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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  $0.40 \text{ cm year}^{-1}$  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 longterm 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

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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 commercial 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 specieś 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 speciesspecific 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<sup>3</sup>) 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 and 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  $1.82 \text{ cm year}^{-1}$  (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 semideciduous 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.

#### 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



Fig. 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).

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.

#### 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, <u>https://www.dynaffor.org/</u>, 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 m 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 Eqns. (3) and (4)).

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

<sup>1</sup> ROC = Republic of the Congo, CMR = Cameroon, CAR = Central African Republic.

# 2.3.3. Long-term periodic field inventories in M'Baiki

Ten permanent plots of 4 ha (200 m  $\times$  200 m) 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  $\geq$  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  $\geq$  80 cm. Thinning consisted of killing all trees of non-commercial species with DBH  $\geq$  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.



Fig. 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).

#### 2.4. 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)).

$$Diameter \ increment = \frac{D_f - D_i}{days/365.25}$$
(1)

It was computed considering either only the diameter observations at the first and last census (denoted hereafter  $\Delta D$ ) 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  $\Delta D$  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  $\geq 20$  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)).

$$\Delta \mathbf{D}_{i,j,m} = \mathbf{e}_j + \mathbf{f}_m + \mathbf{g}_{j,m} + \varepsilon_{i,j,m}$$
(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  $(c_i)$  as independent categorical variables.

$$\Delta \mathbf{D}_{i,j,t} = \mathbf{b}_j + \mathbf{c}_t + \varepsilon_{i,j,t} \tag{3}$$

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 ( $\alpha = 0.05$ ) and thus not included in the models presented here. The inventories in MBaiki 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 ( $g_t(year_y) = 0$ ).

$$dD_{i,t,y} = f(D_{i,y}) + g_t(year_y) + \alpha_{i,t} + \varepsilon_{i,t,y}$$
(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<sup>-1</sup> (std. dev. = 0.81 cm) in logged forest in Makalaya and only about 0.37 cm year<sup>-1</sup> (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<sup>-1</sup> and 1.14 cm year<sup>-1</sup>. 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

#### Table 2

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

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

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%).

# 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 =  $1.18 \text{ cm.year}^{-1}$ ) 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%.

# 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 and 0.83 cm year<sup>-1</sup> in the control treatment and between 0.83 and 1.63 cm year<sup>-1</sup> 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<sup>-1</sup> (188%) higher than in the control. In the other sites, increment differences ranged between 0.55 cm year<sup>-1</sup> and 0.26 cm year<sup>-1</sup> (144–230%, Table 3). Restricting analysis to measurements of the 4 years after logging provided similar results: for M'Baïki 0.39 cm.year<sup>-1</sup> (203% increase) and for Northern Congo 0.55 cm.year<sup>-1</sup> (200%).



Fig. 3. Variability of *T. scleroxylon* diameter increment across sites and logging treatments. The dashed horizontal gray line indicates the diameter increment  $(0.9 \text{ cm year}^{-1})$  as fixed by the Cameroon government for the calculation of stock recovery rate. Numbers indicate the sample sizes for each boxplot.



**Fig. 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.



**Fig. 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).

#### 3.4. 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.

### 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,

#### 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<sup>2</sup>) and residual standard error ( $\sigma$ ).

Site	n	Logged effect	Estimate ± CI	Logged + thinne	ed effect Estimate ± CI	P-value	$\mathbb{R}^2$	σ
M'Baïki Makalaya Mbang Northern Congo	136 140 166 77	0.426 0.733 0.260 0.484	$\pm 0.243$ $\pm 0.354$ $\pm 0.092$ $\pm 0.236$	0.544	± 0.217	$\begin{array}{c} 6.3810^{-6} \\ 5.6110^{-6} \\ 1.3110^{-7} \\ 1.1110^{-4} \end{array}$	0.166 0.141 0.205	0.546 0.778 0.422





**Fig. 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 80 cm). 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  $\pm$  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.

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 shadetolerant 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 longterm 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 (MBaiki 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 longlasting 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:  $0.40 \,\mathrm{cm \, vear^{-1}}$  in Southern Cameroon (Ma'an, see Table 2) and  $0.83 \text{ cm year}^{-1}$  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 (604-632 m 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.

### 6. Data Availability

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

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### Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.01.042.

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