Survival and growth of high-value timber species planted in Central African rainforest logging gaps

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Abstract

Logging gaps could provide suitable conditions for enrichment plantation of timber species. However, there is little data on the long-term performance of planted species, particularly in Central Africa. In this study, we assessed the performance of 15 species planted in 198 logging gaps in a forest logging concession of South-Eastern Cameroon. A total of 2,304 trees were monitored for up to 14.3 years or 19 years. We assessed the influence of species, species guild, age and tree size on tree survival and growth using linear mixed-effects models. Survival rates varied across species, age and species guild. Five species (*Detarium macrocarpum* Harms*,* *Erythrophleum suaveolens* (Guill. & Perr.) Brenan, *Terminalia superba* Engl. & Diels, *Baillonella toxisperma* Pierre and *Prioria oxyphylla* (Harms) Breteler) had annual survival rates greater than the average, with more than 80% of the trees planted had survived after 14.3 to 19 years. On the other hand, all *Entandrophragma cylindricum* (Sprague) Sprague individuals had died after 14.8 years. Diameter and height growth also varied across species, age and guild. *Terminalia superba* had the highest diameter (16 mm.yr^{-1}) and height (103 cm.yr^{-1}) increments. *Lovoa trichilioides* Harms and *B. toxisperma* had diameter increments higher than 2 mm.yr^{-1} while *E. utile*, *L. trichilioides*, *E. suaveolens*, *E. angolense* and *Mansonia altissima* (A.Chev.) A.Chev. had height increments higher than 15 cm.yr^{-1}. This study thus recommends enriching logging gaps of South-Eastern Cameroon with a pioneer species, *T. superba*. The use of other species (e.g., *B. toxisperma*, *E. suaveolens* and *D. macrocarpum)* could only be considered if maintenance can be regularly carried out.

Keywords: Forest concessions, logging gap, enrichment planting, tree performances, Cameroon, tropical silviculture

1. Introduction

In Central Africa, logging has focused on very few species for decades, with six species accounting for more than 80% of the total production (Ruiz et al., 2005; BAD-FRMi, 2018; Duhesme et al., 2022). Even if such selective logging has a limited impact on forest cover and biodiversity (Putz et al., 2012), the timber volume of exploited species has depleted through harvest cycles (Gourlet-Fleury et al., 2013). Several measures have been proposed to address this issue, including the promotion of lesser-known timber species as alternative timber resources (Horne, 2013; Karsten et al., 2014), and forest plantations to supplement the regeneration of exploited species (Schulze, 2008; Doucet et al. 2016; Brown et al. 2020; Ilunga-Mulala et al., 2025). The latter option might additionally provide environmental services, such as carbon sequestration or the non-timber resources production for local communities (Cerullo and Edwards, 2019).

Logging gaps could offer suitable conditions for tree planting in production forests (Schulze 2008; Negreros-Castillo and Mize, 2008; Ouédraogo et al., 2014; Fayolle et al., 2015; Schwartz et al. 2017a; Costa et al., 2021). They allow more light to reach the lower vegetation strata and could then create more favourable conditions for the regeneration of light-demanding species (Jans et al., 1993; Numata et al., 2006; Swaine and Agyeman, 2008). As gaps are generally of limited size, not only pioneer species can regenerate within gaps but also mid-successional species (Brokaw, 1985), especially those that can tolerate moderate light levels. Although logging remove on average 1-2 trees per hectare every 25-30 years in the Congo Basin (FRMi, 2018), forest concessions covers wide area allowing large-scale enrichment activities.

The size of these gaps depends on many parameters, including the harvested species, topography and logging method. If reduced impact logging (RIL) practices are implemented, and this is mandatory in FSC-certified forest companies, the gap size is smaller than in conventional logging (Pena-Claros et al. 2008; Medjibe et al. 2011; Bonnell et al. 2011; Imai et al. 2012). In tropical forests, the average area of logging gaps is estimated at 270 m² but it can reach 544 m² (Schulze and Zweede, 2006; Doucet et al., 2009). By targeting large canopy trees, logging gaps usually creates larger gaps than those created by natural tree fall (Felton et al., 2006; Karsten et al., 2013) whose average area ranges from 90 to 250 m² (Yamamoto, 2000).

The enrichment of logging gaps faces the problem of identifying species that could successfully develop in this environment. Planted trees face three major challenges: (*i*) gap gradual closure (Beckage & Clark, 2003); (*ii*) competition from woody and herbaceous vegetation resulting from the germination of the soil seed bank, and the development of established seedlings (Makana and Thomas, 2005; Zébazé et al., 2023; Doucet et al., 2009; Malizia and Grau, 2008); (*iii*) wildlife damages, mainly by duikers and elephants (Nichols et al., 1998; Howlett and Davidson, 2003; Makemba et al., 2022). Those factors reduce the growth and survival of planted trees (Toledo-Aceves and Swaine, 2008a; Rozendaal et al., 2020). Consequently, the selected species should be fast-growing, able to tolerate mid-light conditions once established and among the less palatable species. Other site-related factors may influence tree performance in the gaps (Ilunga-Mulala et al., 2025). The topography, for example, can influence soil moisture and the local microclimate (Baker et al., 2003; Agyeman et al., 2010)

In the tropics, enrichment of logging gaps is not a new topic. The first experiments were conducted in Amazonia (e.g., Schulze, 2008; Keefe et al., 2009; Navarro-Cerrillo et al., 2011;

Schwartz et al., 2013; Schwartz et al., 2017b; Costa et al., 2021) and South-East Asia, with some promising results (e.g., Okimori et al., 2006; Sovu et al., 2010; Millet et al., 2013). In Central Africa, short-term (< 6 years) successes were reported for few species when competition was reduced by regular maintenance and the absence of large mammals (e.g., Doucet et al., 2009; Ouédraogo et al., 2014; Fayolle et al., 2015; Ilunga-Mulala et al., 2025).

In most cases, the long-term monitoring of reforested gaps was limited to less than 5 years (Ilunga-Mulala et al., 2025) because of its difficulties and associated cost (Akwasi Duah-Gyamfi et al., 2014). Therefore, the factors affecting plantation success in gaps remain to be identified. In Central Africa, long-term studies on gap enrichment are needed, especially in the current context where multiple reforestation/afforestation initiatives (e.g., REDD+, AFR100 etc.) have been launched (Brancalion and Holl, 2020; Ilunga-Mulala et al., 2021; Sloan, 2024; Bourgeois et al., 2024). Such studies could reduce the risk of investment losses due to a poor match between selected species and planting environment.

The aim of this study is to address the current knowledge gap on the long-term performance (14 to 19 years) of trees planted in logging gaps in Central Africa. Specifically, it seeks to answer the following questions: (1) Which planted tree species demonstrate good survival and/or growth rates in logging gaps, making them suitable candidates for gap enrichment? (2) How do tree growth and survival rates of the planted trees vary through time? (3) How reliable is species guild classification in guiding the selection of tree species for gap enrichment?

2. Materials and methods

2.1. Study area and environmental conditions

The study area (Fig. 1) consisted of forest management units (FMUs 10-030, 10-041 and 10-044) managed by Pallisco Company, FSC-certified since 2008. It was in the Haut-Nyong department, close to the city of Mindourou, Eastern region of the Republic of Cameroon (between 3°01′ N and 3°44′ N, and 13°20′ E and 14°31′ E), at an average elevation of 620.4 ± 18.3 m. The climate was classified as Am according to the Köppen classification (Beck et al., 2018), with the mean annual temperature and rainfall of 23.2°C and 1,640 mm, respectively (Gorel et al., 2019). Rainfall was distributed in two distinct rainy seasons (August-December and March-June; Daïnou et al., 2011), and reached 494 mm in the warmest quarter (Noce et al., 2020). The geological substrate consisted of Precambrian schistoquartzitic rocks, composed of gneiss, migmatite and micaschist from low Precambrian (Vleminckx et al., 2017). Soils were ferralsols weathered reddish or yellowish (Fétéké et al., 2004), acidic (pH values often <4) and had very low exchange capacity (Vleminckx et al., 2017; Mantel et al., 2023).

The study forest was semi-deciduous, classified as Moist Central Africa (Fayolle et al. 2014) and Moist Forest (Gorel et al., 2022), characterised by a high presence of tree species from the *Fabaceae*, *Annonaceae* and *Malvaceae* families (Réjou-Méchain et al., 2021). Letouzey (1985) described the area as a transition forest between the evergreen and the semi-deciduous forests with canopy trees dominated by species of *Meliaceae*, *Malvaceae* and *Cannabaceae* families.

In Central Africa, elephants and duikers were the main species browsing and damaging seedlings. Elephants were rare in the region. They were only seen at certain times along migration corridors. Different species of Duikers were found in the study area, including yellow-backed duiker (*Cephalophus silvicultor*), blue duiker (*Philantomba congica*) and red duiker (*C. callipygus* and *C. castaneus*) (Houngbégnon et al., 2023).

2.2. Study species

We selected 15 tree species (Table 1), based on the following criteria: *(i)* the species was naturally present in the selected concessions and (*ii*) its timber had commercial value. Among the species that met those criteria, we preferentially selected the species that produce nontimber forest products (fruits, edible caterpillars, medicine, etc.) and with high interest for local communities (*Baillonella toxisperma* Pierre, *Entandrophragma cylindricum* (Sprague) Sprague, and *Erythrophleum suaveolens* (Guill. & Perr.) Brenan). We considered also two species that were listed in CITES Appendix II (*Afzelia bipindensis* Harms and *Pericopsis elata* (Harms) Meeuwen). We additionally aimed to balance the number of selected species per species guild: pioneer, non-pioneer light-demanding and shade-tolerant species according to Hawthorne (1995).

Table 1. Characteristics of study species and the number of study gaps (*n*), average size of 265.8 ± 175.4 m² (Doucet et al., 2009), with corresponding individuals. The species guild is either pioneer (P), non-pioneer light-demanding (NPLD) or, shade-tolerant (ST). The pilot names are presented according to the ATIBT (2016) nomenclature with additional common name in brackets for some species.

Species	Pilot names	Family	Guild	*n* gaps spacing (3m x 4m)	*n* gaps spacing (2m x 4m)	Number of individuals
Afzelia bipindensis Harms	Doussié	Fabaceae	NPLD	10	-	100
Baillonella toxisperma Pierre	Moabi	Sapotaceae	NPLD	20	15	563
Bobgunnia fistuloides (Harms) J.H.Kirkbr. & Wiersema	Pao rosa	Fabaceae	P	7	-	70
Detarium macrocarpum Harms	Mambodé	Fabaceae	P	4	-	21
Diospyros crassiflora Hiern	Ebène d'Afrique	Ebenaceae	ST	9	-	90
Entandrophragma angolense (Welw.) C.DC.	Tiama	Meliaceae	NPLD	10	-	100
Entandrophragma cylindricum (Sprague) Sprague	Sapelli	Meliaceae	NPLD	10	-	100
Entandrophragma utile (Dawe & Sprague) Sprague	Sipo	Meliaceae	NPLD	10	15	342
Erythrophleum suaveolens (Guill. & Perr.) Brenan	Tali	Fabaceae	P	-	15	141
Lovoa trichilioides Harms	Dibétou	Meliaceae	NPLD	10	-	100
Mansonia altissima (A.Chev.) A.Chev.	Bété	Malvaceae	NPLD	18	-	119
Milicia excelsa (Welw.) C.C.Berg	Iroko	Moraceae	P	-	10	202
Pericopsis elata (Harms) Meeuwen	Afrormosia (Assaméla)	Fabaceae	P	-	15	156
Prioria oxyphylla (Harms) Breteler	Tchitola	Fabaceae	ST	10	-	100
Terminalia superba Engl. & Diels	Limba (Fraké)	Combretaceae	P	10	-	100
Total				128	70	2,304

2.3. *Planting*

Tree planting was carried out within gaps created by logging. The shape and size of the logging gaps varied depending on the logged tree size and species. The average size of the gaps was 265.8 ± 175.4 m² (Doucet et al., 2009). Trees were planted in the centre of the gaps between 2004 and 2009 with a single species per gap (Fig. 1; Table 1). Planted seedlings were produced in the nursery of the Pallisco Company. Seeds were harvested on well-conformed local mature trees and sown in polyethylene bags. After germination, the growth of the seedlings was monitored in the nursery. Once the seedlings reached 40 cm in height (after 7 to 12 months in average), the most vigorous trees were transplanted in logging gaps. Shade-tolerant species (*D. crassiflora* and *P. oxyphylla*) were planted in the smallest gaps as they were assumed to tolerate low-light conditions. At contrast, pioneer species were planted in the largest gaps.

