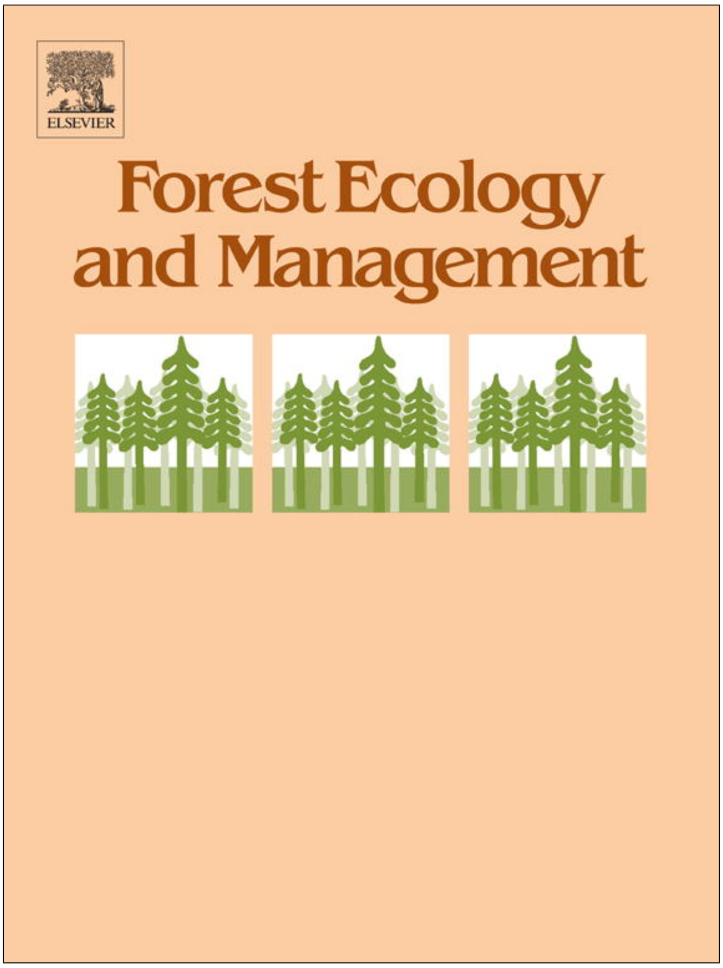
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Tree-ring analysis of an African long-lived pioneer species as a tool for sustainable forest management

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ABSTRACT

Improved forest management in the tropics is hampered by the limited availability of quantitative data, especially in tropical Africa. Important management parameters such as the minimum logging diameter (MLD), the associated biological rotation age (BRA) and the timing of silvicultural treatments are too often based on merchantable dimensions and state regulations instead of ecological data and tree growth. This study combines inventory data and bootstrapped tree-ring curves of natural and planted trees of the long-lived pioneer species *Terminalia superba* Engl. & Diels. A growth-oriented MLD was calculated, and the need and timing of silvicultural treatments was estimated based on the analysis of growth releases and suppressions. Study sites were situated in the Congolese Mayombe forest and western Ivory Coast. Tree rings from 41 natural forest trees (stem discs) and 29 plantation trees (increment cores) were measured, along with diameter and height measurements. Planted and natural forests showed considerable differences in mean growth rate and growth curves. More than 50% of the trees nevertheless reached the canopy without growth releases or suppressions, confirming that *T. superba* does not require intensive management. The growth-oriented MLD not only differs considerably between sites but bootstrapping revealed large differences within forest regions/types. Furthermore, volume-based MLD and BRA are on average larger than basal area-based calculations. The modified monocyclic management system is suggested, especially for planted forests with light-demanding, fast-growing tree species. One small-scale thinning during the juvenile phase is recommended before a final harvest that includes all trees above the growth-oriented MLD. The introduction of sustainable management for *T. superba* therefore primarily depends on forest type and cannot be generalized at the species level.

1. Introduction

Tropical forests hold about half of the world's terrestrial biomass (Pan et al., 2011). These forests need to be managed properly if they are to supply the necessary resources in addition to performing their social and ecological functions. These functions should be described and well-balanced in management plans. This is a complicated task, especially in the tropics, where complex forest structures (Whitmore, 1990), increasing human pressure (Iloweka, 2004), and a lack of systemic research are common. Moreover, every year millions of hectares of tropical forest are lost or seriously degraded. Although the amount of sustainably managed forest increased slightly worldwide between 2005 and 2010 and even tripled in Africa, these forests only account for less than 8% of the world's forests area (Blaser et al., 2011). Successful sustainable management depends on the collection of quantitative data. This study will focus on one of the main elements within the framework of sustainable management – sustained yield – in keeping with the principle that log removal should not exceed the capacity of the growing population to replace the removed tree volume (Sands, 2005).

Timing of log removal should mostly be based on the biological rotation age (BRA) and the adjoined minimum logging diameter (MLD). Governments, scientists, and others define the MLD differently. Legally, the MLD is mostly defined as the minimum diameter cutting limit for tree species. This means that the MLD is not calculated, but fixed by national regulations and/or set at values that coincide with merchantable wood volumes (Sist et al., 2003; Schöngart, 2008). From a scientific point of view, the MLD is calculated based on tree growth. For example, Junk et al. (2011) defined the MLD in the Amazonian floodplain forests as the diameter at the age of maximum current volume increment rates. This study follows Philip (1994) and Rondeux (1999), who define the optimum MLD as the diameter at the age of maximum mean volume or basal-area increment rates. This age of maximum mean increment rates corresponds with the BRA.

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Both volume and basal-area based calculations depend on tree growth data, collected periodically in permanent sample plots (PSPs) or during one inventory with extraction of stem discs or increment cores for tree-ring analysis. Although tree rings are not always easy to distinguish in the tropics (Schweingruber, 1988), they have proven to be a reliable management tool (Baker et al., 2005; Schöngart et al., 2007; Schöngart, 2008). Because of the frequent occurrence of tree-ring anomalies, Brienen and Zuidema (2005) recommend the use of stem discs for tree-ring analysis. Sampling stem discs is not only destructive, it is also difficult, because logging in the tropics is not straightforward. This mostly results in small sample sizes with large variability in growth rate. Computer simulations such as bootstrapping (Efron, 1979; Brienen et al., 2006; Rozendaal et al., 2010) are useful tools to counter such variability and make a more reliable estimate of the MLD.

The definition of sustainable forest management nevertheless involves more than the calculation of annual allowable cut and the calculation of the MLD (Sist et al., 2003). Silvicultural treatments often improve diameter/volume increments (Peña-Claros et al., 2008; Villegas et al., 2009), but the timing and number of these treatments is usually only based on experimental modelling and national regulations. Again, tree-ring data can be used to, e.g., calculate and study the presence and frequency of so-called growth releases and suppressions. The definition of these major changes in growth rates is based on the percentage of growth change, with thresholds for growth releases and suppressions (Nowacki and Abrams, 1997; Brienen and Zuidema, 2006). Those releases and suppressions mark critical moments in the trees' lifespan (Baker et al., 2005; Brienen and Zuidema, 2006) when management could influence the growth of trees positively.

