



## Tree growth and mortality of 42 timber species in central Africa

Gauthier Ligot<sup>a,\*</sup>, Sylvie Gourlet-Fleury<sup>b</sup>, Kasso Dainou<sup>a</sup>, Jean-François Gillet<sup>a</sup>, Vivien Rossi<sup>b,c,i</sup>, Mathurin Mazengué<sup>e</sup>, Stevy Nna Ekome<sup>f</sup>, Yanick Serge Nkoulou<sup>g</sup>, Isaac Zombo<sup>h</sup>, Eric Forni<sup>b,d</sup>, Jean-Louis Doucet<sup>a</sup>

<sup>a</sup> Forest is Life, TERRA, Gembloux Agro-Bio Tech, Université de Liège, Gembloux, Belgium

<sup>b</sup> UPR Forêts et Sociétés, Université de Montpellier, CIRAD, Montpellier, France

<sup>c</sup> UPR Forêts et Sociétés, CIRAD, Yaoundé, Cameroon

<sup>d</sup> UPR Forêts et Sociétés, CIRAD, Brazzaville, Congo

<sup>e</sup> Mokabi SA, BP 97, Impfondo, Congo

<sup>f</sup> CEB Precious Wood, Libreville, Gabon

<sup>g</sup> Pallisco CIFM, Douala, Cameroun

<sup>h</sup> CIB-Olam, BP 41, Ouesso, Congo

<sup>i</sup> UMMISCO, Université Yaoundé I, Yaoundé, Cameroun

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### ABSTRACT

Tree growth and mortality are two central processes in mixed and structurally complex moist tropical forests, yet accurate estimates of the variables needed to model them remain sparse and scattered. It is thus still difficult to predict forest evolution at a local scale and build reliable management plans. To help fill this gap, for 1–7 years we annually monitored 21,180 trees belonging to 42 species exploited for timber production in Central Africa. We made new species-specific estimates of diameter increments and mortality rates, and investigated how tree growth varied with tree size and logging history. We compared our results with the legal values of diameter increments, mortality rates, and minimum cutting diameters used to build forest management plans in Cameroon. Diameter increment was found to vary with tree size for most of the species studied. The relationships between diameter increment and tree size were mostly humpback-shaped. The trees with diameters close to or lower than the reference minimum cutting diameter generally grew faster than the average. We also found that tree growth could slow for 1–2 years after timber exploitation and was then spurred for at least 5 years. The tree growth response to logging was nevertheless species-specific. This study provides new estimates of tree diameter increments and mortality rates that could help make more accurate forest projections and draw up sustainable management plans in Africa.

### 1. Introduction

In Central Africa, tropical rainforest covers 184.7 million hectares, of which 53 million hectares (28%) are currently exploited for timber production (FRMi, 2018). These exploited forests deliver key ecosystem services. They capture about 0.7 t of carbon per hectare per year (Hubau et al., 2020), harbor an extremely broad species diversity including key pollinators of tropical crops, regulate regional weather and freshwater quantity and quality (Brandon 2014), and provide livelihoods for at least 100 million people (De Wasseige et al., 2015). These forests are typically managed with logging, harvesting 1 or 2 large trees per hectare every 25–30 years. To ensure the sustainability of the timber production, sets

of variables and criteria have been adopted in national regulations (Picard et al., 2012). However, like in other tropical forest biomes (Piponiot et al., 2019), concerns have been raised about the depletion of the harvestable stocks and the expected loss of timber production profitability (Karsenty and Gourlet-Fleury, 2016), highlighting the need for in-depth analysis of management strategies with forward-looking approaches.

Tree growth and mortality are two central processes for predicting the dynamics of mixed and structurally complex tropical rainforests. However, these processes are seldom routinely estimated or accurately modeled. First, estimating them requires long-term monitoring in difficult field conditions (Picard and Gourlet-Fleury, 2008). Second, their

\* Corresponding author.

E-mail address: [gligot@uliege.be](mailto:gligot@uliege.be) (G. Ligot).

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modeling is difficult because tree growth and mortality depend on numerous abiotic and biotic factors that are also seldom assessed, especially over large areas. Tree growth and mortality depend, among other factors, on the availability of light, nutrients, and water. However, these resources vary critically in space (e.g., variability in soil features) (e.g., Baribault et al., 2012; Jucker et al., 2018) and time (e.g., annual rainfall regime) (e.g., Battipaglia et al., 2015; Breugel et al., 2011; McDowell et al., 2018) and are shared unevenly among competing trees (Muller-Landau et al., 2006). The diversity and structural complexity that characterize most tropical forests (Leigh, 1975) make predicting the effects of biotic and abiotic factors on individual performance highly challenging. Tree growth and mortality are also affected by human activities and natural disturbances whose frequencies and magnitudes are changing (Battipaglia et al., 2015; McDowell et al., 2018).

Although new remote sensing technologies may help to better describe local tree environments (Chambers et al., 2007; Jucker et al., 2018; Ndamiyehe Ncutirakiza et al., 2020), most models of tree growth and mortality rely today on a few explanatory variables that can be routinely assessed during field inventories. These are mostly tree species, forest types, regions, and occasionally tree size and competition indices. Tree growth and mortality can be estimated per species or species group (e.g., Chao et al., 2008; Claeys et al., 2019; Gourlet-Fleury et al., 2005; Hérault et al., 2011), forest type or region. These estimates are then used to calibrate models of forest dynamics and to simulate the development of forests of known structure and composition (Claeys et al., 2019; Picard et al., 2009).

In Central Africa, simulating forest dynamics over one cutting cycle with this approach has been extensively used to assess the sustainability of timber exploitation (Picard et al., 2012). The industrial production of timber is based on periodic harvesting (cutting cycle about 25–30 years) of a few species that are commercially valuable, and trees whose diameter exceeds a species-specific threshold (minimum cutting diameter) (Nasi et al., 2012). This management system (polycyclic harvest system) is viable only if the stock (i.e., number, volume, and quality) of harvestable trees recovers between cuts (Picard et al., 2009) and if forests continue delivering their different ecosystem services in the long term (Cerutti et al., 2016; Miteva et al., 2015; Nasi et al., 2012). Estimating stock recovery has thus become an important task of sustainable forest management and is enforced by national regulations and certification schemes (Nasi et al., 2012).

Since the mid-1900s, periodic tree monitoring and tree ring analyses have been carried out to study variability in tree growth across species and regions in Central Africa. De Madron et al. (2000) reviewed these studies and collected a total of about 50 estimates of annual diameter increment for 17 species. Ten years later, Picard and Gourlet-Fleury (2011) made a second, in-depth review of the available data and literature. They collected a total of 1713 estimates of annual diameter increment for 296 species. In both reviews, substantial differences were reported among estimates depending on species, site, forest type, disturbance history, tree size, and methodology.

Fewer studies have reported estimates of mortality rates. Picard and Gourlet-Fleury (2011) found a total of 537 estimates for 220 species. The paucity of accurate information prevented them from making separate estimates for undisturbed and disturbed forests. They also found no differences between species with contrasting light requirements and concluded that the commonly used mortality rate of 1% remained acceptable.

Despite the impressive work already done in collecting and analyzing field data, estimates of tree increment and mortality rates remain sparse (about six estimates of tree growth per species), scattered, and representative of only particular sites in a vast forest biome. It is therefore likely that most forest management plans are based on locally biased values of tree growth and mortality rates. The degree and extent of these biases remain to be further quantified.

