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Growth determinants of timber species *Triplochiton scleroxylon* and implications for forest management in central Africa

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ABSTRACT

The sustainability of the polycyclic logging system in tropical forests has been increasingly questioned for a variety of reasons, and particularly in central Africa as commercial species, mostly light-demanding long-lived pioneer species, usually fail to recover a stable number of large trees after exploitation. Several factors are known to affect tropical tree demographic processes, like tree growth, survival and recruitment. Tree growth has particularly been showed to depend on ecological conditions, tree genetics, and competition with surrounding vegetation, as well as tree size or ontogeny. Yet, due to the paucity of available data, the importance of such factors is unclear and usually ignored when estimating future timber yields. To fill this gap, we chose to evaluate the variability in growth of one African long-lived pioneer and commercially very important species: *Triplochiton scleroxylon* K. Schum, gathering a broad dataset composed of tree ring data recorded in one site in Cameroon and periodic field inventory data recorded in seven sites across central Africa. In total, we analyzed 13,225 records of annual tree diameter increments recorded over 920 trees from seven sites in Cameroon, Republic of the Congo and Central African Republic. We evaluated (*i*) to what extent the average growth of trees that reach harvestable dimensions differs from population average and (*ii*) to what extent past perturbations influence the growth of remaining trees. We found the diameter growth of *T. scleroxylon* to be remarkably variable and this study provided an unprecedented quantification of the magnitude of some key growth determinants. In unlogged forests, the diameter increment of *T. scleroxylon* ranged between 0.40 cm year^{-1} in Southern Cameroon and 0.83 cm year^{-1} in South-Eastern Cameroon. The diameter increment was weakly related to tree size but increased twofold from unlogged to logged forests. Perturbation caused by logging stimulates growth of *T. scleroxylon* for at least 10-15 years. Finally, harvestable timber stock of large-sized *T. scleroxylon* was found to be constituted by trees that grew in average twice faster than trees of the entire extant population. As more and more inventory data become available, quantifying these effects could be replicated for other timber species and in other sites, to improve the accuracy of future timber resource estimates and improve forest management guidelines.

1 INTRODUCTION

Timber exploitation in tropical forests contributes to local development and, when conducted in a sustainable way, can ensure the long-term preservation of forest cover, biodiversity and ecosystem services (Nasi *et al.*, 2012; Miteva *et al.*, 2015; Cerutti *et al.*, 2016). With the aim to attain sustainable timber exploitation, tropical forests are often exploited under polycyclic systems and following criteria set in management plans. These criteria usually include the length of the cutting-cycle, maximum exploitation intensities, and species-specific minimum cutting diameters. Their values are either fixed by national regulations (e.g. the cutting cycle in Cameroon is fixed to 30 years), forest certification schemes or set by forest managers to ensure an acceptable level of stock recovery rate for each commercial species. The stock recovery rate is the ratio between the potentially exploitable stock at the end of the cutting cycle to that at the beginning of the cutting cycle. It expresses the balance between harvest and natural renewal of the potentially exploitable stock (Picard *et al.*, 2009). Despite the efforts to attain the sustainability of polycyclic systems, its effectiveness has increasingly been questioned for a variety of reasons, but particularly because commercial species usually fail to recover the initial exploited timber volume or tree number (Putz *et al.*, 2012; Gourlet-Fleury *et al.*, 2013b; Bourland *et al.*, 2015; Groenendijk *et al.*, 2017; Romero and Putz, 2018).

Predicting stock recovery rates is thus a key aspect of sustainable forest management. Yet, this task requires species-specific data on the autecology and demography of comercial species, that is, data on how diameter distributions, growth, mortality and recruitment rates vary for a given species (Karsenty and Gourlet-Fleury, 2006; Picard *et al.*, 2009). However, these data remain poorly quantified for tropical species including those exploited for timber. Ultimately, this paucity of information hinders our ability to predict future timber stocks to correctly inform forest management decisions. Decisive information is mostly sparse on (*i*) how tree growth varies between individuals within a population (Brienen and Zuidema, 2007; Rozendaal *et al.*, 2010; Groenendijk *et al.*, 2017); (*ii*) how growth varies across a species´ range and the environmental conditions driving this variation (Brienen and Zuidema, 2005; Therrell *et al.*, 2007; Wagner *et al.*, 2016; Locosselli *et al.*, 2017; Rosa *et al.*, 2017); and (*iii*) how species growth is affected by previous forest disturbances (natural or anthropic) (Gourlet-Fleury *et al.*, 2013b).

Recent studies have indeed raised concerns about applying fixed values of annual diameter increment for all individuals within a species in the computation of timber stock recovery rates (Brienen and Zuidema, 2007; Rozendaal *et al.*, 2010; Groenendijk *et al.*, 2017). Individuals of the same species show substantial variability in growth throughout their lifetime with some individuals sometimes showing persistent fast growth (Brienen and Zuidema, 2007; Groenendijk *et al.*, 2017). Although only few indivuals eventually grow faster than population average, it has been showed that the fast growers can constitute the majority of the individuals that reach harvestable size (Brienen and Zuidema, 2007; Rozendaal *et al.*, 2010). Brienen and Zuidema (2007) have then showed how these differences can be incorporated in simulation of timber stock recovery rate to provide more realistic predictions in Bolivia. In addition, tropical tree growth depends on topographic, edaphic and changing climatic conditions (Brienen and Zuidema, 2005; Therrell *et al.*, 2007; Wagner *et al.*, 2016; Locosselli *et al.*, 2017; Rosa *et al.*, 2017) as well as past natural and anthropic disturbances (Gourlet-Fleury *et al.*, 2013b). All these sources of variation are usually not considered in simulations of stock recovery rates. For example, in Cameroon, these simulations are performed using legally fixed species-specific diameter increments that do not vary across Cameroonian environmental conditions (Ministère de l'Environnement et des Forêts, 1998). A better understanding of these factors is clearly needed to enhance sustainable forest management.

Here, we combine growth data from periodic field inventories and tree ring analyses to quantify the variability of tree growth within populations, between different areas, and under different management history, to provide a basis for more accurate calculations of future timber resources in central Africa. As a study case, we evaluated the growth of *Triplochiton scleroxylon*

K. Schum (Malvaceae), a widespread (Bongers *et al.*, 1999), long-lived pioneer associated to fertile soils (Veenendaal *et al.*, 1996) and commercially important species, being the third most exploited species in central Africa (Bayol *et al.*, 2012).

Analyzing the different factors affecting tree growth, we address the following questions. (*i*) To what extent trees that attain harvestable dimensions have grown faster than population average? (*ii*) To what extent does tree growth depend on past logging conditions? We assume that few fast-growing individuals reach the canopy and harvestable dimension whereas most trees strive under the canopy and ultimately die before reaching harvestable dimension. Moreover, according to the reported results in the experimental plots in M'Baïki (Jardin, 1995), we expect strong post-logging growth releases that may last at least 10 years. Here, we address and discuss these questions and expectations using a broad dataset composed of tree ring data recorded in one site in Cameroon and field inventory data recorded in seven sites located in three central African countries .

2 MATERIAL AND METHODS

2.1 STUDY SPECIES

T. scleroxylon (Malvaceae) is a large deciduous tree species with low wood density (320 – 440 kg/m^3) named Obeche, Samba, Wawa or Ayous (Palla and Louppe, 2002). It can reach 50 m in height and 2 m in diameter and develops large buttresses at its trunk base (Hall and Bada, 1979; Siepel *et al.*, 2004). It is locally relatively abundant throughout the semi-deciduous forests of central Africa (Fayolle *et al.*, 2012), and also widespread in West Africa (Bongers *et al.*, 1999). *T. scleroxylon* is more abundant in well drained, ferruginous and fertile soils, often at altitude less than 500 m a.s.l. and never above 900 m a.s.l.. Areas in its spatial range have a seasonal climate with a marked dry season, rainfall ranging between 1100-1800 mm and temperature between 20 and 35°C (Hall and Bada, 1979). *T. scleroxylon* can grow relatively quickly, with annual diameter increment ranging up to 1.82 cm.year^{-1} (Jardin, 1995). *T. scleroxylon* easily colonizes open areas and regenerates for some time in early successional forests, but often fails to regenerate under the (disturbance) conditions in unlogged and logged forests (Hall and Bada, 1979; Karsenty and Gourlet-Fleury, 2006). Additionally, good fructifications are irregular and supra-annual (Palla and Louppe, 2002) which may further hamper regeneration.

2.2 STUDY SITES

Data were collected in seven sites in central Africa, representative of a wide range of tropical forests. All sites but Ma'an correspond to semi-deciduous forests and are characterized by one or two dry seasons per year (Fig. 1). In Ma'an, forests are evergreen with about 20% more rainfall than the others (Table 1, Fig. 1). In all sites but M'Baïki, the geological basement consists of low Precambrian schistoquarzitic rocks with additional old volcanic intrusions in Ma'an or covered with quaternary alluvial deposits in the alluvial plains of Kabo and Mbirou (Gillet and Doucet, 2012); M'Baïki is located on a large plateau with sandstone-quarzite bedrock (Ouédraogo, 2011). In all sites, the resulting soils are classified as Ferralsols and Acrisols (Jones *et al.*, 2013). For the sake of clarity, the three sites in the Republic of the Congo were hereafter pooled together in graphical illustrations.