This study explores the use of combined growth data from a forest inventory and tree-ring analysis to formulate recommendations for sustainable management of West and Central African forests. The studied tree species is the long-lived pioneer *Terminalia superba* Engl. & Diels. This species has a vast natural distribution area, stretching from Sierra Leone to Angola (Groulez and Wood, 1985). Due to its fast growth, straight stems, and high commercial heights (Groulez and Wood, 1985), large plantations were installed in the Democratic Republic of Congo (DRC) beginning in 1948. *T. superba* is listed by the International Tropical Timber Organisation (ITTO) as one of the major tropical species traded and is used for, among other things, interior joinery, furniture, veneer, and plywood (Groulez and Wood, 1985). The presence of distinct annual tree rings in Central and West Africa (Mariaux, 1969; De Ridder et al., 2013) allows us to raise the following research questions:

(1) Is it possible to suggest silvicultural treatments based on tree-ring patterns of a long-lived pioneer species? If so, can the need and the timing of these treatments be determined based on the analysis of growth releases and suppressions?
(2) How do MLD and BRA vary within and between sample sites? Is it possible to define one MLD for all forest regions/types, similar to current regulations?
(3) Combining the results of the first two research questions, is there an important difference in the management of a planted or a natural forest? In other words, does the introduction of sustainable management with silvicultural treatments and a final harvest based on MLD/BRA depend on forest region/type or can it be generalised at the species level?

2. Material and methods

2.1. Study sites

All study sites belong to the Guineo–Congolian regional centre of endemism (White, 1983). The Ivorian study sites are part of the evergreen moist rainforest. The Congolese study sites are situated within a drier semi-evergreen rainforest. A map with detailed information is available in De Ridder et al. (2013).

The three Congolese study sites are situated on the southern border of the Mayombe Forest, which covers the western parts of Gabon, the Republic of Congo, the DRC and Cabinda (Angola). Two study sites were chosen within the Luki Biosphere Reserve (05°30′ to 05°45′S and 13°07′ to 13°15′E). The first study site in Luki is a natural forest stand; the second is located in Monzi, 15 km away, in a *T. superba* plantation established between 1955 and 1957. Plantations were installed at planting distances of 8×12 m and no structured management was carried out (De Ridder et al., 2010). A third study site was selected in a natural forest stand in Tshela, about 70 km to the north. All study sites were situated at altitudes below 300 m above sea level. The average annual precipitation, based on precipitation data from the Luki climate station from 1959 to 1996, is 1168 mm, but some years are particularly dry. The region is characterised by a dry season of 4–5 months (May to September–October) and a short period with less precipitation (January–February). The proximity of the ocean and the associated high relative humidity likely buffer the intensity of the dry season. Temperatures oscillate around 26 °C in the rainy season and drop to a minimum of 20 °C in the dry season. The soils of the Luki Reserve are classified as orthic Ferralsols, while Tshela is characterised by ferric Acrisols (FAO, 2008). Most soils are argillaceous, with a pH of between 4 and 6 and a C/N of between 4 and 9.

In western Ivory Coast (06°07′ to 07°15′N, 07°30′ to 08°15′W), four study sites are situated in natural forests (mostly secondary forests), some of them more than 100 km apart. Study sites were situated between 200 and 370 m above sea level. The average annual precipitation, based on precipitation data from six climate stations from 1959 to 1996, is 1650 mm. In this region, the dry season generally lasts for 3 months (December to February). In July and August, a period of less precipitation is observed. Relative humidity drops about 20% in the dry season. Annual mean temperature is 25 °C, with a minimum of 18 °C in January and a maximum of 33 °C in February/March (Van Oldenborgh and Burgers, 2005). Soils have a pH of between 4 and 7 and a C/N of 8–12, and are classified as Ferralsols and Acrisols, i.e., typical acid soils for tropical lowlands (FAO, 1986).

2.2. Sampling and tree-ring analysis

Stem discs and increment cores were collected for tree-ring analysis. In natural forests, a total of 12 stem discs from the Mayombe and 29 stem discs from western Ivory Coast were sampled. Trees' stem height (until the first branch) and diameter were measured in the natural forests. In the plantations of the Mayombe, two perpendicular increment cores were taken per tree, but no stem height or diameter measurements are available. Tree rings were measured on 60 plantation trees. All samples were air dried to prevent fungal infestation, and increment cores were frozen for 2 weeks to prevent insect infestation. Stem discs were too large for freezing and therefore only superficially disinfected before storage in the Tervuren Xylarium. All discs and cores were sanded with grits increasing gradually from 50 to 600 or 1200.

The procedure for tree-ring measurements is described in detail in De Ridder et al. 2013). Ring widths were measured to the nearest 0.01 mm using a stereo-microscope and a Lintab measuring device with TSAP-Win software (Rinn, 2003). Approximate age is therefore known for the sampled trees, in addition to diameter. For increment cores without pith, it is better to use the number of rings than approximate age. Missing pith was not corrected for due to many samples with pith eccentricity and large variations in juvenile ring-widths. The time necessary to grow to the sampling height is not taken into account. Therefore, tree ages are slightly underestimated.

2.3. Analysis of growth changes

Basal-area growth rather than diameter growth was used to calculate growth events, as *T. superba* has a known age trend, especially in plantations (De Ridder et al., 2013). Based on the tree-ring data, the percentage of growth change was calculated with Nowacki and Abrams's formula (1997):

$$GC_i = [(M_2 - M_1)/M_1] \times 100 \quad (1)$$

where GC_i is the percentage of growth change for year i, M_1 the preceding 10-year mean basal-area growth (including the year of change) and M_2 is the subsequent 10-year mean basal-area growth. For example, for GC_{1979}: M_1 is the mean from 1970 to 1979, whereas the mean for M_2 is from 1980 to 1989. Brienen and Zuidema (2006) defined a growth release as a growth increase of more than 100%, and a growth suppression as a growth decrease of at least 50%. A growth release lasting for at least 5 years is regarded as sustained. Growth changes were calculated for individual trees and the mean growth curves for the forest regions/types. In classical dendrochronology, tree-ring series are synchronised by calendar date. To answer the current research questions, however, mean growth curves for each forest region/type were constructed by synchronising individual tree-ring series by age. The patterns of canopy accession presented by Brienen and Zuidema (2006) were used to classify all sample trees:

- 'No (sustained) release'. Canopy accession occurred without major growth changes. A slight growth release (<5 years) is allowed and this pattern is often found in trees where light since seedling stage was never limited.
- 'One sustained release'. At least one growth release (>5 years or preceded by a growth suppression) is distinguished, due to, e.g., a gap in the canopy.
- 'One suppression'. Trees reach the canopy after one growth suppression. Usually, this type of tree has fast initial growth, followed by a strong growth decrease.
- 'Multiple releases and suppressions'. Canopy accession takes place after several growth releases and suppressions. Successful growth into the canopy involves repeated growth shifts, probably due to canopy dynamics.

