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ORIGINAL PAPER

Performance of native tree species in plantations: a synthesis for the Guineo-Congolian region

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Abstract In the rainforests of the Guineo-Congolian region, several native tree species have been tested in plantations established with different silvicultural methods and objectives. The results of these experiments remained scattered, hampering our ability to identify the key drivers of variability in survival and growth of planted species. In this study, we carried out a systematic review of the literature. From 45 selected studies, a database was compiled of 89 native tree species planted in different forest types (evergreen, semideciduous and transition). The data included plantation age, survival, height and diameter growth. For each species, information was collected on the planting method (understorey, line planting, gap, degraded area, regrowth and clear-cut), and species functional traits (species guild, dispersal mode, wood density and leaf phenology). Tree survival, height and diameter growth were modelled using linear mixed-effect models. Tree survival depended mainly on plantation age, and mortality was the highest in the seven first years. However, survival did not significantly depend on planting method or species traits. In the study plantations, height and diameter growth depended on planting method and species guild. Diameter growth was negatively correlated with wood density. Pioneer, non-pioneer light-demanding and shade-tolerant species grew faster in diameter when planted in degraded areas and clear-cuts. Pioneer species grew the fastest in gaps. Although we did not find an effect of forest type on tree survival and growth, the variability between sites was substantial. This study provides empirical evidence that planting methods need to be adapted to the species guild.

Keywords Planting · Enrichments · Traits · Growth rates · Survival

Introduction

In African rain forests, logging is selective and in legal logging concessions, only eight species and 1–2 ind. ha^{-1} every 25–30 years account for more than 90% of the total harvest (FRMi 2018). However, despite the adoption by national governments of new forest legislation and commitments to sustainable forest management, decades of forest stand creaming or high grading has led to a scarcity of some commercial species (Fredericksen 1998; Dickinson and

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Whigham 1999; Degen et al. 2006; Putz et al. 2012; Doucet et al. 2016; Umunay et al. 2019).

Proponents have argued that the regeneration of harvested species should be promoted by developing sylviculture based on the planting of native species (Doucet et al. 2016; Ilunga-Mulala et al. 2021). Such plantations are particularly important for pioneer species that thrive best in large openings which are rare in natural forests (Makana and Thomas 2005; Schwartz et al. 2013; Ouédraogo et al. 2014, 2018; Fayolle et al. 2015).

From the early twentieth century, tree plantations have been proposed as solution to reduce forest biodiversity loss, promote sustainable timber production and, more recently, increase carbon sequestration in degraded areas (Jacovelli 2014; Ceccon et al. 2016; Pirard et al. 2016; McEwan et al. 2020; Brown et al. 2022; Hua et al. 2022; Banin et al. 1867). In the context of climatic crisis, large-scale planting has been presented as an important solution (Bastin et al. 2019; Brown et al. 2020). However, it must be well planned and executed (Brancalion and Holl 2020; Holl and Brancalion 2020). In Africa, forest restoration initiatives are increasing and require support to achieve their objectives (e.g., REDD + and AFR100). AFR100, for example, has pledged to restore 100 million ha by 2030 (https://afr100.org/) by expanding tree plantations (Fagan et al. 2022). Plantations of native species started in colonial times but never on a large scale due to installation and maintenance costs. Moreover, many plantation have not been thinned, which complicates productivity assessment (Brunck et al. 1990). Nevertheless, given the renewed interest in planting initiatives, these plantations can provide important information on the technical plans best suited to providing high-quality wood, optimizing carbon sequestration and maintaining biodiversity.

The success of forest plantations depends on several factors related to species ecology, functional traits, environment (light, climatic and soil characteristics), planting and maintenance methods. For tropical species, a substantial part of variability in tree survival and growth is explained by tree functional traits (Gray et al. 2019; Shen et al. 2019; Jiang and Jin 2021). Planting methods have been reported to critically affect sapling growth and survival (Fétéké et al. 2015; Forbes et al. 2020). In the Guineo-Congolian region, six planting methods have been used: understorey planting, line planting, gap planting, degraded area planting, regrowth and clear-cut planting (Table 1). The factors affecting the survival and growth of planted trees remain little studied (e.g., Donis 1956; Dupuy 1990; Zaou et al. 1998) although such information is required to ensure plantation success.

In plantations and natural forests, species guilds and competition are key factors for tree performance. The guild reflects the ability of a species to survive and develop under specific light conditions (Hawthorne 1995). Controlling the development of competitive vegetation is one of the most important factors for the success of plantations (Catinot 1965b; Ouédraogo et al. 2014; Fayolle et al. 2015). Herbaceous species and pioneer tree species such as *Musanga cecropioides* R.Br. ex Tedlie or *Macaranga* spp. can strongly impede the development of timber plantations (Catinot 1965b; Doucet et al. 2009). They grow vigorously and compete with the planted species, especially under high light conditions (Nichols et al. 1998). Controlling the competition of pioneer species has been implemented using specific

Table 1 Description of the study planting methods

Methods	Description
Understorey (Fig. 1a)	In the forest understorey, herbs, lianas and saplings less than 4 m height are removed and seedlings planted at 4.5 m × 4.5 m to 10 m × 10 m (Makana and Thomas 2005; Toledo-Aceves and Swaine 2008)
Line planting (Fig. 1b)	2 to 5-m-wide paths are cleared, and seedlings planted along a line every 2 to 5 m. The paths are spaced 20 to 25 m apart (Bergeroo-Campagne 1958a, 1958b; Dupuy and Koua 1993; Dupuy 1998)
Gap (Fig. 1c)	Natural treefall and logging gaps (with area varied between 61 and 500 m^2) are planted (Makana and Thomas 2005; Lopes et al. 2008; Doucet et al. 2009). Occasionally additional trees are cut to increase the gap area up to 5000 m^2 (Coates and Burton 1997). 5 to 1000 trees are planted per gap, depending on gap size
Degraded area (Fig. 1d)	In a highly degraded forest, valuable species and all trees with dbh > 50 cm are identified and protected, and the understory is clear-cut using chainsaws, machetes (Doucet et al. 2016), and in some cases, bulldozers. Monospecific or mixed plantings are planted at 2.5 m × 2.5 m to 6 m × 4 m spacing on an area of 0.5 to 2 ha, generally along roadsides (Donis 1956; Liegois 1959; Doucet et al. 2016)
Regrowth (Fig. 1e)	Prior to the plantation, large trees are manually cut down or weakened (Beligné 1986; Dupuy 1998). The natural regeneration of trees of interest are preserved. Between 80 and 800 trees are planted per ha (e.g., studies by Bergeroo-Campagne 1958a; Beligné 1986; Opuni-Frimpong et al. 2008, 2014; Ngueguim et al. 2016). The plantation area is variable and ranges from 0.25 to more than 1 ha
Clear-cutting (Fig. 1f)	The forest is clearcut with chainsaws, machetes, bulldozers or other heavy machinery and seedlings planted afterwards. The seedlings grow in open conditions (Coates 2002; Cazzolla Gatti et al. 2015). Spacing between trees is generally 3 m × 3 m or 4 m × 4 m

planting methods, plantation spacing and adapting maintenance frequency (Catinot 1965b).