To help fill this gap, for 1–7 years we annually monitored 21,180 trees belonging to 42 species, all except one of which were exploited for

timber production, in eight sites in Central Africa. We made new estimates of diameter increments and mortality rates, and we investigated how tree size and logging history could affect tree growth and mortality rates to assess whether these factors deserved more place in forest dynamics simulations.

## 2. Materials and methods

### 2.1 Sites

Trees were sampled in eight sites in three countries: five in Cameroon, one in Gabon and two in the Republic of the Congo. Each site was located in a forest concession (Fig. 1). The sites spanned a climatic gradient ranging from evergreen forest (e.g., Ma'an and Bambidie) to semi-deciduous forests (e.g., Mbang) (Réjou-Méchain et al., 2021) characterized by varying dry seasons with annual rainfall ranging across sites (Fig. 1). The soils were composed of a geological basement of low Precambrian sedimentary and metamorphic rocks (Table 1) with the resulting soil classified as ferralsol, Acrisol, Plinthosol, or Gleysol (Jones et al., 2013). Logging history also varied across sites. Some sites were in undisturbed forests where practically no anthropic perturbation occurred during the last century, whereas other sites were in forests where industrial logging likely occurred several times during the last century.

### 2.2 Tree sampling and measurements

In the eight sites (Table 1), tree sampling was performed in forest units of about 500 ha. The logging history of each forest unit was classified as unlogged, logged, or unlogged-then-logged. Unlogged forest units were areas where no industrial exploitation had occurred for at least 20 years before the first measurement. Logged forest units were areas exploited 0–7 years before the first measurement. Unlogged-then-logged forest units were areas classified as unlogged at the first census but logged during the monitoring period. In both logged and unlogged-then-logged forest units, we checked that logging occurred in the same year in the entire forest unit.

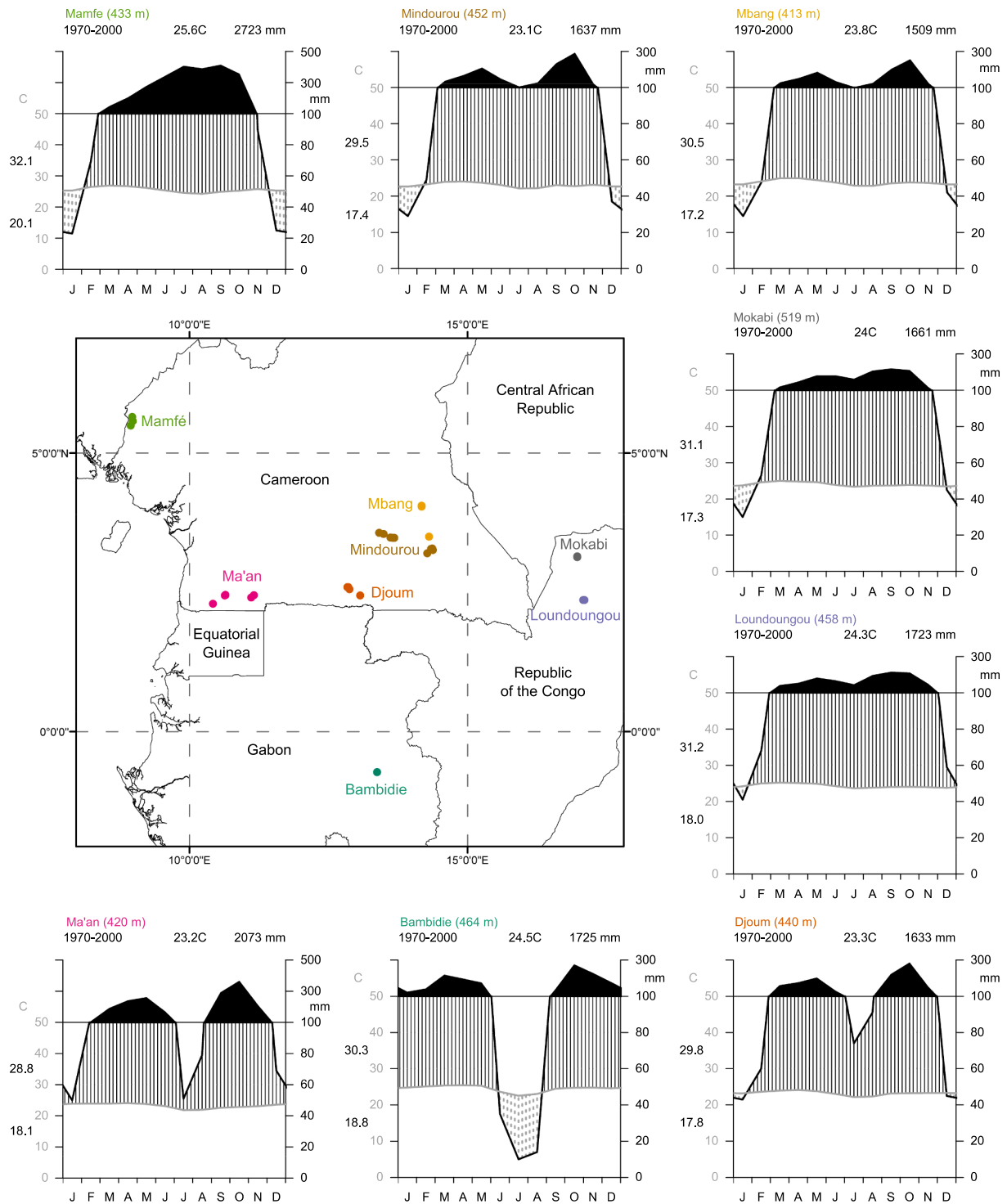
For each selected forest unit, a set of studied species was defined. All the studied species except *Greenwayodendron suaveolens* (Engl. & Diels) Verdc. were commercially important timber species. *Greenwayodendron suaveolens* was selected because it could be found in all sites.

For each selected species and forest unit, we sampled and measured a total of 200 trees with 20 trees per 10 cm diameter class ([10–20[, [20–30[, ..., [100, +∞[). The field crew advanced through the forest units and sampled trees until the target number of trees per diameter class and species was reached. They avoided selecting trees of the same diameter class that were close to each other. The trees were sampled independently of their health status, trunk shape, or tree crown position. Senescent understory trees with trunk irregularities were thus sampled alongside healthy canopy trees.

With this sampling strategy, we collected a large dataset with repeated measures for 21,180 trees. The total number of trees sampled per species ranged widely. For relatively scarce species (*Chrysophyllum beguei*, *Milicia excelsa*, *Bobgunnia fistuloides*, *Nauclea diderrichii*, *Khaya anthotheca*), we sampled fewer than 100 trees in one site, while for other species, more than 1000 trees were sampled across different sites and forest units (*Greenwayodendron suaveolens*, *Entandrophragma cylindricum*, *Erythrophloeum suaveolens*, *Pterocarpus soyauxii*). On average, we sampled 481 trees per species and 189 trees per species and site. Such a dataset could not have been readily obtained by measuring trees in plots because of the very large number of plots required.

The differentiation of two species of *Erythrophloeum* was difficult: they were assigned following the maps of Gorel et al. (2019) or to the *Erythrophloeum* sp. taxon in one site (Djoum) where the two species coexisted (Gorel et al., 2019).

