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Using tree-ring data to improve timber-yield projections for African wet tropical forest tree species

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ABSTRACT

Worldwide, over 400 million hectares of tropical forests are set aside for timber production. Several certification schemes exist to ensure more sustainable exploitation and large areas of production forests are currently certified. Under such schemes, logging companies are required to evaluate whether species are not overexploited and, if necessary, adapt their logging activities. However, the data needed to project exploitation intensities – growth, mortality and regeneration rates of trees – are scarce or non-existent. Tree-ring analysis provides lifetime species-specific growth data that can be used to allow or improve the projections of timber availability during following logging cycles. In this study, we integrated growth data from tree rings with logging inventory data to forecast timber yields in the next harvest round for four timber species in Cameroon. We compared projections using tree-ring data with projections using fixed growth rates, as set by law and customarily applied in Cameroon. Additionally, we assessed the effect of increasing logging cycles and of using filed-based species-specific logging intensities on the next cycle's yield projections. Under current logging practices, timber volumes available at next logging cycles are projected to be 21–36% of the volumes obtained at first harvest. Simulations using fixed rates often resulted in lower yields with lower volume ingrowth from trees that were below minimum cutting diameters in the first harvest. Lengthening the logging cycle increased yield predictions during the next harvests, but yields were still not sustained over time. This problem can be resolved by using species-specific logging intensities, which led to projected yields of up to 73% of the initial harvested volume. The growth data provided by tree-ring analysis allows conducting such species-specific projections and thus helps to provide the knowledge base necessary for sustainable forest management. Yet, the low overall yields are a concern to forest conservation, as loss of economic value may lead to conversion of forests to other land uses.

1. Introduction

Tropical forests harbour a rich biodiversity and hold almost half of the world's terrestrial biomass (Pan et al., 2011). Simultaneously, these forests are an important source of timber and large tracts of tropical forest – 403 million hectares – are being logged or have been assigned for logging in the near future (Blaser et al., 2011). In many tropical countries, forestry legislation aim to ensure logging operations do not affect long-term economic, societal and ecological functions of forests (Estève, 2001), and often require the development of management plans prior to exploitation (Nasi et al., 2006). Several international certification schemes (e.g., FSC, PEFC, OLB, etc.) have also been set up to evaluate the sustainability of logging, guarantee socio-economic benefits and safeguard the future of forest areas. Currently, the area of logging concessions with some form of certification accounts for only 8% of the world's forests, with only a small worldwide increase in area between 2005 and 2010 (Blaser et al., 2011). The area of certified forests in Africa has, however, more than tripled in the same period, from 1.48 to 4.63 million hectares (Blaser et al., 2011).

Under certification schemes, logging is usually performed in polycyclic logging systems, in which the largest individuals in a forest parcel are selectively logged and the parcel is allowed to regrow for several years, i.e., for the length of the logging cycle. Logging cycle length may be either fixed by national legislation (typically 20–40 years) or adjusted per forest type (Nasi et al.,

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2006). Additionally, only one part of all potentially exploitable trees can be logged (i.e., there is a maximum logging intensity) and a species-specific minimum diameter threshold to log trees (Minimum Cutting Diameter, MCD) is also usually set (Nasi et al., 2006). Logging companies are required to evaluate whether the combination of logging cycle length, intensity, and MCD results in the sustainable exploitation of a species.

In many countries in the Congo Basin in Central Africa, sustainability of exploitation is assessed using stock recovery rate calculations (Picard et al., 2009). These calculations use the vital rates (i.e., growth and mortality) and current population structure of a species to forecast the number of trees available for harvest after one logging cycle, compared to the number harvested at the first logging round (Durrieu de Madron et al., 1998). To attain sustainable stocks, recovery rates should equal 100%. If needed, the MCD of a species is increased, as cycle length and maximum logging intensity are often fixed by law (e.g., in Cameroon at 30 years and 80%, respectively). Alternatively, assessments of sustainability of exploitation can also be performed on logged volumes instead of on the number of trees. Such timber-yield projections provide an indication whether exploited volumes can be sustained in the next harvest round (Brienen and Zuidema, 2006) and thus provide a more complete picture of timber exploitation. Despite their relevance, such calculations exist only for a limited set of tropical tree species worldwide (Putz et al., 2012) and they are nearly absent for African species (De Ridder et al., 2013). This shortage of studies is worrisome, given the importance of sustainable management for conserving forested areas and maintaining biodiversity of tropical forests (Edwards et al., 2011; Putz et al., 2012).

The basis for calculating timber yields is ultimately the ecological information on the vital rates for each exploited species (e.g., growth rates, regeneration and survival), which is commonly obtained from monitoring trees in Permanent Sample Plots (PSPs). Plot data has limitations when used to estimate species-specific growth rates and tree ages, especially for commercial tree species (Picard et al., 2010). Commercial species usually occur in low densities per hectare (Poorter et al., 1996; Hall et al., 2003) and, combined with the relative small size (typically one hectare) and short monitoring period of most PSPs (typically a few years to a few decades), this implies that vital-rate data is collected for only a very small number of trees of these commercial species. Thus, for many commercial species, accurate and long-term data on survival, ages and growth rates are lacking or of poor quality.

Tree-ring analysis offers a reliable and relatively fast tool to assess tree ages (at logging) and to measure growth rates covering the entire life-span of trees. These data have been used to improve calculations of future timber yields (Brienen and Zuidema, 2006; Schöngart, 2008) and assess the sustainability of timber exploitation for several species in South America (Brienen and Zuidema, 2006; Schöngart, 2008; Rozendaal et al., 2010). Despite the long-known potential for tree-ring analysis in Africa (Mariaux, 1967), such calculations exist for only one African species (i.e., *Terminalia superba*; De Ridder et al., 2013). Given the strong increase in demand for timber from Africa and the increase in certified African forests (Blaser et al., 2011), it is important that such calculations are performed for more species.

Tree-ring derived growth data has the additional advantage that it documents the persistent growth differences between individuals: it shows which individuals are the consistently fast-growing, and which the slow growers. These growth differences among individuals within a species lead to large variation in tree ages at harvestable sizes, and fast-growing trees contribute disproportionally to future timber yields (Brienen and Zuidema, 2007; Rozendaal et al., 2010). Including persistent growth-differences in timber yield predictions provides more realistic estimates of future yields compared to calculations using fixed growth rates (Brienen and Zuidema, 2007), thus improving the assessment of logging sustainability. Finally, tree ring data can also be used to determine the size range of future crop trees, which may attain harvestable sizes in one logging round trees and thus need to be protected or tended.

In this study, we use tree-ring data for four Cameroonian tree species to project future timber yields. For each of these species we use the observed size distribution in a logging concession and combine this with growth data to predict future yields under five distinct logging scenarios. The scenarios are based on the current Cameroonian national logging legislation, but vary in the growth data being used (legally fixed or tree-ring based), the length of the cutting cycles (the current 30-year cycle used in Cameroon or cycles of 40 and 60 years), and in the logging intensities (maximum allowed intensity or an intensity that is based on *in situ* timber availability). We address the following questions:

- Under current logging regulations, what proportion of timber extracted at first harvest will be available in the next standard harvest round for four timber species in Cameroon and do these proportions change when using legally fixed or tree-ring based growth rates?
- How do these proportions change for the different species when increasing logging-cycle lengths to 40 and 60 years?
- What is the effect of changing the logging intensities on future timber yields?

We collected lifetime growth data for four timber species in Cameroon using tree-ring analysis and used a bootstrapping approach to simulate future timber yields. We then compared different logging scenarios: from a base model following the parameters set by Cameroonian legislation (MINEF, 2001) to alternatives based on tree-ring growth data, varying logging cycle lengths and applying field-based logging intensities. Additionally, we determined the diameter ranges of future crop trees and assessed the number of years trees have grown between reaching MCD and being logged, an indication of how long wood volume has ‘accumulated’ after trees passed MCD.

