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SPECIAL ISSUE PAPER

Enrichment of Central African logged forests with high-value tree species: testing a new approach to regenerating degraded forests

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ABSTRACT
In natural forests of Central Africa, several studies indicate a dramatic decrease in commercial trees, including species of concern for conservation. Enrichment planting with these species will favor both the long-term recovery of their populations and biodiversity conservation in logged forests. In this study, we analyzed the survival and growth of 23 species in plantations. Fourteen 0.2–1.1 ha mixed species plantations consisting of single-species 15 × 15 m blocks were studied for 5 years in a logging concession of southeastern Cameroon. The plantation design considered both species light requirements and sensitivity to damage by pests. To identify the best species for enrichment planting, we assessed both species performance and plantation costs. We also tested for relationships between species traits and species performance. Mean annual diameter growth increments ranged from 1.67 to 42.9 mm. No significant relationship was found between growth and survival. Herbivory by wild Bovidae was the main cause of mortality and should be carefully considered in rehabilitation efforts. We found a significant negative relationship between wood density and maximum growth rate. The other traits tested were not good predictors of species performance in plantations. The two best-performing species, *Triplochiton scleroxylon* and *Terminalia superba*, could reach the minimum cutting diameter during a 30-year cutting cycle. Costs were high and mechanized site preparation is suggested to reduce them. Widespread adoption of such plantations will only occur if financial incentives or national regulations for assuring regeneration are implemented.

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1. Introduction

More than 400 million hectares of tropical forest are designated for timber production. Most of them have been or will be selectively logged. In their meta-analysis, Putz et al. (2012) emphasized that although 85–100% of species of mammals, birds, invertebrates, and plants remain after selective logging, timber volumes decline by about 65% after the first harvest if the same species are again harvested. This depletion of logged species is of growing concern and many commercial species are now listed in the International Union for Conservation of Nature (IUCN) red list (e.g., Bourland et al. 2012). Post-logging silvicultural treatments, including planting of high-value species, would need to be applied in order to reestablish or conserve the timber biodiversity of forest stands. This paper analyzes the survival and growth of such high-value species in simple mixture in plantations in Central Africa.

Central African moist forests cover around 180 million hectares, and 26% of this area is licensed for commercial use by logging companies (De Wasseige et al. 2012). In most countries, logging companies must comply with an updated legal framework, including a detailed management plan based on tree inventories, estimates of recovery rates, planned felling cycles, and site-specific minimum cutting diameters (MCDs) (Bayol & Borie 2004; Fargeot et al. 2004). In the Congo basin, logging is very selective, with only six logged species accounting for 75% of total timber volume (Ruiz Pérez et al. 2005). Timber extraction rates per unit area are low (on average 6 m^3 and less than two trees per hectare), associated damages are about 10%, and vegetation recovery is rather fast (Ruiz Pérez et al. 2005).

In spite of the logging regulatory framework and limited extraction, the continuity of supply of key timber species in Central Africa is in question. Although biomass can recover quickly after logging (i.e., 20 years), regaining exploitable wood volume is much slower (Chazdon 2003). In a long-term study at the M'Baïki silvicultural experiment in the Central African Republic, trees available for exploitation decreased dramatically after a first cutting cycle of 24 years (Gourlet-Fleury et al. 2013). For two important timber species,

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modeling the populations dynamics under a repeated felling regime showed a decrease in exploitable stock linked to decline of the target populations, indicating that the traditional logging regime is far from sustainable (Karsenty & Gourlet-Fleury 2006).

In Central Africa, forest managers face two major issues: (i) the difficulty of recovering the timber stock 20–30 years after logging (i.e., after a complete cutting cycle) and (ii) the lack of regeneration in the pioneer species that make up most of the harvest because of natural decline of their populations with increasing stand age. According to Gourlet-Fleury et al. (2013), reducing the felling intensity or even doubling the length of the cutting cycle will not ensure recovery of these pioneer species, but only hasten their decline due to further natural reductions in regeneration.

Silviculture may help recover timber stock. In a 24-year experiment, Gourlet-Fleury et al. (2013) assessed the effect of thinning (mean of 21 trees thinned ha^{-1}, and 6.6 m^2 ha^{-1} of basal area removed) on forest structure and dynamics. They concluded that thinning combined with logging significantly increased gain in biomass, but it had no effect on gain in timber stock at the end of the first felling cycle. However, these treatments should promote gains in timber stock in subsequent cycles. In the same experiment, Ouédraogo et al. (2011) explained that thinning enhanced the growth and survival of nonpioneer light demanders or shade-bearers, to the detriment of pioneer species.

If thinning fosters the growth of nonpioneer saplings, other techniques are necessary to regenerate pioneer timber species, which probably establish after larger perturbations such as cultivation and subsequent abandonment (Doucet 2003; Van Gemerden et al. 2003; Biwolé et al. 2015). In some areas, late secondary growth rather than pristine forests are indicated by abundant large pioneer tree species such as *Pericopsis elata* and *Triplochiton scleroxylon*, which were included in our study (Gillet & Doucet 2013; Biwolé et al. 2015; Bourland et al. 2015). Management techniques such as enrichment planting have been recommended to promote these species (Fayolle et al. 2014; Ouédraogo et al. 2014).

Planting success was a major preoccupation for foresters in the mid-twentieth century in Africa. Many trials were based on a few or even a single species (e.g., *Khaya* spp., *Tarrietia utilis*, Dupuy & Koua 1993; Dupuy & Chézeaux 1994) sometimes planted on huge areas (e.g., *Aucoumea klaineana* in Gabon, Brunck et al. 1990). In spite of good results, these plantations were abandoned because of labor costs and because management plans were considered sufficient to ensure sustainable forest management. Today, increasing pressure on tropical forests and global concerns about the maintenance of ecosystem services (including timber production, biodiversity, and carbon), again focus attention on yield, and also on restoring biodiversity in production forests (Parrotta et al. 1997). Approaches to restoring tropical forest ecosystems vary depending on the amount of forest and soil degradation, residual vegetation, and desired restoration outcomes (Chazdon 2008).

Stanturf et al. (2014) proposed the term ‘rehabilitation’ for restoring desired species composition, structure, or processes to an existing but degraded ecosystem. There are several methods of rehabilitation including enrichment planting or planting after partial overstory removal. In such planting, species mixtures are desirable for both improving biodiversity and the range of goods and services as well as limiting pest-induced damages (Piotto et al. 2004; Potvin & Gotelli 2008). Different kinds of mixtures exist. Simple mixtures consist of two or more species planted in single-species blocks or rows (Stanturf et al. 2014). Such mixtures are useful on sites with distinct gradients in environmental factors such as drainage or light. Species must thus be selected according to the site conditions (Stanturf et al. 2014).