Each sampled tree was marked and located, and its diameter



**Fig. 1.** Location of the study sites and forest units in Central Africa with the Walter and Lieth diagrams corresponding to one of the forest units of each site. Climatic data were extracted from the WorldClim 2 database (Fick and Hijmans, 2017) and processed with the Climatol R package (Guijarro, 2019). The gray lines show mean monthly variation in temperature. The black lines show mean monthly variation in rainfall. The black areas depict rainy seasons. The dotted areas depict dry seasons.

measured. The field crew painted an identifying number on the tree trunk and recorded its coordinates using a GPS unit (GARMIN™ GPSMAP 64). The diameter was measured with a tape to the nearest millimeter. The point of measurement (POM) was also painted on the tree trunk (Fig. 2). For trees with buttresses and other stem irregularities at breast height (1.3 m), the POM was raised 1 m above the buttresses or up to 4.5 m in height for the species known to rapidly develop tall buttresses (Fig. 2). If buttresses or any other obstructive features (e.g.,

liana, wounds) reached the POM during the census interval, then a new POM was established higher, and the diameter was thereafter measured only at this new POM.

### 2.3 Diameter increment

#### 2.3.1 Data cleansing

For most trees, the diameter was measured annually at least three

**Table 1**

Description of the main features of each site. The last column gives a subjective index of the relative intensity of past anthropic disturbances ranging from 0 (undisturbed forests where practically no anthropic perturbation occurred during the last century) to 3 (forest where industrial logging likely occurred several times during the last century). The country names in the site column are abbreviated (Cameroon = CMR, Gabon = GAB, Republic of the Congo = COG).

Site	Topography	Geology and soil	Forest type adapted from Réjou-Méchain et al. (2021)	Forest structure and main distinguishing species	Anthropic disturbance index
Mamfé, CMR	Mamfé Basin	Nitisols, nutrient rich, dark red, deep, well-drained soils derived from metamorphic rocks.	Atlantic evergreen forest	Old dense secondary forest with <i>Lophira alata</i> (and Caesalpinioideae)	1
Ma'an, CMR	South Cameroonian tableland	Yellow, partially hydromorphic or shallow orthic ferralitic soils derived from Early Precambrian rocks.	Mixed evergreen	Old secondary forest with <i>Lophira alata</i> (and Caesalpinioideae)	2
Mindourou, CMR	South Cameroonian tableland	Mixed with red or yellow ferralitic soils derived from Early Precambrian rocks.	Semi-deciduous-evergreen transition	Old and young mixed secondary forest with <i>Terminalia superba</i> , <i>Mansonia altissima</i> , <i>Triplochiton scleroxylon</i> , <i>Pericopsis elata</i> , <i>Baillonella toxisperma</i> , <i>Desbordesia glaucescens</i> and <i>Celtis</i> spp.	1
Djoum, CMR	South Cameroonian tableland	Modal orthic red soils derived from Early Precambrian rocks <sup>8</sup> .	Semi-deciduous-evergreen transition	Mixed secondary forest with <i>Distemonanthus benthamianus</i> , <i>Cylicodiscus gabunensis</i> and <i>Celtis</i> spp.	3
Mbang, CMR	South Cameroonian tableland	Red or yellow ferralitic soils derived from Early Precambrian rocks.	Semi-deciduous	Old secondary forest with <i>Mansonia altissima</i> , <i>Sterculia rhinopetala</i> and <i>Celtis</i> spp.	3
Bambidie, GAB	Old sedimentary basins of Franceville and Okondja	Ferralitic cambisols, mostly shallow clay soils with very low nutrient retention capacity.	Mixed evergreen	Old secondary forest with <i>Aucoumea klaineana</i> , <i>Dacryodes buettneri</i> (and Caesalpinioideae)	1
Loundougou, COG	Congo Basin	Quaternary alluvial deposits, mixed clay and sand yellow poor ferralitic soils.	Semi-deciduous-evergreen transition with temporally flooded and terra firma forests, including open canopy Marantaceae forests and monodominant (semi-)evergreen dense forests.	Old mixed secondary forest with <i>Celtis</i> spp., <i>Erythrophleum suaveolens</i> and <i>Petersianthus macrocarpus</i> and almost intact <i>Gilbertiodendron dewevrei</i> monodominant forests	1
Mokabi, COG	Carnot tableland	Red sandy, deep and well drained soils will low capacity to retain nutrients and water.	Evergreen-semi-deciduous transition on sandstone.	Dense primary forest with <i>Manilkara maboensis</i> and <i>Cleistanthus caudatus</i>	0

times (i.e., in at least 2 years, see Suppl. Table 1). For each tree we fitted a linear model of tree diameter ( $d_i$  expressed in cm) as a function of the time interval since the first record  $t_i$  expressed in years, Eq. (1):

$$d_i = a + b \times t_i + \varepsilon_i \quad (1)$$

where  $a$  and  $b$  were the fitted parameters and  $\varepsilon_i$  the residuals. The fitted values of  $b$  provided estimates of the annual diameter increment. This relationship was first used to identify outliers and salient observations that needed to be verified ( $\varepsilon_i > 1.5$  cm and Cook's distance  $> 1$ ) (Fox and Weisberg, 2011). In Mokabi, the trees were measured only twice ( $d_0$  and  $d_i$ ) and this procedure could not be applied. In this site, the increments ( $\Delta d$ ) were computed with Eq. (2) and we discarded increments of rank lower than the 1<sup>st</sup> percentile or higher than the 99th percentile:

$$\Delta d = \frac{d_i - d_0}{t} \quad (2)$$

### 2.3.2 Treatment assignment of diameter increments

All increments computed from the data collected in logged and unlogged forest units were assigned to the logged or unlogged treatment, respectively. In unlogged-then-logged forest units, the treatment was either logged or unlogged depending on observation dates and date of logging (Fig. 3). The date of logging was not precisely known. We knew only the calendar year during which the logging occurred, so we took 30 June of that year as the logging date.

### 2.3.3 Diameter increment estimate

After data cleansing, we fitted Eq. (1) again for each combination of tree, POM and treatment. The slope coefficients  $b$  of the fitted models were our estimates of diameter increment. For some combinations of tree and treatment, more than one increment could be obtained if the POM was raised during the monitoring period. In this case, we averaged the different estimates. The use of linear regressions to estimate the diameter increment was found to best take account of all observations (e.g., not only the first and last) and to handle observations that were unevenly distributed along the monitoring period.

### 2.4 Mortality rate

For each forest unit, the considered period was the longest census interval in the unlogged treatment ranging between 1 and 7 years. In unlogged-then-logged forest units, we kept only the records that were made before the exploitation year. Dead trees were defined as trees whose location the field crew could confidently find and whose death they confirmed. Trees that were not found were not counted either as dead or surviving. This choice was made to avoid confounding dead trees with trees that were alive but not found or located in an area that had for example become inaccessible.

We focused on the mortality rates computed for the unlogged conditions because we had fewer data in the logged conditions. The mortality rates computed for the logged conditions are given in supplementary materials (Supplementary Material 7).

The mortality rate ( $\lambda$ ) was calculated using Eq. (3) (Condit et al.,





Fig. 2. Measurement of tree diameter above buttresses with a tape.

1995):

$$\lambda = \frac{\ln(N_0) - \ln(N_t)}{t} \quad (3)$$

where  $N_0$  is the number of trees measured at the first census and  $N_t$  is the number of surviving trees after  $t$  years. We computed one estimate of  $\lambda$  per species and site thus aggregating the observations made in different forest units and during different census periods.  $t$  is the arithmetic mean of the census period length observed for the surviving trees. Condit et al. (1995) demonstrated that using the arithmetic mean provides reliable estimates.