2. Materials and methods

2.1. Study area

Samples were collected inside the adjacent 2011 and 2012 cutting blocks of the FSC-certified (Forest Stewardship Council) logging concession 11.001, of Transformation REEF Cameroon (TRC, 2008). This concession lies in the Southwest Region of Cameroon, adjacent to Korup National Park (Fig. 1), at approximately 5°23′N, 9°10′E. Although a large area in the North-west of the concession was previously exploited in the 1980s, our sampling area consisted of primary forest without signs of major disturbances or previous exploitation. The vegetation consists of semi-deciduous Guineo-Congolian lowland rainforest (∼200 m a.s.l.; cf. White, 1983) dominated by Leguminosae–Caesalpinioideae, with a canopy height of ca. 40 m (and emergent trees up to 53 m). Regional climate is equatorial, with a unimodal rainfall distribution and a dry season from December to February (monthly rainfall <100 mm). Total annual precipitation averages ∼4000 mm (Nchanji and Plumptre, 2001) and mean annual temperature averages 26.7 °C (range: 25.7–29 °C). See the climatic diagram (Mamfé weather station; cf. Walter and Lieth, 1960) in Fig. 1.

2.2. Study species, sample collection and ring measurements

In the period of June 2010 to May 2012 we collected samples of four timber species known to produce annual growth rings

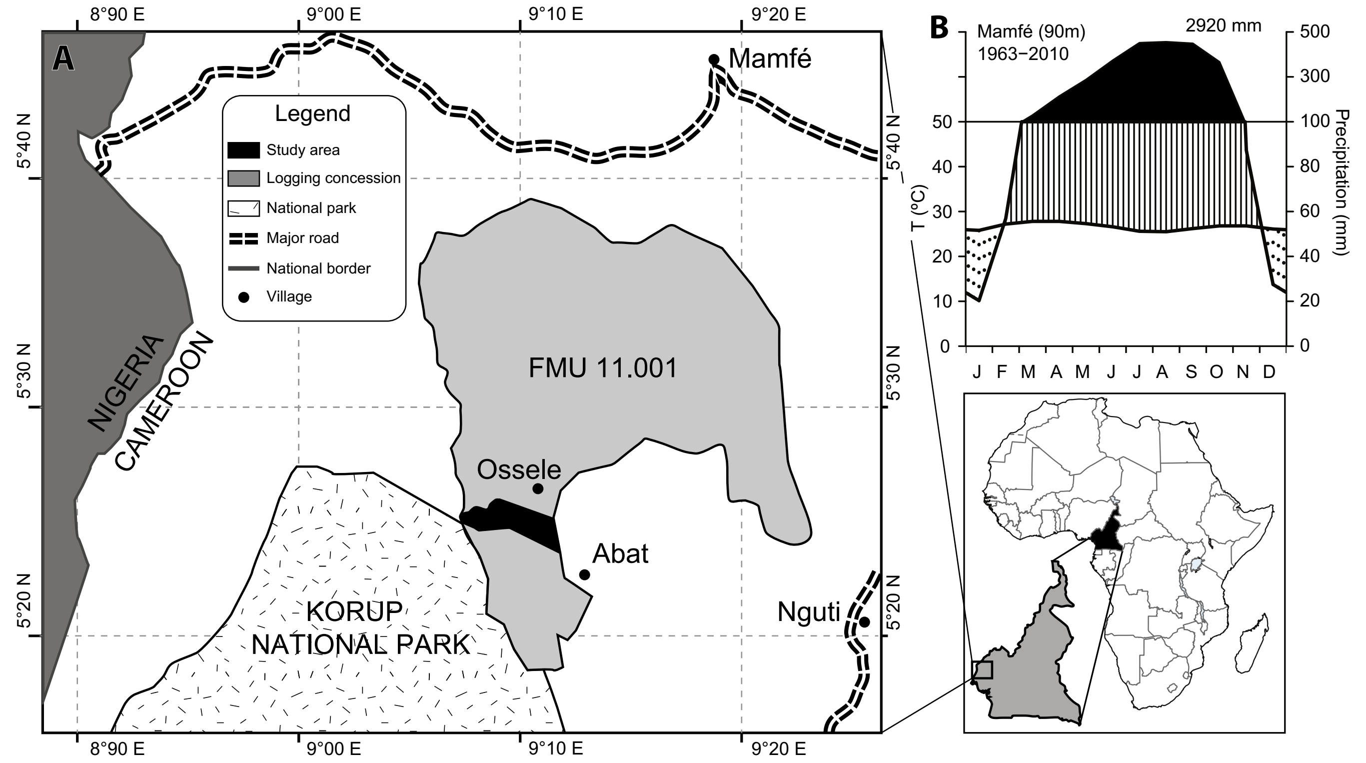

Fig. 1. (A) Location of study site: Forest Management Unit 11.001 (light grey) and the sampling area (black). Inlay shows the location of the study site in Cameroon. Roads, national borders and national parks are also shown. (B) Climate diagram (cf. Walter and Lieth, 1960; period 1968–2009) for the Mamfé Airport weather station, indicating the rainy (>100 mm month-1; black area) and dry seasons (rainfall < temperature, dotted area).

(Groenendijk et al., 2014) and that were being commercially exploited (Table 1). These species vary in their use, commercial value and abundances in the forest. For two species, we collected ~100 individuals: *Brachystegia eurycoma* Harms, *Daniellia ogea* (Harms) Rolfe ex Holl. For *Terminalia ivorensis* A. Chev. we collected 63 samples and for *Entandrophragma utile* (Dawe & Sprague) Sprague 10 individuals (Table 1). These two species were not abundant in the area, but have high commercial value (Lemmens et al., 2012). Each sampled tree was georeferenced (Garmin GPS60X) and its diameter at breast height (dbh) was measured.

We collected most samples (~90%) in previously unlogged parts of the FMU (TRC, 2008) not showing apparent signs of past disturbances (e.g., from logging, agriculture, or fire). For trees that were logged, we collected cross-sectional discs (ca. 30% of the samples), as working with discs allows identifying the presence of wedging (rings that merge on certain parts of the circumference of the tree) and intra-annual growth variations. For trees not being logged and for smaller trees (below MCD) we collected cores (in three to four directions) using 5.15 mm increment borers (Suunto and Haglof). Samples were usually taken at 1 m height or above anomalies or buttresses and we sampled all trees >5 cm dbh. All samples were air dried and surfaces prepared to allow for growth-ring identification by polishing them (with increasingly finer sandpaper; grain 40–1000) or using a large sliding microtome (Gärtner and Nievergelt, 2010). Ring boundaries were assessed and marked by naked eye or under a stereo microscope (magnification 16–40×) and ring-widths measured on scanned images with 1600–2400 dpi resolution (Epson Expression 10000XL). Samples were often wetted and/or scanned laying on a film of water on the scanner plate to increase ring visibility. Ring widths were measured using the software WinDendro Regular (Regent Soft, Canada) in three to four radii per tree (for details of ring measurements see

Table 1

Growth and age characteristics of five commercial tree species from Southwest Cameroon. Provided are: species name; number of trees collected (as cross sections or discs), average diameter growth rates measured from tree rings, growth rates legally fixed and used for timber projections in Cameroon, ages to reach Minimum Cutting Diameter (MCD), guild (cf. Poorter et al., 2006) and the main uses of wood.

Species	Family	Commercial name	#Samples (as disc)	Growth rate rings (cm yr^{-1}, ±SD)	Growth rate fixed (cm yr^{-1})	Age MCD[*] (range)	Guild[**]	Main uses wood
Brachystegia eurycoma	Fabaceae (C)	Ekop Naga	128 (32)	0.56 ± 0.48	0.5	100 (48–135)	PST	Plywood, interior[a,b]
Daniellia ogea	Fabaceae (C)	Faro	105 (18)	0.43 ± 0.35	0.7	148 (77–214)	ST	Plywood[a,b]
Entandrophragma utile	Meliaceae	Sipo	10 (10)	0.72 ± 0.40	0.5	126 (79–203)	LLP	Veneer, furniture[a,b]
Terminalia ivorensis	Combretaceae	Framiré	62 (52)	0.96 ± 0.71	0.7	45 (21–91)	LLP	Furniture, plywood[a,b]

[*] Minimum Cutting Diameter (MCD) is 60 cm, except for *E. utile* = 80 cm.
[**] Guilds: PST = Partially shade tolerant, ST = Shade tolerant, LLP = Long-lived pioneer.
[a] Lemmens et al. (2012).
[b] CIRAD (2012).