However, there is little data on site tolerance and growth in Africa as emphasized in the meta-analysis of Piotto (2008). The use of functional traits could help to predict species performance in plantations. Plant functional traits, in particular specific leaf area (SLA), seed size, wood density, and tree height at maturity (H_{max}), are often good predictors of tree growth rates within communities (Poorter et al. 2008). For example, functional traits could predict tree growth and survival in plantings in Mexico (Martínez-Garza et al. 2013). While the relationships may not hold over a broad area, among tree species in a local area, those with high SLA, small seeds, low wood density, and high H_{max} tend to have fast growth rates (Poorter et al. 2008; Paine et al. 2015).

In this study, we test a forest rehabilitation method using simple mixtures of high-value timber species planted after manual removal of the understory in degraded forests in southeastern Cameroon. In 2014, we analyzed the survival and growth of 23 species planted between 2009 and 2012 in 14 mixed-species plots. We addressed the following questions: (i) How do the selected species perform in simple mixtures? (ii) Is it possible to use plant functional traits to select the best candidates for mixed plantation? (iii) What is the cost of these plantations?

2. Methods

2.1. Study area

The study area is located in the province of Eastern Cameroon (between 3°01′ N and 3°44′ N; 13°20′ E and 14°31′ E). The study plantations were established in Forest Management Units 10–041, 10–042, 10–044, 10–039, 10–030, and 10–031, managed by the FSC-certified Pallisco Company. According to Worldclim (2015), annual rainfall is ca. 1640 mm with two distinct rainy seasons (August–November and March–June), and the mean annual temperature is 23.1°C (Hijmans et al. 2005). The topography is undulating with elevation varying between 500 and 650 m. The geological substrate consists of volcanic intrusions and metamorphic rocks, and soils are classified as Ferralsols (Jones et al. 2013). The forest is mostly semi-deciduous and has been classified as *Celtis* forest by Fayolle et al. (2014). It is spatially heterogeneous in species composition and degraded by recent (<50 years) or long-term (>200 years) human disturbances (Morin-Rivat et al. 2014). Due to the lack of regeneration of commercial light-demanding species, enrichment plantings have been recommended for this forest by Fayolle et al. (2014). The host forest company has included enrichment plantings in its environmental policy since 2009 in order to promote the regeneration of the logged species in the framework for certification.

2.2. Study species

We selected 23 high-value species for planting (Table 1), based on their use as high-value timber or nontimber forest products (fruits, edible caterpillars, medicine, etc.). Many of them are considered as threatened by the IUCN (http://:www.iucnredlist.org/), and one is included in CITES Appendix II (*P. elata*, https://www.cites.org/eng/app/appendices.php). We gathered information on qualitative traits (deciduousness, regeneration guild, dispersal) from Hawthorne (1995) and Meunier et al. (2015). We extracted information on quantitative traits from several databases. Seed mass was obtained from Seed Information Database Version 7.1 (available from: http://data.kew.org/sid/). Wood density was extracted from the Dryad global wood density database (Chave et al. 2009; Zanne et al. 2009). Maximum height and diameter were computed from Meunier et al. (2015). If data were not available at the species level, we used the most frequent or mean

Table 1. Characteristics and functional traits of the species used in this study.

Species	Family	IUCN status^1	Main uses	Leaf phénology^2	Guild^3	Dispersal mechanism	Wood density (g·cm^{-3})	D_{max} (m)^4	H_{max} (m)^5	Seed mass (mg)
Afzelia bipindensis Harms	Fabaceae	VU	Timber	De	NPLD	Animal	0.73	1.5	40	**4977**
Amphimas pterocarpoides Harms	Fabaceae	NA	Timber	De	NPLD	Wind	0.66	1	45	
Autranella congolensis (De Wild.) A. Chev.	Sapotaceae	CR	Timber	De	NPLD	Animal	0.78	2	50	NA
Baillonella toxisperma Pierre	Sapotaceae	VU	Timber/fruits/oil	De	NPLD	Animal	0.72	3	60	NA
Bobgunnia fistuloides (Harms) J.H. Kirkbr. & Wiersema	Fabaceae	EN	Timber	Ev	P	Animal	0.87	0.8	25	**96**
Cylicodiscus gabunensis Harms	Fabaceae	NA	Timber	De	P	Wind	0.78	2	60	NA
Detarium macrocarpum Harms	Fabaceae	NA	Timber	De	P	Animal	0.57	1.5	50	**9613**
Distemonanthus benthamianus Baill.	Fabaceae	NA	Timber	De	P	Wind	0.61	1.2	40	NA
Entandrophragma angolense (Welw.) C. DC.	Meliaceae	VU	Timber	De	NPLD	Wind	0.46	1.5	50	376.6
Entandrophragma cylindricum (Sprague) Sprague	Meliaceae	VU	Timber/edible caterpillars	De	NPLD	Wind	0.57	2	60	311.5
Entandrophragma utile (Dawe & Sprague) Sprague	Meliaceae	VU	Timber	De	NPLD	Wind	0.53	2	60	425
Erythrophleum suaveolens (Guill. & Perr.) Brenan	Fabaceae	NA	Timber/edible caterpillars	De	P	Unassisted	0.84	1.5	40	702.2
Khaya anthotheca (Welw.) C. DC.	Meliaceae	VU	Timber	De	NPLD	Wind	0.50	1.5	60	258
Lophira alata Banks ex C. F. Gaertn.	Ochnaceae	VU	Timber/edible caterpillars	De	P	Wind	0.88	1.5	50	1300
Mansonia altissima (A. Chev.) A. Chev.	Sterculiaceae	NA	Timber	De	NPLD	Wind	0.56	0.9	30	322
Milicia excelsa (Welw.) C.C. Berg	Moraceae	NT	Timber	De	P	Animal	0.56	1.5	55	3
Nauclea diderrichii (De Wild. & T. Durand) Merr.	Rubiaceae	VU	Timber	Ev	P	Animal	0.65	1.2	35	1.7
Pericopsis elata (Harms) Meeuwen	Fabaceae	EN	Timber	De	P	Wind	0.64	1.3	40	333
Piptadeniastrum africanum (Hook. f.) Brenan	Fabaceae	NA	Timber	De	NPLD	Wind	0.61	2	60	NA
Pseudospondias microcarpa (A. Rich.) Engl.	Anacardiaceae	NA	Fruits	De	NPLD	Animal	NA	0.6	20	NA
Pterocarpus soyauxii Taub.	Fabaceae	NA	Timber	De	NPLD	Wind	0.66	1.5	50	**531**
Terminalia superba Engl. & Diels	Combretaceae	NA	Timber	De	P	Wind	0.46	1.5	50	95
Triplochiton scleroxylon K. Schum.	Malvaceae	LC	Timber/edible caterpillars	De	P	Wind	0.33	2	50	301.2

Values in bold were calculated at the genus level.