Canopy accession is secured because long-lived heliophilous species such as *T. superba* are known for their strong growth towards the light, and are usually part of the main canopy (pers. obs.). The proportion of trees belonging to each of these patterns is calculated for each forest region/type. Also the age, the year in which, and the diameter at which the growth releases/suppressions take place, is recorded. Precipitation (Van Oldenborgh and Burgers, 2005; De Ridder et al., 2013) in years with growth releases/suppressions is compared with precipitation in years without such major growth changes to check whether the influence of climate can be neglected, as stated by Nowacki and Abrams (1997), using the 10-year time spans for the calculation of growth releases/suppressions.

2.4. Minimum logging diameter (MLD) and biological rotation age (BRA)

The MLD represents the diameter at which maximum mean annual growth increment occurs (Philip, 1994; Rondeux, 1999). In this study, maximum annual increments of basal area and volume were calculated (Fig. 1) and the resulting MLDs were compared for the different forest regions/types.

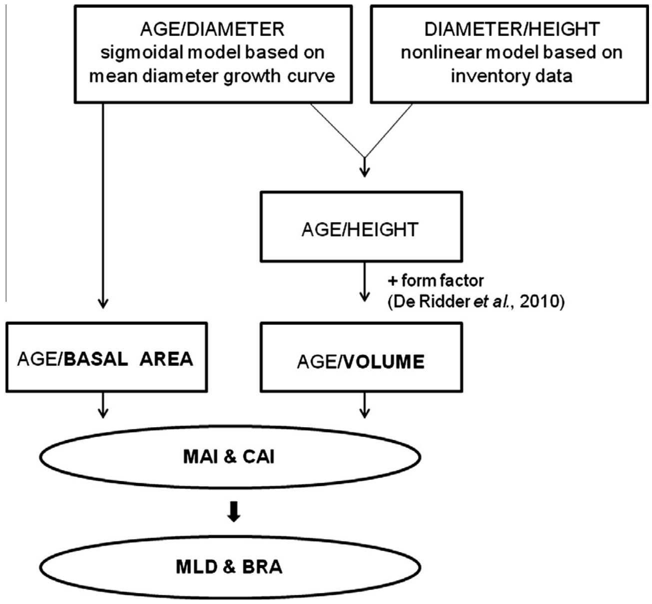

Fig. 1. Flowchart illustrating the calculation of the minimum logging diameter (MLD) and the biological rotation age (BRA), based on maximum annual increments of basal area and volume. MAI: mean annual increment and CAI: current annual increment.

The general procedure described by Philip (1994), Rondeux (1999), and Schöngart (2008) was applied for the MLD based on maximum annual volume increments. A sigmoidal nonlinear regression was fitted to the mean diameter growth curve (age–diameter) of the Mayombe plantations as well as the natural forests of Ivory Coast and the Mayombe (Verhulst, 1838; Schöngart et al., 2007; Schöngart, 2008), whereas a nonlinear regression was fitted to the diameter–height data (Schöngart et al., 2007; Schöngart, 2008). The volume at each age was then calculated as the product of basal area, stem height, and a fixed form factor, previously published in De Ridder et al. (2010). From the cumulative volume growth (CG_V), the current (CAI_V) and mean annual volume increment (MAI_V) were calculated (Philip, 1994; Rondeux, 1999):

$$CAI_V = CG_{V(t+1)} - CG_{V(t)} \quad (2)$$

$$MAI_V = CG_{V(t)}/t \quad (3)$$

An optimal volume production of the tree is found at the intersection of the CAI_V and MAI_V-curves, coinciding with the optimum MAI_V. The age at which the peak in MAI_V occurs corresponds with a specific diameter on the modelled mean diameter growth curve, i.e. the minimum diameter limit for optimal exploitation rates or the MLD. In addition to the optimal volume growth, CAIs and MAIs can also be calculated (Eqs. (2) and (3)) for basal area (Philip, 1994; Rondeux, 1999).

Abovementioned procedure for calculation of MLD/BRA based on actual datasets, was repeated for bootstrapped growth curves. The bootstrap procedure as described in Brienen et al. (2006) was implemented in Matlab® (version R2011a). In total 1000 MLDs were calculated, each based on a set of simulated growth curves equal to the original amount of measured growth curves. Growth curves were simulated in 5 year intervals, as such including total autocorrelation. The mean growth curve of each forest region/type thus is simulated a 1000 times. MAIs and CAIs of volume and basal area were calculated on these simulated growth curves and histograms of MLD/BRA values are generated. The method of Brienen et al. (2006) was slightly modified by implementing continuous random sampling of the growth rate, in between the minimum and maximum growth rate found within a growth class, instead of using the measured values. Diameters were truncated at 60 cm for calculations of MLD/BRA in the natural and planted Mayombe trees. A maximum age of 40 year in the plantations and 50 years in all natural forests was used as older trees were rare and are given too much importance at higher ages, especially regarding the specific growth of the sampled trees.

3. Results

3.1. Growth characteristics of natural and planted T. superba

In both forest regions/types, tree ring analyses were successful (De Ridder et al., 2013). A concise summary of the growth characteristics can be found in Table 1. All study regions had normally distributed diameters ($p > 0.05$). The diameter distribution of the natural forests approximately followed a negative exponential curve whereas the diameter distribution of plantations followed a more Gaussian curve, as expected for natural and planted forests.

Comparing the mean diameter growth of the three study regions, the natural forest Mayombe trees grow significantly faster than the plantation trees and the natural forest Ivorian trees ($p < 0.01$) (Table 1). However, until the age of approx. 25 years, tree growth appears high and similar in Ivory Coast and the natural Mayombe forest but significantly higher than in the plantation ($p < 0.01$) (Fig. 2). Mean diameter growth after 40 years is still lower in the plantations but the differences are no longer significant. Mean diameter growth curves of bootstrapped simulations are very similar to the original mean diameter growth curves in the Mayombe. Only in Ivory Coast, diameter growth seems slightly overestimated until 25 years but quite underestimated afterwards (Fig. 2).

The individual diameter growth curves (Fig. 3) show that the variability in growth is high, especially in the Ivorian trees and in the Mayombe plantations. No difference is found between the two natural forests, based on the individual diameter growth curves. In the plantation, however, two separate groups are noticed (Fig. 3c): trees with diameters smaller or larger than 30 cm. The smaller diameters are significantly younger than the larger diameters (34 years versus 43 years, $p < 0.05$). Also, the larger trees grow significantly faster than the smaller trees ($p < 0.001$).

Mean diameter growth and age show negative correlations for natural forests whereas positive correlations characterise the plantation (Table 2). The same is true for mean diameter growth and diameter relations.