Groenendijk et al. (2014)). Growth rates were averaged for all radii and converted to diameter growth rates.

The quality and accuracy of the tree-ring measurements was assessed by crossdating. Crossdating consists of matching patterns of variation in ring-widths between different ring-width series and can be performed within trees (i.e. among different radii) and between different trees. Within-tree crossdating helps identifying wedging and 'false' rings and ensures the same (number of) rings are measured between different radii. While internal crossdating was successful for most samples, crossdating among trees proved challenging for all species, and building tree-ring width chronologies was impossible for our study species (Groenendijk et al., 2014). Radiocarbon dating confirmed annual nature of ring formation for three species: *B. eurycoma*, *D. ogea* and *E. utile* (Groenendijk et al., 2014). For *T. ivorensis* and *E. utile* the annual nature of ring formation had been previously demonstrated by Détienne et al. (1998) in Cameroon, and for the *E. utile* trees used in this study, with oxygen isotope chronologies (van der Sleen et al., 2015). Note that tree ages used here are slightly underestimated as we do not include a correction for the time trees require to growth to sample height.

2.3. Projecting future population structures

The basis to predict future timber yields were projections of the population structure of each species after one logging cycle (e.g., after 30 years). Current population structures (i.e., the number of individuals per diameter class), were derived from the inventories of the logging company and from our own measurements in 16 circular plots of ~1 ha (see Groenendijk et al., 2014). For trees >20 cm, the primary sources for diameter distributions were two inventories carried out by the logging company: one systematic inventory of all trees >MCD in the 2011 and 2012 cutting blocks, and another stratified throughout the entire logging concession (for trees >20 cm) using 946 plots of ~0.5 hectare (TRC, 2008). In both inventories, the diameter of trees was estimated by inventory crews within 10-cm diameter windows. We corroborated these distributions, and completed them for trees smaller than 20 cm, using the size distributions measured in our sampling plots (Groenendijk et al., 2014).

For the projections of future diameter distributions, we generated a 'current population' of 500 individuals according to the species' size distributions in the field, and every individual was assigned a random diameter within the size class. We based our projections on a fixed number of individuals instead of on a fixed area (cf. Rozendaal et al., 2010), to account for the large differences in abundances of trees per hectare between the species (Fig. 2 and Table 2).

2.4. Fixed and tree-ring based growth rates

To assess the effect of using different types of growth data on projected timber yields, we used fixed and tree-ring based growth rates to forecast future population structures. The fixed growth rates were based on the growth rates set by Cameroonian law (MINEF, 2001) to be used for timber yield predictions. These growth rates do not depend on tree size and are set to be 0.5 cm yr^{-1} for *B. eurycoma* and *E. utile* and 0.7 cm yr^{-1} for *D. ogea* and *T. ivorensis*. The tree-ring based data were obtained through tree-ring analysis for our species (Groenendijk et al., 2014). The number of trees measured varied (Table 1) and was rather low for *E. utile*, with only ten trees measured. To ensure a similar amount of growth data for all species and to increase the number of growth trajectories, we performed bootstrap simulations using the tree-ring data and generated 1000 growth trajectories for each species, following the approach by Brienen and Zuidema (2006). We incorporated growth autocorrelation by randomly choosing a growth rate for the current year from trees that were in the same 'growth rate class' in the previous year (i.e., using a 1-year time interval) from a diameter window of 10 cm around the current tree diameter (i.e., 5 cm above and below). These growth trajectories reflect the age/size variation in growth for each species and incorporate the variation in growth among individual trees (i.e., growth autocorrelation). Incorporating this growth variation leads to realistic growth variation in the simulated trajectories and thus to more reliable estimates of timber yields (Brienen and Zuidema, 2007; Rozendaal et al., 2010). Growth simulations were conducted in Matlab 7.9 (The Mathworks Inc.).

Finally, we projected the sizes of trees after one logging round by assigning one of the bootstrapped growth trajectories to each of the 500 trees in our 'current population'. For the final population structure, we applied an annual mortality chance of 1% randomly on all trees, e.g., the fraction of trees that survived in the 30-year logging cycle scenario was $(0.99)^{30}$. This mortality chance is also fixed by the Cameroonian administration (MINEF, 2001) and in range with rates found in the adjacent Korup National Park (Fig. 1) for trees >50 cm dbh: between 0.0 and 6.3% yr^{-1} (average 1.4%, n = 1651; Newbery et al., 2013). Mortality of juvenile trees is usually higher than that of adult trees, but may be in the same range (e.g., 1.1% per year; Newbery et al., 2013), but we do not account for this difference in our simulations.

2.5. Calculations of timber volume

To simulate future yields, we calculated timber volumes for the current and future population structures for each species. For the two most logged species in the 2011 cutting block – *B. eurycoma* (n = 933 trees) and *T. ivorensis* (n = 52) – we calculated species-specific relationships between dbh and log volume using data from the logging company. We established the relationship between dbh and volume using third-degree polynomial functions. For the two other species – *E. utile* (n = 6) and *D. ogea* (n = 35) – the number of trees logged was too low to calculate reliable relationships and the average relationship between dbh and volume for all trees logged that year was used (n = 3186). These volumes represent bole volumes in the forest (i.e., round wood) and incorporate the dbh-stem height relationship and the taper of the stem. These calculations, however, do not account for sapwood volume (usually discarded) nor for losses during the bole transformation at the sawmill (i.e., sawn wood). We do not account for these factors as we assume that changes in sawn-wood yields will be proportional to the changes in volume yields.

2.6. Logging scenarios

We created different scenarios to assess the effects of data type, logging-cycle length and logging intensity on future timber yield. To simulate the current logging conditions in Cameroon, our 'standard' scenario had a cycle length of 30 years and we applied the maximum allowed logging intensity of 80%. We use this standard scenario as a basis to assess the effect of using fixed and the tree-ring based growth rates. To assess how future timber volume changes under longer logging cycles, we simulated two scenarios with longer cycle lengths of 40 and 60 years, using again the maximum logging intensity. Finally, to assess the effect of changing logging intensities on future yields, we applied the standard 30-year cycle but used species-specific logging intensities based on field measurements. For the simulations using longer logging cycles and species-specific logging intensities we used the tree-ring data only, as these data provide accurate and realistic growth rates.