Mortality rates computed over different census interval lengths are not rigorously comparable,  $\lambda$  having been reported to decrease with  $t$  owing to population heterogeneity (Lewis et al., 2004). The data series were too short to compute  $\lambda$  for a fixed period of 5 years as recommended by Lewis et al. (2004). Consequently, as Lewis et al. (2004) propose, we additionally report the standardized 1-year mortality rates using Eq. (4).

$$\lambda_{\text{corr}} = \lambda \times t^{0.08} \quad (4)$$

As mortality rate is generally very low (<1%), accurate estimates of mortality rates require large samples of trees monitored over long periods. For some combinations of site and species, the number of monitored trees was below 100, which was judged too low to compute

accurate mortality rates (Picard and Gourlet-Fleury, 2008). Here we thus show only the estimates of mortality rates computed for the combinations of site and species with more than 100 monitored trees.

## 2.5 Statistical analyses

### 2.5.1 Confidence intervals of mean diameter increments

Mean diameter increments were computed for each combination of species, treatment, and site. Confidence intervals of mean diameter increments were computed assuming a normal distribution of the observations. This assumption did not hold for all samples, but these confidence intervals were mostly used for illustrative purposes.

### 2.5.2 Comparison with reference values

Most management plans are drawn up assuming that tree growth rates are constant for the concerned diameter classes within a species. In some cases, reference values of tree growth rates are defined by local government such as in Cameroon (Ministère de l'Environnement et des Forêts, 1998). In Gabon and Congo, forest managers mostly used reference values from the literature (e.g. Picard and Gourlet-Fleury, 2011). However, locally, these estimates may be biased because tree growth varies substantially within such vast territories. To assess this bias, we compared our computed estimates of diameter increment with the values defined by the Cameroon government. This choice was essentially arbitrary but justified in that most of our study sites were in Cameroon. This should be considered as one study case. We tested the differences between our estimates and the reference values using the Wilcoxon rank sum test and correcting the obtained  $p$ -values for multiple tests by applying the Benjamini and Hochberg correction (Benjamini and Hochberg, 1995).

### 2.5.3 Tree size and site effects in unlogged forests

We tested whether diameter increment varied with tree diameter with an additive mixed model fitted for each combination of species and site for which at least 20 trees were monitored Eq. (5):

$$\Delta d_{j,s} = a + s(d_{j,s}) + \alpha_s + \epsilon_{j,s} \quad (5)$$

where  $\Delta d_{j,s}$  is the diameter increment of tree  $j$  in site  $s$ .  $a$  is a fixed number,  $s(d_{j,s})$  is a fixed non-linear smooth function of tree diameter, and  $\alpha_s$  is a random site effect. Using a smooth function had the advantage of needing no assumption about the nature of the relationship between diameter increment and initial tree diameter. To avoid model overfitting, we used cubic regression splines and forced a relatively simple overall shape (using only four base functions). The model was fitted using the mgcv package in R version 1.8-33 (Wood, 2006).

### 2.5.4 Diameter increment in logged and unlogged forests

We tested whether diameter increment was higher in logged than in unlogged forests for all combinations of site and species for which diameter increment could be computed in both conditions. In unlogged-then-logged forest units, the same trees were measured in both treatments. The null hypothesis could then be tested with Wilcoxon signed rank sum tests (non-parametric paired tests). In the other forest units where different trees were measured in the unlogged and logged treatment, we tested the treatment effect with Kruskal-Wallis rank sum tests for each combination of site and species. The  $p$ -values obtained were

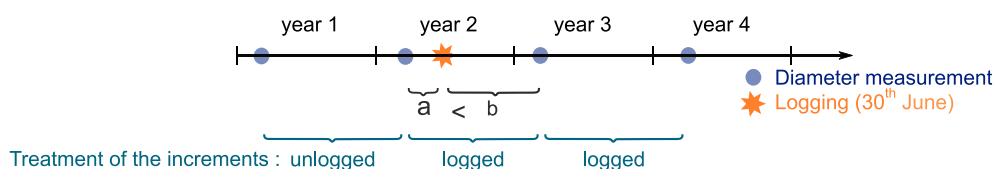


Fig. 3. Treatment assignment of the computed diameter increments. Here, the second increment is assigned to the logged treatment because the period before the logging is shorter (a) than the period after the logging (b).

corrected for multiple tests using the Benjamini and Hochberg correction.

The effect of logging on diameter increment was further examined by computing the differences between the mean diameter increment observed in logged and unlogged conditions. In particular, we analyzed the variation of the logging effect with the time elapsed between the censuses and the logging. The logging effect was also found to depend on both tree size and species, but as no general pattern was found, we placed this analysis in the [supplementary material \(Supplementary Material 6\)](#).

### 2.6 Mortality rate confidence intervals

The credible intervals ( $\alpha = 0.05$ ) of mortality rates were computed using a Bayesian framework (Kruschke, 2014). Assuming that the number of surviving trees ( $N_t$ ) in a population of  $N_0$  trees is the outcome of  $N_0$  Bernoulli trials and using an uninformative beta prior  $B(1, 1)$ , the posterior distribution became the beta distribution  $B(N_0 + 1, N_0 - N_t + 1)$  from which the credible interval bounds of  $N_t$  could be computed using the quantiles 2.5% and 97.5%. The credible intervals of mortality rates  $\lambda$  were then computed with Eq. (3).