3.2. Analysis of growth changes

At the individual tree level, the canopy accession pattern 'no sustained release' is found in more than 50% of all trees, independent of the forest region/type (Fig. 4). The second most important

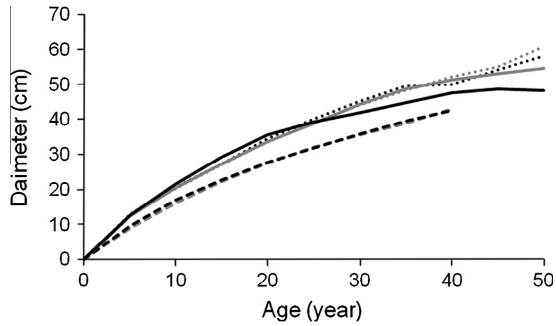

Fig. 2. Mean diameter growth curves for the natural forest of Ivory Coast (solid line), the natural forest of the Mayombe (dotted line) and the plantation of the Mayombe (dashed line). Diameter growth curves were truncated at 60 cm in the Mayombe, and at 50 years for natural and 40 years for planted forests. The equivalent bootstrapped mean growth curves are shown in grey.

canopy accession patterns is 'one sustained release', found in 20–25% of the natural trees, whereas growth suppressions are more frequent in planted forests (ca. 20%). At the forest region/type level, no growth releases/suppressions were found in the mean basal-area growth curves.

Trees without growth releases/suppressions or one suppression reached the canopy on average after 18 years. Trees with one release or multiple releases and/or suppressions reached this diameter significantly later, after 25–30 years. Trees with the most abundant accession pattern (no sustained release) are significantly younger (40 compared to 54 years) and faster-growing (1.33 compared to 0.99 cm year^{-1}) than the trees with other accession patterns ($p < 0.05$). Trees with one suppression are older (44 years) and slower-growing (1.03 year^{-1}) than trees without major growth changes but only the difference in growth rate is significant.

Growth suppressions were not related to one principal diameter or age class (data not shown) when based on basal-area increments. In all three forest regions/types, growth releases occurred mostly between 10 and 20 year and between 10 and 30 cm (Fig. 5a and b).

In the plantations, the longest growth releases were found in the 1970s and the longest growth suppressions from 1993 to 1997. In Ivorian natural forests, growth releases were longest during 1974–1986. Natural Mayombe trees did not have a sufficient number of growth releases and suppressions to distinguish peak periods for growth releases and suppressions.

3.3. Minimum logging diameter (MLD) and biological rotation age (BRA)

Diameter and stem height of Ivorian trees showed no relation (Table 2) and could not be modelled. Therefore, in Ivory

Table 1
Growth characteristics of the natural forest in western Ivory Coast, the natural forest of the Mayombe, and the plantation in the Mayombe based on the original growth data.

	Natural forest Ivory Coast	Natural forest Mayombe	Plantation Mayombe
Number of samples with distinct tree rings	29	12	29
Mean diameter (cm)	56 ± 11	57 ± 15	41 ± 12[b]
Mean stem height (m)[c]	17 ± 8 (19)	23 ± 2 (7)	No data
Mean age (years)	55 ± 43[a]	47 ± 38	40 ± 6
Mean diameter growth (cm year^{-1})[d]	0.70 ± 0.27 (114)	1.32 ± 0.42 (50)	1.09 ± 0.52 (49)
Mean diameter growth first 25 years (cm year^{-1})	1.58 ± 0.41	1.61 ± 0.30	1.27 ± 0.34
Mean diameter growth first 40 years (cm year^{-1})	1.21 ± 0.31	1.24 ± 0.19	1.15 ± 0.16

[a] The number of tree rings was estimated for three stem discs with unclear, degraded or rotten rings around the pith.
[b] The mean diameter was reconstructed from the increment cores.
[c] Between brackets is the number of sampled trees.
[d] This is the mean diameter growth derived from the mean diameter growth curve, of which the length in years is given between brackets.

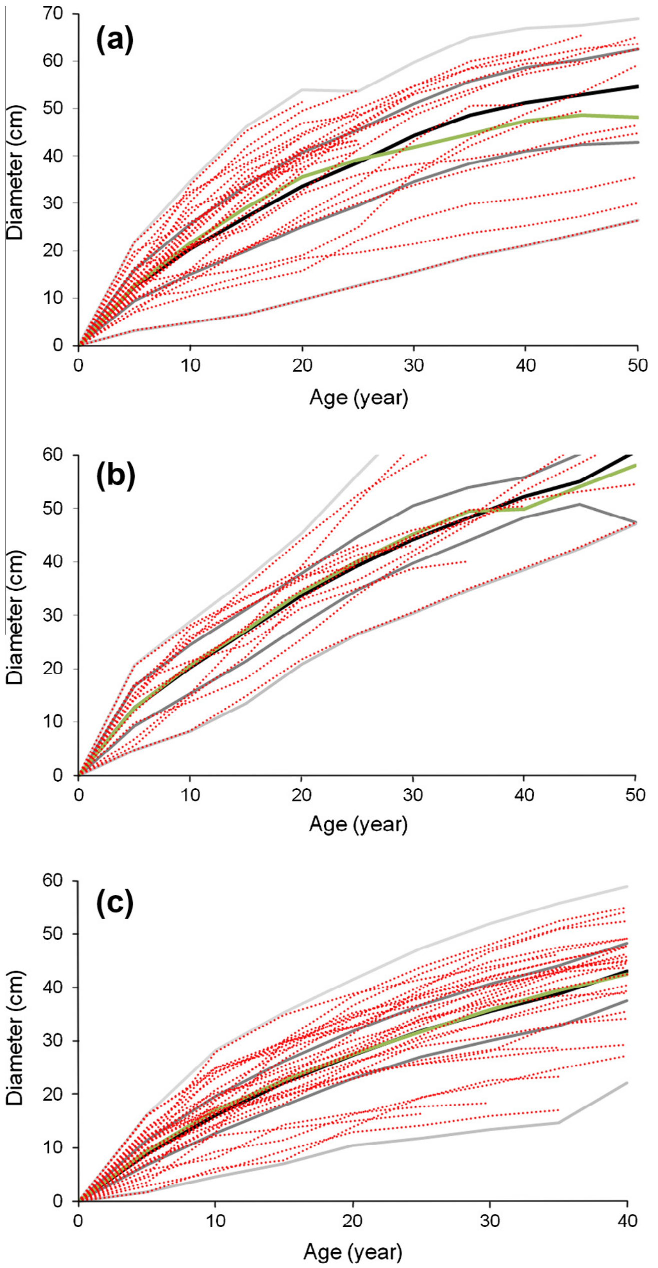

Fig. 3. Individual diameter growth curves for the three study regions with (a) the natural forest in Ivory Coast, (b) the natural forest in the Mayombe, and (c) the plantation in the Mayombe. The dotted red lines are the original individual growth curves, the green solid line is the mean growth curve based on the these individual growth curves and the black line is the mean growth curve based on bootstrapped simulations. The two light grey lines delimit the range of all simulations and the two dark grey lines delimit the range of the mean growth curves based on a set of simulations equal to the amount of original individual growth curves available (1000 mean growth curves, each based on a subset of simulations).