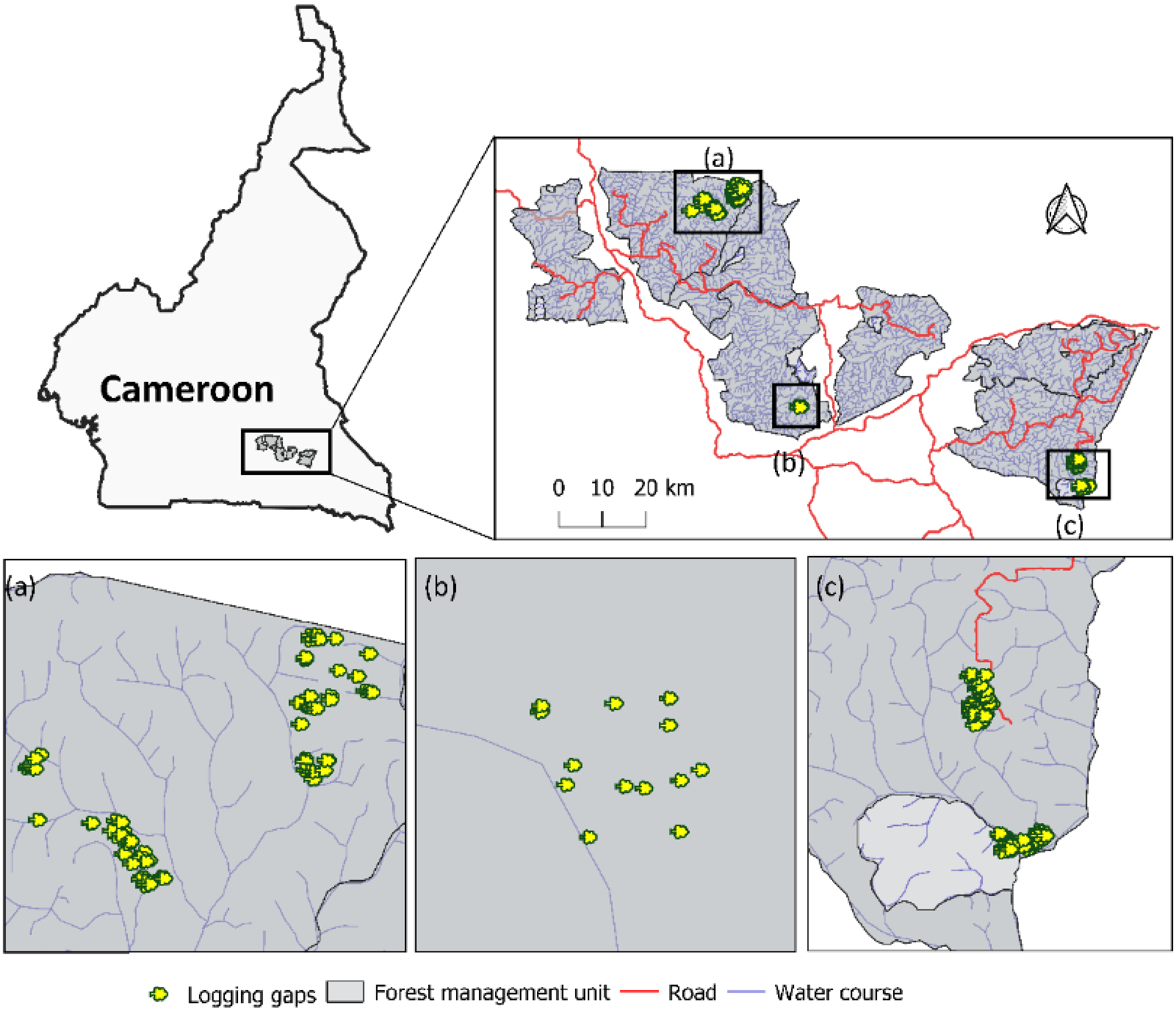

Fig. 1. Location of the study logging gaps in the South-Eastern Cameroon

Two plantation spacings were used (3 m x 4 m and 2 m x 4 m) and 4 to 11 seedlings of a single species were planted in the logging gaps of 207 to 271 m², 15 to 41 seedlings in the gaps of 271 m² to 400 m², and up to 89 seedlings in the gaps larger than 400 m² (Table 1).

After 12 months, competing vegetation in the entire planting area of the gap was cut only once using a machete.

2.4. Data collection

Survival, diameter (at 10 cm and at 1.3 m from the collar) and height were recorded for each tree at each measurement campaign. Total height was measured from the collar to the terminal bud of the trunk using a Vertex IV dendrometer for the trees taller than 2 m or using a ruler for the trees shorter than or equal to 2 m. Diameter was measured directly with a calliper (for trees with a diameter less or equal to 8 cm) or with a girth tape (trees with diameter larger than 8 cm).

Four measurement campaigns were carried out: one immediately after planting, one 1-2 years after planting, one 2.3-6 years after planting and one 14.3-19 years after planting (Table 2). Some gaps were not monitored at the 2.3-6 years after planting due to logistical issues. Data were collected between 2004 and 2010, depending on the year of planting in each gap. The final monitoring occurred in 2023. The measurements were carried out mostly between January and April, and in few cases between September and October. The extent of these periods was linked to operational constraints related to the access to the different remote areas where roads were closed after logging.

Different abiotic variables were also collected such as gap topography (Table S1). Nevertheless, as no significant relationships could be found with these variables, we do not present these analyses in this manuscript.

Table 2. Monitoring periods for each study species.

Species	Monitoring periods		
	1-2 years	2.3-6 years	14.3-19 years
Afzelia bipindensis	x		x
Baillonella toxisperma	x	x	x
Bobgunnia fistuloides	x		x
Detarium macrocarpum	x	x	x
Diospyros crassiflora	x		x
Entandrophragma angolense	x		x
Entandrophragma cylindricum	x		x
Entandrophragma utile	x	x	x
Erythrophleum suaveolens	x	x	x
Lovoa trichilioides	x		x
Mansonia altissima	x	x	x
Milicia excelsa	x	x	x
Pericopsis elata	x		x
Prioria oxyphylla	x		x
Terminalia superba	x		x

2.5. Data calculation

At each monitoring time and for each gap, we computed the survival rate S_t (%) with Eq. 1. We then computed the annual survival rate S_{an} (%) with Eq. 2 (Sheil et al. 1995).

$$S_t = \frac{N_t * 100}{N_0} \qquad (1)$$

$$S_{an} = 100 - \{[1 - \left(\frac{N_t}{N_0}\right)^{\frac{1}{t}}] * 100\} \quad (2)$$

Where N_0 and N_t were population counts at the beginning and at the measurement time t in years, respectively.

Mean diameter and height were averaged for each gap to ensure having the same number of observations per gap. Mean diameter increment (ΔD in mm yr^{-1}) and mean height increment (ΔH in cm yr^{-1}) were computed using Eq. 3:

$$\Delta y = \frac{\bar{y}_{t=m} - \bar{y}_{t=n\,(m>n)}}{(m-n)/365.25} \qquad (3)$$

with $\bar{y}$ being the mean diameter (or height) of trees planted in a common gap and measured at two different censuses t_n and t_m (in days). Δy was computed over the different possible periods. As a large number of trees had not reached 1.3 m in diameter during censuses, the mean diameter increment was computed using diameters measured at 10 cm above the ground.

2.6. Statistical analysis

Survival rate (S_{an}), diameter increment (ΔD) and height increment (ΔH) were modelled using linear mixed-effects models (LMM) to account for the variability across species and gaps. The models were fitted with the *lmer* function of the "lme4" (version 1.1-30) R package (Bates et al., 2015). We considered only the gap (ρ_j) as random effect while species (S_i), species guild (G), period (A) and their interactions were analysed as fixed effects (Eq. 4, 5).

$$y'_{ij} = \mu + b_{1,A_{ij}} + b_{2,S_{ij}} + b_{3,A_{ij}*S_{ij}} + \rho_j + \varepsilon_{ij} \qquad (4)$$

$$y'_{ij} = \mu + b_{1,A_{ij}} + b_{2,G_i} + b_{3,A_{ij}*G_i} + \rho_j + \varepsilon_{ij} \qquad (5)$$

With $\rho_j \sim \mathrm{N}(0, \sigma_\rho^2)$ and $\varepsilon_{ij} \sim \mathrm{N}(0, \sigma_\varepsilon^2)$

Parameters b_1, b_2 and b_3 were the model fixed coefficients. y_{ij} were the responses variables computed for each gap j and species i. The responses variables ΔD, ΔH and S_{an}, were transformed using respectively: $y' = \log_e(y + 1)$, $y' = \sqrt{y}$, and $y' = \sin^{-1}\sqrt{y}$. The best models were selected using a stepwise approach examining the Akaike Information Criterion (AIC), and likelihood ratio tests using the *anova* function of the "lme4" (version 1.1-30) R package (Bates et al., 2015). A Tukey-adjusted *post-hoc* test was used to compare the predicted means of each factor and interaction using the *emmeans* function of the "emmeans" (version 1.8.1-1) R package. To account for potential heterogeneity that could arise from differences in individual growth across the three periods tested, Eq. 4 was additionally fitted separately for each period. The conditional and marginal R^2 were computed to assess the proportion of variance explained by the model with the random effects (conditional R^2) or without them (marginal R^2). They were computed with the *r.squaredGLMM* function of the “MuMIn” (version 1.47.1) package (Barton, 2022). We performed all analyses in the statistical software R version 4.2.1 (R Core Team, 2022), using the “ggplot2” (version 3.3.6) package (Wickham, 2016) for plotting.

3. Results

3.1. Tree survival rates

For all species, the mean annual survival rate (S_{an}) varied significantly across periods ($F = 90.7$, p-value < 0.001) and species ($F = 11$, p-value < 0.001) (Table 3). The mean annual survival rate was 92.4 ± 11.7% 1-2 years after planting (t_1). It slightly decreased through time. This decreased was nevertheless not significantly lower during the second period (2.3-6 years after planting) than during the first period (t_2; 91.9 ± 17.4%; $t = -1.9$; p-value = 0.065). It was then significantly lower with the data recorded during the last campaign (14.3-19 years after planting, t_3; 60.3 ± 45%; $t = -12.9$; p-value < 0.05) (Fig. 2a and Table S2). At t_3, *D. macrocarpum* had the highest annual survival rate (98.3%), followed by *E. suaveolens* (97.5%), *T. superba* (94.6%), *B. toxisperma* (89.8%), *P. oxyphylla* (85%) and *A. bipindensis* (81%) (Fig. 2a). The annual survival rate of the other species was less than 80% and all *E. cylindricum* trees were dead at t_3 (0% of survival; Fig. 2a). Among the eight species with annual survival rates above the mean (92.4%) at t_1, four species (*M. excelsa*, *P. elata*, *M. altissima* and *E. utile*) showed a decline in survival at t_3 (Fig. 2a and Table S3). In contrast to the other species, *T. superba* increased its annual survival rate between t_1 and t_3 (Fig. 2a).