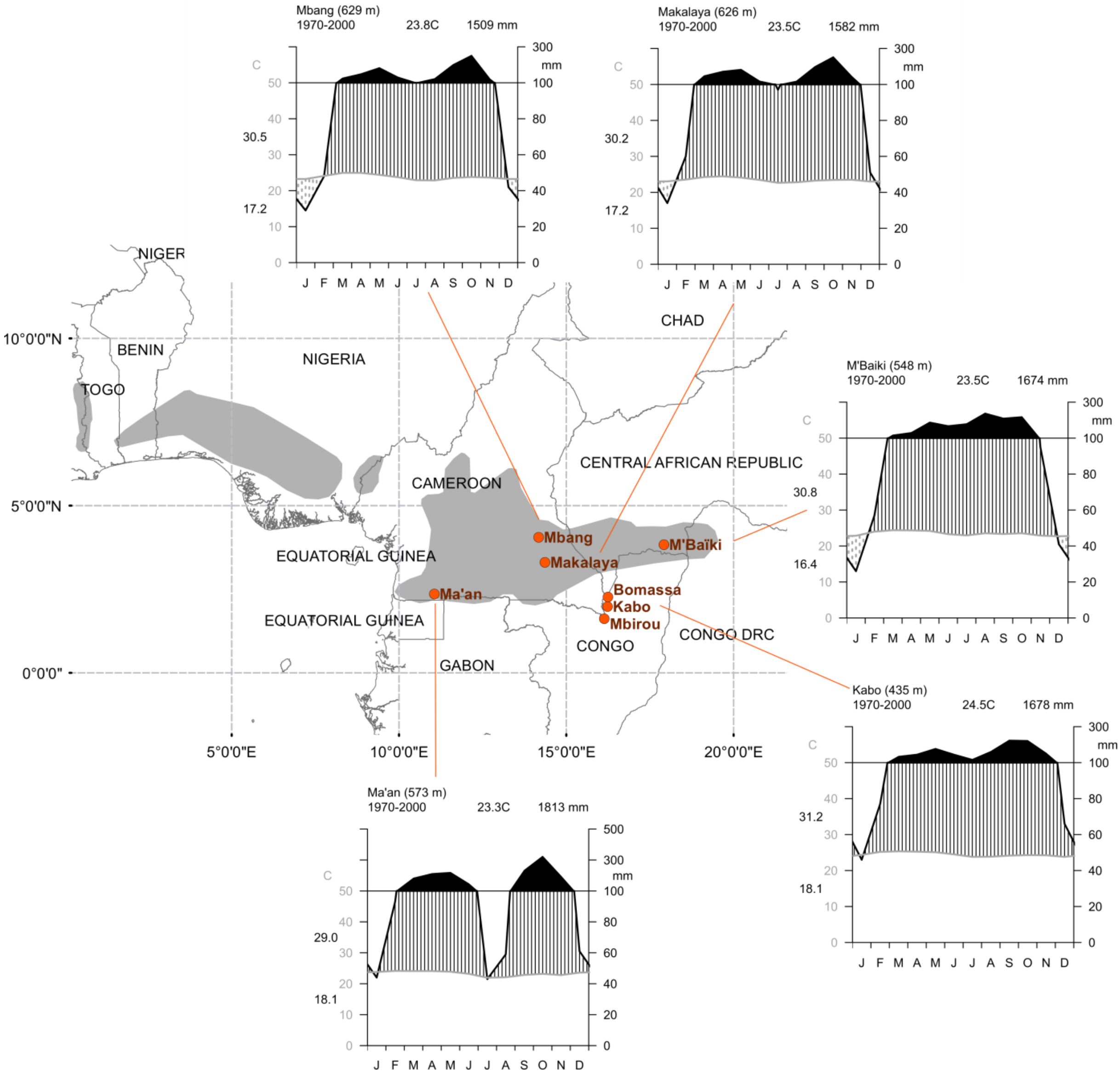

Figure 1: Location of the study sites in western central Africa with the reported distribution of *T. scleroxylon* (shaded area) as defined by Hall and Bada (1979). Walter and Lieth climatic diagrams are given for each study site or group of close sites (Bomassa , Kabo and Mbirou in Northern Congo). Climatic data were extracted from the WorldClim 2 database (Fick and Hijmans, 2017).

2.3 GROWTH DATA

We used three sources of growth data: (i) tree rings, (ii) short-term periodic field inventories carried out in the different study sites (iii) and long-term periodic field inventories carried out in the experimental plots of M'Baïki (Table 1). All these approaches have inherent biases (Bowman *et al.*, 2013) when assessing long-term growth responses of trees, especially when assessing growth of extant large trees (Sheil *et al.*, 2017). By crossing the information from different data sources we hope to, in part, apprehend these biases.

2.3.1 TREE RING ANALYSES

A total of 25 trees were selected in one logging concession in Mbang (Cameroon). In May 2015, the trees were felled, and stem disks were collected above buttresses. According to the protocol described by Latte *et al.* (2015), green-wood orthoimages of the stem disks were created, the disks were cut in bars that were sanded up to 400 grit size, scanned with 1800 DPI resolution. Tree rings were identified on the images and measured in two directions using ArcMap (ArcGIS 9.3; ESRI, Redlands, CA, USA)(Fig. 2). Diameter growth of *T. scleroxylon* has a marked annual periodicity and growth boundaries consist of a marginal parenchyma band, 1 to 4 cells wide (Iyamabo, 1971; Détienne and Mariaux, 1976). To ensure measurement quality, we measured tree rings in different radii per tree and cross-dated measurements within and between trees. We built a chronology that synthesized the common annual signal shared by different trees using TSAP (Rinntech©, Germany) and dplr R package version 1.6.5. (Bunn *et al.*, 2017). Finally, we calculated diameter growth by multiplying the mean annual ring width of each individual by two.

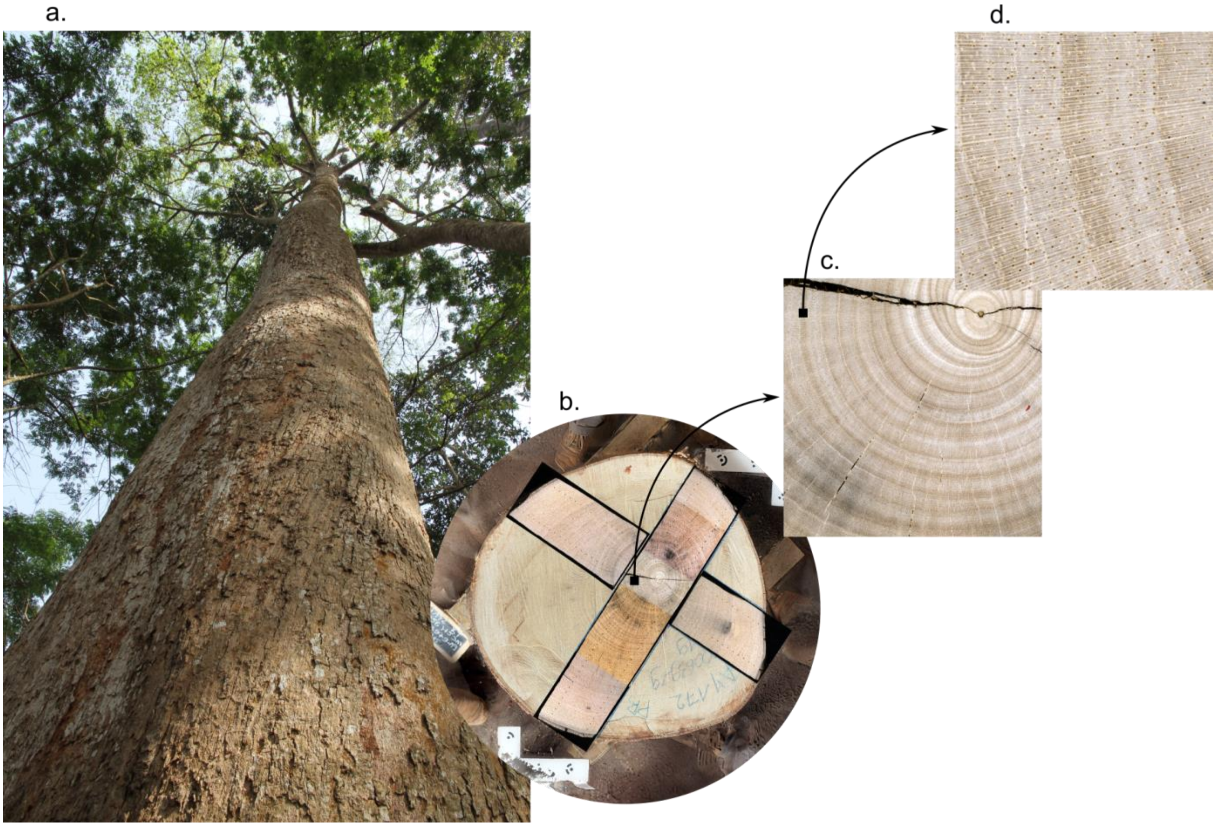

Figure 2: Illustrations of an Ayous tree, (a) a dry wood shrinkage-free image of a stem cross-section (Latte *et al.*, 2015), (b) tree rings (c) and a zoom on distinct tree rings (d).