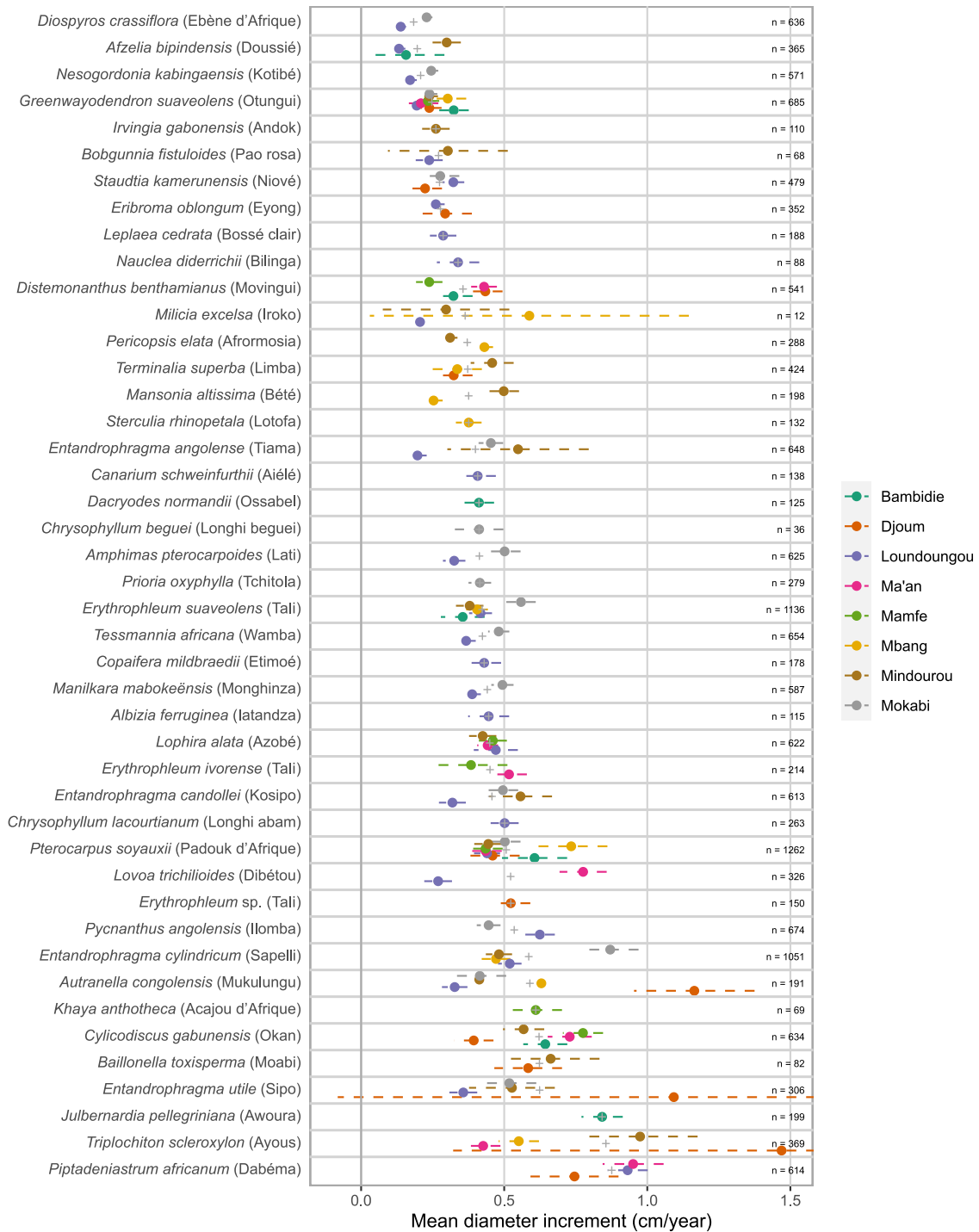


Fig. 4. Variability of diameter increment estimates across species and sites. The points show the mean diameter increment by species and site. The error bars are 95% confidence intervals. The species are ordered by increasing mean diameter increment (gray crosses). The total number of monitored trees per species is shown on the right.

### 3 Results

#### 3.1 Mean diameter increments in unlogged forests

Diameter increments varied considerably across the study species and sites (Fig. 4, Suppl. Table S1). In unlogged forests, we assessed the diameter increment of 17,297 trees. The averaged estimates per study species and site ranged from 0.13 cm/year (*Afzelia bipindensis* in Loundoungou) to 1.47 cm/year (*Triplochiton scleroxylon* in Djoum). The mean

of the census period length was 3.3 years and ranged from 0.9 (*Irvingia gabonensis* in Mindourou) to 6.8 years (*Lophira alata* in Mindourou).

Most study species were sampled in a limited number of sites. In the unlogged treatment, most species were monitored in fewer than four sites. Only two species were monitored in all sites (*Greenwayodendron suaveolens* and *Pterocarpus soyauxii*), three species in five sites (*Cylicodiscus gabunensis*, *Autranella congolensis* and *Erythrophleum suaveolens*) and five species in four sites (*Triplochiton scleroxylon*, *Lophira alata*, *Distemonanthus benthamianus*, *Entandrophragma cylindricum* and



Fig. 5. Ratio of observed mean diameter increment to the corresponding reference value. The ratios are computed for each species and site. A ratio value of 100% means that the observed increment is the same as the reference value. A ratio value of 200% means that we measured an increment double the reference value. The error bars flanking the points denote the 95% confidence intervals. The p-value level associated with the Wilcoxon rank sum tests is shown with circles and triangles. The species are ordered by increasing mean value of this ratio (gray crosses). The total number of monitored trees per species is shown on the right.

*Entandrophragma utile*).

Substantial differences in the estimates of diameter increment were observed across sites and for most species (Fig. 4). This variation was modeled for all species that were monitored in several sites ( $\alpha_s$  in Eq. (5)). The site effect was found to be significant in most cases. It was not significant for only four species three of which (*Eribroma oblongum*, *Austranella congolensis* and *Baillonella toxisperma*) were monitored in only two sites and one (*Staudtia kamerunensis*) in three sites. The maximum standard deviation of  $\alpha_s$  was 0.6 cm/year (*Triplochiton scleroxylon*, Suppl. Table S2). No general pattern was evidenced. The between-site variation was species-specific: some sites favored some species and disfavored others (Fig. 4). For example in Mbang, *Austranella congolensis* grew fastest, whereas *Entandrophragma cylindricum* growth was slowest (Fig. 4).

A few species exhibited remarkably low between-site variability, for example *Greenwayodendron suaveolens* and *Lophira alata*, which we measured in respectively eight and four sites. For these two species, our estimates ranged from 0.19 to 0.32 cm/year and from 0.42 to 0.47 cm/year, respectively.

We compared the species-specific estimates of diameter increment

obtained in the unlogged treatment with the reference values (cf. Section 2.5.2). Differences were found between the estimates and the reference values of diameter increments. These differences ranged from  $-0.5$  cm/year to  $0.8$  cm/year. We also expressed these differences in relative values by computing the ratio of our estimates to these legal values (Fig. 5). This ratio ranged from 33% to 291%. Some of our diameter increment estimates were thus 3 times lower or higher than the reference values. 46% and 23% of our estimates were respectively significantly lower or higher than the corresponding reference values.

### 3.2 Diameter increment across tree size in unlogged forests

Eq. (5) was fitted for all species to test whether diameter increment depended on tree size. The significance level of the smooth function  $s()$  is given in supplementary material (Suppl. Table S2) and significant relationships ( $p < 0.05$ ) are shown in Fig. 5. Significant relationships were found for 29 species over the 43 tested taxa. The relationships were mostly non-linear (edf mostly  $> 1$  in Table S2 and Fig. 5). For most species showing a significant  $s()$  term, the diameter increment peaked for diameter classes relatively close to or below the reference minimum