The mixed effect model (Eq. 5 and Table S4) showed that tree survival depended on species guild ($F = 4.2$, p-value < 0.05), and period ($F = 104$, p-value < 0.001). Pioneer species had significantly a higher annual survival rate than non-pioneer light-demanding species ($t = -2.9$; p-value < 0.01). The marginal and conditional R^2 of the model were 25% and 39%, respectively (Table S4).

Table 3. Parameter estimates of the linear mixed models examining the effect of species (15 species, Table 1), period (factoring in tree levels: 1-2 years, 2.3-6 years and 14.3-19 years, respectively) and tree size (tree diameter or height) on survival rates, height and diameter increments (Eq. 4). DF are the degrees of freedom for the fixed effects. Significant relationships are denoted with * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

		Annual survival		Diameter increment		Height increment	
Fixed effects	DF	*F*-value	*p*-value	*F*-value	*p*-value	*F*-value	*p*-value
Species (S_i)	14	11.0	***	30.04	***	28.60	***
Period (A_t)	2	90.73	***	7.21	***	32.64	***
S_i* A_t	19	-	-	9.33	***	9.34	***
Models statistics							
R^2c (%)		40.8		73.1		71	
R^2m (%)		40.3		64.7		61.3	

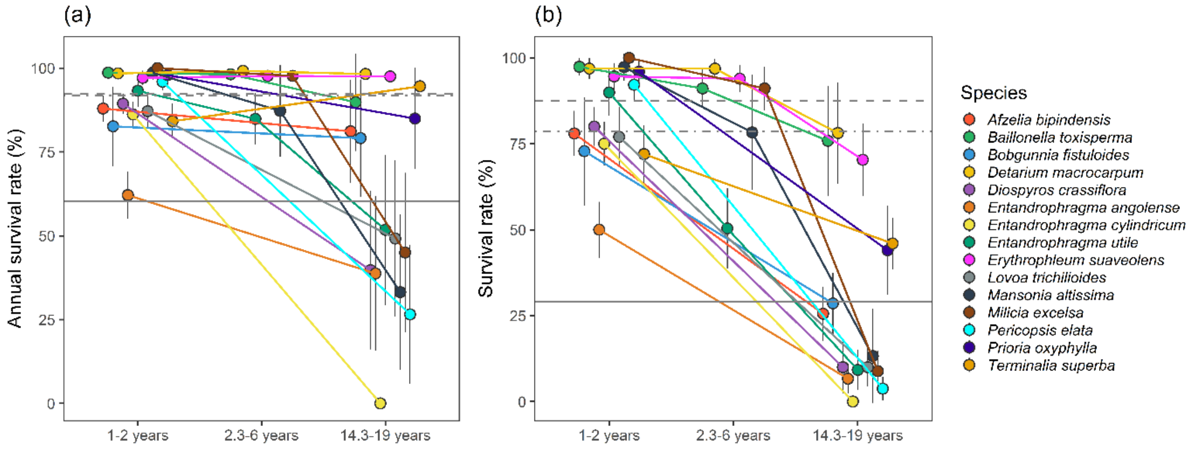

Fig. 2. Average (and standard deviations) planted tree (a) annual survival rate (S_{an}), and (b) Survival rate (S_t) over three monitored periods for the 15 study species. The dashed, dot-dashed and solid horizontal lines indicate the overall means for periods 1-2 years, 2.3-6 years and 14.3-19 years, respectively.

3.2. Annual diameter increment

For all species, the mean diameter increment was 2.9 ± 4.1 mm.yr^{-1} and varied significantly across species ($F = 30$, p-value < 0.001) and periods ($F = 7.2$, p-value < 0.001), with a significant interaction between period and species ($F = 9.3$, p-value < 0.001). The best model (Eq. 4; Table 2) explained 68% and 73% of variance (the marginal and conditional R^2, respectively). The mean diameter increment was the highest (3.4 mm.yr^{-1}) at t_1 and decreased in the following periods. It was significantly lower at t_2 (1.9 mm.yr^{-1}; $t = -9.5$; p-value < 0.001) but not significantly lower at t_3 (2.9 mm.yr^{-1}; $t = 1.4$; p-value $= 0.171$) as outlined on Fig. 3a and Table S2. The effect of age between periods was not significant at t_1 ($t = 1.54$; p-value $=$ 0.127) or t_2 ($t = -1.55$; p-value $= 0.128$), but was marginally significant at t_3 ($t = -2.04$; p-value $= 0.044$) (Table S5).

Terminalia superba had the highest diameter increments across all periods with an increase that was not significant between t_1 and t_3 ($t = 1.58$; p-value $= 0.116$). At t_1, *T. superba* had significantly the highest diameter increment (13.6 ± 8.0 mm.yr^{-1}; $t = 12.6$; p-value < 0.001; n = 20), followed by *M. excelsa* (6.7 ± 1.9 mm.yr^{-1}; $t = 8.2$; p-value < 0.001; n =10), *P. elata* (5.1 ± 2.2 mm.yr^{-1}; $t = 8.2$; p-value < 0.001; n = 30), *B. toxisperma* (4.9 ± 2.4 mm.yr^{-1}; $t = 6.8$; p-value < 0.001; n =16), *B. fistuloides* (3.2 ± 1.8 mm.yr^{-1}; $t = 4.5$; p-value < 0.001; n = 13), and *E. suaveolens* (2.6 ± 1.0 mm.yr^{-1}; $t = 4.8$; p-value < 0.001; n = 28). The other species had diameter increments lower than 2 mm.yr^{-1} (Fig. 3a and Table S6). Among the six monitored species at t_2 (*B. toxisperma*, *M. excelsa*, *E. suaveolens*, *M. altissima*, *E. utile* and *D. macrocarpum*), *B. toxisperma* had the highest diameter increment (2.7 mm.yr^{-1}) followed by *E. suaveolens* (2.6 mm.yr^{-1}) and *M. altissima* (2.0 mm.yr^{-1}). The other species had diameter increments of less than 2 mm.yr^{-1} (Fig. 3a and Table S6).

At t_3 (Table 4), *T. superba* had the highest diameter increments (15.8 ± 6.6 $mm.yr^{-1}$, n = 10), followed by *L. trichilioides* (3.2 ± 1.0 $mm.yr^{-1}$, n = 5) and *B. toxisperma* (2.8 ± 3.6 $mm.yr^{-1}$, n =20). The other species had diameter increments lower than 2 $mm.yr^{-1}$ (Fig. 3a and Table S6).

Comparing the diameter increments between species guilds (Eq. 5 and Table S4) at t_1 and t_3 (where all species were monitored), pioneer species showed significantly higher diameter increments than non-pioneer light-demanding species at t_1 (5.9 ± 5.5 $mm.yr^{-1}$, n =105 and 1.8 ± 2.1 $mm.yr^{-1}$, n =99; $t = 9.1$; p-value < 0.001). This difference was no longer significant at t_3 (4.8 ± 7.1 $mm.yr^{-1}$, n =41 and 2.1 ± 2.4 $mm.yr^{-1}$, n = 56; $t = 2.3$; p-value = 0.063) (Fig. 4a). Shade-tolerant species had significantly lower diameter increment (0.9 ± 0.6 $mm.yr^{-1}$, n =35) than pioneer species at t_1 ($t = 8.3$; p-value < 0.001), but the difference was not significant when compared to non-pioneer light-demanding species ($t = 2.1$; p-value = 0.087). At t_3 shade-tolerant species grew significantly slower than pioneer species ($t = 4.4$; p-value < 0.001) and non-pioneer light-demanding species ($t = 3.1$; p-value < 0.01, Fig. 4a). The model statistics are shown in Table S4.

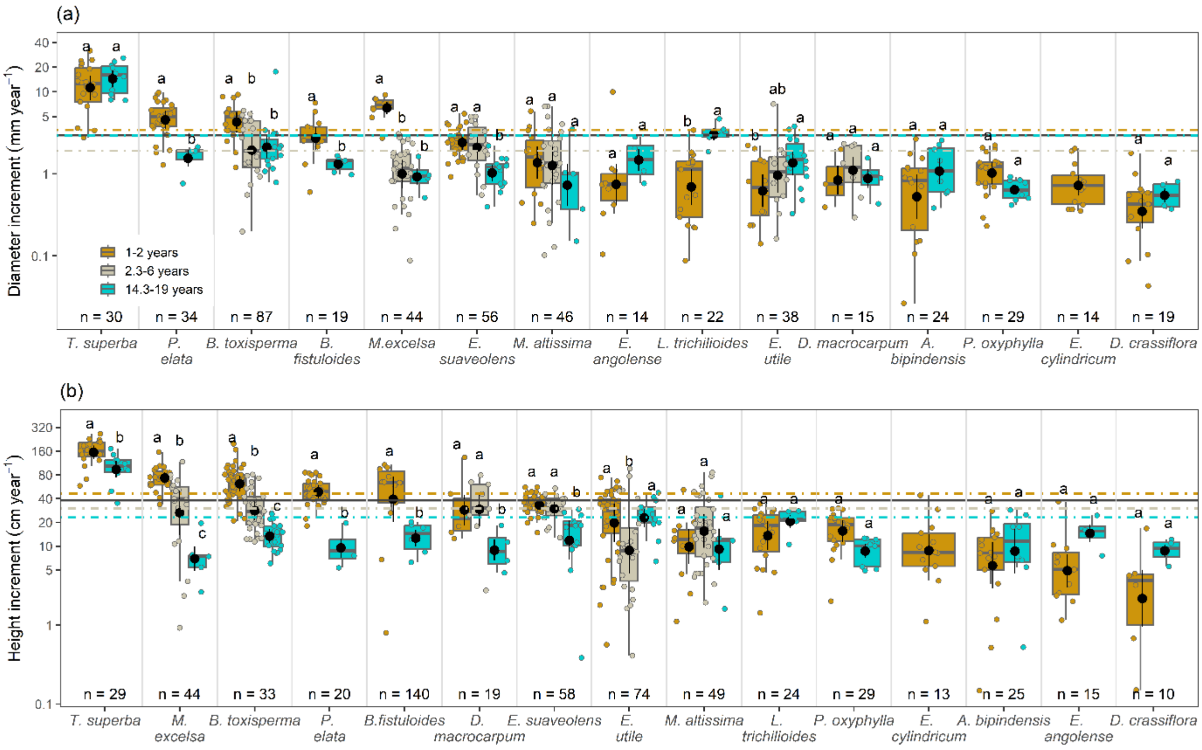

Fig. 3. Growth of 15 native tree species planted in logging gaps. Distinct coloured boxplots are (a) diameter and (b) height increments of planted trees monitored 1-2 years, 2.3-6 years and 14.3- 19 years after planting. The *y*-axis is plotted with a natural logarithmic scale. The coloured points (*n*) are the mean increments of each gap and census. The black dots are the species-specific mean increment surrounded by bars denoting the corresponding standard deviation. Significant differences are shown by different letters using Tukey-adjusted post-hoc test (more details on Table S6 and S7). The black solid horizontal lines indicates the overall mean for the 3 monitoring periods (2.95 mm.yr^{-1} and 38.11 cm.yr^{-1} for diameter and height increments, respectively). Line colours correspond to the mean values of the monitoring periods.

Table 4. Sizes (diameter and height) of the studied species at the end of the monitoring time (age). *n* is the number of gaps and Sd is the standard deviation. Final measurements of all species were conducted between January and April 2023.