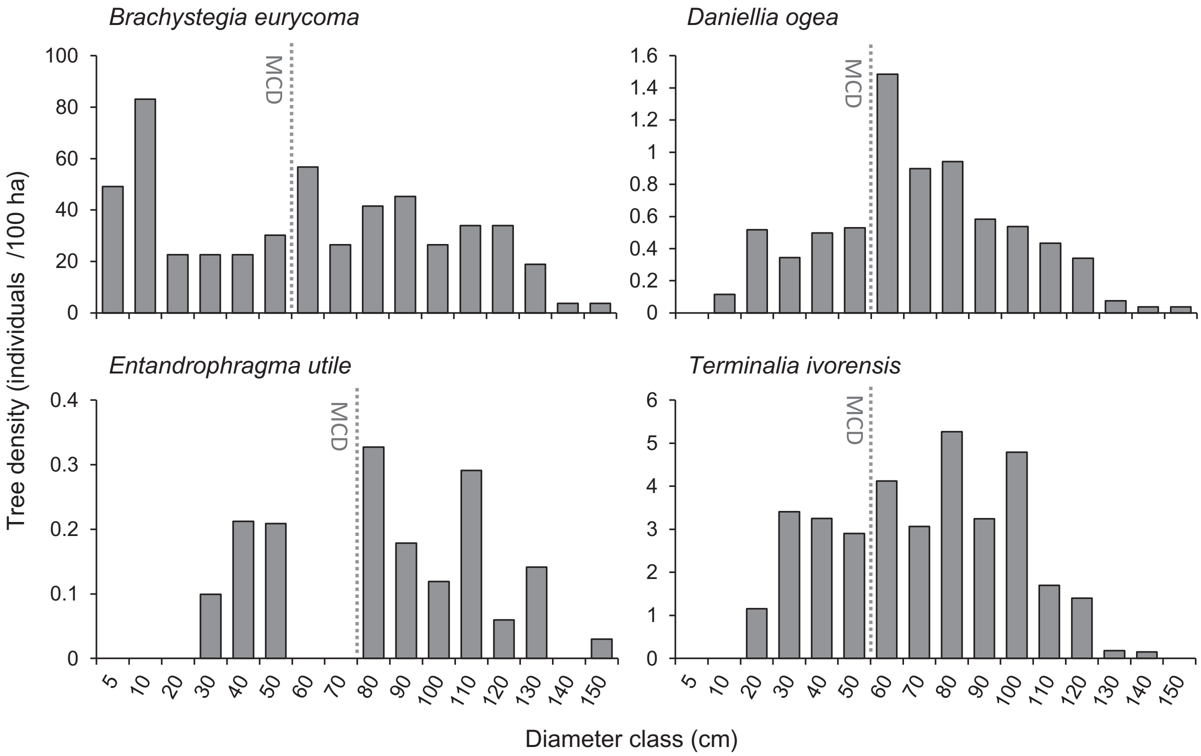

Fig. 2. Density of trees per 10-cm diameter classes for four Cameroonian timber species. Tree densities were obtained from forest inventories in two annual cutting blocks (~3260 hectares) for above their minimum cutting diameters (MCD, dotted vertical lines); in 946 inventory plots of ~0.5 ha across the logging concession for trees >20 cm diameter; and using 16 plots of ~1 ha for smaller diameters. Note the varying scales of the y axes.

Table 2

Number of stems above minimum cutting diameter (MCD) and logging intensities for four species inventoried and logged in the 11.001 concession of TRC Cameroon (2011 cutting block, ca. ~1630 hectares). Non-exploitable are trees growing on steep slopes, within 25 m of rivers, or with crooked or rotten stems. Logging intensity is the percentage of exploitable trees that were ultimately logged.

Species	Inventoried (all >MCD)	Non-exploitable	Exploitable (in % of all)	Logging intensity (in % of exploitable)	Exploited volume (in m^3)
Brachystegia eurycoma	2356	625	1731 (73%)	933 (54%)	12,741
Daniellia Ogea	113	27	86 (76%)	33 (38%)	456
Entandrophragma utile	10	3	7 (70%)	6 (86%)	117
Terminalia Ivorensis	137	25	112 (82%)	52 (46%)	798
All species[a]	8542	2305	6237 (73%)	3187 (51%)	40,654

[a] Includes all 72 species being exploited in the concession.

To determine the species-specific logging intensities, we determined the intensities for each species based on the inventory of the logging company and data on which trees were logged. Depending on factors such as commercial demand for a species' timber, stem quality, etc. the actual intensities of logging may vary between species or between years. We calculated these species-specific intensities based on the number of trees inventoried and logged in the 2012 cutting block. Inventories usually take place in the year prior to exploitation. During inventories, all trees above MCD are tagged, their diameter is estimated and each tree is classified as exploitable or non-exploitable. A tree is classified as non-exploitable when having rotting or strongly crooked stems, growing on steep slopes, or when growing 25 m from rivers. Additionally, not all the trees considered exploitable are harvested during logging operations: certain species have varying commercial demands over time, larger trees are preferentially logged (TRC unpublished data; Van Rheenen, 2005), and trees may be spared if heavily covered in lianas (for safety reasons) or if rotting is noted prior to logging that was not recorded during inventory. Any tree that is cut down is considered exploited, including trees discarded for having rotten stems (noted after logging) and trees used for bridges. We calculated species-specific logging intensities as the proportion of exploitable trees that are actually exploited, thus assuming that trees considered non-exploitable during inventory will fall in the same category for the following logging cycles. Thus, the intensities we use, although higher than if calculated using all trees, provide a much more realistic estimate of the proportion of exploited over exploitable trees in the forest.

2.7. Timber yield calculations

For each of logging scenarios we simulated an initial logging round on the 'population' of 500 individuals by randomly choosing trees from >MCD according to the logging intensities applied. We then simulated a second logging round incorporating the growth of all trees remaining after the first round: those below MCD and the trees above MCD remaining after the first round. Next, we calculated future timber yields by dividing the exploitable volumes projected in the second logging rounds with the volumes exploited in the first round. As timber yields were calculated for virtual populations, our results provide estimates of second harvest volumes relative to the first round's volume (see Table 2). We also calculated what proportion of the volume at second harvest was determined by the ingrowth of trees <MCD (i.e., the 'commercial ingrowth') or by the trees that remained from the first harvest (i.e., those that were not logged). For each scenario, we repeated these calculations 10 times (i.e., for 10 'populations' of 500 trees), to calculate average projected timber yields and avoid that results were affected by the (random) choice of trees to be logged.

2.8. Future crop trees and accumulated growth years

Finally, we used the growth data from tree-rings to determine the size range of future crop trees and to assess the number of years trees have grown after reaching MCD. The size range of future crop trees can be used as an information basis for forest managers to determining the size ranges of trees that need to be protected or tended during current logging activities. These trees may attain harvestable sizes in one logging round (here 30 years) and it is thus important to protect them during exploitation. We determined this diameter range by calculating the size of trees 30 years before reaching MCD, based on the tree-ring data.

We also calculated how many years trees have grown between reaching MCD and being logged, as an indication of how long wood volume has 'accumulated' after trees have passed MCD. If this age is much larger than the logging cycle, this suggests yields may not be sustained in the next logging cycles. These ages were again calculated using the tree-ring data, simply as the difference in the age of a tree when logged, minus its age when reaching MCD.

3. Results

3.1. Stem densities over the diameter classes

Stem densities varied strongly between species, for instance in the 2011 cutting block, *Brachystegia eurycoma* showed ~235 more trees above MCD than *Entandrophragma utile* (Table 2). Population structures also varied between species: *B. eurycoma* was the only species showing regeneration (i.e. with individuals in the smaller diameter categories), while the other three species showed hump-shaped diameter distributions (Fig. 2; Vlam et al., 2016). Additionally, the population structure of *E. utile* lacked individuals in the diameter classes of 60 and 70 cm, just below MCD.

3.2. Growth rates and ages at logging

Growth rates and ages to reach minimum cutting diameters (MCD) varied within and among species. Average growth rates ranged between 0.43 cm yr^{-1} for *Daniellia ogea* and 0.96 cm yr^{-1} for *Terminalia ivorensis* (Table 1). Growth rates also varied across trees within species, inducing large variation in tree ages to reach MCD (Fig. 4). For instance, for *T. ivorensis* ages of trees to reach MCD varied more than fourfold: from 21 to 91 years (average of 45 years), while for *D. ogea*, the slowest growing species ages ranged from 77 to 214 years, on average 148 years (Table 1). Lifetime growth patterns varied between species. *T. ivorensis* trees show a growth pattern typical for light-demanding species, with growth that is fast (>1 cm yr^{-1}) in the juvenile phase but decreased with age (Fig. 3). *B. eurycoma*, *E. utile*, and *D. ogea* presented growth patterns characteristic of more shade-tolerant species, with growth that is slow for juveniles but increased at intermediate diameters (Fig. 3).

Growth rates measured from tree-rings also differed from those used by the Cameroonian administration to calculate timber yields. For *B. eurycoma* and *E. utile* measured growth rates were higher than the set rate of 0.5 cm yr^{-1} (*grey lines*, Fig. 3), while *D. ogea* showed growth consistently below the set rate of 0.7 cm yr^{-1} (*black lines*, Fig. 3). For *T. ivorensis*, measured growth was above the set rate for trees <80 cm dbh and fluctuated around it for larger trees (*black lines*, Fig. 3). Simulated growth trajectories showed similar average growth rates and variation as the tree-ring data (Fig. 4). However, for *B. eurycoma* simulated growth showed less variation than the original tree-ring data, i.e., the spread in measured data (grey lines) was somewhat higher than for the simulated data (red lines; Fig. 4).