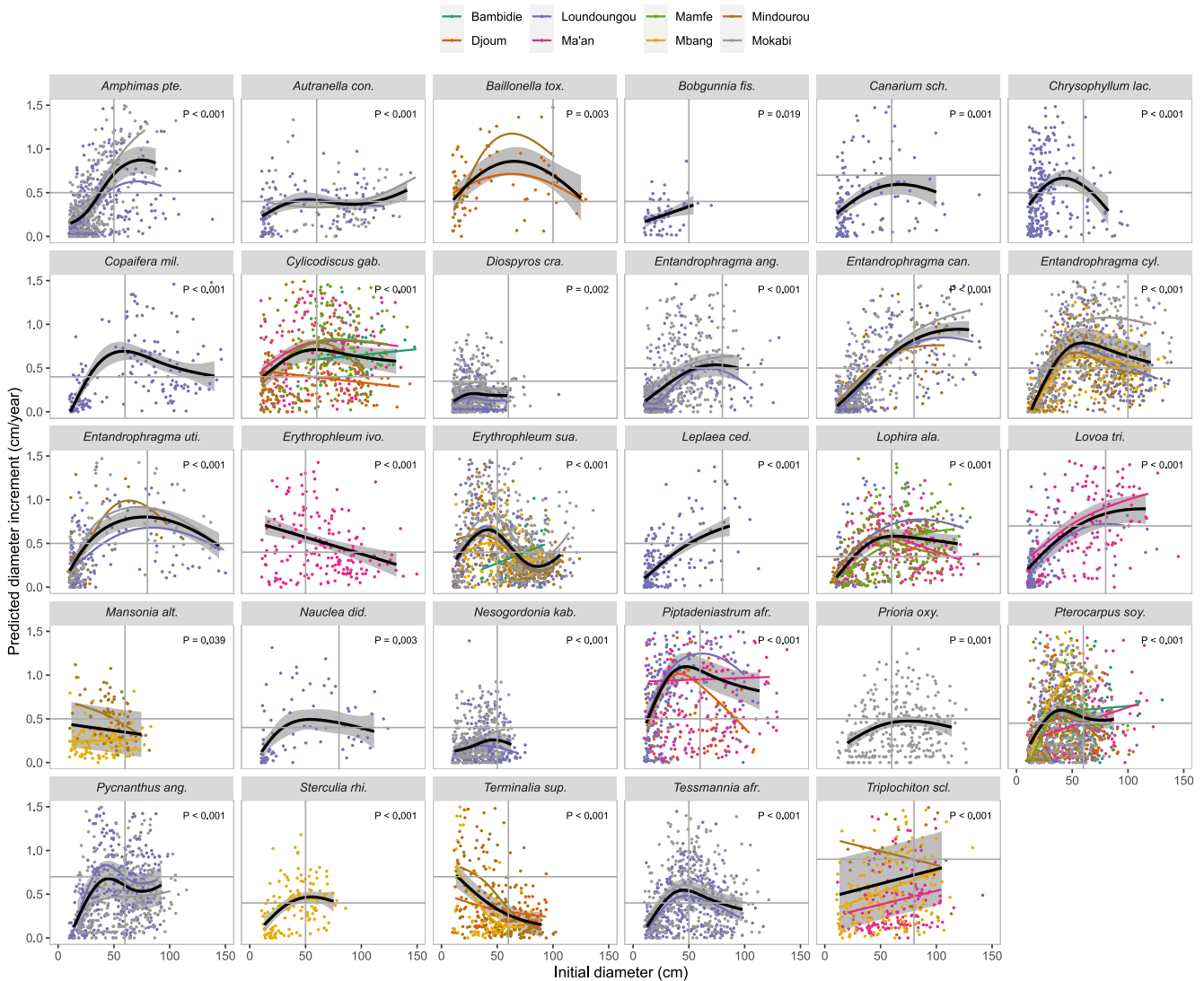


Fig. 6. Relationships between diameter increment and initial diameter. The relationships are shown only for the 29 species for which the relationship was significant ( $s()$  term in Eq. (5)). For the other 14 taxa, the relationships are shown in Supplementary Material (Figure S2.1). Black lines show the prediction of the model described in Eq. (5). Colored lines show predictions of site-specific models. The horizontal and vertical gray lines indicate the species-specific reference values of diameter increment and minimum cutting diameter.



cutting diameter. For these diameter classes (where increment peaked), the predicted diameter increment was generally higher than the reference diameter increment (e.g., *Lophira alata*, *Entandrophragma cylindricum*, *Cylicodiscus gabunensis*). The percentage of explained variance averaged around 19% and ranged from 6% to 50% (Suppl. Table S2).

### 3.3 Diameter increment in logged and unlogged forests

In logged forests, we assessed the diameter increment of 8453 trees. The averaged estimates per study species and site ranged from 0.1 cm/year (*Diospyros crassiflora* in Loundoungou) to 1.59 cm/year (*Triplochiton scleroxylon* in Mindourou). The mean of the census period length was 2.4 years and ranged from 0.9 (*Greenwayodendron suaveolens* in Mamfe) to 7.2 years (*Entandrophragma cylindricum* in Mindourou).

The logging effect ranged from  $-0.46$  to  $0.62$  cm/year (Suppl. Table S4). Very different effects were found depending on tree species and site. In Bambié, we found a negative effect of logging for a notable proportion of the species, whereas positive effects were mostly found in Mindourou. In all sites except Mindourou, forest logging occurred less than 4 years before the monitoring period (Fig. 7). This result therefore suggests that tree response to logging was site-specific or depended on the time elapsed between logging and the monitored period. To illustrate this second explanation, we computed the Pearson correlation coefficient between the logging effect and the time elapsed between logging and the censuses. The correlation coefficient was  $0.46$  and was significant (Fig. 7).

### 3.4 Tree mortality rates in unlogged forests

We computed mortality rates by examining a total of 15,860 trees of 36 species that were monitored during varying census periods in the eight sites (Fig. 8). The mean of the census period length was 2.8 years and ranged from 0.6 (*Piptadeniastrum africanum* in Ma'an) to 7 years (*Lophira alata* in Mindourou). Only 242 dead trees were recorded. The overall mortality rate was approximately 0.56% ( $\lambda_{\text{corr}} = 0.60\%$ ). Differences in  $\lambda$  and  $\lambda_{\text{corr}}$  were noted among sites and species but as the differences were negligible (Table S4) we continued with  $\lambda$ . Most values (80%) of our 74 estimates of  $\lambda$  were not statistically different from 1%. Fourteen (19%) estimates of  $\lambda$  were lower than 1% and only one was greater than 1% (1.4%, *Mansonia altissima*).

## 4 Discussion

Using a particular sampling strategy, a large dataset of repeated tree

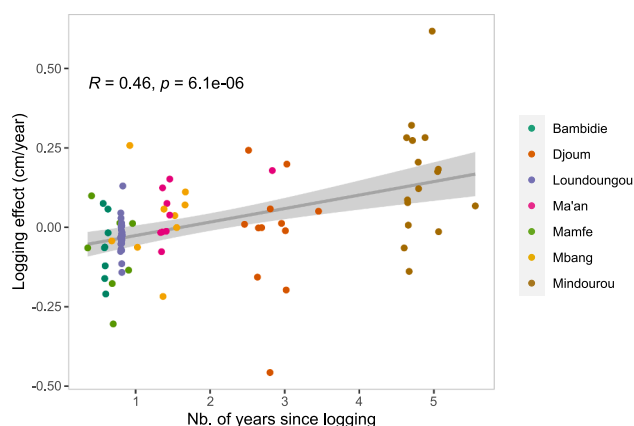


Fig. 7. The logging effect is seen to increase with the time elapsed between logging and the monitored growing period in the logged treatment. The logging effect corresponds to the difference between the growth observed in the logged and unlogged treatments. In this figure, one point corresponds to the logging effect observed for one species and one site.

measures was collected to compute estimates of tree diameter increments and mortality rates of 42 timber species in Central Africa. First, this study provides estimates of diameter increments averaged by species, site, treatment, and size class (Suppl. Table S1, Suppl. Table S2) together with mortality rates averaged by site and treatment (Suppl. Table S5, Suppl. Table S7) that can be directly used to forecast forest development and for example to compute the recovery rate of harvestable stocks between cutting cycles. Second, this dataset casts light on the potential biases in forest projections using reference values of tree diameter increments and mortality rates and applying them to site, tree size, logging history, and over time.

### 4.1 There was a substantial within- and between-site variability in tree growth rates

Tree growth in unlogged forests was found to vary remarkably across sites, species and individuals. We computed 112 estimates of annual diameter increments in forests that had not been exploited for timber for at least 20 years before the censuses. For most species, we noted that diameter increment varied across sites (Fig. 4). The magnitude and sign of this site effect was not the same among the study species. Some sites favored some species and disfavored others, likely depending on species ecology (Baribault et al., 2012). Given the limitations of our tree sample (cf. Section 3.1), we could not model this spatial variability in diameter increment. We could therefore only provide increment estimates for the combinations of the species and sites we studied.