				Diameter (cm)			Height (m)		
Species	Planting year	Age (year)	*n*	Mean ± Sd	Min	Max	Mean ± Sd	Min	Max
Afzelia bipindensis	2008	14.8	8	2.6 ± 1.2	1.5	4.4	2.5 ± 1.3	1.0	4.3
Baillonella toxisperma	2004-2005	19.0	20	6.3 ± 4.9	2.4	26.1	5.1 ± 0.9	3.2	6.8
Bobgunnia fistuloides	2008	14.9	6	2.8 ± 0.5	2.0	3.2	3.5 ± 0.8	2.6	4.3
Detarium macrocarpum	2005	17.9	4	3.1 ± 0.7	2.4	4.1	3.4 ± 0.4	3.0	3.9
Diospyros crassiflora	2008	14.9	4	1.4 ± 0.2	1.2	1.6	1.5 ± 0.3	1.1	1.9
Entandrophragma angolense	2008	14.3	4	3.1 ± 1.1	1.7	4.3	2.4 ± 0.9	1.2	3.4
Entandrophragma cylindricum	2008	14.8	10	-	-	-	-	-	-
Entandrophragma utile	2004-2008	19.0	14	3.6 ± 1.4	1.6	5.8	4.3 ± 1.7	1.8	6.6
Erythrophleum suaveolens	2007	15.8	13	2.9 ± 0.7	1.7	4.6	3.6 ± 1.2	1.7	5.7
Lovoa trichilioides	2008	14.9	5	5.0 ± 1.3	3.3	7.0	3.6 ± 1.1	2.0	4.6
Mansonia altissima	2005	18.0	5	3.9 ± 2.5	2.0	8.1	4.1 ± 3.1	1.4	9.5
Milicia excelsa	2004	18.4	5	2.8 ± 0.9	1.6	3.7	2.7 ± 1.0	1.8	4.4
Pericopsis elata	2008	14.9	4	4.2 ± 0.5	3.5	4.5	3.1 ± 0.8	2.4	4.2
Prioria oxyphylla	2008	14.8	9	1.6 ± 0.2	1.3	1.8	2.1 ± 0.3	1.6	2.5
Terminalia superba	2008	14.8	10	23.8 ± 8.4	13.4	34.8	17.1 ± 5.4	7.7	24.4

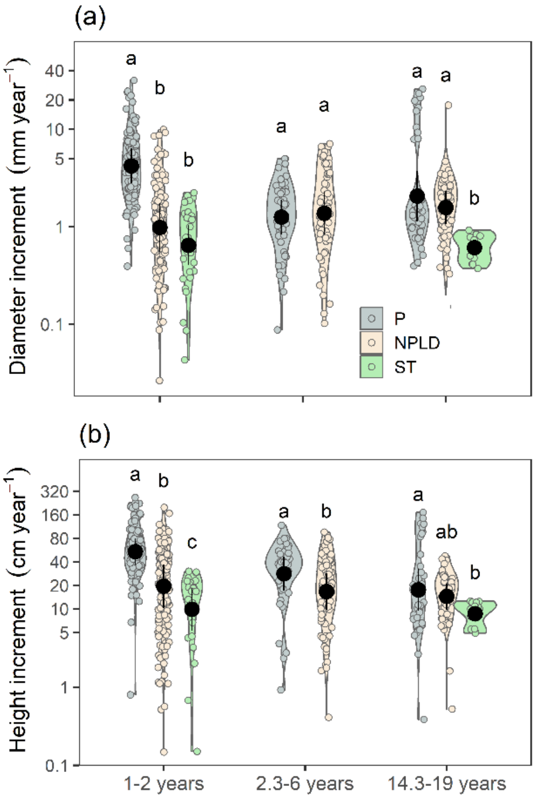

Fig. 4. Diameter and height increments of planted species in logging gaps, grouped by guild: P, pioneer; NPLD, non-pioneer light-demanding; and ST, shade-tolerant species. The *y*-axis is plotted with a natural logarithmic scale. The black dots with standard deviations are the means of (a) diameter and (b) height increments. The significant differences are shown by different letters using Tukey-adjusted post-hoc test. Shade-tolerant species were not monitored between 2.3 to 6 years.

3.3. Annual Height increment

The mean height increment varied significantly across species ($F = 28.6$, p-value < 0.001) and periods ($F = 32.6$, p-value < 0.001), with a significant interaction between period and species ($F = 9.3$, p-value < 0.001). The selected best model (Eq. 4; Table 2) explained 61.3% and 71% of variance (the marginal and conditional R^2, respectively). The mean height increment was the highest (46.7 cm.yr^{-1}) at t_1 and decreased in the following periods. It was significantly lower at t_2 (30.1 cm.yr^{-1}; $t = -5.3$; p-value < 0.001) and at t_3 (23.2 cm.yr^{-1}; $t = 0.83$;

p-value = 0.407) as outlined (Fig. 3b and Table S2). The age effect between periods was not significant at t_1 (t = -0.50; p-value = 0.617) or t_3 (t = -0.55; p-value = 0.585), but was significant at t_2 (t = -2.91; p-value < 0.01) (Table S8). *T. superba* had the highest height increments across periods (Fig. 3b). Seven species (*T. superba*, *M. excelsa*, *P. elata*, *B. fistuloides*, *B. toxisperma*, *D. macrocarpum* and *E. suaveolens*) had significantly higher height increments at t_1 than t_3 (Fig. 3b and 7).

At t_1, *T. superba* had significantly higher height increment (165.0 ± 54.0 cm.yr^{-1}; t = 15.9; p-value < 0.001) than *M. excelsa* (77.3 ± 26.9 cm.yr^{-1}; t = 8.8; p-value < 0.001), *B. toxisperma* (68.2 ± 32.4 cm.yr^{-1}; t = 9.5; p-value < 0.001), *B. fistuloides* (59.4 ± 34.1 cm.yr^{-1}; t = 6.6; p-value < 0.001) and *P. elata* (51.9 ± 18.1 cm.yr^{-1}; t = 7.6; p-value < 0.001). The other species had a height increment lower than 45 cm.yr^{-1} (Fig. 3b). Among the six monitored species at t_2, *M. excelsa* had significantly higher height increment (42.9 ± 30.2 cm.yr^{-1}, n =19) than *D. macrocarpum* (39.6 ± 24.8 cm.yr^{-1}; t = 3.1; p-value < 0.01), *B. toxisperma* (33.2 ± 19.9 cm.yr^{-1}; t = 0.3; p-value = 0.791), *E. suaveolens* (32.0 ± 11.8 cm.yr^{-1}; t = 3.4; p-value < 0.001), *M. altissima* (23.5 ± 21.5 cm.yr^{-1}; t = 5.0; p-value < 0.001) and *E. utile* (19.3 ± 25.8 cm.yr^{-1}; t = 2.0; p-value < 0.05) (Fig. 3b and Table S7).

At t_3 (Table 4), *T. superba* had significantly the highest height increments (103.0 ± 41.2 cm.yr^{-1}, n = 10), followed by *E. utile* (25.7 ± 11.6 cm.yr^{-1}, n = 13), *L. trichilioides* (21.8 ± 7.1 cm.yr^{-1}, n = 5), *E. suaveolens* (16.3 ± 8.6 cm.yr^{-1}, n = 13), *E. angolense* (15.8 ± 7.0 cm.yr^{-1}, n = 4) and *M. altissima* (15.2 ± 16.5 cm.yr^{-1}, n = 5). The other species had height increments of less than 15 cm.yr^{-1} (Fig. 3b), and significant effects are presented on Table S7.

Height increment was negatively correlated with tree height for *B. toxisperma* (r = -0.55; p-value < 0.001), *E. suaveolens* (r = -0.39; p value < 0.001), *M. excelsa* (r = -0.51; p-value <

0.001), *P. elata* (r = -0.54; p-value < 0.001), *P. oxyphylla* (r = -0.61; p-value < 0.001) and *T. superba* (r = -0.39; p-value < 0.05), but positively correlated with height for *M. altissima* (r = 0.56; p-value < 0.001; Fig. 5). The other species did not have significant correlations between height increment and tree height.

The height increments varied between species guilds at t_1 and t_3 (Eq. 5 and Fig. 4b). Pioneer species had significantly greater height increments than non-pioneer light-demanding at t_1 (70.4 ± 53.1 cm.yr^{-1}, n =118 and 34.6 ± 32.6 cm.yr^{-1}, n =163; t = 7.9; p-value < 0.001), and this difference was no longer significant at t_3 (34.5 ± 43.8 cm.yr^{-1}, n =42 and 17.9 ± 10.3 cm.yr^{-1}, n = 55; t = 2.23; p-value < 0.063) (Fig. 4b). Shade-tolerant species had significantly lower height increments (14.9 ± 9.2 cm.yr^{-1}, n =26) than pioneer species at t_1 (t = 7.1; p-value < 0.001), and non-pioneer light-demanding species (t = 2.7; p-value < 0.05). At t_3 the height increment of shade-tolerant species (9.2 ± 3.0 cm.yr^{-1}, n = 13) was also significantly lower than that of pioneer species (t = 2.5; p-value < 0.05), but the difference was not significant when compared to non-pioneer light-demanding species (t = 1.1; p-value = 0.524; Fig. 4b and Table S4).

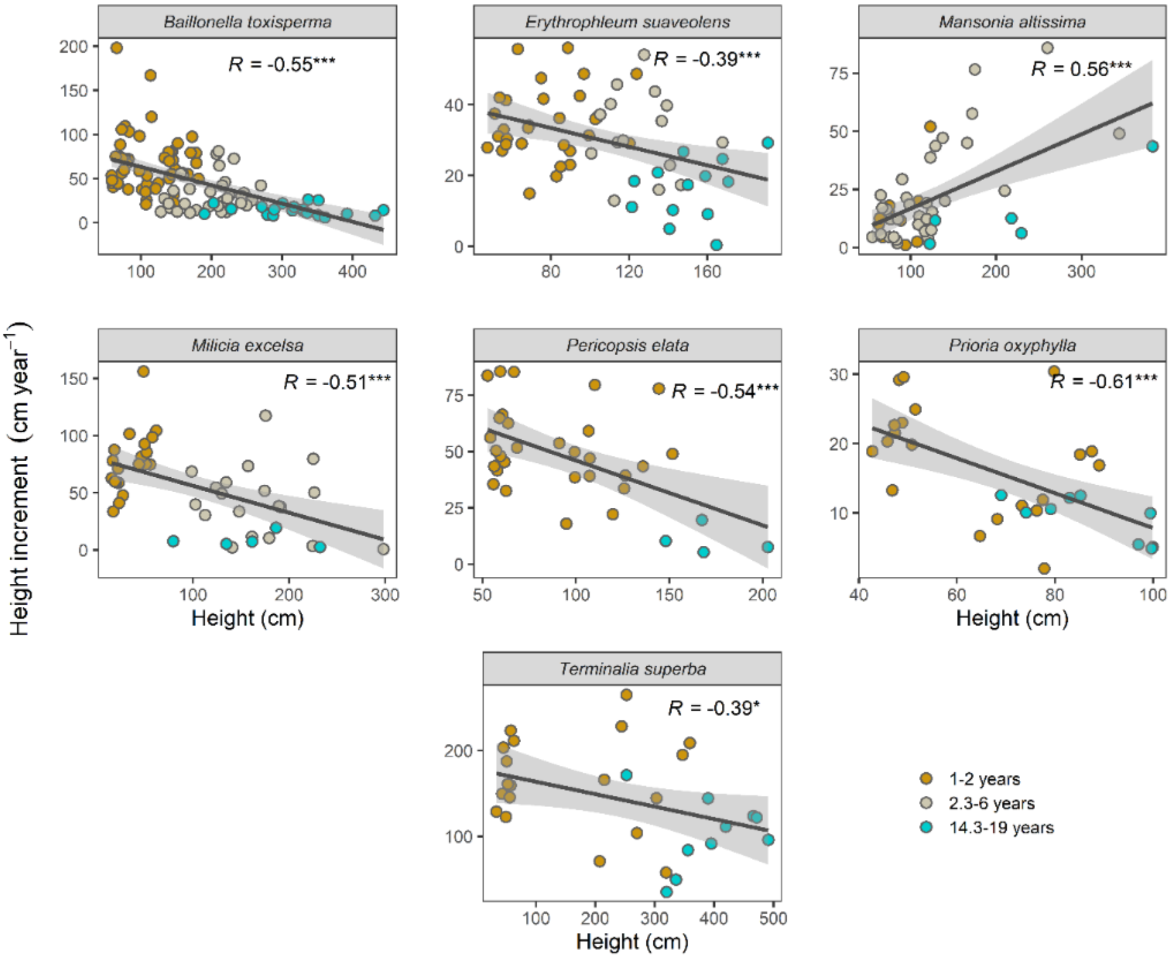

Fig. 5. Significant relationships between height increments and tree height for seven species planted in logging gaps in south-eastern Cameroon. The grey area around the line shows the 95% confidence interval. The correlation coefficient and the corresponding *p*-value (*$p < 0.05$; ***$p < 0.001$) are provided.