Other factors that can affect the growth and survival of trees are genetics and site conditions, in particular, soil and climate but also the growth of competition (Clark et al. 1999; Vleminckx et al. 2015; Amani 2018). Such interactions have nevertheless been understudied.

In this paper, we synthesize plantation trials and identify the key factors of the Guineo-Congolian species performance according to different planting itineraries. More specifically, we reviewed studies of plantation performance, aggregating the results in a single dataset to: (1) synthesis the growth and survival performance of native tree species planted in moist forests of the Guineo-Congolian region; (2) test whether these performance metrics varied across species and sites; and (3) test whether the performance metrics depended on environmental conditions, planting methods and species traits.

Materials and methods

Literature search

Literature relating to forest plantations carried out in the Guineo-Congolian region and using native species was searched using the following engines: Scopus, CAB Abstracts, Bielefeld Academic Search Engine (BASE), and Agritrop. Selected articles had been published before November 17, 2022. Following the suggestion of Petrokofsky et al. (2015), the following keyword combinations were used: (plantation* OR planting OR enrichment OR reforest*) AND (Africa* OR tropical Africa* OR central Africa* OR west Africa*) AND (increment OR biomass OR growth OR survival OR silviculture*) AND (forest* OR seedling). We supplemented these search engines with Google Scholar and the archive of Africa Museum (https://zenodo.org/records/10013908) using the same keywords on November 20, 2022. A few additional articles were identified from the references of the selected articles. Keywords were entered in the search engines in English and French as several tropical African countries are French-speaking. We obtained 23,373 peer-reviewed articles, theses, technical reports or book chapters, from which we eliminated duplicates according to the PRISMA flow diagram (Fig. S1).

Next, we checked that the topic of the selected articles met the following criteria: (a) the experiment had to be conducted in the Guineo-Congolian region as delimited in Droissart et al. (2018); (b) the focus was on local tree species; (c) trees were planted and not naturally regenerated; (d) quantitative data about their survival and growth performance were available; (e) the planting methods were described, and (f) trees were planted in a forest environment, i.e., agroforestry plantations were not included. When the same dataset or plantation experiment was used in several publications, only the data from the latest one was considered. If any useful information was missing from the article or book, the corresponding author was contacted to provide additional data.

Data extraction

A limited number of studies have compared the species-specific performance of planted trees between different planting methods. However, it is difficult to estimate the effect size of the planting methods (Lajeunesse 2011, 2015; Lortie et al. 2015; Gurevitch et al. 2018; Kawamura et al. 2021). However, the majority of these studies only provided species records for survival and growth associated with a single planting method.

The collected records were grouped into categories based on planting methods according to the level of disturbance (Table 1). Such an approach is recommended for meta-analyses when the aim is to have a broad view of the effect of each factor tested (Paquette et al. 2006; Gurevitch et al. 2018; Cook-Patton et al. 2020; Bukoski et al. 2022) and avoids vote-counting methods (Gurevitch et al. 1992, 2018; Nakagawa and Santos 2012).

The data provided as figures, numbers, tables or graphs in the articles was extracted and compiled in an Excel database. The image processing software, Image J 1.53 (Schneider et al. 2012), was used to extract survival, height and diameter growth data from graphical illustrations. For studies that did not provide numerical geographic coordinates of the experimental sites, the coordinates were calculated by georeferencing the map using QGIS 3.26.3 or were estimated from the site name and description (Table S1). For each record, we also extracted the forest type (mostly evergreen, semi-deciduous and transitional between evergreen and semideciduous) following Gond et al. (2013) and Réjou-Méchain et al. (2021) (Table S1) and climate data (Noce et al. 2020).

For each publication, the following information was recorded: geographic location, site name, planting method, species, plantation age, number of individuals, initial diameter, initial height, survival rate, and height and diameter increments. For each species, the taxonomy was adapted to the version of the African plant database of November 28, 2022 (available from: https://africanplantdatabase.ch/en/search/). The scientific names of the study species are listed in Table S2, with their pilot names corresponding to the ATIBT (2016) nomenclature. We identified the corresponding species guild, dispersal mode and leaf phenology according to Fayolle et al. (2012), Meunier et al. (2015), Doucet et al. (2016) and Daïnou et al. (2021). For the few species whose data were lacking, expert opinions were requested

(Jean-François Gillet and Jean-Louis Doucet, comm. pers.). The selected traits showed tree light use and installation strategy, crucial for their performance. Species were classified according to their (a) species guilds: pioneer, non-pioneer light-demanding and shade-tolerant as described by Hawthorne (1995); (b) leaf phenology: deciduous (including briefly deciduous) and evergreen; and (c) dispersal mode: animal, wind or unassisted. The Global Wood Density Database was used to compute the average wood density of each species (Zanne et al. 2009). Plantation maintenance was not considered in the analyses because the protocols varied widely between studies.

Data calculation

For each species, site and treatment, the annual survival rate S_{an} (%) was determined with Eq. 1 (Sheil et al. 1995).

$$S_{an} = 100 - \left[\left(1 - \left(S_t\right)^{\frac{1}{t}}\right) \cdot 100\right], S_t = \frac{N_t}{N_0} \tag{1}$$

where S_t, N_0 and N_t were the survival rate over a period of t years, the initial and final numbers of individuals, respectively.

Annual diameter (ΔD) (mm year^{-1}) and height (ΔH) increments (cm year^{-1}) were computed using Eqs. 2 and 3, respectively.

$$\Delta D = \frac{D_t - D_0}{t} \tag{2}$$

$$\Delta H = \frac{H_t - H_0}{t} \tag{3}$$

where, D_0 and H_0 the initial records of diameter and height, D_t and H_t the diameter and height monitored at time t (years).

Statistical analyses

The means and standard deviations of the response variables (survival rate, height and diameter increments) were calculated for each studied factor level. Linear mixed-effects models (LMMs) were then fitted to compute the variability of the survival rate ($S_{an_{ij}}$), height (ΔH_{ij}) and diameter (ΔD_{ij}) increments of species i in location j. An intercept-only model was fitted with site and species as random effects (Eq. 4). The "species" factor was treated as a random effect, as the aim was not to compare species with each other, as the number of observations for some species was too low. Explanatory variables were added, considering the "species" factor as a fixed (S_i, Eq. 5) or random (α_i) effect (Eq. 6), to determine the resulting impact on model robustness, keeping the site (β_j) as a random effect. The explanatory variables were plantation age (A), planting method (M), species guild (G), forest type (F), dispersal mode (D), wood density (W), leaf phenology (L) and the interaction between planting method and species guild. We used the same random effect structure as in the intercept-only models. The results of all models were analysed using the *anova* function of the "stats" R package. 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.

