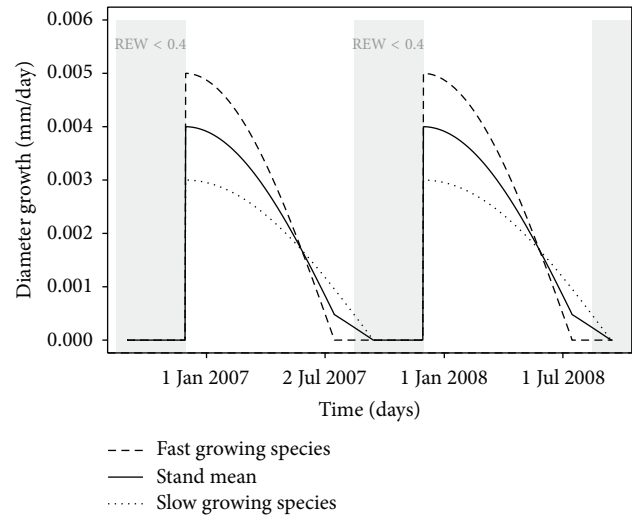

Figure 2: A theoretical representation of the shape of tree diameter growth dynamics of the mean community (solid line), of the fast growing species (dashed line) and slow growing species (dotted line), under the assumption of the paper and supported by the results. The mean value of tree growth for the community is based on the data.

the ageing of leaves, for example, through a decreasing exponential, should be explored. In order to develop predictive model of CO_2 fluxes between the forest and the atmosphere; further investigations are needed as tree growth is one of the demographic variables, and trees may respond to climate change in other demographic dimensions, for example, mortality and reproduction, that may or may not show similar climate interactions.

4.5. Conclusion. With the absence of extreme climatic events during our study, we cannot conclude that a composition change is expected. However, our results join the recent finding that smaller, denser-wooded trees are able to maintain their functioning in drought conditions [33, 60]. In such cases where climate variation is regular and implies quite thin variance explanation, using traits in analysis must be done with the traits closer to the processes. For example, N, P, and K are very correlated but only N improves the model, probably because this trait is closest to the process linking tree growth and climate, as N is a proxy of the maximum photosynthetic rate and maximum growth rate [38]. Among the climate variables, we found no effect of trait interaction with temperature on tree growth. The mean temperature at our site is near the optimal range for photosynthesis and is stable throughout the year. But, if temperature follows the expected increase for the 21st century [69], temperature will impact tree growth by reducing photosynthesis kinetics [9].

In this study, each growth measurement is assumed to be independent of others. This is a strong, but common, assumption for growth modeling. Our results suggest that a single heavy rain in the dry season does not have the same effect on tree growth as a heavy rain in the wet season. This practically compels one to analyse tree growth with

dynamic models. In the absence of extreme climate events, trait-based community dynamic models appear to be the only way to investigate extreme climatic scenarios, such as those predicted for the 21st century. Such modeling approaches, combined with experiments on unusual extreme events [70], are urgently needed to test the sensitivity of tropical forests to climate change.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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