2.3.2 SHORT-TERM PERIODIC FIELD INVENTORIES

In several forest concessions in Cameroon and in the Republic of the Congo (Fig. 1), transects were established in unlogged and logged forests to monitor tree growth and phenology yearly (DynAfFor project, https://www.dynaffor.org/, Table 1). For the needs of this study and because there might be no completely undisturbed forests in central Africa (Morin-Rivat *et al.*, 2017), unlogged forests were defined as forests that have not been exploited on an industrial scale recently. For the 3 sites in Cameroon, the last known exploitation occurred at least 39 years before the first census. For the 3 sites in the Republic of the Congo, the last exploitation occurred 15-20 years before the first census. Along these transects, tree sampling was carried out to ensure obtaining about 10-20 trees per diameter class in each site (Picard and Gourlet-Fleury, 2008). The diameter was measured with a tape to the nearest millimeter and a permanent mark was placed on tree trunk to ensure that diameter was monitored every year at the same height. For trees with buttresses and other sort of stem irregularities at breast height (1.3 m), the point of measurement (POM) was raised 1 meter above the buttresses. For each tree, we kept for the analyses only the longest diameter series without any change in POM.

Table 1: Characteristics of the study plots and transects with country code, site name, treatment, number of monitored trees (n_{tree}), number of observed annual increments (n_{incr}), initial and final years of the studied censuses, date of the last known exploitation, data used to test whether large extant trees were fast growers (conditional growth effect, model eq. 2) and the magnitude and duration of logging effect on tree growth (models eq. 3 and 4).

Country[1]	**Site**	**Treatment**	**n_{tree}**	**n_{incr}**	**Census period**	**Cutting dates**	**Cond. effect**	**Logging effect**	**Logging effect duration**
ROC	Bomassa	Logged	6	59	2006-2016	2006		X	
ROC	Bomassa	Logged	12	116	2006-2016	2006		X	
ROC	Kabo	Control	20	240	2004-2016	1985		X	
ROC	Kabo	Control	25	272	2004-2016	1985		X	
CAR	M'Baïki	Control	54	1148	1984-2016			X	X
CAR	M'Baïki	Logged	38	809	1984-2016	1984		X	X
CAR	M'Baïki	Logged+Thinned	58	1023	1984-2016	1985-1987		X	X
CMR	Ma'an	Control	147	834	2011-2017				
CMR	Makalaya	Control	35	97	2014-2017			X	
CMR	Makalaya	Logged	115	339	2014-2017	2011		X	
CMR	Mbang	(*Tree rings*)	25	6803	….-2015	*(unknown)*	X		
CMR	Mbang	Control	180	1058	2009-2015	1970	X	X	
CMR	Mbang	Logged	180	127	2015-2017	2014		X	
ROC	Mbirou	Control	25	300	2004-2016	1989		X	

[1] ROC = Republic of the Congo, CMR = Cameroon, CAR = Central African Republic

2.3.3 *Long-term periodic field inventories in M'Baïki*

Ten permanent plots of 4-ha (200m × 200m) were established in 1982 nearby the city of M'Baïki, in the Central African Republic, in two protected forests (Boukoko and La Lolé). All trees with a diameter ≥ 10 cm were individually marked, geo-referenced and identified. The girth was measured with a tape to the next half centimeter and a permanent mark was placed on tree trunk to ensure that diameter was monitored every year at the same height. From 1984 to 1990, the diameter increment of some large trees with irregular stems remained unmeasured. For trees with buttresses and other sort of stem irregularities at breast height (1.3 m), the POM was raised 50 cm above the buttresses in the regular part of the stem and up to the permanent height of 4.50 m later on (Gourlet-Fleury *et al.*, 2013b). The plots have been yearly monitored since 1982 (except in 1997, 1999, 2001 and 2013, 2014 for political and socio-economic reasons). The 10 plots were assigned to three different silvicultural treatments according to a random block design: control (3 plots), logging (3 plots), logging and thinning (4 plots). Logging occurred in 1984-1985 and thinning in 1986-1987, with no other logging or thinning activities performed ever since. Logging consisted in harvesting trees of commercial species with DBH ≥ 80 cm. Thinning consisted of killing all trees of non-commercial species with DBH ≥ 50 cm using poison girdling, removing lianas, and all *Musanga cecropioides* (in one of the plots). Further information about the experimental design, forest structure in the plots (tree density, basal area and biomass) and composition (dominant species and diversity) can be found in Ouédraogo (2011), Gourlet-Fleury *et al.* (2013b) and Gourlet-Fleury *et al.* (2013a). In the present study, we used the longest diameter series recorded on each monitored *T. scleroxylon* trees without any change in POM from 1984 to 2016.

2.4 Diameter increment computation

Annual diameter increment was computed as the difference between diameters measured at two different censuses (D_i and D_f) divided by the period length expressed in number of days (*days*, eq 1).

$$Diameter\ increment = \frac{D_f - D_i}{\#days/365.25} \qquad \text{Eq. 1}$$

It was computed considering either only the diameter observations at the first and last census (denoted hereafter ΔD) or between all possible censuses (dD). The first approach suited well to analyze tree growth with the observations carried out along the permanent transects. Using ΔD has the advantage of reducing noise due to measurement inaccuracy and removing temporal autocorrelation, while neglecting the variation of tree size within the monitoring period. This approach is, however, justified when using diameter increment computed over a limited time period and when using relatively wide size classes as explanatory variables. The variable dD was used to analyze growth releases using the long-term data obtained from the M'Baïki experiment (32 years) and tree ring data.

2.5 STATISTICAL ANALYSES

To answer our two research questions, we used different statistical methods and different data subsets that are detailed below. In all data subsets, only trees with diameter ≥ 20 cm and < 100 cm were considered to ensure having enough observations for each combination of diameter classes, sites and perturbation treatments.

2.5.1 LARGE-SIZED TREES VERSUS POPULATION AVERAGE

To evaluate whether the diameter increment of trees that attained large dimensions was higher than the population average, we compared inventory and tree ring data gathered before forest logging in 2014, in Mbang. In total, 180 trees were periodically monitored over 6 years before logging and 25 of these were sampled in 2014 for tree-ring analyses. We assumed the past growth of the 25 sampled trees to represent the growth of trees that attain large sizes. To reduce the effect of autocorrelation in tree ring data, annual diameter increments were averaged by diameter class and tree. For each diameter class, the growth of the inventoried trees between 2009 and 2014 was assumed to represent the average growth of *T. scleroxylon* population in Mbang. The difference between conditional and population diameter increment was tested performing an ANOVA of tree growth as a function of diameter classes (e_j), sampling method (f_m) and the interaction ($g_{j,m}$, eq. 2).

$$\Delta D_{i,j,m} = e_j + f_m + g_{j,m} + \varepsilon_{i,j,m} \qquad \text{Eq. 2}$$

With i, j, and m the indices for tree individual, diameter class and method (field diameter measurement *versus* tree rings). $\varepsilon_{i,j,m}$ is the random error assumed to follow a normal distribution $N(\mu=0,\sigma)$.

This test also assumes that growing conditions remained unchanged through time: i.e. the growing conditions experienced by extant juvenile trees are assumed to be similar to the conditions experienced by extant large trees at the same size (i.e. when juvenile, about 100 years ago). To partially relax this assumption, we additionally computed the proportion of trees within the population that showed the same growth average than the one of the felled trees. This effect, the conditional growth of extant large trees, was further tested with the null hypothesis being the absence of difference between the two samples (tree monitoring *versus* tree rings) using pairwise comparison of marginal means and Tuckey post-hoc tests.

2.5.2 IMPORTANCE OF LOGGING EFFECT

We tested whether tree growth is stimulated after logging activities using two different approaches, as for one of the study sites (Mbang) trees in logged and control conditions were not independent. In this site, the same trees were monitored before and after logging while in the other sites, different trees were monitored in logged and control conditions. For the Mbang site, we performed a paired Student T-test on tree growth before and after logging for the same trees. For the other sites, we ran an ANOVA (eq. 3) with tree size (b_j) and logging effect (c_t) as independent categorical variables.

$$\Delta \mathrm{D}_{i,j,t} = \mathrm{b}_j + \mathrm{c}_t + \varepsilon_{i,j,t} \qquad \text{Eq. 3}$$

With i, j, and t being the indices tree individual, diameter class and treatment. $\varepsilon_{i,j,t}$ is the random error assumed to follow a normal distribution $N(\mu=0,\sigma)$. This model was fitted for each site separately.

To account for an eventual non-linear relationship between tree size and tree growth, we performed analysis using discrete size classes of 20 cm in diameter. We also fitted additive models (GAM) with tree size as a continuous variable, which provided very similar results (not shown). The interaction between tree size and logging conditions was never significant (α = 0.05) and thus not included in the models presented here. The inventories in M´Baiki and in Northern Congo were carried out during longer periods (32 years and 12 years respectively) than in the other sites (about 4 years). To verify that the monitoring period length did not affect our results, we repeated the ANOVA for a standard period of maximum 4 years.