Coast, the volume based MLD was not calculated. For the natural and planted forests of the Mayombe such a regression was possible ($R^2 \geqslant 0.37$, $p < 0.01$). For the plantations without height measurements, the diameter-height regression from a large plantation inventory of *T. superba* by De Ridder et al. (2010) was used.

Based on actual and simulated growth curves, the optimum MAI_V and MAI_{BA} of the Mayombe plantations is lower than in natural forests (Fig. 6) and this optimum is reached about 15 years

Table 2
Correlations of age, diameter, height, and mean diameter growth. Mean diameter growth is defined as twice the mean tree-ring width of the tree-ring series. The number of samples included in the Pearson correlation is given between brackets.

	Natural forest Ivory Coast	Natural forest Mayombe	Plantation Mayombe
Diameter–height	−0.05 (19)	0.79* (7)	No data
Age–diameter	0.70*** (29)	0.34 (12)	0.77*** (29)
Age–mean diameter growth	−0.78*** (29)	−0.78** (12)	0.36 (29)
Diameter–mean diameter growth	−0.60*** (29)	−0.29 (12)	0.87*** (29)

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

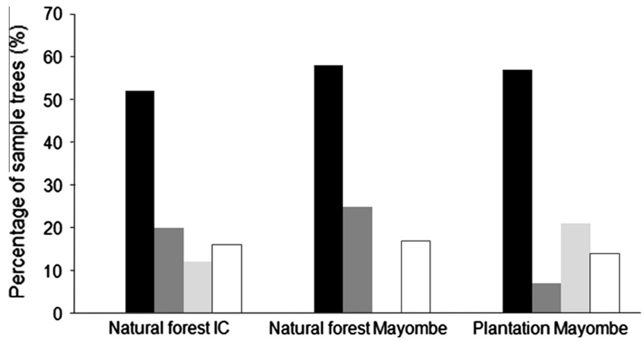

Fig. 4. Percentage of accession patterns, based on basal-area increments. Black bars represent 'no sustained releases', dark grey bars represent 'one sustained release', light grey bars represent 'one suppression', and white bars represent 'multiple releases and suppressions'.

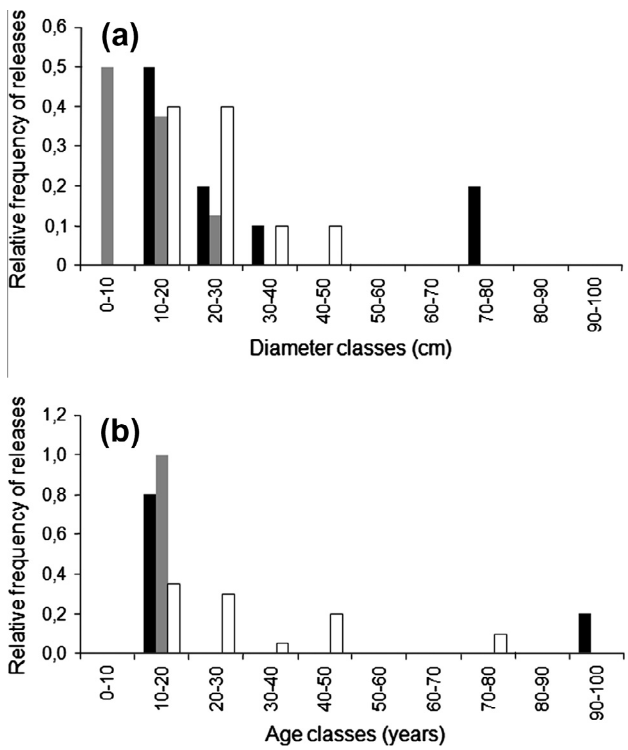

Fig. 5. Relative number of growth releases (%) compared to the total number of trees/region: (a) for diameter classes, (b) for age classes based on basal-area increments, in the three forest regions/types. Black bars represent the natural Mayombe forest, grey bars the plantation in the Mayombe, and white bars the natural forest in Ivory Coast.

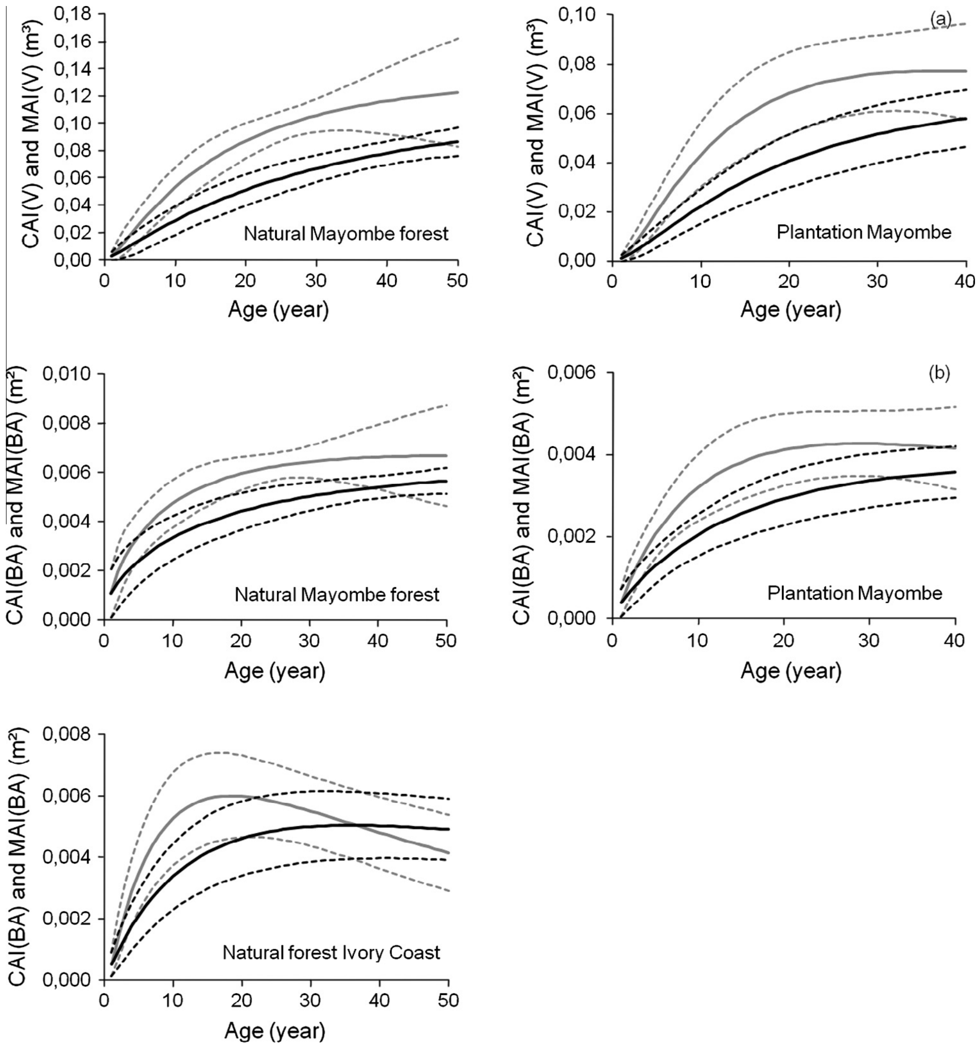

Fig. 6. Current (CAI: grey line) and mean (MAI: black line) annual increments of bootstrapped data and 95% confidence intervals (dashed lines) for the three forest types/regions. Based on (a) volume, graphs were calculated for natural and planted Mayombe forests. Based on (b) basal area, graphs were calculated for natural Mayombe forest, planted Mayombe forest, and Ivorian natural forest.