3.3. Timber-yield projections

We combined diameter distributions with growth data to project future timber yields for four species in Cameroon under different scenarios: using different input growth data, logging cycle length, and logging intensities. First, we assessed the effect of using simulated growth data versus fixed growth rates on future yields. Under the standard logging scenario – with a cycle of 30 years and maximum logging intensity of 80% – yields at second harvest were rather low irrespective of using fixed or tree-ring based growth data (Fig. 5). For all species, projected yields in the second harvest round were between 21% and 36% of the volumes at first harvest (Fig. 5). Commercial ingrowth (i.e., volume ingrowth from trees <MCD at the first harvest that grew above MCD in the second) was quite low and the largest proportion of the future yields originated from the 20% of trees not logged in first harvest (black bars; Fig. 5). For *E. utile*, projections using fixed growth rates did not show any new ingrowth, i.e., none of the trees below MCD attained exploitable diameters within the 30-year logging cycle. For *D. ogea*, total yield projections were higher when using fixed growth rates but commercial ingrowth was nearly identical to the projections using tree-ring data.

Second, we assessed the effect of increasing the logging cycle length on future yields by predicting future yields under varying cycle length of 30, 40 and 60 years. These predictions were per-

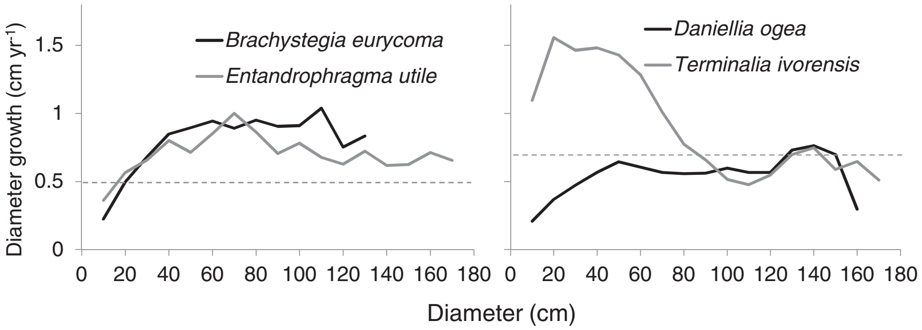

Fig. 3. Diameter growth rates calculated from tree-ring measurements for four timber species in Cameroon. Dotted lines indicate the fixed growth rates used for yield simulations in Cameroon: 0.5 cm yr^{-1} for *B. eurycoma* and *E. utile*; and 0.7 cm yr^{-1} for *D. ogea* and *T. ivorensis*.

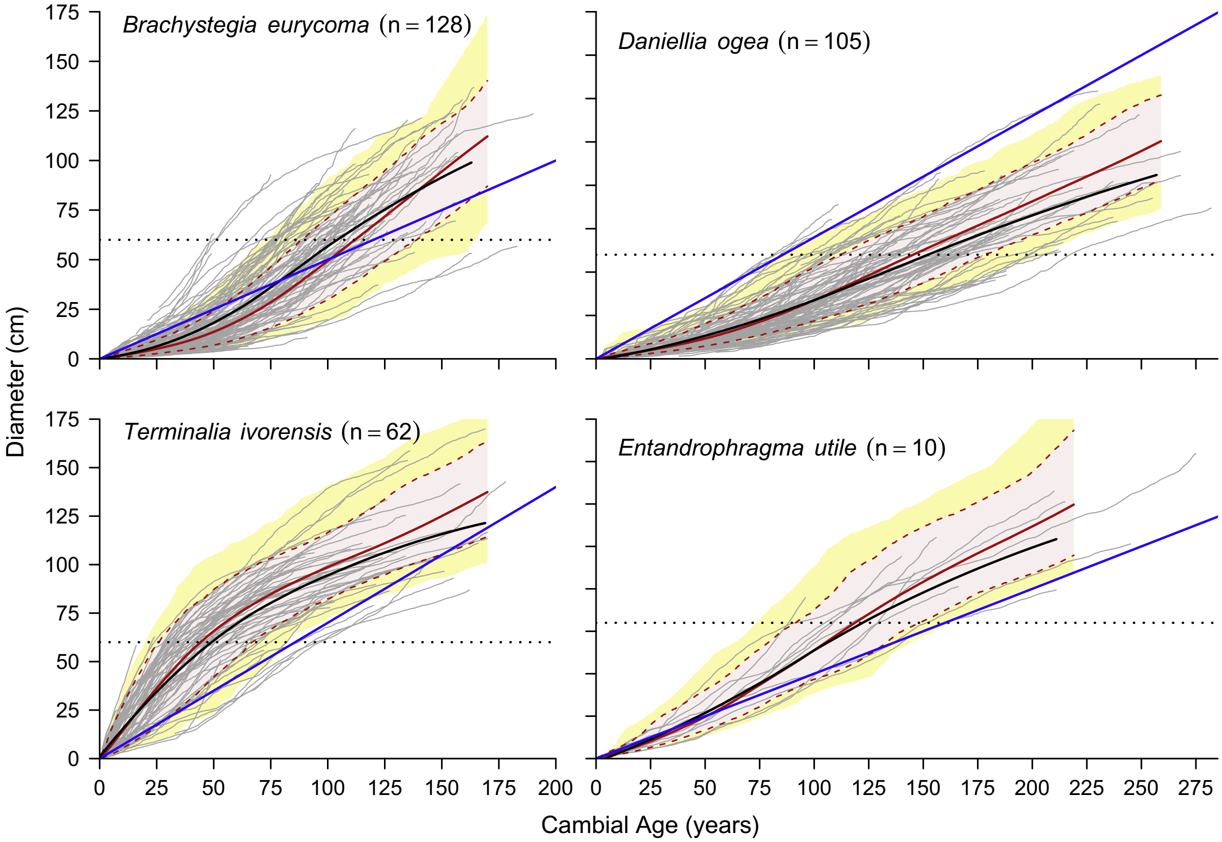

Fig. 4. Measured and simulated tree-growth trajectories. Grey lines: growth trajectories measured with tree-ring analyses; black lines: mean growth trajectory from tree-rings; continuous red lines: mean of simulated trajectories; dashed red lines and pink areas: the 95% confidence interval of simulated trajectories; and yellow shading: highest and lowest simulated diameters per age. Horizontal dotted lines indicate minimum cutting diameters (80 cm for *E. utile* and 60 cm for the other species) and blue lines the fixed growth rates used for yield simulations as set by the Cameroonian administration. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

formed using the tree-ring based growth data and a logging intensity of 80%. Increasing logging cycle length usually resulted in increased timber yields. However, these increases were not very strong and yields at second harvest remained under 48% of the volume extracted at first harvest for all species, even for the longest cycle of 60 years (Fig. 5). Under longer cycles, the share of the future yields originating from the commercial ingrowth changed, becoming larger with increasing cycle length (grey bars, Fig. 5). The share arising from trees not logged in the first round varied per species (black bars, Fig. 5): it remained rather stable for *E. utile*, irrespective of cycle length; it decreased for *B. eurycoma*; and remained rather constant for *D. ogea* and *T. ivorensis*.

Finally, we assessed future timber yields using species-specific logging intensities as realized during the practice of exploitation in the forest concession. We calculated and applied the following species-specific intensities: 54% for *B. eurycoma*; 38% for *D. ogea*; 86% for *E. utile*; and 46% for *T. ivorensis*. These percentages are calculated relative to the number of exploitable trees in the forest and thus not to the total number of trees inventoried (Table 2). Using the field-based intensities and the standard logging cycle of 30 years, timber yields predictions increased remarkably for *B. eurycoma, D. ogea* and *T. ivorensis*, increasing from 24–36% to 52–73% (Fig. 5). On the other hand, yield decreased slightly for *E. utile*, from 25% to 21%, as the intensity of logging increased from 80% to 86%. Across all species, commercial ingrowth was similarly low for both intensity scenarios: on average ~7.5% of the volume logged at first harvest (grey bars, Fig. 5). The increase in yields were thus solely resulted from a larger number of trees that remained after first harvest. The share of future yields from remaining trees increased from on average 20% of the volume logged at first harvest to 45% (black bars, Fig. 5).