[1] IUCN status: CR, critically endangered; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered.

[2] Deciduousness: De, deciduous; Ev, evergreen.

[3] Guild: P, pioneer; NPLD, nonpioneer light demanding.

[4] Maximum diameter.

[5] Maximum height.

value at the genus level (Slik et al. 2008). Most of the focal species (20 out of 23) were deciduous, pioneer or nonpioneer light demanders, and dispersed by wind or animals. Among the study species, seed mass varied between 2 (*Nauclea diderrichii*) and 9613 mg (*Detarium macrocarpum*). Wood density ranged from 0.33 (*T. scleroxylon*) to 0.88 $g{\cdot}cm^{-3}$ (*Lophira alata*), with an average of 0.63 $g{\cdot}cm^{-3}$. Maximum diameter at breast height (dbh) ranged from 0.6 (*Pseudospondias microcarpa*) to 3.0 m (*Baillonella toxisperma*) and maximum height ranged from 20 (*P. microcarpa)* to 60 m (*B. toxisperma, Cylicodiscus gabunensis, Entandrophragma cylindricum, Entandrophragma utile, Khaya anthotheca, Piptadeniastrum africanum*).

2.3. Experimental design

From 1 January 2009 to 31 December 2014, during the wet season, the forest company planted 53 plots (totaling 44.4 ha) with seedlings grown in nurseries. These plots were established in the most degraded areas along principal or secondary roads (Figure 1). These locations facilitated plot maintenance and preserved forest cover in less disturbed areas.

The planting design was a 'simple mixture, multiple species, single cohort planting' as defined by Stanturf et al. (2014). Planting followed these four steps. First, the high-value species and all other species with a dbh >50 cm were identified and protected. Second, the understory was clear cut by a team of 10 workers using machetes or a chainsaw. Third, the species planted were selected based on their shade tolerance (P, NPLD sensu Hawthorne 1995, Table 1), their availability in the nurseries, and canopy openness at the sites. Fourth, for each plot, species were established in blocks according to the visually evaluated canopy cover by the team supervisor following the recommendations of Hawthorne (1995) and Meunier et al. (2015). Planting was done in 15 × 15 m single-species blocks using 25 seedlings per species planted 3 m apart in a block (Figure 2). Planted seedlings were around 50 cm high.

Within each plot, species blocks were alternated to minimize the effects of parasites and predation. *Milicia excelsa, Entandrophragma* spp., and *K. anthotheca* are extremely sensitive to parasites (gall-forming insects and/or shootborers) (Bosu et al. 2006; Opuni-Frimpong et al. 2008). In the first year, maintenance cleaning was done every four months. In the second year, two cleanings were performed every six months, and one cleaning was done at the end of the third year. Future thinning will be necessary to promote the best tree in each species block, the width of a block (15 m) being roughly the diameter of one mature crown.

We analyzed the performance of the 23 species in 14 plots planted between 2009 and 2012, out of the 53 original plots (Table 2). The size of the selected plots ranged from 0.2 to 1.1 ha, and the number of species varied from 2 to 10 per plot. At plantation establishment, canopy cover was estimated above each planted seedling with a clinometer. The presence (1) or absence (0) of vegetation in the following height intervals – 0–10 m, 10–20 m, and >20 m – was visually assessed. The sum was calculated to obtain a canopy cover index in a range from 0 (full open) to 3 (full cover). After plantation establishment, the proportion of seedlings planted in fully open areas (total cover index = 0) was 75% (SD = 18%), including 81% for pioneer and 62% for nonpioneer species.

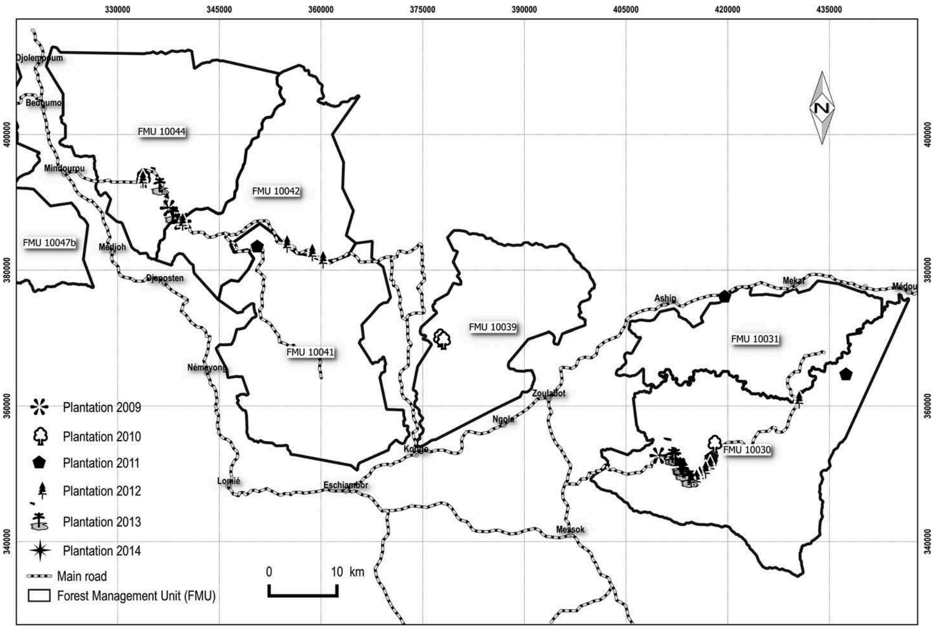

Figure 1. Location of the enrichment plantings between 2009 and 2014 in the Pallisco management units, southeastern Cameroon.