The models were fitted with the *glmer* function of the "lme4" (version 1.1-30) R package (Bates et al. 2015) with a Gaussian family. In all these analyses, S_{an} values were $2 \times$ *arcsine square root* transformed while ΔH and ΔD values were $ln + 1$ transformed, so that the residuals were approximately normally distributed.

$$y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij} \tag{4}$$

$$\begin{aligned} y_{ij} = \mu &+ b_1 A_{ij} + b_{2,S_{ij}} + b_{3,M_j} + b_{4,G_i} + b_{5,F_j} + b_{6,D_i} \\ &+ b_{7,W_i} + b_{8,L_i} + b_{9,M_j * G_i} + \beta_j + \varepsilon_{ij} \end{aligned} \tag{5}$$

$$\begin{aligned} y_{ij} = \mu &+ b_1 A_{ij} + b_{2,M_j} + b_{3,G_i} + b_{4,F_j} + b_{5,D_i} + b_6 W_i \\ &+ b_{7,L_i} + b_{8,M_j * G_i} + \alpha_i + \beta_j + \varepsilon_{ij} \end{aligned} \tag{6}$$

With $\alpha_i \sim \mathrm{N}\left(0, \sigma_\alpha^2\right)$; $\beta_j \sim \mathrm{N}\left(0, \sigma_\beta^2\right)$ and $\varepsilon_{ij} \sim \mathrm{N}\left(0, \sigma_\varepsilon^2\right)$.

Where y are transformed response variables annual survival rate, height and diameter increments, μ the model intercept, b the slope parameters for the different explanatory variables. α_i and β_j the random effects of species and sites and ε_{ij} the residual error of the model. The best models were selected using a stepwise approach examining the Akaike Information Criterion (AIC), the Bayesian Information Criterion (BIC) and the likelihood ratio tests using the *anova* function of the "Stats" package. Variables that were not significant were removed from the final models (M, G, F, D, W and L for annual survival rate; *F, D, W, and L* for height increment and A, F and L for diameter increment). As expected, given the low number of observations for certain species, models with species and sites as random effects were better than those considering the species as fixed effect and only the site as random effect (Table 2). We selected the models:

$$S_{an_{ij}} = \mu + b_1 A_{ij} + \alpha_i + \beta_j + \varepsilon_{ij} \tag{7}$$

$$\Delta H_{ij} = \mu + b_1 A_{ij} + b_{2,M_j} + b_{3,G_i} + b_{4,M_j * G_i} + \alpha_i + \beta_j + \varepsilon_{ij} \tag{8}$$

$$\Delta D_{ij} = \mu + b_{1,M_j} + b_{2,G_i} + b_{3,D_i} + b_4 W_i + b_{5,M_j * G_i} + \alpha_i + \beta_j + \varepsilon_{ij} \tag{9}$$

Table 2 AIC, BIC, X^2 values and P values (likelihood ratio test) are given for the models, including the site and species as random effect (Eq. 6) and the species as the fixed effect and only the site as random effect (Eq. 5) for survival rates, height and diameter increments. The best models are in bold

Models	Annual survival rates				Height increment				Diameter increment			
	AIC	BIC	X^2	P value	AIC	BIC	X^2	P value	AIC	BIC	X^2	P value
Site and species as random effect (Eq. 6)	335.2	356.3	102	0.0553	1265.6	1361.5	136.35	< 0.001	1034.5	1138.2	118.45	< 0.001
Only the site as random effect (Eq. 5)	394.97	756.4			1293.2	1746.6			1054.1	1455.9		

for survival rates (Eq. 7), height (Eq. 8) and diameter (Eq. 9) increments. 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 (marginal R^2). They were computed with the *r.squaredGLMM* function of the "MuMIn" (version 1.47.1) package (Barton 2022). The plots were drawn with the "ggplot2" (version 3.3.6) package (Wickham 2016). All statistical analyses were performed using the R statistical environment (version 4.2.1.) (R Core Team 2022) (Fig. 1).

Results

Overview of the dataset

There were 40 published papers, one book and four theses that met our criteria (Table S1). They provided 687 observations (n_{obs}) with 494 records of survival, 578 of height and 556 of diameter increments of 89 native species belonging to 24 families in nine countries across 38 sites in the Guineo-Congolian region (Fig. 2). The most studied country was Cameroon (23%) in Central Africa and Ghana (9%) in West