The within-site variability was also substantial and highlighted the influence of various other factors (Fig. 6). This was expected because the tropical forests studied display a high level of compositional and structural complexity (Leigh, 1975; Richards, 1952). Tree performance (growth and survival) is known to depend critically on the size, proximity, and density of neighboring trees, and on the availability of resources (Baribault et al., 2012; Battipaglia et al., 2015; Jucker et al., 2018), which is changing over time (e.g., owing to disturbances and climate change) (McDowell et al., 2018; Zuidema et al., 2020). We did not attempt to model tree performance in response to changing local growing conditions (e.g., owing to climate change). Instead we assumed that the monitored trees were randomly selected across different forest types so that contrasting species-specific estimates could be obtained. This approach was also practical because the covariates required to describe the local environment (e.g., competition indices, liana loads) are not routinely assessed in inventories or implemented in the models used by forest managers. It has also been shown that the effect of species identity on tree growth can outweigh that of competition for other resources such as light (Laurans et al., 2014).

### 4.2 Legal tree growth rates can be overestimated

In the absence of local estimates of tree growth, forest management plans are built using reference values, such as those set by the Cameroon administration (Ministère de l'Environnement et des Forêts, 1998). In this study, we compared reference values of annual diameter increment with our observed diameter increment averaged by site and species. Our analysis revealed that differences between the reference values and the averaged observations could range substantially, from 33% to 290%. In almost half (46%) of the studied combinations of species and sites, the trees grew more slowly than expected from the reference values. This high proportion of overestimated increment references is of concern, because using them can lead to overestimation of population recovery in management plans (Picard et al., 2008). We note nevertheless that such overestimation does not concern all species: opposite observations were also made but for only 23% of the study cases. For example, for *Baillonella toxisperma* and *Cylicodiscus gabunensis*, the reference diameter increment was lower than the observed increment in most studied sites (Fig. 6).

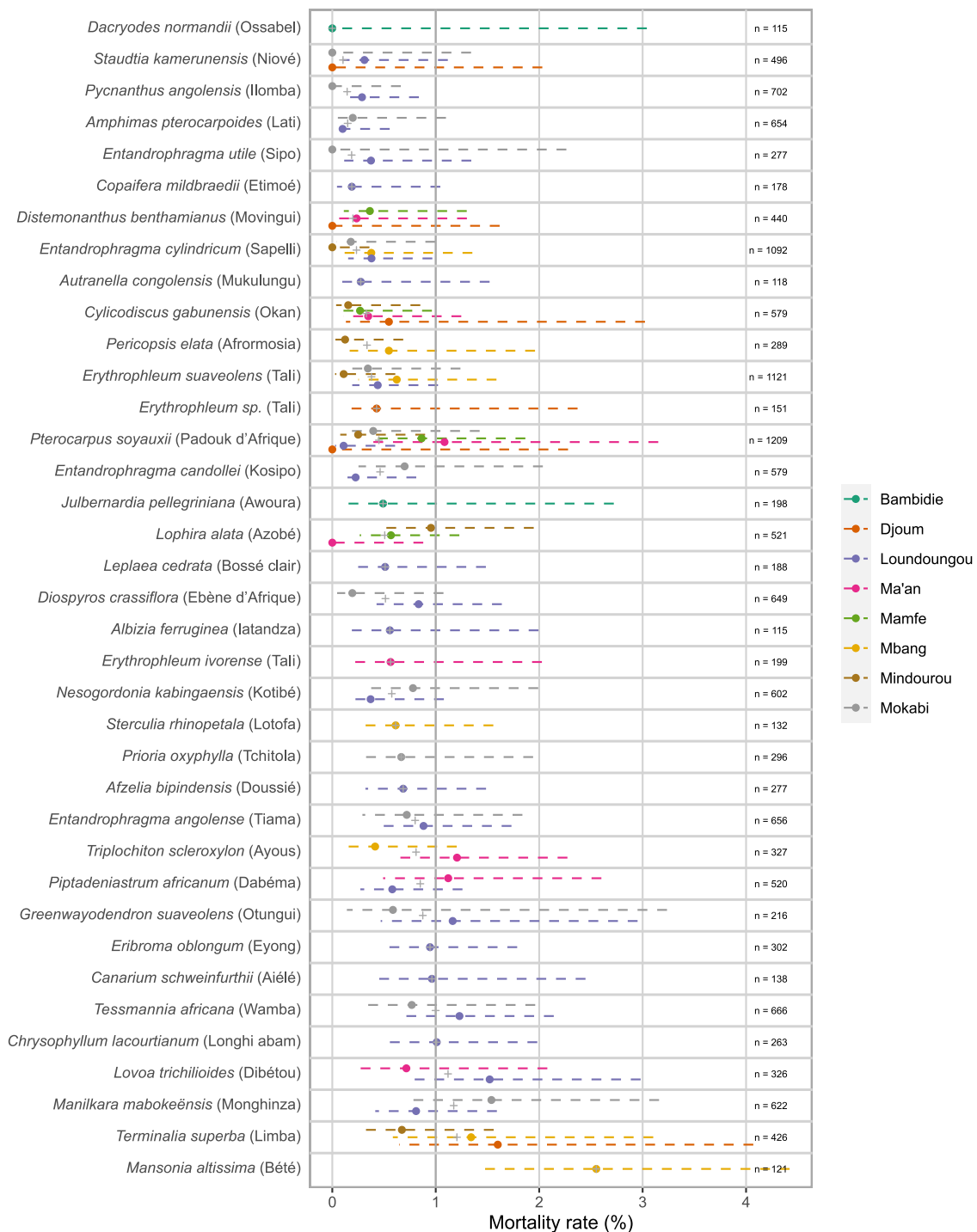


Fig. 8. Estimates and 95% credible intervals of the mortality rates. The total number of monitored trees per species is given next to the credible intervals.

#### 4.3 Logging stimulates temporary tree growth and the magnitude of this effect varies greatly over time

Tree growth is likely affected by disturbances including logging but such responses vary in time (Gourlet-Fleury et al., 2013; Héroult et al., 2010; Vidal et al., 2016). Gourlet-Fleury et al. (2013) found in M'Baiki (Republic of Central Africa) that over 24 years after logging, the average above-ground biomass production in the logged plots was twice that observed in the control plots. Using data from the same experiment but focusing on *Triplochiton scleroxylon*, Ligot et al. (2019) confirmed that diameter growth followed the same pattern. They further stated that the

growth response rapidly increased after logging and then gradually decreased. In total, the positive growth responses lasted over 10–15 years (Ligot et al., 2019). In this study, we were able to further refine this pattern. Examining diameter increment recorded 1 or 2 years after logging, we found no or even negative growth response. We hypothesize that immediately after logging, diameter growth rate decreases slightly (Fig. 7) owing to an adaptation to the new growing conditions and possibly to logging damage (Shenkin et al., 2018). In the subsequent years, the increment might progressively increase before reaching a maximum growth rate, and finally revert to the level observed in unlogged forests as suggested by other studies (de Graaf et al., 1999;

Gourlet-Fleury et al., 2013; Ligot et al., 2019).