2.5.3 LOGGING EFFECT DURATION

We then tested the duration of the logging effect on tree growth. We used the data from M'Baïki where trees have been monitored for 32 years after logging and computed the diameter increment between all possible censuses (*dD*). We fitted a generalized additive mixed model (GAMM) of $dD_{i,j,t}$ including a smooth function of tree diameter ($f(D_{i,y})$), a smooth function of census year for each treatment ($g_t(year_y)$) and a random individual effect ($\alpha_{i,t}$) accounting for data autocorrelation (Eq. 4). To avoid model overfitting, the smooth function of tree diameter used thin plate splines with a dimension basis of 3 whereas the smooth function of census year used cubic regression splines. This model was used to test the null hypothesis being that variation of tree growth is constant through time across all treatments ($g_t(year_y)$=0).

$$\mathrm{dD}_{i,t,y} = \mathrm{f}(\mathrm{D}_{i,y}) + \mathrm{g}_t(\mathrm{year}_y) + \alpha_{i,t} + \varepsilon_{i,t,y} \qquad \text{Eq. 4}$$

With *i, t,* y the indices for tree, treatment and census year. $\alpha_{i,t}$ and $\varepsilon_{i,t,y}$ are random variables assumed to follow normal distributions $N(\mu=0,\sigma)$.

All analyses were implemented in the R statistical environment version 3.3.2 (R Core Team, 2016) using mainly *lme4* version 1.1-12 (Bates *et al.*, 2013) and *mgcv* version 1.8-17 (Wood, 2006) packages.

3 RESULTS

3.1 GROWTH DATA

Diameter increment computed from field inventory data varied substantially across sites, treatments and diameter classes (Table 2, Fig. 3). Mean diameter increment was for example about 1.63 cm year^{-1} (std. dev. = 0.81 cm) in logged forest in Makalaya and only about 0.37 cm year^{-1} (std. dev. = 0.38 cm) in unlogged (control) forest in Northern Congo.

The 25 trees sampled in Mbang for tree ring analyses were 90-229 years old with an average of 121 years old. Their diameter ranged between 89 and 118 cm with an average of 101 cm. Mean diameter increment ranged between 0.45 cm year^{-1} and 1.14 cm year^{-1}. Among-tree variability was also substantial (Fig. 4). On average, sampled trees reached the minimum cutting diameter of 80 cm (in Cameroon) in 88 years, with a range of 57-139 years (Fig. 4). A chronology was successfully built for 8 of these trees indicating that a common signal is shared by these trees and that tree rings were well identified (results not shown). This chronology had satisfying parameters for the Expressed Population Signal (EPS=0.74), correlation between tree-ring series (r=0.31) and the percentage of year-to-year matching growth variation (Gleichlaeufigkeit, GLK=54%).

Table 2: Mean and standard deviation of estimated diameter increment per site and treatment. Also shown the number of considered trees (n_{tree}) and annual increments (n_{incr}). All estimates except one in Mbang (tree rings) were computed using inventory data.

Site	**Treatment**	**n_{tree}**	**n_{incr}**	**Mean** cm year^{-1}	**Std. Dev.** cm year^{-1}
M'Baïki	Control	21	545	0.54	0.30
M'Baïki	Logged	19	425	0.87	0.43
M'Baïki	Logged+Thinned	25	475	1.13	0.79
Ma'an	Control	130	618	0.40	0.36
Makalaya	Control	31	87	0.83	0.53
Makalaya	Logged	91	305	1.63	0.81
Mbang	Control	145	858	0.58	0.44
Mbang (*tree rings*)	Control	25	5761	0.86	0.16
Mbang	Logged	113	113	0.83	0.61
Northern Congo	Control	60	702	0.37	0.38
Northern Congo	Logged	16	16	0.85	0.57

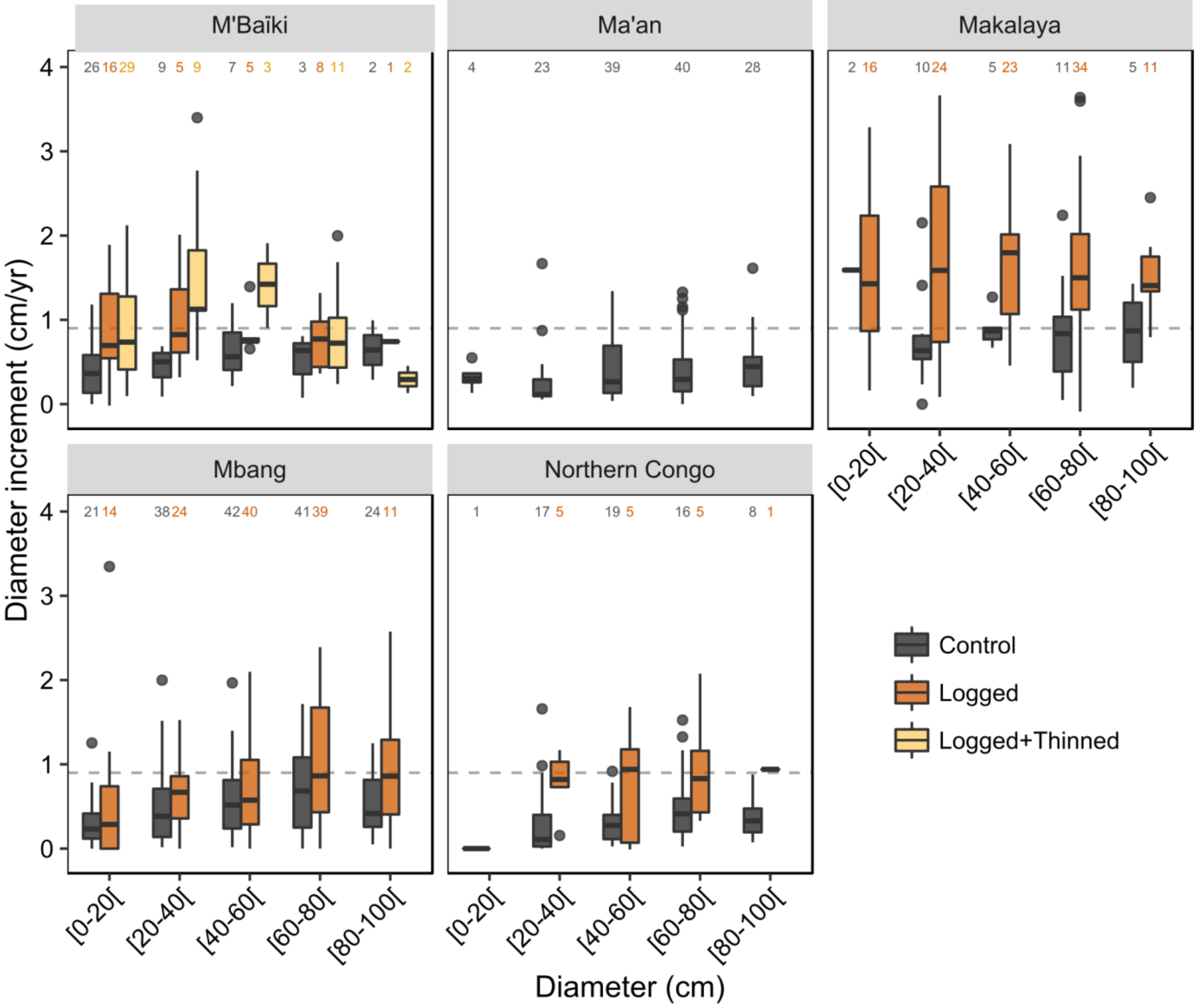

Figure 3: Variability of *T. scleroxylon* diameter increment across sites and logging treatments. The dashed horizontal gray line indicates the diameter increment (0.9 cm year^{-1}) as fixed by the

Cameroon government for the calculation of stock recovery rate. Numbers indicate the sample sizes for each boxplot.

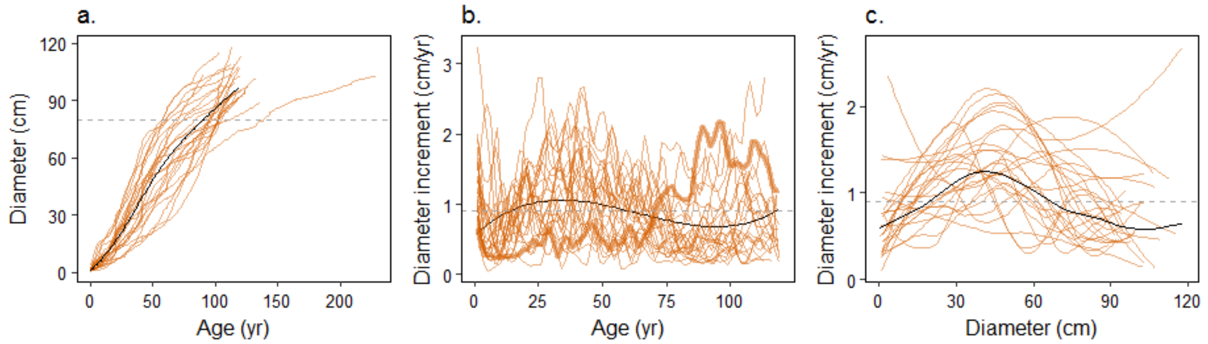

Figure 4: Diameter increment trajectories of 25 *T. scleroxylon* trees sampled in Mbang for tree ring analysis (one line per tree), showing different diameter-age trajectories (a), diameter increment-age relationships (b); and smoothed diameter increment-diameter trajectories (c). The thicker line in plot b shows the growth trajectory of a single tree that is used as an example in the discussion. The black solid lines indicate the smoothed average trend highlighting (c) that diameter growth peak at diameters between 20 and 60 cm. Dashed horizontal gray lines denote the minimum cutting diameter of 80 cm used in Cameroon (a) and diameter increment (b and c) fixed by the Cameroon government.