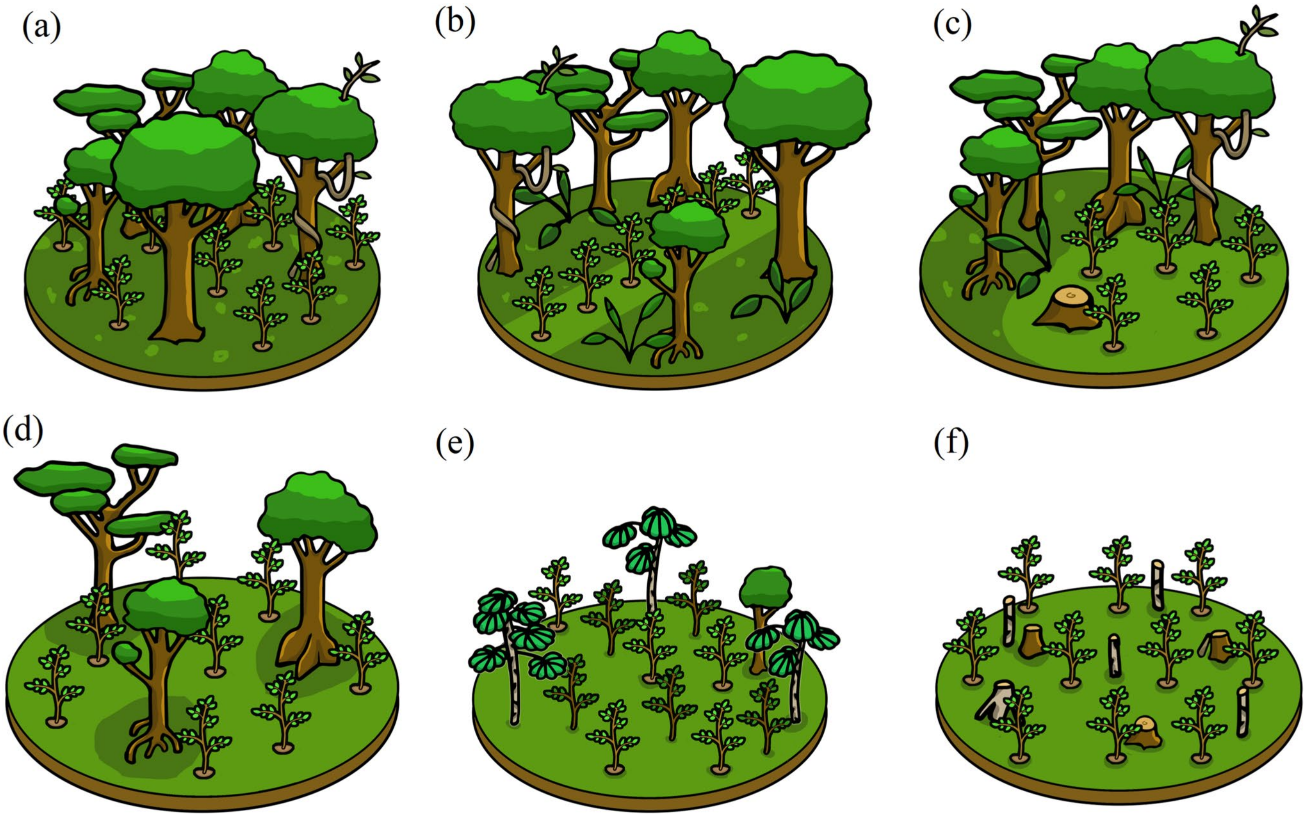

Fig. 1 Illustration of the studied planting methods: **a** understorey, **b** line planting, **c** gap, **d** degraded area, **e** regrowth and **f** clear-cutting. See Table 1 for more details

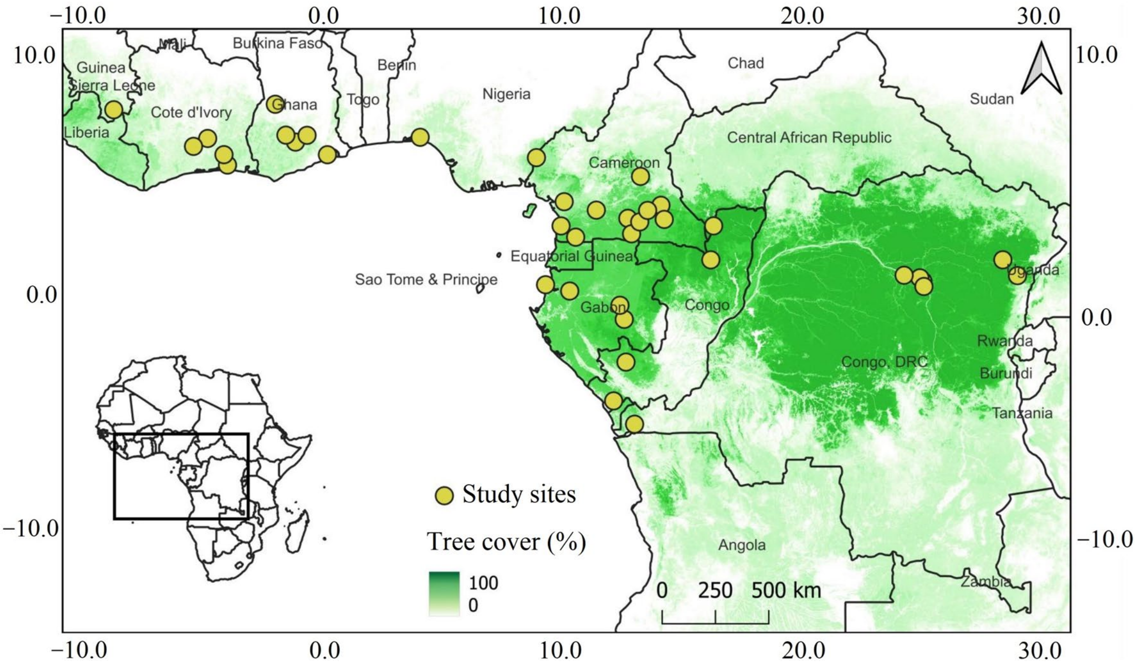

Fig. 2 Location of the study sites (Hansen et al. 2013)

Africa (Fig. 2). Survival, height and diameter increment values of species were not equally distributed across sites. In the study sites, the average annual rainfall was 1662 ± 320 mm and average temperature 31.5 ± 1.7 °C according to the bioclimatic data (Noce et al. 2020). The evergreen forest had the most observations (49%), followed by the semi-deciduous (28%) and the transitional forest (22%).

In general, tree species were planted within their natural distribution area. Only 21 observations (3% of total records) concerned the plantation of species outside of their natural range. We collected information on 28 pioneer, 40 non-pioneer light demanding and 21 shade-tolerant species. Non-pioneer light demanding species was the most studied guild ($n_{\mathrm{obs}} = 338$) before pioneer ($n_{\mathrm{obs}} = 269$) and shade-tolerant species ($n_{\mathrm{obs}} = 80$). Species were mostly dispersed by wind (58.4%) or by animals (32.8%) and rarely classified as unassisted (8.8%).

Average heights and diameters (mean ± standard deviation) were 8.1 ± 8.4 m and 12.6 ± 12.1 cm, respectively. The mean stand age was 12.1 ± 18.1 years (ranging from 0.5 to 80 years). *Pericopsis elata* (Harms) van Meeuwen and *Khaya ivorensis* A. Chev. were the most frequently observed species, accounting for 12.1 and 9.0% of all records, respectively. For 16 species, only one observation could be found (2.3% of total records). These species are: *Amphimas ferrugineus* Pierre ex Pellegr., *Antrocaryon micraster* A.Chev. & Guillaumin, *Antrocaryon nannanii* De Wild., *Berlinia confusa* Hoyle, *Chrysophyllum lacourtianum* De Wild., *Chrysophyllum perpulchrum* Mildbr. ex Hutch. & Dalziel, *Coelocaryon preussii* Warb., *Dacryodes normandii* Aubrév. & Pellegr., *Eribroma oblongum* (Mast.) Pierre ex A.Chev., *Funtumia elastica* (P.Preuss) Stapf, *Nesogordonia kabingaensis* (K.Schum.) Capuron ex R.Germ., *Newtonia leucocarpa* (Harms) G.C.C.Gilbert & Boutique, *Parinari excelsa* Sabine, *Pouteria aningeri* Baehni, *Ricinodendron heudelotii* (Baill.) Pierre ex Heckel and *Scorodophloeus zenkeri* Harms.

Annual survival rate

Survival rates depended significantly on plantation age ($F = 18.43$, $P < 0.001$; Table 3). This relationship was non-linear as the survival rate rapidly increased with age in young plantations and fluctuated little in plantations older than seven years (Fig. 3).