later in plantations (data not shown). The actual MLDs of plantations and natural forests in the Mayombe appear similar but the distributions of simulated MLDs show considerable differences (Fig. 7): the actual MLD for natural forests is located in the left part of the distribution whereas the actual MLD for the plantations is located near the maximum of the distribution. In general, the MLD and BRA of natural forests associated with the optimum MAI_{BA} result in lower values than those associated with the optimum MAI_V. Ivorian trees had the lowest MLDs and shortest BRAs, based on basal area calculations. In the latter case, the calculated MLD differed clearly from the distribution of MLDs.

The actual MLD of natural Mayombe trees based on volume is found beyond the actual dataset but extrapolations are small. The actual BRA of natural and planted forests of the Mayombe is also found at ages higher than 40 or 50 years but all values are part of the distribution of simulated BRAs. Histograms of the BRAs are not shown in Fig. 7 because the distributions are similar to those of the MLDs.

Some simulations of growth curves did not lead to a logical MLD/BRA (values <10 cm or years and values >200 cm or years). The percentage of inconclusive simulations was about 25% in natural Mayombe forests and about 7% in planted Mayombe forests. All simulations lead to logical MLDs/BRAs in Ivory Coast.

4. Discussion

4.1. Analysis of temporal growth patterns

Pioneer species such as *T. superba* often have a known and strong age trend, especially in planted forests (De Ridder et al., 2013). Ring widths are subject to a decrease over time, even when approximately the same cross-sectional area of wood is added (Stan and Daniels, 2010). Because of this size-related trend, the M_1 values were relatively larger for smaller diameter trees when ring widths as opposed to basal-area increments were used. Stan and Daniels (2010) concluded that the calculation of growth releases/suppressions with basal-area increments was more appropriate for sites with large inter- and intra-species variability in tree size, similar to the variability in our forest regions/types.

Generally, at tree level, the canopy accession pattern of 'no sustained release' is most abundant and can be linked to the light-demanding and fast-growing character of the tree species (Brienen and Zuidema, 2006). More than half of the planted and natural *T. superba* trees reached the canopy without suppressions or releases, suggesting that competition for light was not a significant problem. In closed moist forests with (non-pioneer) shade-tolerant species, releases are mostly recorded (Simkin and Baker, 2008). Our study

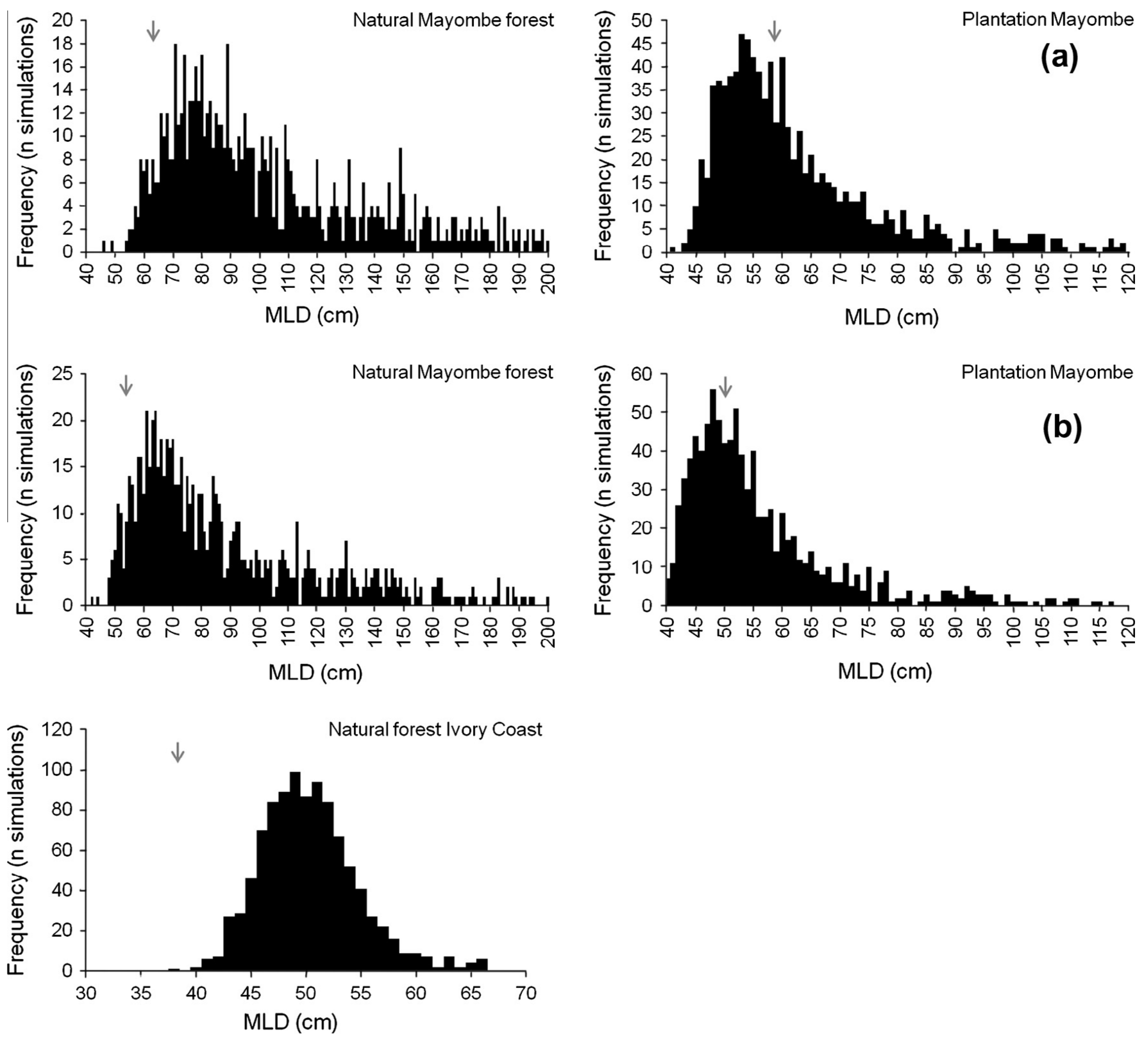

Fig. 7. Histograms of minimum logging diameters (MLDs) based on (a) volume and (b) basal area. The arrow indicates the value of the MLDs based on the original sample dataset.

found growth releases mostly take place during the juvenile phase, as did Brienen and Zuidema (2006). They suggested two causes that could also apply for *Terminalia* trees: larger temporal shifts in light levels for trees in the understorey; or, and more likely, weaker responses by large trees to increased light levels. Next, Brienen and Zuidema (2006) also found suppressions in larger trees that could be provoked by, e.g., liana manifestation or forking, two common phenomena observed for *T. superba* trees. Trees with multiple growth releases and/or suppressions were also found, however, so canopy accession patterns differ not only between but also within species, as is reported by Baker and Bunyavejchewin (2006) and Brienen and Zuidema (2006).