3.2 LARGE-SIZED TREES VERSUS POPULATION AVERAGE

Growth of juvenile trees that have attained large dimensions was substantially higher than the population average of extant trees (fitted model of eq. 2). These differences were significant for trees belonging to the 20-40 cm (diff = 0.745, 148%) and 40-60 cm (diff = 0.765, 131%) diameter classes (P<0.001, Fig. 5), but not for larger size classes. Moreover, diameter increment peaked around diameters between 20 and 60 cm (Fig. 4c).

On average, growth from tree rings was significantly higher than that of trees in plots. However, some individuals within the inventoried population grew as fast as the felled trees at the same size. We quantified what proportion of the extant population in the inventories grew as fast as the (successful) large trees from which we obtained tree ring data. For the diameter class 20-40 cm, this was the case for 18% of the individuals (n=7, growth = 1.18 $cm.year^{-1}$) and in the class 40-60, for 14% of the individuals (n=6). In contrast, diameter increment converged between inventories and ring data for the larger classes: in the class 60-80, 63% of individuals in the inventories showed a similar or slightly higher diameter increment than from ring data, and in the 80-100 this went up to 93%.

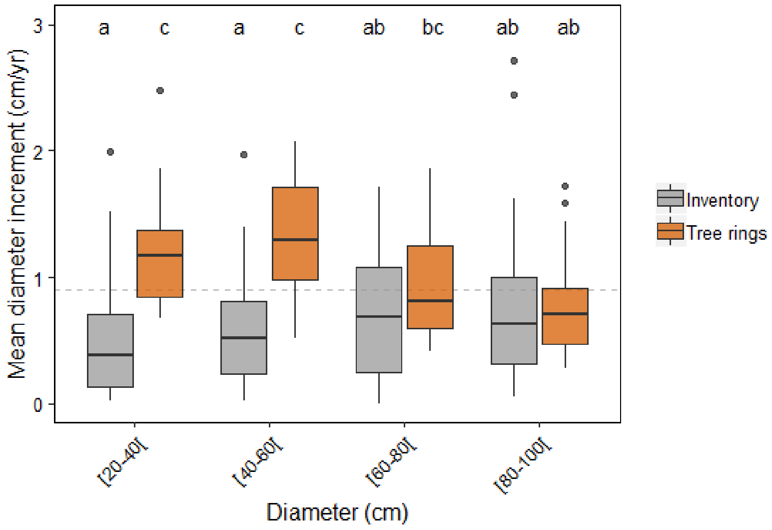

Figure 5: Diameter increment per diameter class in Mbang from two different data sources: inventory data from 152 trees, and tree ring data from 25 extant large trees. Extant large trees grew significantly faster than population average when they had a diameter less than 60 cm. Observations were beforehand averaged per tree and diameter class. Letters denote the results of the post-hoc Tuckey test of model of eq. 2.

3.3 LOGGING EFFECT

Using inventory data, we compared diameter increments in unlogged (control) and logged forests. In all study sites, trees in the logged treatment grew significantly faster than trees in the control treatment. Diameter increments averaged by site and treatment ranged between 0.37-0.83 cm year^{-1} in the control treatment and between 0.83-1.63 cm year^{-1} in the logged treatment (Table 2). Growth stimulation after logging was highest in Makalaya: diameter increment in the logged treatment was 0.73 cm year^{-1} (188%) higher than in the control. In the other sites, increment differences ranged between 0.55 cm year^{-1} and 0.26 cm year^{-1} (144-230%, Table 3). Restricting analysis to measurements of the 4 years after logging provided similar results: for M'Baïki 0.39 cm.year^{-1} (203% increase) and for Northern Congo 0.55 cm.year^{-1} (200%).

Table 3: Model parameter and 95% confidence intervals of the logging effect on annual diameter increment. In Makalaya, Northern Congo sites and M'Baïki, we fitted a linear ANOVA model (eq. 2) to test for this effect (parameter c_t in eq. 2) whereas we applied a paired Student T test in M'Bang. Also shown the number of sampled trees (n), P-value of including the logging effect in the model, determination coefficient (R^2) and residual standard error (σ).

		Logged effect		Logged+thinned effect				
site	**n**	**Estimate ± CI**		**Estimate ± CI**		**P-value**	**R²**	**σ**
M'Baïki	136	0.426	± 0.243	0.544	± 0.217	$6.38\ 10^{-6}$	0.166	0.546
Makalaya	140	0.733	± 0.354			$5.61\ 10^{-6}$	0.141	0.778
Mbang	166	0.260	± 0.092			$1.31\ 10^{-7}$		
Northern Congo	77	0.484	± 0.236			$1.11\ 10^{-4}$	0.205	0.422

3.4 LOGGING EFFECT DURATION

In the M'Baïki site, we also found a positive effect of logging and thinning. In the initial years after the logging and thinning treatments, diameter growth of *T. scleroxylon* was higher in both the logged and logged+thinned plots compared to the control plots. Increment decreased slightly over time in the control and logged treatments (Fig. 6). In the logged treatment this decrease was particularly marked about 15 years after logging, after which growth rates reached similar levels as in the control. In the logged+thinned treatment, mean diameter increment increased in the four years immediately after logging (1984-1988) and thinning (1986) and remained high in this treatment for about 15 years. After 15 years (from 2000 onwards, Fig. 6), growth rates rapidly decreased.

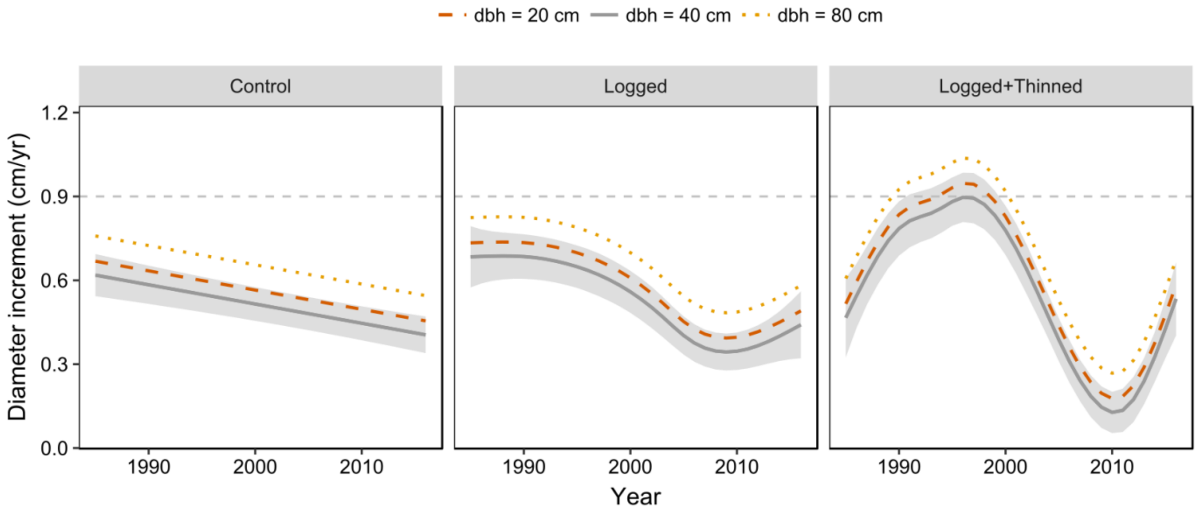

Figure 6: Post-logging diameter increment predicted by a generalized additive mixed model (eq. 3) over time and for the three treatments of the M'Baïki experiment and for three specific initial diameters (20, 40 and 80cm). Thinning occurred in 1986-1987, two years after logging and the first study census. The curves correspond to model predictions excluding the random effect. The shaded areas correspond to the prediction for dbh = 40 cm ± the standard error. For the sake of clarity, the standard error of the other two curves was not displayed. The dashed horizontal gray line indicates the diameter increment fixed by the Cameroon government for the stock recovery calculations.

4 DISCUSSION

Using data from periodic field inventories from three different countries in central Africa as well as tree ring data, we identified key factors affecting the growth of a long-lived pioneer tree species, *T. scleroxylon*. With these analyses we provide a more rigorous basis to develop silvicultural guidelines to reach sustainable forest exploitation.