Bt	Bt	Bt	Bt	Bt	Ea	Ea	Ea	Ea	Ea	Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	Bt	Bt	Bt	Bt	Bt	42
Bt	Bt	Bt	Bt	Bt	Ea	Ea	Ea	Ea	Ea	Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	Bt	Bt	Bt	Bt	Bt	39
Bt	Bt	Bt	Bt	Bt	Ea	Ea	Ea	Ea	Ea	Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	Bt	Bt	Bt	Bt	Bt	36
Bt	Bt	Bt	Bt	Bt	Ea	Ea	Ea	Ea	Ea	Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	Bt	Bt	Bt	Bt	Bt	33
Bt	Bt	Bt	Bt	Bt	Ea	Ea	Ea	Ea	Ea	Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	Bt	Bt	Bt	Bt	Bt	30
Ec	Ec	Ec	Ec	Ec	Nd	Nd	Nd	Nd	Nd	Ts	Ts	Ts	Ts	Ts	Me	Me	Me	Me	Me	Ka	Ka	Ka	Ka	Ka	Ts	Ts	Ts	Ts	Ts	Ec	Ec	Ec	Ec	Ec	27
Ec	Ec	Ec	Ec	Ec	Nd	Nd	Nd	Nd	Nd	Ts	Ts	Ts	Ts	Ts	Me	Me	Me	Me	Me	Ka	Ka	Ka	Ka	Ka	Ts	Ts	Ts	Ts	Ts	Ec	Ec	Ec	Ec	Ec	24
Ec	Ec	Ec	Ec	Ec	Nd	Nd	Nd	Nd	Nd	Ts	Ts	Ts	Ts	Ts	Me	Me	Me	Me	Me	Ka	Ka	Ka	Ka	Ka	Ts	Ts	Ts	Ts	Ts	Ec	Ec	Ec	Ec	Ec	21
Ec	Ec	Ec	Ec	Ec	Nd	Nd	Nd	Nd	Nd	Ts	Ts	Ts	Ts	Ts	Me	Me	Me	Me	Me	Ka	Ka	Ka	Ka	Ka	Ts	Ts	Ts	Ts	Ts	Ec	Ec	Ec	Ec	Ec	18
Ec	Ec	Ec	Ec	Ec	Nd	Nd	Nd	Nd	Nd	Ts	Ts	Ts	Ts	Ts	Me	Me	Me	Me	Me	Ka	Ka	Ka	Ka	Ka	Ts	Ts	Ts	Ts	Ts	Ec	Ec	Ec	Ec	Ec	15
Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Eu	Eu	Eu	Eu	Eu	Db	Db	Db	Db	Db	Nd	Nd	Nd	Nd	Nd	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	12
Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Eu	Eu	Eu	Eu	Eu	Db	Db	Db	Db	Db	Nd	Nd	Nd	Nd	Nd	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	9
Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Eu	Eu	Eu	Eu	Eu	Db	Db	Db	Db	Db	Nd	Nd	Nd	Nd	Nd	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	6
Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Eu	Eu	Eu	Eu	Eu	Db	Db	Db	Db	Db	Nd	Nd	Nd	Nd	Nd	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	3
Ma	Ma	Ma	Ma	Ma	Ka	Ka	Ka	Ka	Ka	Eu	Eu	Eu	Eu	Eu	Db	Db	Db	Db	Db	Nd	Nd	Nd	Nd	Nd	Me	Me	Me	Me	Me	Ma	Ma	Ma	Ma	Ma	0
AI	AH	AG	AF	AE	AD	AC	AB	AA	Z	Y	X	W	V	U	T	S	R	Q	P	O	N	M	L	K	J	I	H	G	F	E	D	C	B	A	

Figure 2. Example of a multispecies plot consisting of 21 single-species blocks. Each block includes 25 seedlings planted 3 m apart. Each seedling is identified by a combination of a letter (*X* axis) and a distance (*Y* axis). Bt, *Baillonella toxisperma*; Db, *Distemonanthus benthamianus*; Ea, *Entandrophragma angolense*; Ec, *Entandrophragma cylindricum*; Eu, *Entandrophragma utile*; Ka, *Khaya anthotheca*; Ma, *Mansonia altissima*; Me, *Milicia excelsa*; Nd, *Nauclea diderrichii*; Ts, *Terminalia superba*.

The survival and diameter of each seedling was recorded each year. For 2–5 years, depending on the plot, diameters of 6540 tagged seedlings were measured at 10 cm above the stem base with a caliper. At the end of the experiment, the crown exposure of each seedling was classified following Dawkins (1958). Code 1 was assigned to fully shaded understory trees, 2 to upper understory trees partly exposed to direct light, 3 to lower canopy trees partly exposed to direct light, 4 to canopy trees fully exposed to light from above, and 5 to fully emergent with no other vegetation in an inverted vertical cone of 45°. All field measurements were performed by the same team.

Plantations yields and costs were estimated for the 53 plots using data from the logging company between 2009 and 2014. The costs for planted and maintained areas were calculated each year. Costs were classified into wages, transport (fuel, maintenance, and depreciation), and materials (machetes, chainsaw, etc.). Costs were also divided into the main operation stages (seedling production, site preparation, planting, and maintenance).

2.4. Data analysis

To quantify tree survival, we estimated the survival function $S(t)$ over time using the nonparametric Kaplan–Meier estimator (Harrell 2001), which gives the probability of an individual seedling surviving to time t, the time since the beginning of the experiment:

$$S(t) = \Pi t_i \leq t(1 - d_i/n_i)$$

where t_i is the time interval, d_i is the number of deaths that occur in the interval t_i, n_i is the number of seedlings that are alive at the end of the interval t_i, and Π is the product operator across all cases less than or equal to t. Since the time from plantation establishment varied among plots and species from 690 to 1740 days, survival at $t = 690$ days was determined for all species.

A total of 17,794 diameter measurements were made on the 4621 trees alive at the end of the monitoring period. The diameter growth was modeled with a linear mixed model. The time period (up to ca. 5 years) was not long enough to justify the use of a nonlinear model (Paine et al. 2012). Because measures of tree diameter were repeated through time, these observations are dependent and correlated with each other. Consequently, including random effects to account for individual tree variability was required. It was achieved using a mixed modeling procedure. Models with fixed and random effects, including a random intercept (α) and a random slope (β), were tested. The best model was selected based on Akaike information criterion comparison of models, and the significance of the difference between pairs of models was tested with the likelihood ratio test. We first identified the best random structure (random slope) and then the best fixed effects (species and species–time interaction) in accordance with Zuur et al. (2009). The equation that was found to give the best mixed linear model, based on the diameter (D) of the seedling (i) belonging to species (s) at the time (t) was

$$D_{ist} = a_s + c_s \times \text{Time} + \beta_{is} \times \text{Time} + \varepsilon_{ist}$$

with a_s and c_s as fixed parameters, β_{is} as a random parameter, and ε_{ist} as the error.