Using the tree-ring data, we also assessed the diameter range of future crop trees under the standard 30-year logging cycle and measured the number of years trees have grown between reaching MCD and being logged. The diameter range from which individuals have the potential to reach MCD differed strongly between species: for *E. utile* future crop trees range from ~40 to 80 cm in diameter whereas for *T. ivorensis*, this range was from 0 to 60 cm, indicating that *T. ivorensis* trees that establish at the first logging cycle may be logged during the following cycle. The number of years trees have grown between passing MCD and being logged also varied between the species: for *B. eurycoma* on average ~30 years, while for *E. utile* on average ~75 years (with a maximum of >175 years).

4. Discussion

In this study, we combined tree-ring data, growth simulations and field-based logging intensities to improve estimates of future timber yields in the next harvest round for four Cameroonian tree species exploited in a polycyclic logging system. Predictions using standard logging scenarios resulted in low volume recuperation (of 21–36% of the volumes at first harvest), both for simulations using fixed growth rates set by Cameroonian law and using tree-ring based growth rates. Overall, simulations using fixed rates resulted in lower yields with lower volume ingrowth from trees below minimum cutting diameters in the first harvest. Increasing the length of the logging cycle increased yield predictions but did not result

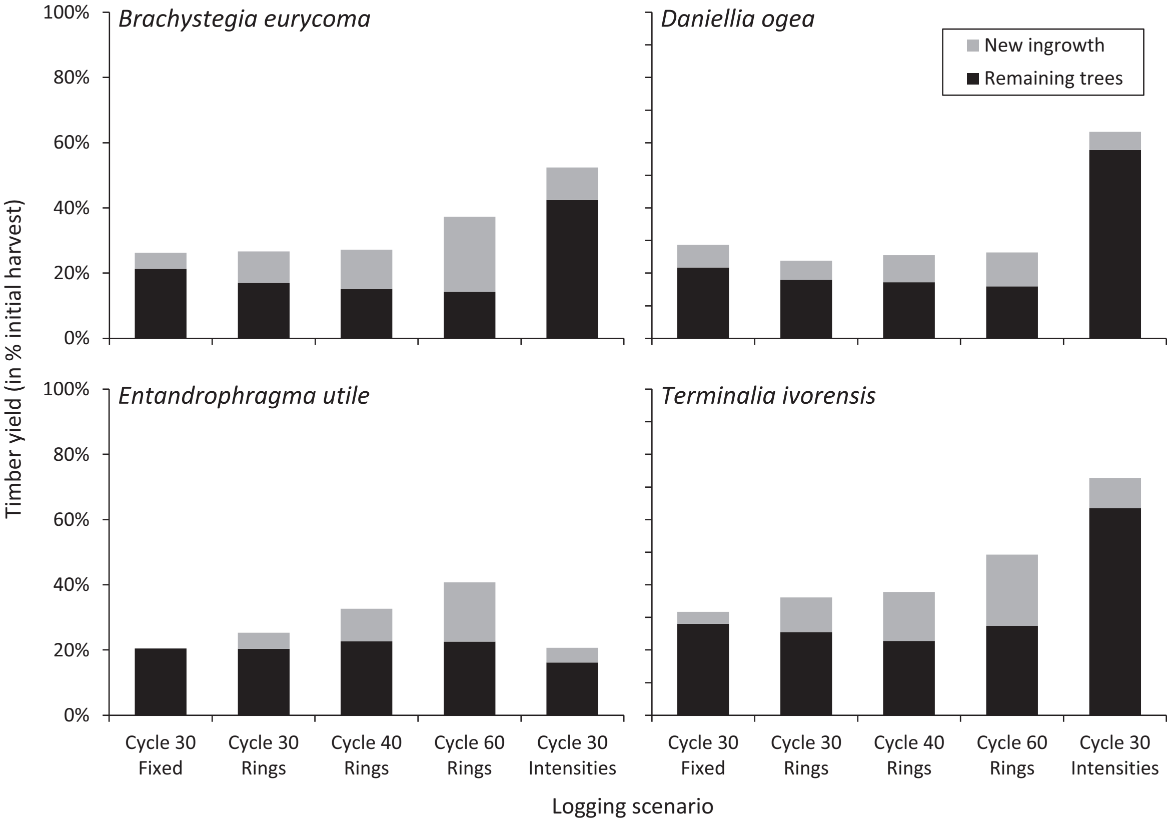

Fig. 5. Predicted timber yields for four commercial tree species from Southwest Cameroon. Results presented for five different logging scenarios: two scenarios under the standard logging cycle of 30 years and maximum allowed logging intensities of 80% used in Cameroon, but using fixed growth rates (Cycle 30 Fixed) or rates measured from tree-rings (Cycle 30 Rings); two scenarios applying longer logging cycle lengths of 40 and 60 years (using tree-ring data and 80% logging intensity); and one scenario with a standard cycle length and species-specific logging intensities based intensities observed in the field (Cycle 30 Intensities). Species logging intensities: *B. eurycoma* = 54%; *D. ogea* = 38%; *E. utile* = 86%; and *T. ivorensis* = 46%. Grey bars represent new volume ingrowth from trees below minimum cutting diameter (MCD) in the first harvest; and black bars the ingrowth from trees not cut at initial harvest (i.e., the remaining trees).

in yields being sustained over time. Changing logging intensities – to the intensities registered in the field – resulted in the largest increases in predicted yields: with yields of up to 73% of the initial harvest volume projected for the next harvest round.

4.1. Robustness of growth simulations and yield projections

Our simulated growth trajectories were rather robust, showing similar average growth rates and variation to the original tree-rings. However, for *Brachystegia eurycoma* the simulated age to reach minimum cutting diameters (MCD) was slightly higher than the measured age and the variation in growth rates was slightly lower. For this species, the projected yields may thus be somewhat conservative, due to the slightly lower growth rates in the simulations compared to actual growth rates but also due to the lower growth variation, which is known to increase future yield projections (Brienen and Zuidema, 2007). The low abundance of *Entandrophragma utile* in the forest and the small sample size (only 10 trees) means that all data for this species – growth simulations, diameter distributions and logging intensities – need to be interpreted with care. For rare species, diameter distributions are very sensitive for the presence/absence of single trees in the sampling plots and extrapolating distributions to large areas thus need caution. Care is thus equally needed when interpreting the timber-yield projections for this species. Nonetheless, we deemed it relevant to also calculate yields for this species due to the commercial valued of *E. utile* (and of the genus) and its presence throughout African tropical forests. Contrastingly, *B. eurycoma* occurred at very high densities in the 2012–2013 cutting blocks, while being nearly absent in other parts of the logging concession (P. Groenendijk, *personal observations*), probably growing gregariously in a similar way as its close Central-African congener *Brachystegia laurentii* (Germain and Evrard, 1956). Simulations for *B. eurycoma*, may thus be only relevant in the specific areas where the species occurs and cannot be extrapolated over the entire FMU.

Our predictions may also underestimate future yields as we do not account for the increase in growth rates that is often reported to occur after logging (Peña-Claros et al., 2008; Gourlet-Fleury et al., 2013), caused by the opening of the canopy. Additionally, disturbances caused by logging could induce a regeneration wave for light-demanding species, such as *Terminalia ivorensis*, that have the potential to reach MCD within one logging cycle and thus boost timber yields.