The mean survival rate (89.1 ± 12.5%) did not vary significantly across planting methods ($F = 0.95$, $P = 0.447$; Fig. 4), species guild ($F = 1.51$, $P = 0.225$), dispersal mode ($F = 0.90$, $P = 0.412$), wood density ($F = 0.71$, $P = 0.404$), leaf phenology ($F = 0.44$, $P = 0.509$) and forest type ($F = 0.81$, $P = 0.447$) (Table S3). The interspecific variability of survival rate was low ($\sigma_{\alpha} = 0.08$) whereas it was substantial between sites ($\sigma_{\beta} = 0.32$) and of the same order of magnitude as the residual variability ($\sigma_{\varepsilon} = 0.31$). A large proportion of the variance was explained by the random effects, as highlighted by the difference between the conditional and marginal R^2 being 58.8 and 11.7%, respectively.

Table 3 Parameters and statistics of the linear mixed models examining the effect of planting methods, species guild, their interaction, plantation age, dispersal mode and wood density on the annual survival rates (Eq. 7), height (Eq. 8) and diameter (Eq. 9) increments

Effect types		Annual survival rate		Height increment		Diameter increment	
		F value	*P* value	*F* value	*P* value	*F* value	*P* value
Fixed effects	Plantation age (A_{ij})	18.43	<0.001	6.63	<0.05	–	–
	Planting method (M_j)	–	–	4.81	<0.001	17.82	<0.001
	Species guild (G_i)	–	–	5.69	<0.01	3.33	<0.05
	Dispersal mode (D_i)	–	–	–	–	3.80	<0.05
	Wood density (W_i)	–	–	–	–	9.31	<0.01
	$M_j * G_i$	–	–	3.50	<0.001	3.02	<0.01
Random effects	Species (σ_α)	0.08		0.24		0.28	
	Sites (σ_β)	0.32		0.48		0.45	
	Residual (σ_ε)	0.31		0.65		0.53	
	R^2 conditional (%)	58.83		48.35		61.93	
	R^2 marginal (%)	11.65		12.09		23.18	

Annual survival rate and height-diameter increments were respectively *arcsine* and *ln* transformed to approach normality. σ_α, σ_β and σ_ε are the standard deviations of the random effects species, sites and residuals, respectively

Height increment

Height increments depended significantly on planting method ($F = 4.81$, $P < 0.001$), species guild ($F = 5.69$, $P < 0.01$), the interaction between these two factors ($F = 3.50$, $P < 0.001$) and plantation age ($F = 6.63$, $P < 0.05$) (Table 3). The overall mean height increment was 66.1 ± 46.1 cm year^{-1} ($n_{obs} = 578$). It was greater for pioneer species (78.4 ± 50.3 cm year^{-1}, $n_{obs} = 221$) than non-pioneer light-demanding species (61.0 ± 42.7 cm year^{-1}, $n_{obs} = 289$); and shade-tolerant species (47.6 ± 34.2 cm year^{-1}; $n_{obs} = 68$). Height increments across planting methods for 84 species are presented in Fig. 5. Plantation age was negatively correlated with height growth ($t = -2.6$, $P < 0.05$; Table S4).

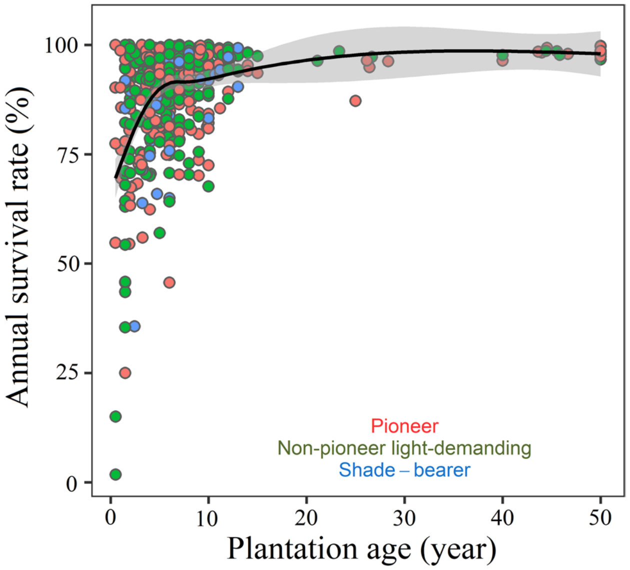

Fig. 3 Relationship between annual survival rate and plantation age. Each point indicates the annual survival rate for each site-species-treatment, coloured according to species guild. The grey area shows the 95% confidence interval

Tukey-adjusted *post-hoc* test for predicted means of each planting method indicated that the difference in height increments of pioneer species was significantly larger in gaps (1.8 ± 1.2 cm year^{-1}; $P < 0.05$), degraded areas (2.1 ± 1.2 cm year^{-1}; $P < 0.001$), and in clear-cuts (1.6 ± 1.2 cm year^{-1}; $P < 0.05$) than for the understory planting method (Fig. 6a, Table S5). For non-pioneer light-demanding species, height increments were significantly larger on degraded areas (1.9 ± 1.2 cm year^{-1}; $P < 0.01$) and in clear-cuts (1.7 ± 1.2 cm year^{-1}; $P < 0.05$) than in gaps (Fig. 6a; Table S5). For shade-tolerant species, height increments were significantly larger on degraded areas (with a difference of 3.4 ± 1.4 cm year^{-1}; $P < 0.01$), in the regrowth (5.2 ± 1.6 cm year^{-1}; $P < 0.01$) and in the understorey (3.7 ± 1.4 cm year^{-1}; $P < 0.01$) than in the gap. No significance difference was found between the others planting methods (Fig. 6a; Table S5).

Height increments did not significantly vary with forest type ($F = 1.48$, $P = 0.238$), dispersal mode ($F = 1.41$, $P = 0.251$), wood density ($F = 1.89$, $P = 0.173$) or leaf phenology ($F = 0.97$, $P = 0.328$) (Table S3). The between-site variability and residual variability of height increment were substantial ($\sigma_\beta = 0.48$ and $\sigma_\varepsilon = 0.65$, respectively). The interspecific variability was low ($\sigma_\alpha = 0.24$; Table 3). A larger part of the variability was explained by the random effects than by the fixed effects; the conditional and marginal R^2 being 48.4 and 12.1%, respectively.