We then extracted the fixed model parameters for each species corresponding to the mean growth value and the best linear unbiased estimate of the random effects (BLUPS) for each individual in order to compute the mean of the growth rate of the best-performing seedlings (i.e., best 10% of stems).

Species performance was represented by mean growth rates (all stems), maximum growth rates

Table 2. Size, openness, planting date, and species combinations (number of planted seedlings) for experimental plots.

Plot number:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Area (ha)	0.4	0.8	1.1	0.3	0.3	0.2	0.5	0.3	0.3	0.5	0.3	0.2	0.3	0.3	5.9
% remaining canopy cover	48.0	42.3	40.0	70.5	13.3	8.2	11.3	15.6	10.0	19.5	17.7	11.9	26.7	21.7	25.5
Planting date	2009 July	2009 October	2010 March	2010 August	2011 November	2012 February	2012 February	2012 February	2012 February	2012 March	2012 March	2012 February	2012 June	2012 June	
Amphimas pterocarpoides										50		25			75
Autranella congolensis													25		25
Baillonella toxisperma					75	50	50	50	50	99		50	50	75	549
Bobgunnia fistuloides								50	25				25		100
Cylicodiscus gabunensis			100							2					102
Detarium macrocarpum				50											50
Distemonanthus benthamianus							25	50	25	50					150
Entandrophragma angolense							25		25						50
Entandrophragma cylindricum				75	75	25	50	50	50	75		25	25	50	500
Entandrophragma utile	40			75	25	50	25	50	50	23			25	25	388
Erythrophleum suaveolens								25							25
Khaya anthotheca			75				75					50			200
Lophira alata													25	25	50
Mansonia altissima	300	650	396	75	75	25	100	50	75	151		50	50	75	2072
Milicia excelsa							75								75
Nauclea diderrichii							50			75					125
Pericopsis elata	60			50	50										160
Piptadeniastrum africanum			50												50
Pseudospondias microcarpa											20				20
Pterocarpus soyauxii			25										25	25	75
Terminalia superba		275	454	50	50	25	50	25	50	75	270	25	50	100	1499
Triplochiton scleroxylon					25	50		25	25						125

(average of best 10% of stems), and mortality rates (all stems).

We tested for significant relationships between species traits and species performance using Pearson correlation for quantitative traits and Kruskal–Wallis analysis for qualitative traits. All statistical analyses were performed within the open source R environment (R version 2.14.1). The 'lme4' package was used for fitting mixed models (Bates et al. 2015).

3. Results

3.1. Species survival and growth

By the end of the experiment, some species experienced high mortality, while others had high survival (Figure 3). The probability of survival at 690 days (Table 3) ranged from 31.2% for *Nauclea diderrichii* (88 dead, 37 living seedlings) to 100% for *Autranella congolensis* (0 dead, 25 living seedlings). After 690 days, the survival rate stabilized (e.g., *P. elata*, at ca. 70%) or decreased further (e.g., *E. cylindricum*).

In the first years, growth trajectories tended to be linear for the 23 study species (Figure 4). The mean annual diameter growth increment (c_s) ranged from 1.67 mm for *M. excelsa* to 42.90 mm for *T. scleroxylon* (Table 3). Although both were planted according to their shade tolerance guild under low canopy cover, the proportion of fully emergent stems (fifth category of Dawkins) was 3% for *M. excelsa* and 61.3% for *T. scleroxylon* (Table 3). For all species considered together, the relationship between survival and growth was positive but not significant ($r = 0.291$, $p = 0.178$).

3.2. Relationships between species performance and traits

We observed only weak correlations between species performance and most functional traits (Table 4). However, we found a significant relationship between the wood density and the maximum growth rate, with fast-growing species tending to have lighter wood. If the fastest growing species (*T. scleroxylon*) was removed from the analysis, the relationship was no longer significant. We also identified a weak, non-significant, correlation between leaf phenology and survival, with deciduous species tending to have a better survival rate than evergreen species. There were however only two evergreen species among the 23 studied species, *N. diderrichii* and *Bobgunnia fistuloides*, with probabilities of survival of 31.2% and 66.0%, respectively, at t = 690 days, below the 73.7% average of the 23 studied species.

3.3. Costs

The forest planting team consisted of 13 people, including two nurserymen and one supervisor. This team was only in charge of the silvicultural activities. As a consequence, the cost per hectare was specific to this team. The team was estimated to be able to plant 10 ha per year and to maintain ca. 60 ha per year (three cleanings on 10 ha the first year following planting, two cleanings on 10 ha in the second year, and the last cleaning on 10 ha in the third year). The total estimated cost per hectare was $7038 (€5585) distributed as follows: wages 69%, vehicles 26% (including depreciation, fuel, and maintenance), and materials 5%. If the total cost was split among the main operation stages, the results were