Growth response to logging is, however, likely to be species- and site-specific. Logging intensity varied within and across sites and was generally lower than observed in other experimental plots such as those in M'Baiki (Gourlet-Fleury et al., 2013). In all sites, only a few species showed a significant growth response (Fig. 7). Depending on site and presumably on forest structure, different species or functional groups could benefit from a canopy opening (Delcamp et al., 2008; Hérault et al., 2010; Peña-Claros et al., 2008; Villegas et al., 2009).

#### 4.4 Variability of tree growth rates across tree ontogeny and due to logging could mitigate overestimated reference values

In line with previous studies, our data found that tree growth could vary greatly throughout ontogeny. According to Hérault et al. (2011), who studied tree growth in Paracou (French Guiana), tree growth trajectories vary greatly among species but for most of them, growth peaks when trees reach about 60% of their maximum size. Like Hérault et al. (2011), we also observed humpback-shaped growth trajectories for most studied species. Interestingly, growth trajectories mostly peaked for diameters close to the reference minimum cutting diameter (Fig. 6). Different minimum cutting diameters are used across countries and regions. Nevertheless, as the growth peaks were generally wide (Fig. 6), this trend should hold true for other countries and regions. In these conditions, the trees with diameter close to the harvestable dimensions grow faster than the average. The trees belonging to the diameter classes just below the minimum cutting diameter will therefore reach harvestable dimension faster than predicted using the reference value. Taking this effect into account, the estimate of population recovery as made in the management plans may underestimate the recovery of the harvestable stock in the short term.

Additionally, estimates of the annual diameter increment based on forest inventories, like those provided by this study, can underestimate the growth of the trees that will survive. We randomly sampled trees by diameter class regardless of the fate of each tree. The successful trees that will reach large dimensions might thus grow faster than the average of the sampled population. In structurally complex forests, the successful trees that reach large dimensions have likely experienced favorable growing conditions through a juvenile selection effect (Swaine et al., 1987; Terborgh et al., 1997) and persistent fast growth (Brienen and Zuidema, 2007; Groenendijk et al., 2017). During their ontogeny, such trees have faster growth and a lower probability of dying than most of the other trees. Using our estimate of the mean diameter increment could therefore also result in underestimation of forest recovery. However, the extent and variability of this bias is difficult to assess and still largely unknown. One solution requires combining diameter increments assessed from tree rings and field inventories (Ligot et al., 2019; Rozendaal et al., 2010).

Similarly, the effect of logging on the growth of remaining trees has been evidenced in many studies (e.g., Gourlet-Fleury et al., 2013) including this one, but this effect is usually ignored in most forest projections. Although further studies are needed to model tree growth response over longer time periods, it seems likely that the effect over one cutting cycle would be positive. Using increment data exclusively from unlogged forest, as recommended by Bracke et al. (2021), might therefore underestimate the true value.

The estimate of diameter increment as provided here might thus be slightly conservative, because its use can underestimate the recovery of the harvestable stock in the short term. Nevertheless, using such estimates of diameter increment to compute the recovery rate of the harvestable timber stock (e.g., with the "Dimako formula", Durrieu De Madron et al., 1998) does not ensure the long-term sustainability of the polycyclic harvest system. Variation in tree mortality and tree recruitment could have even more importance in long-term simulations (Picard et al., 2009). Additionally, the evolution of timber quality is usually ignored even though this form of management gradually depletes the

stocks of the most valuable trees (Picard et al., 2012).

#### 4.5 Using a fixed mortality rate of 1% seems acceptable but further efforts are required to predict it more accurately

Tree mortality depends on many factors (McDowell et al., 2018) and remains very challenging to assess and model. Monitoring tree mortality requires monitoring large tree populations for long periods. As tree mortality rate is intrinsically low (0.5–2% in Chao et al. (2008) and Lewis et al. (2004)), only a few dead trees can be recorded annually even if a large number of trees are monitored. In this study, despite monitoring over 15,000 trees for 2.8 years on average, we observed only 317 dead trees scattered across eight sites and 36 species. The number of sampled trees and the monitoring duration were likely too small to confidently and statistically evidence differences in mortality rates across species, sites, or other factors.

Our results here again support taking a mortality rate of 1% to perform forest projections (Picard and Gourlet-Fleury, 2011). Most of our estimates of mortality rates were not statistically different from 1% (Supplementary Material 7). Clearly, using a constant value across sites, species and tree size is a simplification. Though mostly statistically insignificant, we observed a substantial variability in the mortality rates across sites and species (Fig. 8). Such variability was expected and has been partly related to forest structure and diversity (Baker et al., 2004; Malhi et al., 2006; ter Steege et al., 2006) of species traits such as wood density (Baker et al., 2004; Chao et al., 2008), tree size, and vigor (Chao et al., 2008).

#### 4.6 Practical recommendations

This study underlines that field monitoring of tree growth and mortality are valuable and provide insight into forest population dynamics. Monitoring nevertheless requires substantial efforts as it must include large numbers of trees and annually repeated measurements over long periods. As recommended by Lewis et al. (2004), we consider that monitoring tree growth and mortality should be performed for at least 5 years, i.e. using a longer census period than here. Repeated measures of tree diameter facilitate the detection of inevitable measurement errors and provide more robust estimates of tree growth that are less affected by inter-annual variability. If periods are too short, too few dead trees will be tallied, and mortality rates cannot be accurately estimated or modeled. Our experience also shows that monitoring thousands of trees annually for 5 years is logistically feasible. Given that forest dynamics can vary substantially across sites, we recommend implementing tree monitoring in each forest enterprise. Such monitoring should be carried out as a priority in unlogged areas. In logged forests, longer monitoring periods could be required as tree growth and mortality are expected to vary substantially for 10–20 years after logging (de Graaf et al., 1999; Gourlet-Fleury et al., 2013; Ligot et al., 2019). In logged forests, the monitoring should also begin immediately after logging to obtain as complete a picture as possible of the tree growth response.

## 5 Conclusion

We performed annual monitoring of more than 20,000 trees in Central Africa to acquire and deliver estimates of tree growth and mortality rates of 42 timber species in logged and unlogged forests. Such estimates and monitoring are essential to better understand the dynamics of tropical forests and to develop sustainable management plans. Moreover, forest management plans in Central Africa are mostly built using species-specific values of annual diameter increment (and mortality rates) and assuming them constant across tree size or over time. This study appraises this assumption and brings key insights into the variability in tree growth with tree size and logging history. We found that the Cameroon legal values of diameter increment were often

overestimated, highlighting the need for a study to provide new estimates of tree growth rates. Additionally, our estimates of mortality rates were mostly lower than the mortality rate usually applied (1%). Although the demography of the overall population could be reliably predicted, the substantial variability in tree growth and mortality across species and sites remains a major brake on accurately predicting how species populations evolve at the local scale.

### CRedit authorship contribution statement

**Gauthier Ligot:** Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft. **Sylvie Gourlet-Fleury:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition, Project administration. **Kasso Dainou:** Methodology, Writing – review & editing. **Jean-François Gillet:** Methodology, Writing – review & editing. **Vivien Rossi:** Methodology, Writing – review & editing. **Mathurin Mazengué:** Resources. **Stevy Nna Ekome:** Resources. **Yanick Serge Nkoulou:** Resources. **Isaac Zombo:** Resources. **Eric Forni:** Resources, Methodology. **Jean-Louis Doucet:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition, Project administration.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary material (estimates of tree growth and mortality rates per species and treatment as well as supplementary analyses) to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119889>. Data and scripts are also available at <https://doi.org/10.18167/DVN1/EBN15Y>.

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