4. Discussion

Enrichment of logging gaps could be considered as an effective option to mitigate the impact of timber exploitation on logged tree populations, but only for species whose planted trees can thrive in gaps (Doucet et al., 2009; Sovu et al., 2010; Millet et al., 2013; Makemba et al., 2022). This latter issue was little documented, and this study brought key elements using 14-19 year-long monitoring of 2,304 planted trees belonging to 15 species including pioneer (P, 6 species), non-pioneer light-demanding (NPLD, 7 species) and shade-tolerant species (ST, 2 species; Table 1). Shade-tolerant species were less represented as at least 90% of the logged species in the Central African region are P and NPLD (Ruiz et al., 2005; Makana and Thomas, 2006).

4.1. High variability in survival rates across species

The survival of the planted trees is expected to vary across species and planting methods (Makana and Thomas, 2005; Hall, 2008; Ilunga-Mulala et al., 2025). Survival varied substantially across species (Fig. 2) and the survival rates was found satisfactory for a very limited set of species. For the other species, the survival rates might have been limited by interspecific competition, light availability, herbivory and insect attacks.

Only four species (*B. toxisperma*, *D. macrocarpum*, *E. suaveolens, T. superba*) had good survival rates, which were in the order of magnitude of previous studies. For these species, 45% of the planted trees survived up to 19 years after planting (annual survival rate $S_{an} \geq 90\%$, Fig. 2b and Table S3).

The survival rates of planted *B. toxisperma* can be high but may critically depends on the availability of light. In our study area, the mean annual survival rate (S_{an}) in gaps of *B. toxisperma* ranged between 90 and 99% (with $S_t = 76 - 97\%$) with the lower survival rates being observed for older plantations. Such good survival rates had already been reported for plantation of *B. toxisperma* in gaps ($S_{an} = 93\%$, Koumba Zaou et al., 1998; Daïnou et al., 2021) and in understorey plantations, i.e. in low-light conditions ($S_t = 94\%$ six years after planting) (Koumba Zaou et al., 1998). According to Daïnou et al. (2021), in central Africa, the survival rate of *B. toxisperma* plantations could be lower in high-light conditions such as in degraded areas ($S_{an} = 87\text{-}89\%$ after six years). Plantations of *B. toxisperma* might therefore perform better in shaded or partially shaded environments, such as in gaps, at least during the first years after the plantation.

High survival rates of *D. macrocarpum*, *E. suaveolens* and *T. superba* had also been reported, although such estimates remains scarce and limited to specific conditions (Doucet et al. 2016; Daïnou et al., 2021). After 14 years, we found that 78% of the *D. macrocarpum* trees had survived (S_t = 97% after six years; S_t = 78% and S_{an} = 89% after 14 years; Table S3). According to Doucet et al. (2016), two years after planting, the survival rate (S_t) of *D. macrocarpum* was about 92% in degraded areas, in Cameroon. Unlike other species, and despite its commercial importance, no other studies have examined *D. macrocarpum* plantations outside Cameroon in the Guinean-Congolian region. Concerning *E. suaveolens*, the survival rate was found to be relatively constant and high over the different monitoring periods (S_{an} = 97%). Some estimates of *E. suaveolens* have been reported for degraded areas (S_t = 88%) after two years (Doucet et al. 2016) and (S_{an} = 97%) after six years (Daïnou et al., 2021) in few sites in Cameroon. Similarly, the observed survival rate of *T. superba* (S_t = 46% after 15 years; S_t = 72% after two years) was nearly equivalent to that estimated in degraded forest (S_t = 51%) in DR Congo (Liegois and Petit 1950) or in Cameroon (S_t = 84%) (Doucet et al. 2016).

The other species had lower survival rates. For instance, the observed survival rates in plantations of *Entandrophragma* spp. ranged between S_{an} = 0 and 52% (S_t = 0 and 9%), 14 to 19 years after planting. *Entandrophragma* spp. are known to exhibit highly variable survival rates in plantations (Dupuy, 1990; Makana and Thomas, 2005; Ilunga-Mulala et al., 2025) and very high mortality rates (S_t = 12 to 37%) have particularly been found for *E. cylindricum* when planted in forest understorey (Hall, 2008).

Light availability was presumably a key limiting factor for the light-demanding species. Indeed, in high-light environments, higher survival rates had been found for *E. cylindricum* at least during the first years after planting (Hubert, 2003; Makana and Thomas, 2005; Cerisier, 2010). Survival (S_t) was estimated at 92% two years after planting (Makana and Thomas, 2005), 77-80% 11-14 years after planting (Liegois and Petit 1950; Beligné 1986) in DR Congo; and 50% 50 years after planting in Cameroon (Owona Ndongo et al., 2009). At contrast, in low-light condition, *E. cylindricum* can have very low survival rates (<37%) as early as six months after planting (Hall, 2008). Though different factors are in play, the limited size of the gaps and their closure through time (Neves et al., 2019) can likely explains the low survival rates observed in gaps, especially for light-demanding species such as *E. cylindricum.*

Seedling predation by herbivores is another possible cause of mortality in forest gaps (Schupp et al., 1989; Hall, 2008; Sovu et al., 2010; Makemba et al., 2022). Duiker (*Cephalophus sp, Philantomba congica*) and sitatunga (*Tragelaphus spekii*) browse leaves (Daïnou et al., 2021), slowing down plant growth and reducing survival rates. These animals can moreover preferentially browse in gaps (Makemba et al., 2022) leading to high browsing rate up to 88% for *E. cylindricum* (Hall, 2008; Blervacq, 2023).

Finally, the survival of several species can be affected by insect attacks. Parasitism by *Phytollyma lata* is very common for *M. excelsa* (Nichols et al., 1999; Bosu et al., 2006; Agyeman et al., 2009) and by *Hypsipyla* spp. for *Etandrophragma* spp. (Hall, 2008; Daïnou et al., 2021). Mortality was high in *M. excelsa* saplings (survival S_t = 9% at 18 years) and there was a significant decline in growth rates over time (Fig. 2b). We identified a few individuals with attacks of the gall-making psyllid which was previously identified as one cause of *M. excelsa* mortality in Cameroon (Fayolle et al., 2015). While parasitism does not necessarily lead to plant mortality, repeated attacks on the terminal bud considerably slow down growth and competitiveness. In Ghana, only 20% of *M. excela* trees survived psyllid attack nine years after planting (Nichols et al., 1998; Bosu et al., 2006).

4.2. Species-specific growth rates in gaps

Only very competitive species are likely able to thrive in gap plantations (Duah-Gyamfi et al., 2014; Navarro-Martínez et al., 2017). In our study, *T. superba* was the only species showing satisfactory growth rates. *Terminalia superba* is known to be a vigorous species showing sustained growth in plantations at different sites (Donis, 1956; Liegois, 1959; Marien and Mallet, 2004; Bosu et al., 2006; De Ridder et al., 2010; Doucet et al., 2016; Akaffou et al., 2021), although this had not yet been demonstrated in logging gaps (Ilunga-Mulala et al., 2025). The observed growth rate was nevertheless higher (16 $mm.yr^{-1}$) than that of larger trees (~4.5 $mm.yr^{-1}$) (Ligot et al., 2022). Its growth potential in plantations was likely limited in gaps. Larger diameter increment were indeed observed in degraded areas (~20 $mm.yr^{-1}$) (Liegois and Petit 1950; Catinot, 1965; Hubert 2003; Doucet et al., 2016).

The growth of the other species were increasingly affected through time by the surrounding competition and canopy closure (Doucet et al., 2009). For instance, the diameter increment of *B. toxisperma* was around 4.9 $mm.yr^{-1}$ the two first years. However, this growth rate declined over time to about 2.8 $mm.yr^{-1}$ after 15 years. It is likely that this species, as many others, could not outcompete the surrounding vegetation (Coomes and Grubb, 1998; Schnitzer et al., 2005; Rozendaal et al., 2020). Several factors such as environmental changes conditions, resource competition and climatic events or disturbances could explain the growth difference between periods. However, the variability in diameter growth between trees ages was not significant between 1-2 years and 2.3-6 years, and marginally significant between 14.3-19 years (Table S5).

Additionally, in the context of predicting the success of tree planting in gaps, our results question the relevance of the growth-survival trade-off between fast-growing species without adaptative structures to resist to stressful conditions and slow-growing species with structures that allow them to tolerate stressful conditions (Meira-Neto et al., 2019; Hérault et al., 2020). Most species exhibiting large growth at the seedling stage have often, indeed, fragile crown architecture. For instance, *M. excelsa* can grow fast, but its fragile crown makes it very vulnerable to falling branches, mammal damages and liana infestation. Yet, in gaps, the species planted must be fast-growing, tolerant to low-light conditions and tolerant to various stem damages. This explains why only a very limited set of species could be successfully planted in gaps. Most other species are rapidly dominated by surrounding vegetation, leading in a reduced allocation of resources to root reserves (Cahill and Casper 2002; Engelbrecht and Kursar, 2003; Madsen et al., 2021). This shift often results in reduced diameter growth, stem resistance, and resistance to herbivory and insect attacks.

In the competitive environment of gaps, it seems particularly important to plant vigorous seedlings. Part of the unexplained growth variation could have been attributed to species-specific genetic variation (Ofori et al., 2007; Ilunga-Mulala et al., 2021; Akaffou et al., 2021; Schmitt et al., 2023; Angbonda et al., 2024) and seedling production methods. In this study, 40-cm-tall seedlings were planted because this method provided good plantation results in degraded forests (Doucet et al., 2016). In gaps, given the low survival rates observed for many species, future studies might evaluate whether planting taller seedlings could be an interesting solution.

Better plantation maintenance could also have improved the performance of planted trees in the gap (Romell et al., 2008; Doucet et al., 2009; Ouédraogo et al., 2014; Neves et al., 2019). Plantation maintenance was only carried out the first years after the planting. During this period, the survival rate was generally higher for most of the study species (Fig. 2). For some other species, including *A. bipindensis*, a species listed in Appendix II of CITES, the initial growth rate was very low (Fig. 3), indicating that plantation maintenance might not have been enough. Nevertheless, increasing plantation maintenance might not always be possible given its cost (Schulze, 2008) and given that plantation might become hardly accessible several years after logging. This is particularly the case in the concessions certified for sustainable management. For these species, plantations should be preferably carried out in easily accessed area such as degraded areas or loading yards along the main permanent roads.