For the yield projections, we used logging intensities based on field data of trees inventoried and actually exploited. However, these field data did not allow to assess what proportion of trees considered exploitable was not logged because of the stem conditions (rotten or malformed), or due to commercial reasons (e.g., for being relatively small or because of low demand for a species' timber). The number of trees marked for exploitation that are considered not-exploitable in the end can be quite significant: in the Amazon 28% of trees (Holmes et al., 2002). As our data did not allow for these quantifications, we included only those trees that were considered not-exploitable during the inventory, possibly leading to overestimations in the yield projections. Our field-based logging intensities also correspond to a specific year (of

2012), but may vary depending on several factors ranging from economic crises to (species-specific) timber demand. More accurate inventories of species specific proportions of exploitable trees and logging intensities, covering several years and large areas (i.e., different logging concessions) would greatly increase the accuracy of yield predictions.

Despite the limitations of our data, we believe that the yield predictions are still accurate and present a large improvement on previous estimates: our simulations were performed using field-based data that incorporate both specific lifetime growth strategies of tree species – instead of fixed and estimated growth rates – as well as realistic and species-specific logging intensities – instead of the fixed maximum allowed intensities.

4.2. Fixed versus tree-ring based growth rates

We compared the effect of simulating logging yields using two types of data: legally fixed and tree-ring based growth rates. The fixed rates used for yield simulations in Cameroon differed from the measured growth rates of all species but *B. eurycoma*. These differences were strongest for *T. ivorensis* and *Daniellia ogea*. Individuals of *T. ivorensis* showed growth rates consistently higher that the fixed rates, especially for trees <80 cm dbh (Fig. 3), sizes critical for future yields. On the other hand, *D. ogea* trees grow consistently slower than the fixed rates (Fig. 3). Using rates that differ from the actual growth of a species, may potentially lead to incorrect decisions on the logging intensity or cutting cycle lengths. Knowledge on growth rates and its variation, and the lifetime growth pattern of a species, can provide crucial guidelines for managers, such as, size ranges of trees to be protected during logging and whether liberation of these future crop trees (e.g., by girdling competing non-commercial trees) may be a valuable silvicultural intervention (De Ridder et al., 2013). Our results show that the size range of future crop trees varies strongly between species: *T. ivorensis* individuals that recruit at first logging may already reach harvestable sizes within one cutting cycle, whereas for the other species these trees 'originated' from ranges starting at ~10–40 cm. Protecting future crop trees of relevant sizes can thus be used to more efficiently apply silvicultural measures in the field to increase future yields.

4.3. Ages to reach minimum logging diameter

Average ages for trees to reach MCD varied strongly among species: from 45 years for *T. ivorensis* to 148 years for *E. utile*. These ages already provide an indication of the yield recuperation potential of a tree species: if ages at MCD far exceed the logging cycle length, volume regrowth may not be sufficient to replenish timber stocks. For *T. ivorensis*, trees reached MCD on average in ~45 years, with the fastest-growing individual reaching it in 21 years. Such relatively low ages to reach MCD, and the corresponding fast growth rates, have also been found for other African light-demanding timber species: ~75 years to reach 80 cm for *Triplochiton scleroxylon* (1.1 cm yr^{-1}; Détienne et al., 1998), 60 years to reach 60 cm dbh for the congener *Terminalia superba* (De Ridder et al., 2013). Similar ages have also been found for several species growing in white-water floodplains in the Amazon: between 17 and 82 years to reach 50 cm (low wood density species; Schöngart (2008)). These low ages to reach MCD for the fast-growing *T. ivorensis*, suggest that timber yields may be sustained in the future (Schöngart, 2008), assuming that recruitment of young individuals is ensured. Sustained yields were also suggested for the fast-growing congener *Terminalia superba*, from forests in Ivory Coast and the Democratic Republic of the Congo (De Ridder et al., 2013).

For the other three species – *B. eurycoma*, *D. ogea* and *E. utile* – ages to reach MCD exceeded the cycle length by a factor of three to five (ages of ~100–150 years, Table 1), suggesting low yield recuperation for these species. For the two Caesalpinioideae, growth rates and ages at MCD, measured from tree-rings, do not exist in wet African forests and are even sparse for other Caesalpinioideae: in the adjacent Korup National Park (Fig. 1), diameter growth rates of 0.48–0.50 cm yr^{-1} were reported for *Microberlinia bisulcata* (Newbery et al., 2013); in Southwest Cameroon, under a rainfall of ~1600 mm yr^{-1}, average growth rates of 0.53 cm yr^{-1} were found for *Erythrophleum ivorense* (Nzogang, 2009), with ages to reach the 50 cm MCD between 61–128 years; in the Democratic Republic of Congo, with ~1200 mm yr^{-1} annual rainfall, diameter growth rates of 0.46 cm yr^{-1} have been reported for *Prioria balsamifera* (Couralet, 2010), but all trees were below 60 cm.

The ages to reach MCD of *E. utile* compare to the ages of 126–172 found for three *Entandrophragma* species (including *E. utile*) in Southwest Cameroon with rainfall ~1600 mm yr^{-1} (Nzogang, 2009). These ages are, however, lower than the ages of ~250 years reported for *Entandrophragma cylindricum* from Central African Republic (Détienne et al., 1998). These high ages suggest that under current logging cycle lengths, timber recuperation for these slow-growing species will be low.

Ultimately, differences in ages to reach MCD between species may in the long run lead to exploitation shifting towards fast-growing species (Valle et al., 2007), as the stock of slow-growing species becomes exhausted. Such shifts in species may have important financial consequences, as fast-growing species tend to have lower wood densities and lower market value (e.g., Schöngart, 2008).

4.4. Timber-yield projections

We simulated five scenarios of timber yields at the next harvest round by varying three aspects: the input data (using fixed growth rates or simulated rates with variation), the logging cycle lengths (cycles of 30, 40 and 60 years), and the variations in intensity of logging (maximum allowed or actual species-specific intensities). The simulations using legally fixed growth rates usually showed lower yield predictions than the simulations using bootstrapped growth trajectories based on tree-ring data (Fig. 5). Only for *D. ogea* did using legally fixed growth rates give higher predictions of future timber yields. These higher predictions arise from the fact that fixed rates for *D. ogea* were also consistently higher than the actual measured rates for all size classes (Fig. 3). The most striking difference between the simulations with fixed versus simulated growth rates is the consistently higher commercial ingrowth (volume growth from trees <MCD) when using the simulated growth data (i.e., 'new ingrowth' grey bars; Fig. 5). These results illustrate the importance of incorporating persistent differences in growth between individuals in yield predictions (Brienen and Zuidema, 2007; Rozendaal et al., 2010) as fast-growing trees contribute disproportionally to timber ingrowth in future cycles (Brienen and Zuidema, 2007).

Increasing logging cycle lengths resulted in increased future yield projections, but did not result in sustained yields. Commercial ingrowth increased under longer logging cycles as trees below MCD had more time to grow to harvestable sizes. Except for *E. utile*, these longer cycles reduced the contributions of the trees remaining after logging, probably due to the accumulated mortality over time. For *E. utile*, the share of future timber volume from the remaining trees increased over time, probably due to the size distribution of *E. utile* (Fig. 2), which showed relatively high numbers of individuals in the size classes 80 and 110 cm, but lacked individuals in the classes 60 and 70 cm. Volume growth for these large trees is fast, due to the third degree relationship between stem diameter and volume, and under longer logging cycles, these trees thus had more time to accumulate stem volume. At longer logging cycles, the role of mortality and regeneration become more important and our predictions do not incorporate these aspects well: mortality is fixed for all species and sizes and regeneration is not accounted for. This limits our simulations for longer logging cycles, especially for *T. ivorensis*, as recruiting individuals of this species have the potential to reach harvestable sizes within one logging cycle. Not accounting for regeneration caused an increasingly underestimation of future yields with increasing logging cycle lengths.