4.1 HARVESTABLE TREES GREW FASTER THAN POPULATION AVERAGE

Comparing the life-time growth history of 25 large trees with the current growth of 180 extant trees in the same site (Mbang), we showed that individuals that attain large sizes grow faster as juveniles than the remainder of the population. This difference was particularly marked in diameter classes <60 cm: past growth of extant large trees when 20 and 60 cm diameter was more than double that of current growth of extant trees of the same size. Such effect has often been hypothesized as the result of a higher survival probability for fast growing juvenile trees, the so called juvenile selection effect (Swaine *et al.*, 1987; Terborgh *et al.*, 1997; Brienen and Zuidema, 2006) and/or due to persistent growth differences between individuals (Brienen *et al.*, 2006; Brienen and Zuidema, 2006). Few studies have, however, formally tested and disentangled these effects (Landis and Peart, 2005; Rozendaal *et al.*, 2010). Here, for the first time, we were able to test these hypotheses using the combination of periodic field inventories and tree-ring data, as suggested by Rozendaal *et al.* (2010). Using only tree-ring data, Rozendaal *et al.* (2010) found a significant juvenile selection effect for 3 out of 5 tropical tree species in Bolivia, while Groenendijk *et al.* (2015) found a significant juvenile selection effect for only 1 over 13 studied species from Cameroon, Bolivia and Thailand. In addition, the juvenile selection effect evidenced by Rozendaal *et al.* (2010) was limited to trees of less than 10 cm in diameter, whereas, here, we observed an effect lasting up to 60 cm in diameter for an African timber tree species. These findings support the idea that the juvenile selection effect might be strong for long-lived light-demanding species, such as *T. scleroxylon*, which was suggested by Rozendaal *et al.* (2010) and Groenendijk *et al.* (2015).

Our results also concur with the higher diameter increments reported from tree-ring analyses (Mariaux, 1972; Détienne and Mariaux, 1976; Jardin, 1995) compared to increments arising from field inventories (De Madron *et al.*, 2000). Fast-growing individuals contribute more to future timber stocks, and using lower average diameter increment of extant (small) trees likely results in biased projections of future timber stocks (Brienen and Zuidema, 2007; Zuidema *et al.*, 2009; Groenendijk *et al.*, 2017). Nevertheless, including the higher growth rates found for extant large trees in stock recovery projections should also be done with care, as they may provide overoptimistic predictions (Zuidema *et al.*, 2009; Groenendijk *et al.*, 2014; Groenendijk *et al.*, 2017). Further comparisons are needed, for other ecological conditions and for species with different growth strategies, in combination with modeling studies (Couralet *et al.*, 2005; Brienen and Zuidema, 2007; Zuidema *et al.*, 2010), to unravel the importance juvenile selection effect and persistent fast growth on tree population dynamics. We suggest comparing tree growth of individuals from all size classes for both the tree-ring analyses and field inventories, as both data sources have potential biases (Bowman *et al.*, 2013). This combination of methods is a robust approach to provide insights on growth differences between the juveniles from the present with those of the past.

4.2 GROWTH STIMULATION AFTER LOGGING LASTED 10 TO 15 YEARS

While positive response to logging has been commonly reported at the community level (Gourlet-Fleury *et al.*, 2013b; Vidal, 2016 #2312; Herault, 2010 #2346), different responses can be expected for different species or functional groups (Peña-Claros *et al.*, 2008; Villegas, 2009 #2167; Herault, 2010 #2346). For example, silvicultural treatment mainly benefited shade tolerant species in a moist forest in Bolivia (Peña-Claros *et al.*, 2008), while stimulating growth of long-lived pioneer species in a seasonally dry forest (Villegas *et al.*, 2009). Additionally, in a wet evergreen forest in French Guiana, silvicultural treatments benefited all functional groups, but most strongly shade-tolerant species (Delcamp *et al.*, 2008) or species with inherent slow growth (Herault *et al.*, 2010).

We found that *T. scleroxylon* – a fast-growing long-lived pioneer species in central African semi-deciduous forests – shows a marked growth response to disturbance. In all study sites, the diameter increment of *T. scleroxylon* in the logged treatment was about twice as high as in the control treatment (Table 2). For the first time, using the long-term datasets in M'Baïki we were able to show that growth responses to past logging last about 10 to 15 years (Fig. 6), i.e. a slightly longer period to what reported de Graaf *et al.* (1999) in an Amazonian tropical rainforest (in Suriname). On top of the growth stimulation induced by selective logging, additional silvicultural interventions further increased *T. scleroxylon* growth rates. After logging, *T. scleroxylon* grew 130% faster in the logged+thinned treatment than in the logged treatments, totaling 210% faster growth than in the control treatment (M´Baiki data, 32 years). This growth stimulation by logging and thinning lasted for about 15 years (Fig. 6). Logging and silvicultural treatments presumably increases resource availability for the remaining trees. Long-lived pioneer species such as *T. scleroxylon* may show stronger responses to disturbances than species from other functional groups. Long-lived pioneers species can survive under the canopy in (semi-)deciduous forests as seasonal canopy variations provide enough light enabling sampling survival (Villegas *et al.*, 2009). These species generally have higher diameter-increment potential than shade tolerant species (Valladares and Niinemets, 2008), and their responses to logging and thinning should thus not be extrapolated to other functional groups. Population-level growth responses of species with aggregated spatial distributions such as *T. scleroxylon*, should also be extrapolated with care. These responses depend on disturbances occurring in the vicinity of a tree. Species with spatially aggregated distributions will have different probabilities to be near a disturbance than species with more evenly or randomly dispersed population. Combining our findings of growth releases with these other aspects will be particularly useful to design silvicultural treatments and promote more sustainable tropical forest exploitation.

4.3 GROWTH IN RELATION TO TREE ONTOGENY AND DISTURBANCES

The growth of tree species has often been assumed to be size dependent. However, the shape of the size-growth relationships critically depends on how growth is expressed (e.g., in diameter, basal area, volume), and particularly whether population-level or individual-level growth is considered (Sheil *et al.*, 2017; Ligot *et al.*, 2018). For population-level diameter increment, most species in French Guiana showed a hump-shaped growth trajectory, with diameter increment peaking at about 60% of their maximum size (Hérault *et al.*, 2011; Fétéké *et al.*, 2015). We hardly found a common growth trajectory for the sampled *T. scleroxylon* trees, irrespective of the type of data (tree rings and inventory). In the tree-ring data, only half of the sampled trees showed a hump-shaped growth trajectory peaking between 20 and 60 cm (Fig. 4c). From the inventory data, the relationship between tree size and growth was weak. Furthermore, the shape of this relationship varied across sites (Fig. 3) underlining the need of local observations of diameter increment to perform accurate prediction of stock recovery rate.

Like other species with low wood density (Hérault *et al.*, 2011), *T. scleroxylon* seems to have a high potential to accelerate its growth, and probably can develop and adapt its crown to increase light capture and maximize growth (Poorter *et al.*, 2006). Using the tree ring data, we indeed found that some individuals showed several periods of long-lasting suppression and growth releases (Brienen *et al.*, 2006), sometimes at late ontogenic stages (e.g., Fig. 4b). For the management of plantations, this result suggests that *T. scleroxylon* should react well to periodic canopy openings, even for large-stature trees. Releases at larger sizes may also explain why we did not find a clear declining trend in diameter increment with tree size (Fig. 4c). Similarly, releases may also explain why we found no clear evidence of a size-related growth stimulation to logging. Logging has typically been reported to promote the growth and survival of intermediate-size trees (Peña-Claros *et al.*, 2008; Gourlet-Fleury *et al.*, 2013b). Yet, for *T. scleroxylon* we found no relation of this growth response with tree size, i.e., the interaction between tree size and silvicultural treatment was never found significant.

4.4 STRONG BETWEEN-SITE GROWTH VARIABILITY

Analyzing tree growth of *T. scleroxylon* in unlogged (control) forests, we observed important differences among trees and sites (Table 2). The average diameter increment of *T. scleroxylon* varied twofold across sites: 0.40 cm year^{-1} in Southern Cameroon (Ma'an, see Table 2) and 0.83 cm year^{-1} in South-East Cameroon (Makalaya). The high diameter increment observed in Makalaya may appear surprising but corroborates the findings of De Madron *et al.* (2000) as well as those of Doucet *et al.* (2016) in young plantations in the same area. Curiously, this site had the highest elevation (604-632m a.s.l), while *T. scleroxylon* has been reported to be more abundant at lower altitudes - <500 m a.s.l. (Hall and Bada, 1979). The two sites with the lowest observed diameter increments were likely in the periphery of the ecological niche of *T. scleroxylon* (Fig. 1): relatively high mean annual temperature in Northern Congo, and high annual rainfall in Southern Cameroon (Ma'an). According to Hall and Bada (1979), the favorable annual rainfall range for *T. scleroxylon* is between 1100 and 1800 mm. Along this gradient of precipitation from semi-deciduous to evergreen forests in central Africa, the limiting factors for *T. scleroxylon* growth likely vary from limited water supply to soil fertility. Presumably, many ecological factors interact and affect tree growth and these relationships could be non-linear.