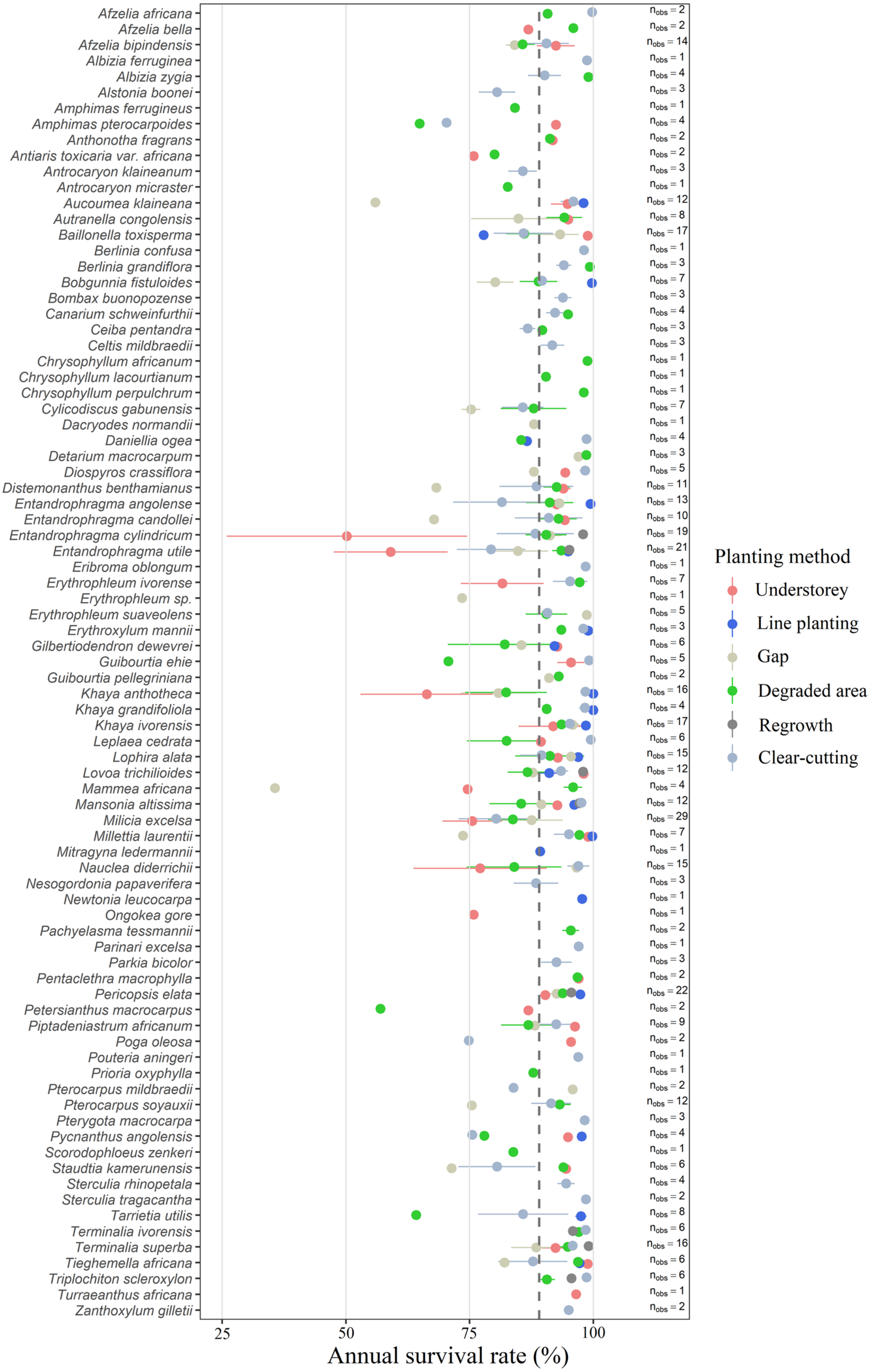

Fig. 4 Means and standard deviations of the annual survival rates of tree species across planting methods. n_{obs} is the number of observations for each species. The dotted vertical line indicates the mean annual survival rate

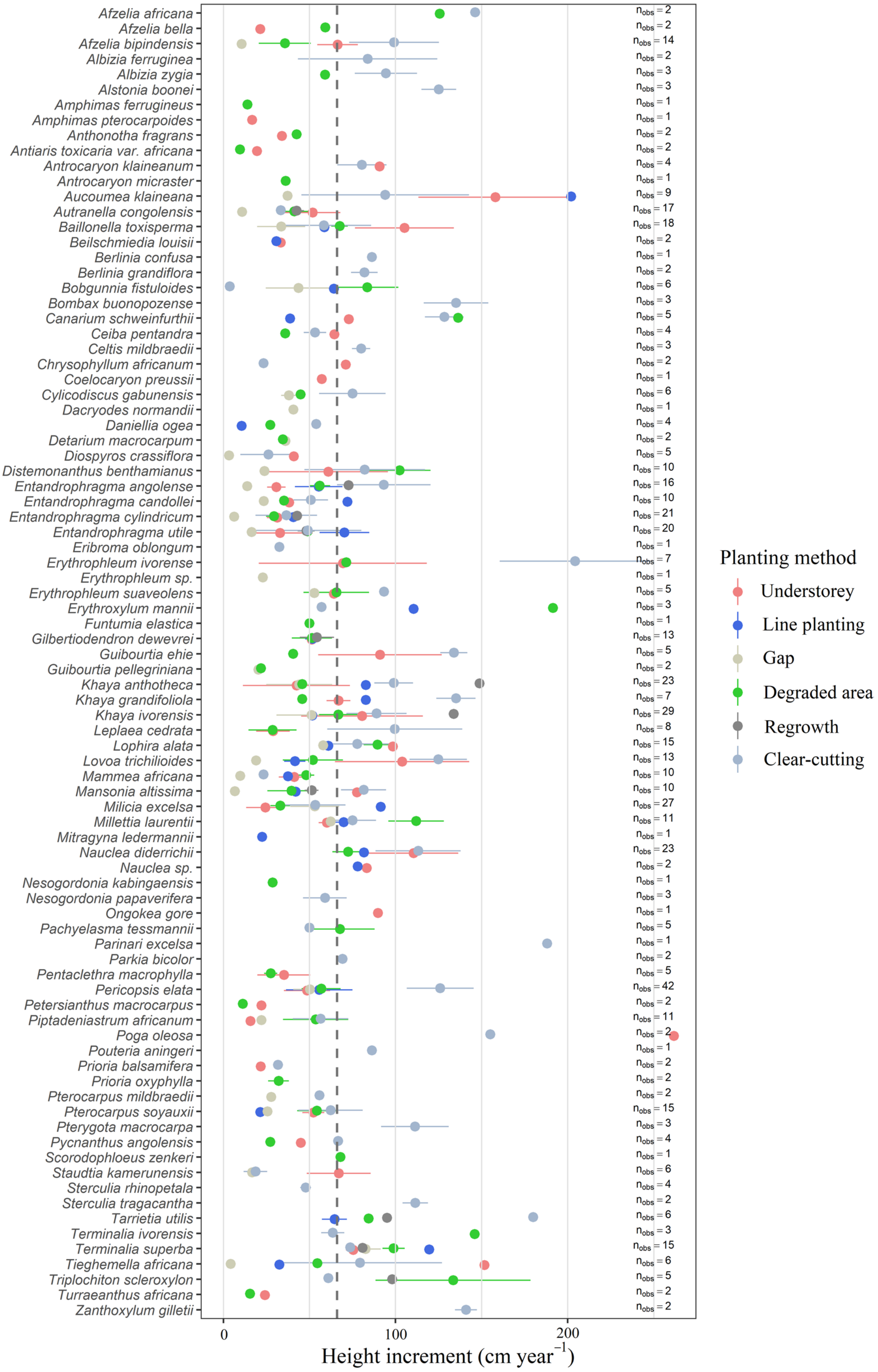

Fig. 5 Means and standard deviations of height increments of species across planting methods. n_{obs} is the number of observations for each species. The dashed vertical line indicates the mean height increment