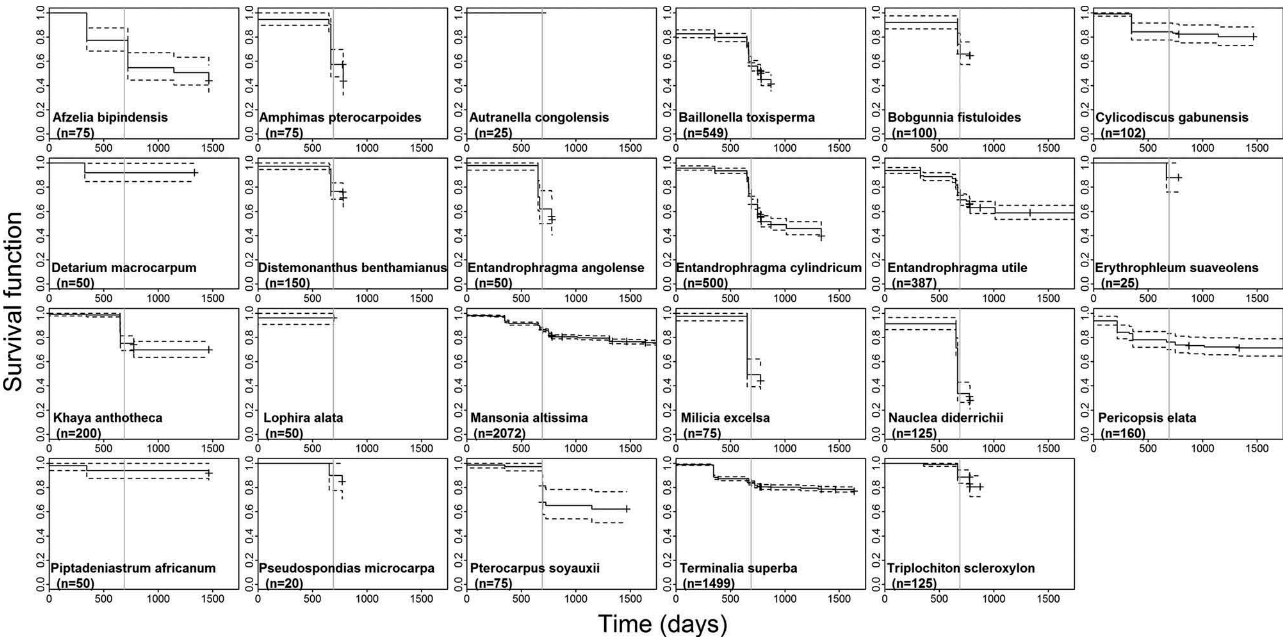

Figure 3. Kaplan–Meier survival estimates over time, with 95% confidence bounds for the 23 studied species. The vertical gray line indicates survival at t = 690 days for comparison among species.

Table 3. For each species, number of observations (*N*), average canopy cover index (from 0, full open, to 3, full cover), average Dawkins index (from 1, lower understory, to 5, emergent), proportion (%) of emergent stems (fifth category of Dawkins), survival at 690 days (% of stems alive), maximum and mean diameter growth rates (in mm year^{-1}), minimum cutting diameter (Cameroon national regulation), and time to reach the minimum cutting diameter given the mean diameter growth rate.

Species	*N*	Average cover index	Average Dawkins index	% emergent	% survival	Max. growth	Growth	Growth SD	MCD (cm)	Time (years)
Afzelia bipindensis	75	0.97	3.4	18.2	54.7	11.21	5.75	1.27	80	139
Amphimas pterocarpoides	75	0.42	3.2	21.1	43.7	5.42	2.42	1.25	50	207
Autranella congolensis	25	0.84	2.4	0.0	100.0	8.76	6.41	1.59	60	94
Baillonella toxisperma	549	0.29	3.5	16.1	58.7	11.65	6.76	0.47	100	148
Bobgunnia fistuloides	100	0.09	3.7	18.5	66.0	16.10	7.77	0.96	50	64
Cylicodiscus gabunensis	102	1.62	2.6	1.2	83.3	9.08	5.10	0.80	60	118
Detarium macrocarpum	50	1.00	2.7	2.2	92.0	6.71	4.53	1.08	50	110
Distemonanthus benthamianus	150	0.21	3.6	23.4	76.0	21.16	10.46	0.73	60	57
Entandrophragma angolense	50	0.33	2.9	0.0	56.0	9.88	3.84	1.48	80	208
Entandrophragma cylindricum	500	0.72	2.7	1.6	72.6	5.10	1.71	0.48	100	585
Entandrophragma utile	387	0.59	2.9	3.3	73.4	12.22	5.00	0.48	80	160
Erythrophleum suaveolens	25	0.27	3.5	22.7	88.0	12.41	7.30	1.64	50	68
Khaya anthotheca	200	0.96	2.8	3.5	74.0	17.20	7.59	0.63	80	105
Lophira alata	50	0.19	3.8	27.1	96.0	18.73	13.64	1.15	60	44
Mansonia altissima	2072	0.93	2.7	6.8	86.4	13.64	7.34	0.18	60	82
Milicia excelsa	75	0.09	3.3	3.0	44.0	2.83	1.67	1.34	100	599
Nauclea diderrichii	125	0.24	3.7	21.6	31.2	17.08	9.54	1.27	80	84
Pericopsis elata	160	0.50	3.4	18.3	73.8	16.12	9.33	0.69	90	96
Piptadeniastrum africanum	50	1.00	2.8	0.0	92.0	19.41	11.42	1.07	60	53
Pseudospondias microcarpa	20	0.00	4.6	70.6	85.0	21.74	16.77	1.87	50	30
Pterocarpus soyauxii	75	0.33	3.2	0.0	81.3	11.80	5.01	1.06	60	120
Terminalia superba	1499	0.45	3.4	20.9	84.0	33.50	19.80	0.22	60	30
Triplochiton scleroxylon	125	0.09	4.4	61.3	83.0	65.96	42.90	0.75	80	19

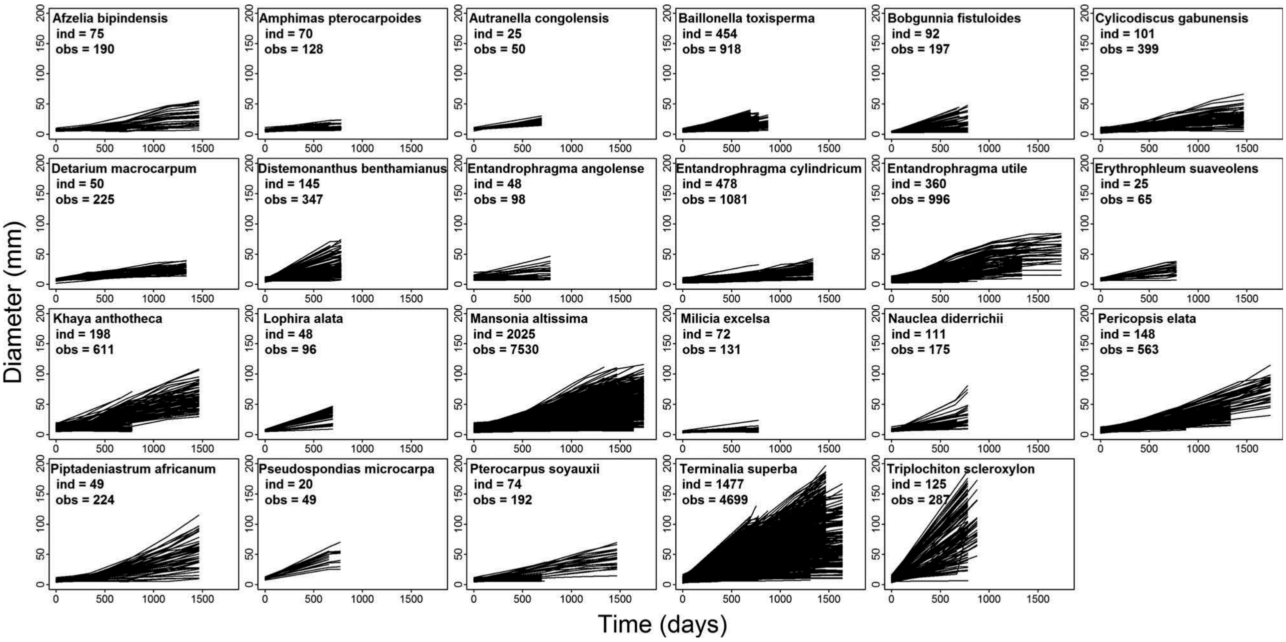

Figure 4. Growth trajectory of the studied species. Number of monitored seedlings (ind.) and total number of measurements (obs.) are given for each species. Depending on the installation date (between 2009 and 2012), the monitoring period varied between plots and ranged from 690 to 1740 days.

as follows: seedling production 11%, site preparation 53%, planting 8%, and maintenance 28%.