5 CONCLUSIONS

Understanding how growth rates of exploited timber species varies across individuals, disturbance history and sites, is key to achieve sustainable forest management. Fast-growing trees strongly drive future harvestable timber stocks (Rozendaal *et al.*, 2010), while slow growers may not reach the canopy or harvestable dimensions within reasonable cutting cycles or before tree senescence. Yet, due to low data availability, the effects of this variation have so far often been ignored in stock recovery rate calculations in central Africa (Groenendijk *et al.*, 2017). This study provides an unprecedented quantification of the magnitude of this variation for the long-lived and valuable timber species *T. scleroxylon*. Growth of *T. scleroxylon* is remarkably variable; it varies strongly between individuals, more than twofold across sites, and responds strongly to logging and thinning with growth stimulation lasting up to 15 years. Our results also suggest that silvicultural treatments such as thinning can be successfully implemented to increase the growth rate of *T. scleroxylon*.

Given variability of tree growth with ontogeny, within a population, and across sites, using fixed diameter increments in stock recovery rate projections will clearly lead to significant local biases. We therefore recommend gathering local growth information and incorporating them in these projections. Quantifying how past logging, the juvenile selection effect and persistent fast growth affect growth for other timber species and sites should be performed with the increasingly available inventory and tree-ring data. Applying this growth variability in combination with other factors that vary locally or temporally (Groenendijk *et al.*, 2017) would lead to more realistic future timber yield projections. This is crucial to propose innovative forest management guidelines to ensure sustainable forest exploitation.

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7 DATA AVAILABILITY

Data and R scripts are available on the CIRAD dataverse repository: http://dx.doi.org/10.18167/DVN1/1TUOBI.

8 REFERENCES

Bates, D., Maechler, M., Bolker, B., Walker, S., 2013. lme4: Linear mixed-effects models using Eigen and S4. In.

Bayol, N., Demarquez, B., De Wasseige, C., Eba’a Atyi, R., Fisher, J.-F., Nasi, R., Pasquier, A., Rossi, X., Steil, M., Vivien, C. (Eds.), 2012. Forest management and the timber sector in Central Africa. Publications Office of the European Union, Luxembourg

Bongers, F., Poorter, L., Van Rompaey, R.S.A.R., Parren, M.P.E., 1999. Distribution of twelve moist forest canopy tree species in Liberia and Côte d'Ivoire: response curves to a climatic gradient. J. Veg. Sci 10, 371-382.

Bourland, N., Cerisier, F., Daïnou, K., Smith, A., Hubau, W., Beeckman, H., Brostaux, Y., Fayolle, A., Biwolé, A., Fétéké, F., Gillet, J.-F., Morin-Rivat, J., Lejeune, P., Tiba, E., Van Acker, J., Doucet, J.-L., 2015. How Tightly Linked Are Pericopsis elata (Fabaceae) Patches to Anthropogenic Disturbances in Southeastern Cameroon? Forests 6, 293.

Bowman, D.M.J.S., Brienen, R.J.W., Gloor, E., Phillips, O.L., Prior, L.D., 2013. Detecting trends in tree growth: not so simple. Trends Plant Sci. 18, 11-17.

Brienen, R.J., Zuidema, P.A., During, H.J., 2006. Autocorrelated growth of tropical forest trees: unraveling patterns and quantifying consequences. For. Ecol. Manage. 237, 179-190.

Brienen, R.J.W., Zuidema, P.A., 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. Oecologia 146, 1.

Brienen, R.J.W., Zuidema, P.A., 2006. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. J. Ecol. 94, 481-493.

Brienen, R.J.W., Zuidema, P.A., 2007. Incorporating persistent tree growth differences increases estimates of tropical timber yield. Frontiers in Ecology and the Environment 5, 302-306.

Bunn, A., Korpela, M., Biondi, F., Campelo, F., Mérian, P., Qeadan, F., Zang, C., 2017. dplR: Dendrochronology Program Library in R. R package version 1.6.5. In.

Cerutti, P.O., Lescuyer, G., Tacconi, L., Atyi, E.a., Essiane, E., Nasi, R., Tabi Eckebil, P.P., Tsanga, R., 2016. Social impacts of the Forest Stewardship Council certification in the Congo basin. Int. J. For. Rev.

Couralet, C., Sass-Klaassen, U., Sterck, F., Bekele, T., Zuidema, P.A., 2005. Combining dendrochronology and matrix modelling in demographic studies: An evaluation for Juniperus procera in Ethiopia. For. Ecol. Manage. 216, 317-330.

de Graaf, N.R., Poels, R.L.H., Van Rompaey, R.S.A.R., 1999. Effect of silvicultural treatment on growth and mortality of rainforest in Surinam over long periods. For. Ecol. Manage. 124, 123-135.

De Madron, L.D., Nasi, R., Détienne, P., 2000. Accroissements diamétriques de quelques essences en forêt dense africaine. Bois For. Trop. 263, 63-74.

Delcamp, M., Gourlet-Fleury, S., Flores, O., Gamier, E., 2008. Can functional classification of tropical trees predict population dynamics after disturbance? J. Veg. Sci 19, 209-220.

Détienne, P., Mariaux, A., 1976. Nature et périodicité des cernes dans le bois de samba. Bois For. Trop. 169, 29-35.

Doucet, J.-L., Daïnou, K., Ligot, G., Ouédraogo, D.-Y., Bourland, N., Ward, S.E., Tekam, P., Lagoute, P., Fayolle, A., 2016. Enrichment of Central African logged forests with high-value tree species: testing a new approach to regenerating degraded forests. Int. J. Biodiv. Sci. Ecosystem Serv. Manage. 12, 83-95.

Fayolle, A., Engelbrecht, B., Freycon, V., Mortier, F., Swaine, M., Réjou-Méchain, M., Doucet, J.-L., Fauvet, N., Cornu, G., Gourlet-Fleury, S., 2012. Geological Substrates Shape Tree Species and Trait Distributions in African Moist Forests. PLoS ONE 7, e42381.

Fétéké, F., Perin, J., Fayolle, A., Dainou, K., Bourland, N., Kouadio, Y.L., Moneye, S.J.J., Bekono, C.-C., Liboum, M.Y., Doucet, J.-L., 2015. Modéliser la croissance de quatre essences pour améliorer la gestion forestière au Cameroun. Bois For. Trop. 325, 5-20.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37, 4302-4315.

Gillet, J.-F., Doucet, J.-L., 2012. A commented checklist of woody plants in the Northern Republic of Congo. Plant Ecology and Evolution 145, 258-271.

Gourlet-Fleury, S., Beina, D., Fayolle, A., Ouédraogo, D.-Y., Mortier, F., Bénédet, F., Closset-Kopp, D., Decocq, G., 2013a. Silvicultural disturbance has little impact on tree species diversity in a Central African moist forest. For. Ecol. Manage. 304, 322-332.

Gourlet-Fleury, S., Mortier, F., Fayolle, A., Baya, F., Ouédraogo, D., Bénédet, F., Picard, N., 2013b. Tropical forest recovery from logging: a 24 year silvicultural experiment from Central Africa. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 368, 20120302.

Groenendijk, P., Bongers, F., Zuidema, P.A., 2017. Using tree-ring data to improve timber-yield projections for African wet tropical forest tree species. For. Ecol. Manage. 400, 396-407.

Groenendijk, P., Sass-Klaassen, U., Bongers, F., Zuidema, P.A., 2014. Potential of tree-ring analysis in a wet tropical forest: A case study on 22 commercial tree species in Central Africa. For. Ecol. Manage. 323, 65-78.

Groenendijk, P., van der Sleen, P., Vlam, M., Bunyavejchewin, S., Bongers, F., Zuidema, P.A., 2015. No evidence for consistent long-term growth stimulation of 13 tropical tree species: Results from tree-ring analysis. Glob. Chang. Biol. 21, 3762-3776.

Hall, J.B., Bada, S.O., 1979. The Distribution and Ecology of Obeche (Triplochiton Scleroxylon). J. Ecol. 67, 543-564.

Hérault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C.E.T., Wagner, F., Baraloto, C., 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species. J. Ecol. 99, 1431-1440.

Herault, B., Ouallet, J., Blanc, L., Wagner, F., Baraloto, C., 2010. Growth responses of neotropical trees to logging gaps. Journal of Applied Ecology 47, 821-831.

Iyamabo, D.E., 1971. Some aspects of girth and radial growth patterns of *Triplochiton scleroxylon* K. Schum. Nigeria agricultural 6, 51-57.

Jardin, J.-L., 1995. Etude de la croissance de l'ayous (*Triplochiton scleroxylon*), du sapelli (*Entandophragma cylindricum*), et du fraké (*Terminali superba*) par analyse de cernes. In, Projet aménagement pilote intégré de Dimako. Ministère de l'environnement et des forêts, Douala, Cameroun.

Jones, A., Breuning-Madsen, H., Brossard, M., Dampha, A., Deckers, J., Dewitte, O., Gallali, T., Hallett, S., Jones, R., Kilasara, M., 2013. Soil atlas of Africa. European Commission, Office of the European Union, Germany.