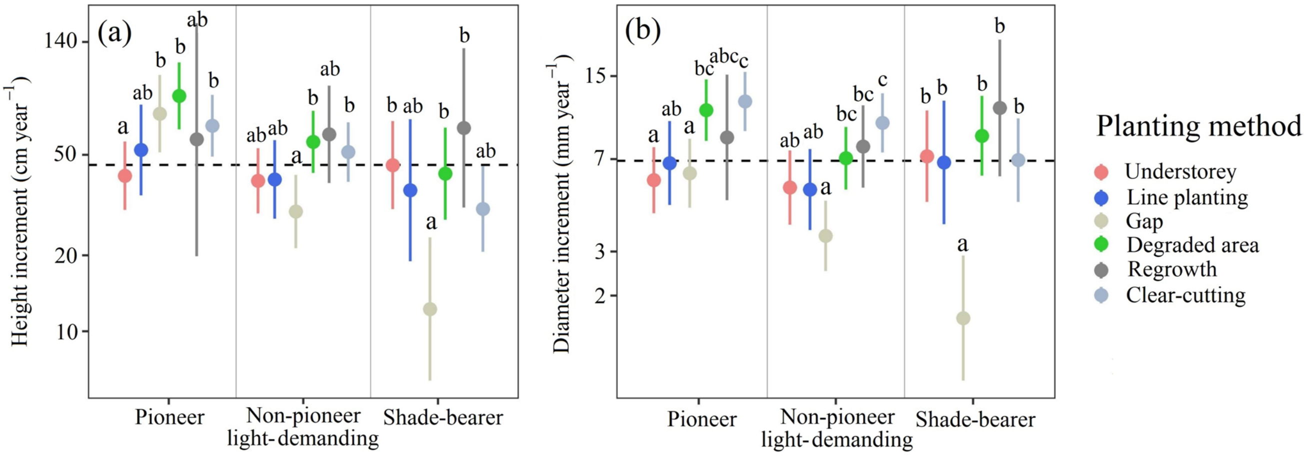

Fig. 6 Effect of planting methods across species guild on **a** height and **b** diameter increments. Points and confidence intervals show the bivariate relationships between planting methods predicted by the selected linear mixed models (Tables S5 & S6). Significant differences are shown by different letters using Tukey-adjusted *post-hoc* test. Y axes are in log$_e$-scale. The dashed horizontal line shows the mean determined by the intercept-only models

Diameter increment

Diameter increments significantly depended on the planting methods ($F = 17.82$, $P < 0.001$), species guild ($F = 3.33$, $P < 0.05$), their interaction ($F = 3.02$, $P < 0.01$), dispersal mode ($F = 3.8$, $P < 0.05$) and wood density ($F = 9.31$, $P < 0.01$) (Table 3). Substantial differences in diameter increments were observed across planting methods for most species (Fig. 7). The correlation between diameter increment and wood density was significantly negative ($r = -0.34$, $P < 0.01$; Fig. 8). The mean diameter increment was 9.3 ± 6.9 mm year^{-1} ($n_{obs} = 556$). It was larger for pioneer species (10.3 ± 7.3 mm year^{-1}, $n_{obs} = 231$) than for non-pioneer light demanding species (8.9 ± 6.4 mm year^{-1}, $n_{obs} = 261$) and shade-tolerant species (6.9 ± 5.8 mm year^{-1}, $n_{obs} = 64$).

The difference in mean diameter increment provided by the Tukey-adjusted *post-hoc* test of pioneer species was significantly larger in degraded areas than in the understorey planting (1.9 ± 1.2 mm year^{-1}; $P < 0.001$) and gap planting (1.8 ± 1.2 mm year^{-1}; $P < 0.01$). Diameter increments observed in clear-cuts were significantly larger than with understorey planting (2.1 ± 1.2 mm year^{-1}; $P < 0.001$), gap planting (1.9 ± 1.2 mm year^{-1}; $P < 0.001$) and line planting methods (1.8 ± 1.2 mm year^{-1}; $P < 0.05$). For the non-pioneer light-demanding species, diameter increment was significantly smaller in gap plantings than in clear-cuts (2.8 ± 1.2 mm year^{-1}; $P < 0.001$), regrowth (2.3 ± 1.2 mm year^{-1}; $P < 0.01$) and in degraded areas (2.0 ± 1.1 mm year^{-1}; $P < 0.001$). Diameter increments were significantly greater in clear-cuts than in line planting (1.8 ± 1.2 mm year^{-1}; $P < 0.01$) and understorey (1.8 ± 1.2 mm year^{-1}; $P < 0.01$). For shade-tolerant species, diameter increments were significantly smaller in the gap plantings than in regrowth (6.9 ± 1.5 mm year^{-1}; $P < 0.001$), degraded areas (5.3 ± 1.3 mm year^{-1}; $P < 0.001$), understorey (4.4 ± 1.5 mm year^{-1}; $P < 0.001$), line planting (4.2 ± 1.5 mm year^{-1}; $P < 0.01$) and clear-cuts (4.3 ± 1.4 mm year^{-1}; $P < 0.001$). No significance difference in diameter increments was found between others planting methods (Fig. 6b; Table S6).

Diameter increments did not significantly vary with age ($F = 1.37$, $P = 0.243$), type of forest ($F = 0.22$, $P = 0.773$) or leaf phenology ($F = 1.13$, $P = 0.352$) (Table S3). Diameter increments varied almost equally between sites ($\sigma_\beta = 0.45$) and residual variability ($\sigma_\varepsilon = 0.53$). The between species variability was low ($\sigma_\alpha = 0.28$) (Table 3). A greater proportion of the variability depended on the random effects than on fixed effects, with the conditional and marginal R^2 being 61.9 and 23.2%, respectively.