Because of the plantation design, the number of expected crop trees was 44 per hectare (44 blocks per hectare with one crop tree per block remaining after thinning). Therefore, the total cost for raising a mature tree from seed was approximated at $160 (€127) in 2014. This figure is probably underestimated because thinning costs were not included. In Cameroon, the MCD ranges from 50 to 100 cm, depending on the species (Table 3). Any projections about the time needed for trees to reach this diameter

Table 4. Relationship between the performance of 23 species (mean and maximum growth, and survival) in plantations and species functional traits.

	Growth	Maximum growth	Survival
Quantitative traits			
Wood-specific gravity	$r = -0.41$ $p = 0.058$	**$r = -0.46$** **$p = 0.030$**	$r = 0.01$ $p = 0.650$
Seed mass	$r = -0.17$ $p = 0.540$	$r = -0.22$ $p = 0.415$	$r = 0.22$ $p = 0.406$
Maximum diameter	$r = 0.03$ $p = 0.883$	$r = 0.04$ $p = 0.868$	$r = 0.11$ $p = 0.609$
Maximum height	$r = -0.14$ $p = 0.539$	$r = -0.10$ $p = 0.638$	$r = 0.08$ $p = 0.710$
Qualitative traits			
Regeneration guild (df = 1)	$\chi^2 = 2.37$ $p = 0.124$	$\chi^2 = 1.37$ $p = 0.242$	$\chi^2 = 0.21$ $p = 0.640$
Deciduousness (df = 1)	$\chi^2 = 0.76$ $p = 0.383$	$\chi^2 = 0.43$ $p = 0.513$	$\chi^2 = 3.05$ $p = 0.081$
Dispersal (df = 2)	$\chi^2 = 0.21$ $p = 0.901$	$\chi^2 = 1.38$ $p = 0.501$	$\chi^2 = 1.72$ $p = 0.422$

Pearson correlation coefficients (r) and associated p-values are given for quantitative traits. Kruskal–Wallis χ^2 and associated p-values are given for qualitative traits. Significant relationships are shown in bold.

are imprecise. But if the average observed growth rates could be maintained with thinning (see Section 4), the time to the MCD would be ca. 19 years for the best-performing species (*T. scleroxylon*) and between 30 and 160 years for most other species.

4. Discussion

4.1. Identification of the best species for enrichment planting

Many plantation methods have been tested since the early twentieth century, but few data are available on species performance in young plantations, even for important timbers like *Entandrophragma* spp. (Dupuy & Mille 1993) or species of concern for conservation like *P. elata* (on CITES Appendix II), *A. congolensis*, and *B. fistuloides* (classified CR and EN in the IUCN red list, respectively). Most of the quantitative information available is from projections of early species growth derived from older trees in plantations of a known age, but with little information on plantation maintenance (Ndongo et al. 2009; Ebuy et al. 2011). Moreover, to avoid bias due to environmental and time variations, multispecies comparison in the same site during the same period has been needed, as was carried out in this study.

We found promising growth rates and high survival rates for some species (e.g., *T. scleroxylon, T. superba*, and *L. alata*). In comparison to other plantations of the same age (maximum 10 years), our estimates of mean annual diameter increment were (i) higher for *T. scleroxylon* (Lapido et al. 1951; Dupuy & Koua 1993), (ii) similar for *T. superba* (Tariel & Groulez 1958; Appiah 2012), and (iii) slightly higher for *L. alata* (Biwolé et al. 2012). For most of the other species, the values we observed were similar or slightly lower than those reported in other studies (Dupuy & Koua 1993; Koumba Zaou et al. 1998; Onyekwelu 2007; Addo-Danso 2010).

The positive (but nonsignificant) relationship between survival and growth was not always consistent with results from other studies. For example, Beckage and Clark (2003) found that species with the highest mortality rates outperformed the other species. On the other hand, in our study, for some species (e.g., *M. excelsa* and *Entandrophragma* spp.), low growth increments were associated with high mortality rates. Attempts to grow *M. excelsa* in plantations have generally failed due to attacks by *Phytolyma lata*, a gall-forming insect. Shade during the first 12–18 months minimizes the development of galls and associated dieback, but repeated attacks in open areas have frequently resulted in high mortality (Nichols et al. 1999; Bosu et al. 2006). Fayolle et al. (2015) have recently recommended planting *M. excelsa* in logging gaps rather than in open areas. Similarly, *Hypsipyla* shoot borers often hamper plantation success for Meliaceae (*Khaya* spp. and *Entandrophragma* spp.) in open areas. In our study, planting *K. anthotheca* under light shade (Table 3) allowed for good growth and reduced mortality, confirming the results obtained by Opuni-Frimpong et al. (2008) in Ghana.

The high mortality rates obtained for the other Meliaceae species (*Entandrophragma* spp.) were not due to shoot borer attack but rather the result of shoots being browsed by wild Bovidae (mainly *Tragelaphus spekii* and *Cephalophus* spp.) (personal observation). Such damage in fallow forests with canopy structure very similar to young plantations has also been reported by Hall (2008). Due to their low re-sprouting capacity, the growth of the injured trees was probably reduced by competing, overtopping vegetation (Table 3). The tradeoffs among survival, growth, and herbivory present a serious challenge for these species (Goodale et al. 2014).

4.2. Relationships between functional traits and species performance

The lack of significant correlations between qualitative functional traits and performance measures might be due to several factors. Variation in regeneration guild was limited; most of the species used were deciduous and light-demanding (either pioneer or nonpioneer), only two species were evergreen, and none was a shade bearer. Martínez-Garza et al. (2013) found that regeneration guild could be used to predict tree growth, but they also emphasized that some nonpioneer species performed nearly as well as pioneers. Functional guilds are not discrete because there is a continuum in such traits as light requirements (Agyeman et al. 1999). The maximum growth of nonpioneer species also occurs in partial to full vertical illumination (Martínez-Garza et al. 2005). Nursery-grown seedlings of nonpioneer species can cope with high light levels and a low water supply, and they grow faster in the open conditions than in shade (Fayolle et al. 2015). The type of dispersal (Table 1) was also a poor predictor of species growth, perhaps because the main dispersal categories can be found in both fast- and slow-growing tropical tree species (Agyeman et al. 1999).