Karsenty, A., Gourlet-Fleury, S., 2006. Assessing sustainability of logging practices in the Congo Basin's managed forests: the issue of commercial species recovery. Ecol. Soc. 11, 26.

Landis, M.R., Peart, D.R., 2005. Early performance predicts canopy attainment accross life histories in subalpine forest tree. Ecology 86, 63-72.

Latte, N., Lebourgeois, F., Claessens, H., 2015. Increased tree-growth synchronization of beech (Fagus sylvatica L.) in response to climate change in northwestern Europe. Dendrochronologia 33, 69-77.

Ligot, G., Gourlet-Fleury, S., Ouédraogo, D.-Y., Morin, X., Bauwens, S., Baya, F., Brostaux, Y., Doucet, J.-L., Fayolle, A., 2018. The limited contribution of large trees to annual biomass production in an old-growth tropical forest. Ecol. Appl. 28, 1273-1281.

Locosselli, G.M., Krottenthaler, S., Pitsch, P., Anhuf, D., Ceccantini, G., 2017. Age and growth rate of congeneric tree species (Hymenaea spp.–Leguminosae) Inhabiting different tropical biomes. Erdkunde 71, 45-57.

Mariaux, A., 1972. Quelques données de croissance en diamètre du samba (Triplochiton scleroxylon K. Schum.) estimées d'après les cernes de 4 arbres exploitaté en Centrafrique. In. Centre Technique Forestier Tropical.

Ministère de l'Environnement et des Forêts, 1998. Guide d'élaboration des plans d'aménagement des forêts de production du domaine forestier permanent de la république du Cameroun. In.

Miteva, D.A., Loucks, C.J., Pattanayak, S.K., 2015. Social and environmental impacts of forest management certification in Indonesia. PLoS ONE 10, e0129675.

Morin-Rivat, J., Fayolle, A., Favier, C., Bremond, L., Gourlet-Fleury, S., Bayol, N., Lejeune, P., Beeckman, H., Doucet, J.-L., 2017. Present-day central African forest is a legacy of the 19th century human history. Elife 6, e20343.

Nasi, R., Billand, A., van Vliet, N., 2012. Managing for timber and biodiversity in the Congo Basin. For. Ecol. Manage. 268, 103-111.

Ouédraogo, D.-Y., 2011. Prédiction de la dynamique forestière à l'aide d'un modèle matriciel qui incorpore la variabilité de la réponse des espèces à l'environnement: application dans une forêt tropicale humide semi-décidue d'Afrique centrale. In. Université Montpellier II-Sciences et Techniques du Languedoc.

Palla, F., Louppe, D., 2002. Obeché. In. CIRAD, Montpellier, p. 6.

Peña-Claros, M., Fredericksen, T.S., Alarcón, A., Blate, G.M., Choque, U., Leaño, C., Licona, J.C., Mostacedo, B., Pariona, W., Villegas, Z., Putz, F.E., 2008. Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. For. Ecol. Manage. 256, 1458-1467.

Picard, N., Banak, L.N., Namkosserena, S., Yalibanda, Y., 2009. The stock recovery rate in a Central African rain forest: an index of sustainability based on projection matrix models. Can. J. For. Res. 39, 2138-2152.

Picard, N., Gourlet-Fleury, S., 2008. Manuel de référence pour l'installation de dispositifs permanents en forêt de production dans le Bassin du Congo. In. COMIFAC/CIRAD, p. 265.

Poorter, L., Bongers, L., Bongers, F., 2006. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. Ecology 87, 1289-1301.

Putz, F.E., Zuidema, P.A., Synnott, T., Peña-Claros, M., Pinard, M.A., Sheil, D., Vanclay, J.K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J., Zagt, R., 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. Conservation Letters 5, 296-303.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. In. R Foundation for Statistical Computing, Vienna, Austria.

Romero, C., Putz, F., 2018. Theory-of-Change Development for the Evaluation of Forest Stewardship Council Certification of Sustained Timber Yields from Natural Forests in Indonesia. Forests 9, 547.

Rosa, S.A., Barbosa, A.C.M.C., Junk, W.J., da Cunha, C.N., Piedade, M.T.F., Scabin, A.B., Ceccantini, G.C.T., Schöngart, J., 2017. Growth models based on tree-ring data for the Neotropical tree species Calophyllum brasiliense across different Brazilian wetlands: implications for conservation and management. Trees 31, 729-742.

Rozendaal, D.M.A., Brienen, R.J.W., Soliz-Gamboa, C.C., Zuidema, P.A., 2010. Tropical tree rings reveal preferential survival of fast-growing juveniles and increased juvenile growth rates over time. New Phytol. 185, 759-769.

Sheil, D., Eastaugh, C.S., Vlam, M., Zuidema, P.A., Groenendijk, P., van der Sleen, P., Jay, A., Vanclay, J., 2017. Does biomass growth increase in the largest trees? Flaws, fallacies and alternative analyses. Funct. Ecol. 31, 568-581.

Siepel, A., Poorter, L., Hawthorne, W., 2004. Ecological profiles of large timber species. In, Biodiversity of West African forests: An ecological atlas of woody plant species. CABI, pp. 391-445.

Swaine, M., Hall, J., Alexander, I., 1987. Tree population dynamics at Kade, Ghana (1968-1982). J. Trop. Ecol. 3, 331-345.

Terborgh, J., Flores, C., Mueller, P., Davenport, L., 1997. Estimating the ages of successional stands of tropical trees from growth increments. J. Trop. Ecol. 13, 833-856.

Therrell, M.D., Stahle, D.W., Mukelabai, M.M., Shugart, H.H., 2007. Age, and radial growth dynamics of Pterocarpus angolensis in southern Africa. For. Ecol. Manage. 244, 24-31.

Valladares, F., Niinemets, U., 2008. Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences. Annual Review of Ecology, Evolution, and Systematics 39, 237-257.

Veenendaal, E., Swaine, M., Lecha, R., Walsh, M., Abebrese, I., Owusu-Afriyie, K., 1996. Responses of West African forest tree seedlings to irradiance and soil fertility. Funct. Ecol., 501-511.

Villegas, Z., Peña-Claros, M., Mostacedo, B., Alarcón, A., J.C.Licona, Leaño, C., Pariona, W., Choque, U., 2009. Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest. For. Ecol. Manage. 258, 971-977.

Wagner, F.H., Hérault, B., Bonal, D., Stahl, C., Anderson, L.O., Baker, T.R., Becker, G.S., Beeckman, H., Souza, D.B., Botosso, P.C., Bowman, D.M.J.S., Bräuning, A., Brede, B., Brown, F.I., Camarero, J.J., Camargo, P.B., Cardoso, F.C.G., Carvalho, F.A., Castro, W., Chagas, R.K., Chave, J., Chidumayo, E.N., Clark, D.A., Costa, F.R.C., Couralet, C., Mauricio, P.H.d.S., Dalitz, H., Castro, V.R.d., Milani, J.E.d.F., Oliveira, E.C.d., Arruda, L.d.S., Devineau, J.L., Drew, D.M., Dünisch, O., Durigan, G., Elifuraha, E., Fedele, M., Fedele, L.F., Filho, A.F., Finger, C.A.G., Franco, A.C., Júnior, J.L.F., Galvão, F., Gebrekirstos, A., Gliniars, R., Graça, P.M.L.D.A., Griffiths, A.D., Grogan, J., Guan, K., Homeier, J., Kanieski, M.R., Kho, L.K., Koenig, J., Kohler, S.V., Krepkowski, J., Lemos-Filho, J.P., Lieberman, D., Lieberman, M.E., Lisi, C.S., Santos, T.L., Ayala, J.L.L., Maeda, E.E., Malhi, Y., Maria, V.R.B., Marques, M.C.M., Marques, R., Chamba, H.M., Mbwambo, L., Melgaço, K.L.L., Mendivelso, H.A., Murphy, B.P., Brien, J.J.O., Oberbauer, S.F., Okada, N., Pélissier, R., Prior, L.D., Roig, F.A., Ross, M., Rossatto, D.R., Rossi, V., Rowland, L., Rutishauser, E., Santana, H., Schulze, M., Selhorst, D., Silva, W.R., Silveira, M., Spannl, S., Swaine, M.D., Toledo, J.J., Toledo, M.M., Toledo, M., Toma, T., Filho, M.T., Hernández, J.I.V., Verbesselt, J., Vieira, S.A., Vincent, G., Castilho, C.V.d., Volland, F., Worbes, M., Zanon, M.L.B., Aragão, L.E.O.C., 2016. Climate seasonality limits leaf carbon assimilation and wood productivity in tropical forests. Biogeosciences 13, 2537-2562.

Wood, S., 2006. Generalized additive models: an introduction with R. CRC press.

Zuidema, P.A., Brienen, R.J.W., During, H.J., Güneralm, B., 2009. Do persistently fast-growing juveniles contribute disproportionately to population growth? A new analysis tool for matrix models and its application to rainforest trees. The American Naturalist 174, 709-719.

Zuidema, P.A., Jongejans, E., Chien, P.D., During, H.J., Schieving, F., 2010. Integral Projection Models for trees: a new parameterization method and a validation of model output. J. Ecol. 98, 345-355.