4.3. Guild provided indications of species performance but was a poor indicator of plantation success

After small-scale disturbance such as in logging gaps, it was expected that early successional species could outperform the other species. Consequently, the species guild was assumed to be an important proxy for choosing the appropriate planting method for species (Ilunga-Mulala et al., 2025).

Nevertheless, we have only depicted weak differences in plantation success across guilds supporting that some pioneer species might be better suited for gap enrichment. Indeed, only one species was found to developed well, *T. superba* (S_{an} = 94.6%) a pioneer species. On average, the pioneer species had higher growth rates than the other species, but the difference was small and only significant the two first years after planting (Fig. 4).

Moreover, putting *T. superba* aside, *B. toxisperma,* a non-pioneer light-demanding species, grew significantly faster than many other species.

Species could have different resource allocation strategies even within the same guild (Poorter and Evans, 1998), which could explain the competitive advantage of *T. superba*. It could have a photosynthetic capacity that may enable efficient light use under the gap conditions, supporting sustained growth. Additionally, *T. superba* may tolerate nutrient-poor soils, especially since the soils are already poor in the studied site (Vleminckx et al., 2017). The only two shade tolerant species, *P. oxyphylla* and *D. crassiflora*, seemed the less adapted showing low growth and survival rates. However, our sample was limited to only 15 species, highlighting the need for similar monitoring for other important pioneer species, including the two most logged in central Africa (*Aucoumea klaineana* Pierre and *Triplochiton scleroxylon* K. Schum).

4.4. Study limitations

While this study provides insight into the performance of species in logging gaps, some limitations remain. Sparse sampling over the 2.3-6 years may have influenced the results. Although abiotic factors may influence tree performance in more variable landscapes, minimal variation in elevation and slope likely explains their lack of significance here, justifying their exclusion from further analysis.

5. Conclusions

Identifying species with high survival and growth rates in logging gap is crucial for the success of gap enrichment. This study provides valuable contributions to the understanding of the survival and growth performance of 15 high-value native tree species planted in logging gaps in Central Africa, based on a long-term monitoring. Among the studied species, *T. superba* was the best performing species in gaps, with a high growth rate (with mean diameter increment of 15.8 mm.yr^{-1}). Its annual survival rate increased through time and reached 94.6%, 14.8 years after planting. Planted *T. superba* trees in logging gaps could survive and grow well. Other planted species such as *B. toxisperma*, *E. suaveolens* and *D. macrocarpum* which had annual survival rates higher than 89% at age between 15.8 and 19 years could survive and grow well in gaps but maintenance must then be carried out regularly.

CRediT authorship contribution statement

Crispin Ilunga-Mulala: Conceptualization, Methodology, Data curation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Gauthier Ligot**: Conceptualization, Methodology, Validation, Writing – review & editing, Supervision. **Achille Bernard Biwolé**: Conceptualization, Methodology, Writing – review & editing, Supervision. **Nils Bourland**: Planting, Writing – review & editing. **Yves Brostaux**: Methodology, Writing – review & editing. **Fousseni Fétéké**: Writing – review & editing. **Yanick Serge Nkoulou**: Writing – review & editing. **Stephane Tchakoudeu**: Writing – review & editing. **Benjamin Cerisier**: Conceptualization, Planting, Methodology, Writing – review & editing. **Guillaume Neve**: Writing – review & editing. **Jean-Louis Doucet**: Funding acquisition, Conceptualization, Methodology, Writing – review & editing, Supervision.

Competing Interests

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

Acknowledgements

This study was supported with the financial assistance of the European Union (CRIS: 2020/419-588) through the project Reforestation of the forest management units of Cameroon (UFA-Reforest), implemented by the Association Technique Internationale des Bois Tropicaux (ATIBT) and Nature+ asbl. It was also made possible with the support of the Applied

Research in Ecology and Social Sciences in Support of the Sustainable Management of Forest Ecosystems in Central Africa (RESSAC) program implemented by CIFOR-ICRAF, and with the financial assistance of the European Union. We thank the hosted company Pallisco-CIFM. Thanks to our field team for their hard work, especially to Nkomo Nkomo David, Mbam Samuel, Kengni Di Clovis, Djompande Crépin and Jean-Yves De Vleeschouwer for logistical assistance.

References

Agyeman, V.K., Ofori, D.A., Cobbinah, J.R., Wagner, M.R., 2009. Influence of *Phytolyma Lata* (Homoptera: Psyllidae) on seedling growth of *Milicia excelsa*. Ghana J. For. 25.

Agyeman, V.K., Swaine, M.D., Thompson, J., Kyereh, B., Duah-Gyamfi, A., Foli, E.G., 2010. A comparison of tree seedling growth in artificial gaps of fifferent sizes in two constrating forest types. Ghana J. For. 26, 14–40.

Akaffou, S.D., Kouame, A.K., Gore, N.B.B., Abessika, G.Y., Kouassi, H.K., Hamon, P., Sabatier, S., Duminil, J., 2021. Effect of the seeds provenance and treatment on the germination rate and plants growth of four forest trees species of Côte d'Ivoire. J. For. Res. 32, 161–169. https://doi.org/10.1007/s11676-019-01064-y

Angbonda, D.M., Ilunga-Mulala, C., Bourland, N., Beeckman, H., Boyemba, F., Hatakiwe, H., Ngongo, J.P., Hardy, O.J., 2024. Inbreeding depression affects the growth of seedlings of an African timber species with a mixed mating reproductive system, *Pericopsis elata* (Harms) Meeuwen. Heredity (Edinb). https://doi.org/10.1038/s41437-024-00709-x

ATIBT, 2016. Nomenclature générale des bois tropicaux. Association Technique Internationale des Bois Tropicaux, Nogent-sur-Marne, France, p 340.

Baker, T.R., Burslem, D.F.R.P., Swaine, M.D., 2003. Associations between tree growth, sol fertility and water availability at local and regional scales in Ghanaian tropical rain forest. J. Trop. Ecol. 19, 109–125. https://doi.org/10.1017/S0266467403003146

Barton, K., 2022. MuMIn: Multi-Model Inference, R Package Version 1.46. 0. 2022.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–51. https://doi.org/10.18637/jss.v067.i01

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future köppen-geiger climate classification maps at 1-km resolution. Sci. Data 5, 1–12. https://doi.org/10.1038/sdata.2018.214

Beckage, B., Clark, Ja.S., 2003. Seedling survival and growth of three forest tree species: the role of spacial heterogeneity. Ecology 84, 1849–1861.

Beligné, V., 1986. Essais de plantations forestiers en forêt de Deng-Deng. Centre de recherches forestières, Nkolbisson, p 54.

Blervacq, R., 2023. Interactions trophiques entre mammifères et espèces ligneuses d'intérêt commercial dans une forêt du sud-est Cameroun. Université de Liège.

Bonnell, T.R., Reyna-Hurtado, R., Chapman, C.A., 2011. Post-logging recovery time is longer than expected in an East African tropical forest. For. Ecol. Manage. 261, 855–864. https://doi.org/10.1016/j.foreco.2010.12.016

Bosu, P.P., Cobbinah, J.R., Nichols, J.D., Nkrumah, E.E., Wagner, M.R., 2006. Survival and growth of mixed plantations of *Milicia excelsa* and *Terminalia superba* 9 years after planting in Ghana. For. Ecol. Manage. 233, 352–357. https://doi.org/10.1016/j.foreco.2006.05.032

Bourgeois, C., MacKenzie, R.A., Sharma, S., Bhomia, R.K., Johnson, N.G., Rovai, A.S., Worthington, T.A., Krauss, K.W., Analuddin, K., Bukoski, J.J., Castillo, J.A., Elwin, A., Glass, L., Jennerjahn, T.C., Mangora, M., Marchand, C., Osland, M.J., Ratefinjanahary, I.A., Ray, R., Salmo III, S.G., Sasmito, S.D., Suwa, R., Tinh, P.H., Trettin, C.C., 2024. Four decades of data indicate that planted mangroves stored up to 75% of the carbon stocks found in intact mature stands. Sci. Adv. 5430, 1–12. https://doi.org/10.1126/sciadv.adk5430

Brancalion, P.H.S., Holl, K.D., 2020. Guidance for successful tree planting initiatives. J. Appl. Ecol. 57, 2349–2361. https://doi.org/10.1111/1365-2664.13725

Brokaw, N.V.L., 1985. Gap-Phase Regeneration in a Tropical Forest. Ecology 66, 682–687.

Brown, H.C.A., Berninger, F.A., Larjavaara, M., Appiah, M., 2020. Above-ground carbon stocks and timber value of old timber plantations, secondary and primary forests in southern Ghana. For. Ecol. Manage. 472, 118236. https://doi.org/10.1016/j.foreco.2020.118236

Cahill, J.J.F., Casper, B.B., 2002. Canopy gaps are sites of reduced belowground plant competition in a productive old field. Plant Ecol. 164, 29–36.

Catinot, R., 1965. Sylviculture tropicale en forêt dense africaine 5e partie: perspectives d'aménagement. Bois Forets des Trop. 104, 17–29. https://doi.org/10.19182/bft1965.100.a18965

Cerisier, B., 2010. Evaluation de divers essais sylvicoles d ' enrichissement des trouées d ' abattage en forêt dense humide camerounaise. Dissertation. Université de Liège.

Cerullo, G.R., Edwards, D.P., 2019. Actively restoring resilience in selectively logged tropical forests. J. Appl. Ecol. 56, 107–118. https://doi.org/10.1111/1365-2664.13262

Coomes, D.A., Grubb, P.J., 1998. Responses of juvenile trees to above- and belowground competition in nutrient-starved amazonan rain forest. Ecology 79, 768–782.

Costa, R., Pinheiro, C., Vidal, E., Schwartz, G., 2021. Technical and financial evaluation of enrichment planting in logging gaps with the high-value species *Swietenia macrophylla* and *Handroanthus serratifolius* in the Eastern Amazon. For. Ecol. Manage. 495. https://doi.org/10.1016/j.foreco.2021.119380

Daïnou, K., Bauduin, A., Bourland, N., Fétéké, F., Doucet, J., 2011. Soil seed bank characteristics in Cameroonian rainforests and implications for post-logging forest recovery. Ecol. Eng. 37, 1499–1506. https://doi.org/10.1016/j.ecoleng.2011.05.004

Daïnou, K., Tosso, F., Bracke, C., Bourland, N., Forni, É., Hubert, D., Mbuya K., A., Loumeto, Jean Joël Louppe, D., Ngomanda, A., Ngomin, A., Tchuante tite, Valérie Doucet, J.-L., 2021. Guide pratique des plantations d'arbres des forêts denses humides d'Afrique. Presses Universitaires de Liège, p 320.

De Ridder, M., Hubau, W., Van Den Bulcke, J., Van Acker, J., Beeckman, H., 2010. The potential of plantations of *Terminalia superba* engl. & diels for wood and biomass production (Mayombe Forest, Democratic Republic of Congo). Ann. For. Sci. 67. https://doi.org/10.1051/forest/2010003

Donis, C., 1956. La forêt dense congolaise et l'état actuel de sa sylviculture. Bull. Agric. du Congo Belge 47, 261–320.