The weak relationship between quantitative functional traits (Table 1) and growth is more surprising because wood density, seed mass, and adult stature are usually considered to be significant predictors of tree growth and mortality for trees with diameter above 10 cm (Poorter et al. 2008). Wood density was negatively correlated with maximum growth rate, but its relationship with mean growth rate was not significant, possibly because too few species were sampled (Poorter et al. 2008).

Growth and mortality rates are often negatively correlated with seed mass. In our experiment, the relationship, although negative, was not statistically significant. Seed size affects survival and indirectly growth since small-seeded species have limited reserves and must quickly deploy roots and leaves to become autotrophic (Poorter et al. 2008). Many small-seeded species have photosynthetic cotyledons and a high SLA, which boosts juvenile growth. But correlation between seed size and growth disappears over time as the initial SLA differences are reduced.

Variation in SLA can be a main driver of interspecific variation in seedling growth rate (Poorter & Bongers 2006), although SLA is only a good predictor at a low irradiance level and not in open sites (Martínez-Garza et al. 2013). Other leaf traits, like leaf dry mass content (LDMC), could be better predictors for open sites, at least for nonpioneer species, because a high LDMC is an adaptation to survive in dry open area conditions (Martínez-Garza et al. 2013). Leaves with higher LDMC have higher moduli of elasticity and thicker and more rigid lignified cell walls than species with lower LDMC. These characteristics allow them to maintain leaf turgor in dry conditions (Martínez-Garza et al. 2013). For the species studied, however, LDMC may not predict growth well due to the overlap in LDMC values between the fast-growing and slow-growing species used in this study. Vanhal (2013) reported LDMC values of 0.51, 0.31, and 0.36 $g \cdot g^{-1}$ for fast-growers *T. scleroxylon, T. superba*, and *L. alata*, respectively, versus LDMC values of 0.30, 0.33, and 0.36 $g \cdot g^{-1}$, for slow growers *Afzelia bipindensis, E. cylindricum*, and *Pterocarpus soyauxii*, respectively.

Maximum size reached by the studied species was also a poor predictor of performance, probably because the relationship between height and growth depends on the ontogenic stage. Light increases with height in forest canopies, and the crowns of taller species receive more light than those of shorter species (Poorter et al. 2008). Nearly all the studied species were able to reach the canopy and the variance in sizes was probably too small to detect any relationship between height and growth. Another architectural feature, such as crown length, might have been a better predictor. Long crown species have a larger leaf area and are more self-shading at midday, thus minimizing photoinhibition due to high leaf temperature (Martínez-Garza et al. 2013).

4.3. Perspectives on supply and costs

Without long-term monitoring, any growth projection is imprecise, but useful estimates can be made. If unthinned, growth for any of the studied species may not be linear over a long time period (Paine et al. 2012). Obiang et al. (2014) showed that growth rates of two species (*A. klaineana* and *L. alata*) decrease when their stems reach 50–70 cm in diameter. However, in mixed plantations, Dupuy and Koua (1993) observed a linear growth rate of *Khaya* spp. until at least 50 cm in diameter. In 50-year-old unthinned plantations, diameter growth rates for the best-performing stems of *Distemonanthus benthamianus* (at 825 surviving stems per hectare (SSH)), *E. cylindricum* (800 SSH), *L. alata* (1375 SSH), *Mansonia altissima* (300 SSH), and *T. scleroxylon* (800 SSH) were 10, 7, 9, 10, and 14 $mm \cdot year^{-1}$, respectively (Ndongo 2006). Given such high growth rates after 50 years, we can assume that the average growth rates we observed can be maintained up to the legal cutting diameter (Table 3) if thinning is performed. The possible time to reach this diameter ranged from 19 years (*T. scleroxylon*) to 599 years (*M. excelsa*). This latter value can be explained by the low growth rate of *M. excelsa* under repeated attacks by *P. lata* in open areas.

In Central Africa, forests remain the property of the State and concessions are licensed to private logging companies for a cutting cycle. In Cameroon, the duration of the cutting cycle is 30 years. Over this period, only two of the studied species would probably reach the MCDs: *T. scleroxylon* and *T. superba* (Table 3). Their average volumes at the MCDs should be 6.3 and 2.8 m^3, if calculated with the volume tables used by the government, $V = 0.000209D^{2,35}$ and $V = 0.000252D^{2,28}$, respectively (Fayolle et al. 2013).

The per tree cost we estimated for raising a mature tree (US$160) is roughly equivalent to the market sales price for 1 m^3 of round wood: average log FOB (Free On Board) prices $163 for *T. scleroxylon* (ITTO 2012) and $128 for *T. superba* (http://database.prota.org). The FOB prices for other species can be much higher (e.g., ca. $350 for *P. elata*, http://database.prota.org) but their growth rates are lower (0.8 m^3 for *P. elata* after 30 years if calculated with the volume table recommended by Fayolle et al. 2013). While our estimates of production costs are rough, they help explain the current financial disincentive for implementing silvicultural operations, as shown in Amazonia by Schulze (2008). The high cost of planting has always been cited as one of the main reasons for the abandonment of this practice in tropical regions. Mechanization could reduce the expensive preparation of the sites (53% of the total cost) and should be tested. Alternatively, gap enrichment planting is relatively inexpensive (Doucet et al. 2009; Schulze 2008). Planting in logging gaps should be favored for some species that have shown good performance in this environment, such as *M. excelsa* or *B. toxisperma* (Fayolle et al. 2015).

5. Conclusions

Simple mixtures could be an effective way to restore biodiversity of timber species and to maintain a long-term supply of goods and services from Central African moist logged forests. Although long-term monitoring is needed to confirm the 5-year results from this study, some native species with high growth and survival rates may perform as well in plantations as exotic species (Dupuy et al. 1999), but the quality of their wood needs to be monitored because the effect of fast growth is unknown (Bhat 2000).

Management costs, and a legal framework for plantations that does not address regeneration, limit plantation establishment. Long-term concessions and lower taxes for logging companies that replant harvested species are prerequisites for employing silviculture both at the larger scale and for day-to-day management.

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Disclosure statement

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