Brienen and Zuidema (2006) suggested that trees without major growth changes reached the canopy in the shortest time, and those with multiple releases and suppressions needed the most time. This was true for *T. superba*. Trees that reach the canopy without showing growth releases/suppressions are younger and faster-growing than the trees with other accession patterns. Although trees with growth suppressions reached the canopy after a similar period, they still grew significantly slower than the trees without distinct growth changes. This phenomenon could be linked to the ‘juvenile selection effect’ that Rozendaal et al. (2010) discuss. They define this effect as the higher chance of fast-growing (juvenile) trees to reach the canopy compared with slow-growing (juvenile) trees.

Growth releases and suppressions based on basal-area growth were also calculated for the three mean basal-area growth curves. This reveals that major growth changes only took place on a small scale, not at the site level. Finally, the influence of precipitation on growth releases/suppressions was analysed and no significant relations were found. The methodology of Nowacki and Abrams (1997), who used large timeframes to rule out the influence of climate, appears to be suitable for *T. superba*.

The lower diameter growth rate in the plantations is remarkable, even if we compare with the bootstrapped mean growth curves (data not shown). Based on the sample trees, the correlations between mean diameter growth and age/diameter show opposite signs for planted and natural forests (Table 2). This is probably caused by the ‘reversed’ patterns of diameter growth rates over time: plantation trees grow slowly during the juvenile phase and have a higher growth rate later on (Table 1), whereas natural forest trees grow quickly during the juvenile phase and slower at older age. Still, not all planted trees had similar growth patterns: evidence is given that fast- and slow-growing trees could be distinguished with a diameter threshold set at 30 cm. This diameter is also known as the diameter at which trees enter the canopy (Clark and Clark, 1999). Although the smaller diameters are significantly younger than the larger diameters, they probably did not regenerate in one specific year below the older trees because the age distribution of the plantations is unimodal Gaussian shape (data not shown). These younger trees clearly tolerated some shade from the larger, older trees. Most likely, planting processes as well as regeneration from old seed trees/replanting played an important role in the stand structure of the plantations. Regeneration under crown cover is rarely met in (long-lived) pioneer species, but Alvarez-Buylla and Martinez-Ramos (1992) also found such natural regeneration of *Cecropia obtusifolia* Bertol., a neotropical pioneer tree.

4.2. Evaluation of the minimum logging diameter (MLD) and biological rotation age (BRA)

One of the most important parameters within the concept of sustained yield is the MLD, a cutting limit that can be calculated based on dendrochronological analysis of tree growth. Although the MLD can also be determined by basal-area increments (Dorado et al., 1997; Verzino et al., 1999; Bogino and Villalba, 2008), studies in the tropics mainly focus on a volume-based MLD (Nebel et al., 2001; Schöngart et al., 2007; Schöngart, 2008; Leoni et al., 2011). Two fundamental conditions for this volume-based MLD are height measurements and the existence of a significant age–diameter and diameter–height relation, as described by Schöngart (2008). Although Metcalf et al. (2009) concluded that size and age were not always associated by using a single parameter, the age–diameter relation was positive in most studies, e.g., Worbes et al. (2003), Baker et al. (2005) and da Fonseca et al. (2009). Our study confirms this positive correlation in the different forest regions/types. However, diameter and height only correlated strongly for the Mayombe plantation and natural forest trees, similar to the results of Leoni et al. (2011) and Worbes et al. (2003).

The use of volume-based CAI and MAI is thus limited by the aforementioned conditions. Height measurements for standing trees are especially prone to large measurement errors (Rondeux, 1999; Chave et al., 2004). There is no need for these measurements if the optimal CAI and MAI of the basal area are used. Basal-area growth was derived from the sigmoidal regression, enabling the calculation of the MLD and BRA for the natural forest in Ivory Coast. The use of a rather limited set of growth curves, however, induces rather large uncertainty on the calculated MLD/BRA, both volume and basal-area based. Therefore, Brienen et al. (2006) developed an original bootstrapping method which was validated on tropical growth curves. Whereas distributions of MLD/BRA are narrow in Ivory Coast and larger in the plantations in the Mayombe, the variation in both values is very large in the natural Mayombe forest, probably due to small sample size (only 12 trees). The sample trees of the different forest regions/types seem nevertheless to be representative for the Mayombe: the generated MLD/BRA histograms show that the mean calculated MLD/BRA is situated within the distribution of simulated MLD/BRA values. Also, there is a high correspondence between the measured and simulated mean growth curve. This correspondence was less clear for Ivory Coast. The 28 trees appear not to be representative for the population and seemingly underestimate the MLD/BRA. Clearly, the influence of growth speed on the MLD calculations is considerable. More individual growth curves are needed at higher age to be able to conclusively decide on the average growth pattern in Ivory Coast.

Generally, the MLDs/BRAs of basal-area based simulations are lower than for volume-based simulations but only small differences are observed in the shape of the distribution of MLDs/BRAs between basal-area and volume-based simulations. Bootstrapping of growth curves as such is useful in tropical forests where sampling is not straightforward and growth variations are usually large. Although the actual MLDs based on a limited dataset can look similar (cf. natural and planted Mayombe forests), the distribution of possible MLDs is quite different for both forest types. Such a mathematical technique however is based on a set of biological principles and depends on the sample trees included and the data limits imposed. Bootstrapping was applied here taking into account certain diameter and age limits. Including the oldest/largest trees, which are actually quite rare too, considerably changes the mean growth curves and the fitted sigmoidal functions that are used to calculate the MAI curves. Also, not all simulations lead to a logical MLD or BRA value, as such pinpointing at the limits of the actual measured tree-ring dataset. Sufficient sampling and thorough knowledge of the actual dataset are essential to cautiously interpret bootstrap results.

The relatively low MLDs and BRAs in Ivory Coast, compared to the natural Mayombe forest, are possibly related to the slightly higher diameter growth during the first two decennia (Fig. 2). The plantations also probably recovered partly after slow growth during the juvenile phase (Table 1, mean diameter growth rates after 25 and 40 years) because BRA is higher but still at a diameter that does not significantly differ from the MLD for natural Mayombe forest.

The growth-oriented MLD/BRA is therefore not only site specific: it can also vary considerably within sites and depends on the growth variable used (volume or basal area). This is in line with the work of Schulze et al. (2008), reporting that a static MLD is not reconcilable with different specific life histories, local population structures, and stem densities.