Doucet, J., Daïnou, K., Ligot, G., Ouédraogo, D., Bourland, N., Ward, S.E., Tekam, P., Lagoute, P., Fayolle, A., Bourland, N., Ward, S.E., Tekam, P., Lagoute, P., Fayolle, A., 2016. Enrichment of Central African logged forests with high-value tree species : testing a new approach to regenerating degraded forests. Int. J. Biodivers. Sci. Ecosyst. Serv. Manag. 3732, 1–13. https://doi.org/10.1080/21513732.2016.1168868

Doucet, J., Kouadio, Y.L., Monticelli, D., Lejeune, P., 2009. Enrichment of logging gaps with moabi (*Baillonella toxisperma* Pierre) in a Central African rain forest. For. Ecol. Manage. 258, 2407–2415. https://doi.org/10.1016/j.foreco.2009.08.018

Duah-Gyamfi, Akwasi, Kyereh, B., Adam, K.A., Agyeman, V.K., Swaine, M.D., 2014. Natural Regeneration Dynamics of Tree Seedlings on Skid Trails and Tree Gaps Following Selective Logging in a Tropical Moist Semi-Deciduous Forest in Ghana. Open J. For. 4, 49–57. https://doi.org/10.4236/ojf.2014.41009

Duah-Gyamfi, A., Swaine, E.K., Adam, K.A., Pinard, M.A., Swaine, M.D., 2014. Can harvesting for timber in tropical forest enhance timber tree regeneration? For. Ecol. Manage. 314, 26–37. https://doi.org/10.1016/j.foreco.2013.11.025

Duhesme, C., Gally, M., Glannaz, S., Hervo, C., Kone, Y., Lescuyer, G., Mbonayem, L., Nakoe, P., Kessy, A.N., Lahann, P., Pasquier, A., Serrano, O., van Loon, T., 2021. L'évolution des filières bois dans le bassin du Congo, in: Etat Des Forêts. pp. 37–78.

Dupuy, B., 1990. Essais de comportement en plantation de 58 especes ivoiriennes de forêt dense humide. Centre technique forestier tropical, Abidjan, p 58., Centre technique forestier tropical.

Engelbrecht, B.M.J., Kursar, T.A., 2003. Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia 136, 383–393. https://doi.org/10.1007/s00442-003-1290-8

Fayolle, A., Ouédraogo, D.-Y.Y., Ligot, G., Daïnou, K., Bourland, N., Tekam, P., Doucet, J.L., 2015. Differential performance between two timber species in forest logging gaps and in plantations in Central Africa. Forests 6, 380–394. https://doi.org/10.3390/f6020380

Fayolle, A., Swaine, M.D., Bourland, N., Comiskey, J.A., Dauby, G., Doucet, J., Kouame, N., 2014. Patterns of tree species composition across tropical African forests. J. Biogeogr. 1–12. https://doi.org/10.1111/jbi.12382

Felton, A., Felton, A.M., Wood, J., Lindenmayer, D.B., 2006. Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. For. Ecol. Manage. 235, 186–193. https://doi.org/10.1016/j.foreco.2006.08.011

Fétéké, F., Nkolong, E., Hubert, D., 2004. Unités forestières d'aménagement 10-041, 10-042 et 10-044 regroupées. Management Plan, Pallisco. Douala, Cameroon.

FRMi, 2018. Vision stratégique et industrialisation de la filière bois en Afrique Centrale, horizon 2030. Rapport de la Banque Africaine de Développement.

Gorel, A.P., Hardy, O.J., Dauby, G., Dexter, K.G., Segovia, R.A., Steppe, K., Fayolle, A., 2022. Climatic niche lability but growth form conservatism in the African woody flora. Ecol. Lett. 25, 1164–1176. https://doi.org/10.1111/ele.13985

Gorel, A.P., Steppe, K., Beeckman, H., De Baerdemaeker, N.J.F., Doucet, J.L., Ligot, G., Daïnou, K., Fayolle, A., 2019. Testing the divergent adaptation of two congeneric tree species on a rainfall gradient using eco-physio-morphological traits. Biotropica 51, 364–377. https://doi.org/10.1111/btp.12646

Gourlet-Fleury, S., Mortier, F., Fayolle, A., Baya, F., Ouédraogo, D., Bénédet, F., Picard, N., 2013. Tropical forest recovery from logging: A 24 year silvicultural experiment from Central Africa. Philos. Trans. R. Soc. B Biol. Sci. 368. https://doi.org/10.1098/rstb.2012.0302

Hall, J.S., 2008. Seed and seedling survival of African mahogany (*Entandrophragma* spp.) in the Central African Republic: Implications for forest management. For. Ecol. Manage. 255, 292–299. https://doi.org/10.1016/j.foreco.2007.09.050

Hawthorne, W.D., 1995. Ecological Profiles of Ghanaian Forest Trees. Tropical forestry papers (29). Oxford forestry institute.

Hérault, B., N’Guessan, A.K., Ouattara, N., Ahoba, A., Bénédet, F., Coulibaly, B., Doua-Bi, Y., Koffi, T., Koffi-Konan, J.C., Konaté, I., Tiéoulé, F., Wourro, F., Zo-Bi, I.C., Louppe, D., 2020. The long-term performance of 35 tree species of sudanian West Africa in pure and mixed plantings. For. Ecol. Manage. 468, 118171. https://doi.org/10.1016/j.foreco.2020.118171

Horne, J., 2013. A guide to lesser known tropical timber species, Horne, J. (2013). A guide to lesser known tropical timber species. Gland: WWF International. Available online at: https://www. worldwildlife. org/publications/guide-to-lesser-known-tropical-timber-species.

Houngbégnon, F.G.A., Gillet, J.F., Michaux, J., Brostaux, Y., Zébazé, D., Lhoest, S., Vermeulen, C., Sonké, B., Doucet, J.L., 2023. Seed dispersal by duikers in selectively logged rainforests: Overlooked dispersal of an important animal community. For. Ecol. Manage. 529, 120650. https://doi.org/10.1016/j.foreco.2022.120650

Howlett, B.E., Davidson, D.W., 2003. Effects of seed availability, site conditions, and herbivory on pioneer recruitment after logging in Sabah, Malaysia. For. Ecol. Manage. 184, 369–383. https://doi.org/10.1016/S0378-1127(03)00161-0

Hubert, D., 2003. Sylviculture des essences de forêts denses humides d’Afrique de l’Ouest. Projet PROGERFOR, République de Guinée-Conakry.

Ilunga-Mulala, C., Doucet, J.-L., Biwolé, A.B., Bourland, N., Ligot, G., 2025. Performance of native tree species in plantations: a synthesis for the Guineo-Congolian region. J. For. Res. 36. https://doi.org/10.1007/s11676-024-01817-4

Ilunga-Mulala, C., Hatakiwe, H., Beeckman, H., Hardy, O.J., Ligot, G., Assumani, D., Ndjele, L., Bourland, N., 2021. Influence of spacing and seed trees on the growth of *Pericopsis elata* saplings during the first twenty months of a planting trial. Biotechnol. Agron. Soc. Env. 25, 32–44. https://doi.org/10.25518/1780-4507.18866

Imai, N., Seino, T., Aiba, S. ichiro, Takyu, M., Titin, J., Kitayama, K., 2012. Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales. Plant Ecol. 213, 1413–1424. https://doi.org/10.1007/s11258-012-0100-y

Jans, L., Poorter, L., van Rompaey, R.S.A.R. Van, Bongers, F., 1993. Gaps and Forest Zones in Tropical Moist Forest in Ivory Coast. Biotropica 25, 258–269.

Karsten, R.J., Jovanovic, M., Meilby, H., Perales, E., Reynel, C., 2013. Regeneration in canopy gaps of tierra-firme forest in the Peruvian Amazon: Comparing reduced impact logging and natural, unmanaged forests. For. Ecol. Manage. 310, 663–671. https://doi.org/10.1016/j.foreco.2013.09.006

Karsten, R.J., Meilby, H., Larsen, J.B., 2014. Regeneration and management of lesser known timber species in the Peruvian Amazon following disturbance by logging. For. Ecol. Manage. 327, 76–85. https://doi.org/10.1016/j.foreco.2014.04.035

Keefe, K., Schulze, M.., Pinheiro, C., Zweede, J.C., Zarin, D., 2009. Enrichment planting as a silvicultural option in the eastern Amazon: Case study of *Fazenda Cauaxi*. For. Ecol. Manage. 258, 1950–1959. https://doi.org/10.1016/j.foreco.2009.07.037

Koumba Zaou, P., Nze, S., Mapaga, D., Delaporte, P., 1998. Croissance de 13 essences de bois d'œuvre plantées en forêt gabonaise. Bois Forêts des Trop. 256, 21–33.

Letouzey, R., 1985. Notice de la carte phytogéographique du Cameroun au 1:500.000. Toulouse.

Liegois, P., 1959. Arboretum de Stanleyville. Bull. Agric. du Congo Belge 50, 35–75.

Liegois, P., Petit, L., 1950. L'Aboretum de Stanleyville. Bull. Agric. du Congo Belge 41, 1–10.

Ligot, G., Gourlet-Fleury, S., Dainou, K., Gillet, J.F., Rossi, V., Mazengué, M., Ekome, S.N., Nkoulou, Y.S., Zombo, I., Forni, E., Doucet, J.L., 2022. Tree growth and mortality of 42 timber species in central Africa. For. Ecol. Manage. 505, 119889. https://doi.org/10.1016/j.foreco.2021.119889

Madsen, C., Kunz, M., von Oheimb, G., Hall, J., Sinacore, K., Turner, B.L., Potvin, C., 2021. Influence of neighbourhoods on the extent and compactness of tropical tree crowns and root systems. Trees - Struct. Funct. 35, 1673–1686. https://doi.org/10.1007/s00468-021-02146-3

Makana, J., Thomas, S.C., 2005. Effects of Light Gaps and Litter Removal on the Seedling Performance of Six African Timber Species. Biotropica 37, 227–237. https://doi.org/10.1111/j.1744-7429.2005.00030.x

Makana, J.R., Thomas, S.C., 2006. Impacts of selective logging and agricultural clearing on forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo. Biodivers. Conserv. 15, 1375–1397. https://doi.org/10.1007/s10531-005-5397-6

Makemba, R.N., Tosso, F., Moupela, C., Ligot, G., Brostaux, Y., 2022. Enrichment of Logging Gaps with High-Value Timber Species : How Far Fertilizer, Biochar and Mammal Predation Affect Performances of *Cylicodiscus gabunensis* Harms Seedlings. Forests 13.

Malizia, A., Grau, R.H., 2008. Landscape context and microenvironment influences on liana communities within treefall gaps. J. Veg. Sci. 19, 597–604. https://doi.org/10.3170/2008-8-18413

Mantel, S., Dondeyne, S., Deckers, S., 2023. World reference base for soil resources (WRB). Encycl. Soils Environ. Second Ed. 1–12. https://doi.org/10.1016/B978-0-12-822974-3.00161-0

Marien, J., Mallet, B., 2004. Nouvelles perspectives pour les plantations forestières en Afrique centrale. Bois Forets des Trop. 282, 67–79.

Medjibe, V.P., Putz, F.E., Starkey, M.P., Ndouna, A.A., Memiaghe, H.R., 2011. Impacts of selective logging on above-ground forest biomass in the Monts de Cristal in Gabon. For. Ecol. Manage. 262, 1799–1806. https://doi.org/10.1016/j.foreco.2011.07.014

Meira-Neto, J.A.A., Cândido, H.M.N., Miazaki, Â., Pontara, V., Bueno, M.L., Solar, R., Gastauer, M., 2019. Drivers of the growth–survival trade-off in a tropical forest. J. Veg. Sci. 30, 1184–1194.