The most striking changes in yields arose from changing logging intensities. Our results suggest that up to 73% of the initial volume logged can be recuperated in the next harvest round. These yields are twice the yields predicted when using maximum intensities and approach volume recuperations measured in situ 20 years after logging in the Amazon (Vidal et al., 2016). Logging intensities have been found to be the most important factor determining forest biomass recovery – and subsequently timber volume recovery – in South American forests (Rutishauser et al., 2015). Reducing logged volumes at first harvest obviously increases future yields, as second harvest volumes are divided by a lower initial logged volume. Additionally, these simulations assume that trees not logged in the first harvest round will be available in the following round, which is not always the case. Trees that may be available in the next round are those (above MCD) that were not logged for being rather small (larger trees are preferentially logged), for a lack of commercial demand, or for safety reasons (e.g., crowns covered with lianas). However, trees with rotten stems, for which rotting was discovered only at logging, will still present rotten stems in the next round and not be available. Despite using the most realistic estimates of logging intensities, our simulations probably overestimate the number of available trees in future logging cycles. Although yields increase when applying realistic field-based intensities with realistic growth trajectories from tree-rings, our results still suggest moderate to strong declines in available timber under common logging practices.

Declining yields are in line with other studies (summarized in Putz et al., 2012), and are considered almost inevitable, as the remaining trees cannot grow back the volume accumulated over many decades within current (or reasonable) logging cycle length of several decades. For our study species, this volume of timber from old trees, also called the ‘primary forests premium’ (cf. Keller et al., 2007), had been accumulated during >50 years (Fig. 6). Species-specific yield declines from first to second harvest may thus be inevitable, but it is essential to avoid forest-level overexploitation of timber resources. Smaller species-level yields should thus not lead to unsustainable forest use, i.e., to the conversion of forests to other land-uses. Increasing logging cycle lengths or minimum cutting diameters (MCD), or decreasing logging intensities, are measures that can ensure a more sustainable forest use. However, increasing logging cycle lengths requires long-term investments, which are hampered by the unstable politico-economical environments in many tropical countries. Increasing the MCD or reducing logging intensities – while maintaining logging cycle length – are then more viable options. Lower than maximum field-based intensities raises hope for sustainable exploitation as future yields projections increased remarkably for these species (up to 73% of initial volume was recuperated). The lower field-based intensities imply that the primary forest premium is ‘spread’ over subsequent logging cycles, increasing the long-term financial viability of timber exploitation. Nonetheless, timber exploitation usually focusses on only a handful of these high-value species (Holmes et al., 2002; Ruiz-Pérez et al., 2005), and we expect that for most of these species logging intensities are consistently high. For *E. utile* – the species with the highest commercial value – actual intensities resembled maximum allowed intensities, with subsequent low predicted yields. For species with high value but low abundances, increasing MCD is then crucial to avoid overexploitation, and the high MCDs for *Entandrophragma* spp. in Cameroon (80–100 cm; TRC 2009) is already an important sylvicultural measure to protect overexploitation.

4.5. Outlook and recommendations

Is the sustainable exploitation of tropical timber resources possible? A bleak picture of low future timber yields appears when comparing timber volumes extracted from the same species between the first and second harvest. Yet, we believe that the focus of attaining sustainability should be ensuring long-term forest-level financial viability of timber exploitation, which goes beyond the second harvest (Zarin et al., 2007) and should include the options to harvest other species. Next, we suggest some measures that support such forest-level sustainable exploitation and recommend steps to improve the monitoring and evaluation of timber exploitation.

Increasing the number of species exploited while lowering logging intensities on the most exploited species is a fundamental step to avoid the overexploitation of timber resources (Putz et al., 2012). Measures to stimulate the use of ‘lesser known species’ are thus highly encouraged (e.g., ITTO, 1990). Silvicultural measures should be executed to enhance the growth rates and successful establishment of the exploited species, especially of high-value timber species. Possibilities include: thinning of the forest after logging (Gourlet-Fleury et al., 2013), liberating future crop trees from lianas and competition (Peña-Claros et al., 2008), enrichment planting or tending of natural regeneration (Doucet et al., 2009; Schwartz et al., 2013). Long-term monitoring is required to evaluate the effectiveness and economic viability of these measures (e.g., Peña-Claros et al., 2008; Gourlet-Fleury et al., 2013) as costs may be high (Mostacedo and Fredericksen, 1999).

Monitoring and evaluating the consequences of timber exploitation is key to ensure a sustainable exploitation of forest resources. Ultimately, many factors drive species-specific future yields: length of the cutting cycle, MCD, logging intensities, local abundances, diameter distribution, and growth and mortality rates. The complexity of factors ultimately requires flexible and adaptive forest management systems, ideally basing decisions of logging intensities and MCDs on local and species-specific vital rates. Yield simulations, as presented here, based on field data that contains variation between individuals and species, are a strong tool to assess the sustainability of timber exploitation. Yet, the accuracy of these simulations depends on accurate input data: growth rates, inventory data and estimations of recruitment and mortality rates. Tree-ring data provide a long-term perspective on tree growth, but there is a pressing need for high-quality and long-term monitoring of all consequences of logging activities on tropical forests (e.g., Peña-Claros et al., 2008; Gourlet-Fleury et al., 2013). Ideally, such evaluations should also incorporate the effects of logging on the regeneration, mortality and growth rates of a tree species (e.g., Verwer et al., 2008; Free et al., 2014; Grogan et al., 2014), for instance by using demographic models (e.g., Zuidema et al., 2010) to incorporate these factors in projections of future timber yields. A shared database of tree vital rate data – growth, recruitment, survival – can provide a leap forward in simulating the consequences of logging. Also, we believe that such data should be made available for forest managers and conservation biologists as soon as possible, as relevant forest management decisions can only be taken using actual, field-based data.

Selectively logged forests retain important environmental values, such as high levels of biodiversity (Berry et al., 2010) and the storage of carbon (Sist et al., 2014). The sustainable use of this natural resource is thus key to conserving the value of tropical for-

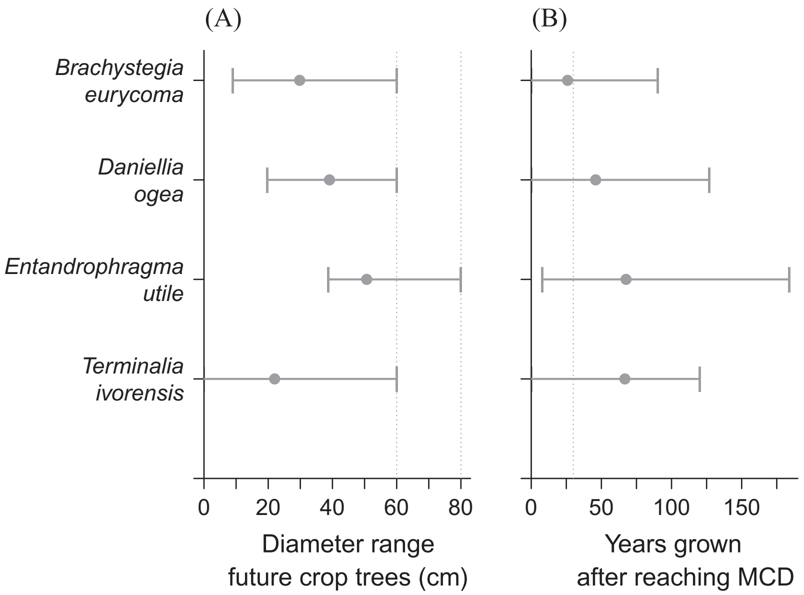

Fig. 6. (A) Diameter range of future crop trees for four timber species from Southwest Cameroon, based on tree-ring analysis. Shown are the ranges and average (dot) diameters of trees 30 years before reaching the Minimum Cutting Diameter (MCD), dashed lines indicate MCDs (80 cm for *E. utile* and 60 cm for other species) (B) Number of years trees have grown between reaching MCD and being logged, dashed line indicate the standard 30-year logging cycle length used in Cameroon.

ests in the future (Edwards et al., 2011). With proper monitoring and financial stimuli, such as higher prices for 'sustainably' logged timber (Meijaard et al., 2005) and payments for ecosystem services, e.g., carbon-offset schemes (e.g., under REDD+; Loarie et al., 2009; Sasaki et al., 2016) tropical forest exploitation can be stimulated and may be sustainable, both financially and ecologically.

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