Nowadays, legal MLD values are static, rather high and often result in increased exploitation (Sist et al., 2003). MLDs are mostly determined by law, whereas BRAs appear less strict. In Liberia and Ghana, the MLD for *T. superba* has been fixed at 70 cm; in Ivory Coast, Gabon, and DRC, at 60 cm. The rotation that is often applied in plantations is 40 years, but under optimum conditions it can be as short as 20–25 years (Kimpouni, 2009). The fixed MLD of 60 cm is part of the simulated range of MLDs for the natural Mayombe forest, although it is located in the left tail of the distribution (Fig. 7). Most of the simulated MLDs for planted Mayombe trees and natural trees in Ivory Coast are smaller than 60 cm, so the legally fixed MLD probably does not lead to overexploitation. The suggested BRA of 40 (Kimpouni, 2009) to 60 years (Humblet, 1946) seems also valid for Ivory Coast and planted Mayombe trees compared with the histograms. Only in the natural forests of the Mayombe it is recommended to use slightly higher BRAs than those suggested (left tail of the distribution).

Finally, the MLD and the associated BRA should also take into account the tree physiology (Sist et al., 2003): the BRA should be larger than the fructification ages of *T. superba*. If trees are being cut earlier, regeneration is hampered. In the Mayombe, fructification takes place from year 23 onwards (Ngueho-Yemele, 2004). In Ivory Coast, fructification is mentioned from the age of 15 years (Ngueho-Yemele, 2004). In all forest regions/types, MAI_V and MAI_{BA} culminate later, thus causing no regeneration problems. Whether MLD/BRA based on volume or basal area is a better choice, with or without bootstrapping, is hard to decide based on this study alone. Based on the calculation of a growth-oriented MLD and knowledge on the forest structure (growth changes), long-term management planning is documented and founded on scientific data.

4.3. Timing and type of silvicultural management

The importance of forest management and the positive influence on growth has previously been demonstrated in Amazonian rainforests (Peña-Claros et al., 2008; Schulze et al., 2008). Long-term growth data are indispensable for such sustainable management plans (Therrell et al., 2007). Not only does tree-ring analysis uncover the behaviour of a long-lived pioneer species, it is especially important to determine the need for and the timing of silvicultural treatments. So far, growth releases/suppressions were not really related to management planning. Brienen and Zuidema (2006) used the growth releases/suppressions in the tropics to evaluate varying growth patterns and age, whereas Baker et al. (2005) used large-scale growth releases/suppressions to study the long-term disturbance history of forests.

Defining one management strategy for natural and planted forests in two distant regions is rather complex because large variations in mean growth rates and growth curves exist between individual trees as well as between different regions/forest types. Still, long-distance relations in growth were found (De Ridder et al., 2013), and, independent of forest type/site, more than half of all planted and natural trees reached the canopy without real growth events.

The theoretical approach for silvicultural treatments in natural and planted forests in the Mayombe and Ivory Coast appears similar. Intensive treatments are not necessary because many trees already reach the canopy at young ages without major growth changes. If treatment is considered, it is preferably recommended in plantations (as production forests) and during the juvenile phase of tree growth because of the 'juvenile selection effect', which has been confirmed using growth releases/suppressions (see Section 4.1). Slow-growing juvenile trees risk remaining slow-growing throughout their lifespans, hampering canopy accession. Two silvicultural treatments can be performed at the same time: removal of lianas, and thinning. In the Mayombe, lianas were a considerable problem in plantations and cutting them could not only avoid forked stems but could also lower the calculated MLD and the associated BRA; a similar effect was mentioned by Nebel et al. (2001). Furthermore, the removal of lianas could reduce the competition for soil water and soil nutrients (Villegas et al., 2009), protect the neighbouring trees, and protect loggers (Putz et al., 2008). Additionally, small-scale thinning of faster-growing trees during the juvenile phase stimulates juvenile growth of slower-growing trees and generates valuable wood volumes for local uses. Herault et al. (2010) confirms that trees with low inherent diameter growth rates benefit the most from gaps, e.g., by thinning. Brienen and Zuidema (2006) as well as Herault et al. (2010) observed that large trees become less dependent on gaps: they intercept more light due to their canopy position. The number of growth releases/suppressions per decade/diameter class also decreases in larger *T. superba* trees. Small-scale thinnings are recommended, as they are completed before the fructification age and regeneration should not be endangered.

There are also other (practical) reasons that support the management of planted *T. superba* forests. First, planted forests are easier to access while trees are still young. Also, the age of trees is generally known, and shows little variation (even-aged forests), enabling foresters to distinguish slow- and fast-growing trees by simply measuring diameters. In natural forests, slower-growing juvenile trees are hard to distinguish from faster-growing juvenile trees because of large variations in growth rates (uneven-aged forests). Small diameters can represent young as well as old trees, and the growth characteristics of other species in natural forests in West and Central Africa are mostly unknown; this makes management planning a lot more laborious.

Thus, even without knowledge on the growth-oriented MLD, it is possible to plan silvicultural treatments based on tree-ring analysis, especially in planted forests. We found different MLDs in different forest regions/types. The Schöngart's modified monocyclic system (2008) for fast-growing, light-demanding tree species could be used in planted forests, with one thinning and a final harvest. This final harvest could remove all trees above the calculated MLD, creating gaps for natural regeneration (Schöngart, 2008). In the natural forests under study, monocyclic systems can be applied for *T. superba* with a MLD/BRA specified per forest region. The structure of natural forests is complex, however, with a wide variety of species and growth patterns, and requires further research.

4.4. Conclusion and perspectives

Tree-ring analysis is a valuable tool for management of natural and planted tropical forests. Growth releases/suppressions based on individual growth curves indicated that *T. superba* does not need intensive management. Only one small-scale thinning needs to be performed in production forests to increase the growth of slower-growing juvenile trees. Actual MLD/BRA values vary considerably among sample sites. Within sites, the range of bootstrapped MLDs varies from 20 cm in the natural Ivorian forest up to 150 cm in natural Mayombe forests. The BRA ranges from 40 years in natural Ivorian forest and 100 years in plantations to more than 200 years in natural Mayombe forest. Based on these results, the introduction of sustainable management can be mainly specified by forest type instead of species level.

Inventories of permanent sample plots (PSP) combined with tree-ring study offer scientists and forest managers the complete picture. Although PSPs are scarce in tropical Africa (Verbeeck et al., 2011), a multitude of variables could be measured periodically, suggesting or evaluating the implementation of silvicultural treatments that promote sustainable management (Peña-Claros et al., 2008; Schulze et al., 2008; Herault et al., 2010). Tree-ring analysis obviously tells the storey of successful trees that survived the seedling stage. Further studies should focus on the germination and mortality rates of seedlings, and their relationship to environmental factors. Regeneration studies are recommended along with enrichment plantings to ameliorate post-logging recovery, which is still poorly documented.

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