Millet, J., Tran, N., Ngoc, V.N., Thi, T.T., Prat, D., 2013. Enrichment planting of native species for biodiversity conservation in a logged tree plantation in Vietnam. New For. 44, 369–383. https://doi.org/10.1007/s11056-012-9344-6

Navarro-Cerrillo, R.M., Griffith, D.M., Ramírez-Soria, M.J., Pariona, W., Golicher, D., Palacios, G., 2011. Enrichment of big-leaf mahogany (*Swietenia macrophylla* King) in logging gaps in Bolivia: The effects of planting method and silvicultural treatments on long-term seedling survival and growth. For. Ecol. Manage. 262, 2271–2280. https://doi.org/10.1016/j.foreco.2011.08.020

Navarro-Martínez, A., Palmas, S., Ellis, E.A., Blanco-reyes, P., Vargas-Godínez, C., Iuit-Jiménez, A.C., Hernández-Gómez, I.U., Ellis, P., Álvarez-Ugalde, A., Carrera-quirino, Y.G., Armenta-montero, S., Putz, F.E., 2017. Remnant Trees in Enrichment Planted Gaps in Quintana Roo, Mexico: Reasons for Retention and Effects on Seedlings. Forests 8, 1–11. https://doi.org/10.3390/f8080272

Negreros-Castillo, P., Mize, C.W., 2008. Regeneration of mahogany and Spanish cedar in gaps created by railroad tie extraction in Quintana Roo, Mexico. For. Ecol. Manage. 255, 308–312. https://doi.org/10.1016/j.foreco.2007.09.052

Neves, L.R., Schwartz, G., Alves, J. do C., Miranda, F., 2019. Post-harvesting silvicultural treatments in canopy logging gaps : Medium- term responses of commercial tree species under tending and enrichment planting. For. Ecol. Manage. 451, 117521. https://doi.org/10.1016/j.foreco.2019.117521

Nichols, D.J., Wagner, M.R., Agyeman, V.K., Paul Bosu, Cobbinah, J.R., 1998. Influence of artificial gaps in tropical forest on survival, growth, and *Phytolyma lata* attack on *Milicia excelsa*. For. Ecol. Manage. 110, 353–362. https://doi.org/10.1016/S0378-1127(98)00299-0

Nichols, J.D., Ofori, D.A., Wagner, M.R., Bosu, P., Cobbinah, J.R., 1999. Survival, growth and gall formation by *Phytolyma lata* on *Milicia excelsa* established in mixed-species tropical plantations in Ghana. Agric. For. Entomol. 1, 137–141. https://doi.org/10.1046/j.1461-9563.1999.00014.x

Noce, S., Caporaso, L., Santini, M., 2020. A new global dataset of bioclimatic indicators. Sci. Data 7, 1–12. https://doi.org/10.1038/s41597-020-00726-5

Numata, S., Yasuda, M., Okuda, T., Kachi, N., Supardi, M.N.N., 2006. Canopy gap dynamics of two different forest stands in a Malaysian lowland rain forest. J. Trop. Ecol. 18, 109–116.

Ofori, D.A., Opuni-Frimpong, E., Cobbinah, J.R., 2007. Provenance variation in Khaya species for growth and resistance to shoot borer *Hypsipyla robusta*. For. Ecol. Manage. 242, 438–443. https://doi.org/10.1016/j.foreco.2007.01.090

Okimori, Y., Kikuchi, J., Hardiwinoto, S., 2006. Effect of Enrichment Planting on Restoring the Logged-Over Dipterocarps in a Tropical Rainforest of Central Sumatra. Plant. Technol. Trop. For. Sci. 231–238.

Ouédraogo, D., Fayolle, A., Daïnou, K., Demaret, C., Bourland, N., Lagoute, P., Doucet, J., 2014.

Enrichment of Logging Gaps with a High Conservation Value Species (*Pericopsis elata*) in a Central African Moist Forest. Forests 5, 3031–3047. https://doi.org/10.3390/f5123031

Owona Ndongo, P.A., Peltier, R., Linjouom, I., Louppe, D., Smektala, G., Béligné, V., Njoukam, R., Tieche, B., Temgoua, L.F., 2009. Plantations de bois d'oeuvre en zone équatoriale africaine : cas de l'arboretum de l'Enef de Mbalmayo au sud du Cameroun. Bois Forets Des Trop. 299, 37. https://doi.org/10.19182/bft2009.299.a20421

Pena-Claros, M., Fredericksen, T.S., Alarcon, A., Blate, G.M., Choque, U., Leano, C., Licona, J.C., Mostacedo, B., Pariona, W., Villegas, Z., Putz, F.E., 2008. Beyond reduced-impact logging : Silvicultural treatments to increase growth rates of tropical trees. For. Ecol. Manage. 256, 1458–1467. https://doi.org/10.1016/j.foreco.2007.11.013

Poorter, H., Evans, J.R., 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. Oecologia 116, 26–37.

Putz, F.E., Zuidema, P.A., Synnott, T., Peña-Claros, M., Pinard, M.A., Sheil, D., Vanclay, J.K., Sist, P., Gourlet-Fleury, S., Griscom, B., Palmer, J., Zagt, R., 2012. Sustaining conservation values in selectively logged tropical forests: The attained and the attainable. Conserv. Lett. 5, 296–303. https://doi.org/10.1111/j.1755-263X.2012.00242.x

R Core Team, 2022. A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, Foudation for Statistical Computing, version 4.2.1. Vienna.

Réjou-Méchain, M., Mortier, F., Bastin, J.F., Cornu, G., Barbier, N., Bayol, N., Bénédet, F., Bry, X., Dauby, G., Deblauwe, V., Doucet, J.L., Doumenge, C., Fayolle, A., Garcia, C., Kibambe Lubamba, J.P., Loumeto, J.J., Ngomanda, A., Ploton, P., Sonké, B., Trottier, C., Vimal, R., Yongo, O., Pélissier, R., Gourlet-Fleury, S., 2021. Unveiling African rainforest composition and vulnerability to global change. Nature 593, 90–94. https://doi.org/10.1038/s41586-021-03483-6

Romell, E., Hallsby, G., Karlsson, A., Garcia, C., 2008. Artificial canopy gaps in a Macaranga spp. dominated secondary tropical rain forest-Effects on survival and above ground increment of four under-planted dipterocarp species. For. Ecol. Manage. 255, 1452–1460. https://doi.org/10.1016/j.foreco.2007.11.003

Rozendaal, D.M.A., Phillips, O.L., Lewis, S.L., Affum-Baffoe, K., Alvarez-Davila, E., Andrade, A., Aragão, L.E.O.C., Araujo-Murakami, A., Baker, T.R., Bánki, O., Brienen, R.J.W., Camargo, J.L.C., Comiskey, J.A., Djuikouo Kamdem, M.N., Fauset, S., Feldpausch, T.R., Killeen, T.J., Laurance, W.F., Laurance, S.G.W., Lovejoy, T., Malhi, Y., Marimon, B.S., Marimon, B.H.J., Marshall, A.R., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Poorter, L., Reitsma, J., Silveira, M., Sonké, B., Sunderland, T., Taedoumg, H., Steege, H., Terborgh, J.W., Umetsu, R.K., van der Heijden, G.M.F., Vilanova, E., Vos, V., White, L.J.T., Willcock, S., Zemagho, L., Vanderwel, M.C., 2020. Competition influences tree growth, but not mortality, across environmental gradients in Amazonia and tropical Africa. Ecology 101, 1–11. https://doi.org/10.1002/ecy.3052

Ruiz, M., Ezzine, D., Nasi, R., Sayer, J.A., Sassen, M., Angoué, C., Gami, N., Ndoye, O., Ngono, G., Nguinguiri, J.-C., Nzala, D., Toirambe, B., Yalibanda, Y., 2005. Logging in the Congo Basin : A multi-country characterization of timber companies. For. Ecol. Manage. 214, 221–236. https://doi.org/10.1016/j.foreco.2005.04.020

Schmitt, S., Hérault, B., Derroire, G., 2023. High intraspecific growth variability despite strong evolutionary heritage in a neotropical forest. Ecol. Lett. 1–12. https://doi.org/10.1111/ele.14318

Schnitzer, S.A., Kuzee, M.E., Bongers, F., 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. J. Ecol. 93, 1115–1125. https://doi.org/10.1111/j.1365-2745.2005.01056.x

Schulze, M., 2008. Technical and financial analysis of enrichment planting in logging gaps as a potential component of forest management in the eastern Amazon. For. Ecol. Manage. 255, 866–879. https://doi.org/10.1016/j.foreco.2007.09.082

Schulze, M., Zweede, J., 2006. Canopy dynamics in unlogged and logged forest stands in the eastern Amazon. For. Ecol. Manage. 236, 56–64. https://doi.org/10.1016/j.foreco.2006.08.333

Schupp, E.W., Howe, H.F., Augspurger, C.K., Levey, D.J., 1989. Arrival and survival in tropical treefall gaps. Ecology 70, 562–564.

Schwartz, G., Falkowski, V., Peña-Claros, M., 2017a. Natural regeneration of tree species in the Eastern Amazon: Short-term responses after reduced-impact logging. For. Ecol. Manage. 385, 97–103. https://doi.org/10.1016/j.foreco.2016.11.036

Schwartz, G., Lopes, J.C.., Mohren, G.M.., Peña-claros, M., 2013. Post-harvesting silvicultural treatments in logging gaps : A comparison between enrichment planting and tending of natural regeneration. For. Ecol. Manage. 293, 57–64. https://doi.org/10.1016/j.foreco.2012.12.040

Schwartz, G., Pereira, P.C.G., Siviero, M.A., Pereira, J.F., Ruschel, A.R., Yared, J.A.G., 2017b. Enrichment planting in logging gaps with *Schizolobium parahyba var. amazonicum* (Huber ex Ducke) Barneby: A financially profitable alternative for degraded tropical forests in the Amazon. For. Ecol. Manage. 390, 166–172. https://doi.org/10.1016/j.foreco.2017.01.031

Sheil, D., Burslem, D.F.R.P., Alder, D., 1995. The Interpretation and Misinterpretation of Mortality Rate Measures. J. Ecol. 83, 331–333.

Sloan, S., 2024. The qualified prevalence of natural and planted tropical reforestation. Commun. Earth Environ. 5. https://doi.org/10.1038/s43247-024-01437-0

Sovu, Tigabu, M., Savadogo, P., Odén, P.C., Xayvongsa, L., 2010. Enrichment planting in a logged-over tropical mixed deciduous forest of Laos. J. For. Res. 21, 273–280. https://doi.org/10.1007/s11676-010-0071-6

Swaine, M.D., Agyeman, V.K., 2008. Enhanced Tree Recruitment Following Logging in Two Forest Reserves in Ghana. Biotropica 40, 370–374.

Toledo-Aceves, T., Swaine, M.D., 2008. Above- and below-ground competition between the liana *Acacia kamerunensis* and tree seedlings in contrasting light environments. Plant Ecol. 196, 233–244. https://doi.org/10.1007/s11258-007-9347-0

Vleminckx, J., Doucet, J.L., Morin-Rivat, J., Biwolé, A.B., Bauman, D., Hardy, O.J., Fayolle, A., Gillet, J.F., Daïnou, K., Gorel, A., Drouet, T., 2017. The influence of spatially structured soil properties on tree community assemblages at a landscape scale in the tropical forests of southern Cameroon. J. Ecol. 105, 354–366. https://doi.org/10.1111/1365-2745.12707

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Second Edition.

Yamamoto, S., 2000. Forest Gap Dynamics and Tree Regeneration. J. For. Res. 5, 223–229. https://doi.org/10.1007/BF02767114

Zébazé, D., Gorel, A., Gillet, J.-F., Houngbégnon, F., Barbier, N., Ligot, G., Lhoest, S., Kamdem, G., Libalah, M., Droissart, V., Sonké, B., Doucet, J.-L., 2023. Natural regeneration in tropical forests along a disturbance gradient in South-East Cameroon. For. Ecol. Manage. 547, 121402. https://doi.org/10.1016/j.foreco.2004.06.007