Discussion

Forty-five studies (Fig. S1) were selected for analyses and provided new insights about plantation success in the moist forests of the Guineo-Congolian region, even though data were limited. Given the size and the heterogeneity of the conditions in the study area, this number is low, underlining that the successful drivers of forest plantations may be understudied. Moreover, these studies mostly (81%) concerned young plantations between 0.5 and 12 years. In addition, several of the 30 most logged species in central Africa (Duhesme et al. 2021) have not yet been sufficiently tested in plantations (e.g., *Cylicodiscus gabunensis* Harms., *Triplochiton scleroxylon* K.Schum., *Guibourtia ehie*

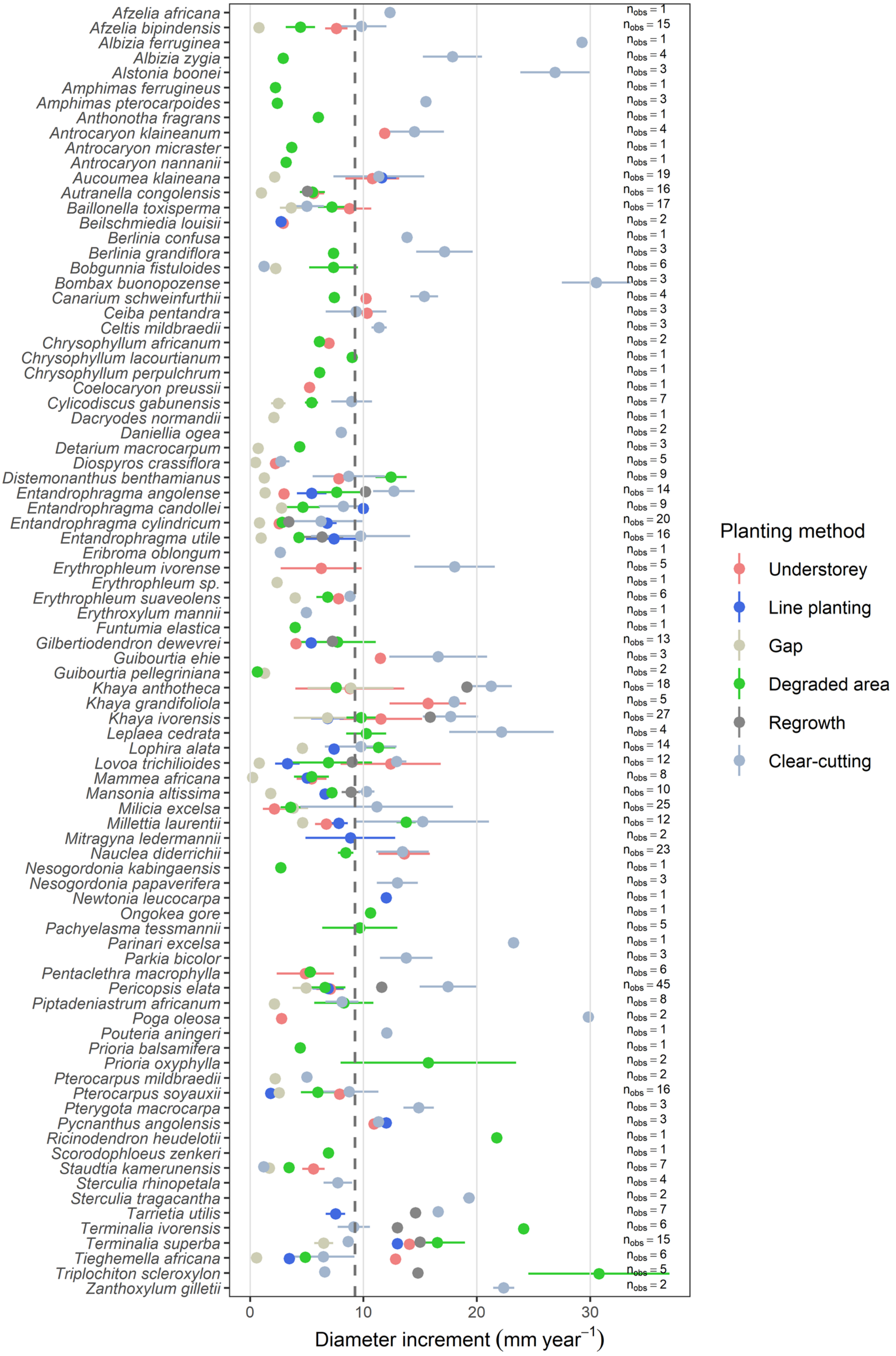

Fig. 7 Means and standard deviations of the diameter increments of species across planting methods. n_{obs} is the number of observations for each species. The dashed vertical line indicates the mean height increment

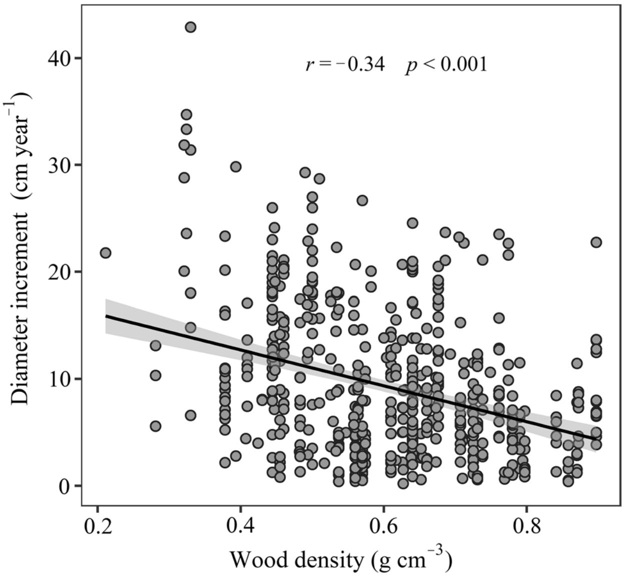

Fig. 8 Correlation between diameter increment and wood density. Each point represents the diameter increment for each site-species-treatment. The grey area is the 95% confidence interval

(A.Chev.) J.Léonard and *Pycnanthus angolensis* (Welw.) Warb. with only 3.3% of the observations). Others were not found in any of the reviewed plantation trials: *Aphanocalyx heitzii* heitzii Pellegr., *Desbordesia glaucescens* (Engl.) Tiegh., *Fillaeopsis discophora* Harms, *Guibourtia tessmannii* (Harms) J.Léonard, *Julbernardia pellegriniana* Troupin, *Prioria balsamifera* (Vermoesen) Breteler and *Tessmannia africana* Harms.

Between site variability in tree performance

Variation in the survival and growth of planted species is expected to be related to the environmental conditions, particularly those characterized by canopy openness (Beckage and Clark 2003; Doucet et al. 2009; Cardoso et al. 2016; Laughlin and Clarkson 2018), by edaphic conditions (Beligné 1986) and rainfall (Baker et al. 2003; van Breugel et al. 2011; Toledo et al. 2011; De Ridder et al. 2013). Our results confirm that substantial differences in plantation performance can be expected across sites, as highlighted by the substantial between-site variability ($\sigma_\beta = 0.32$; 0.48 and 0.45 for survival, height and diameter increments, respectively; Table 3). Significant site-related differences (seven sites) in tree growth were also observed for *Aucoumea klaineana* Pierre in Gabon and Congo according to Obiang Engone et al. (2013).

The residual variability (within species and site) was also substantial for survival, height and diameter increments, indicating that within-site local conditions (soil fertility, competition, herbivory) can greatly affect plantation performance (Jiang and Jin 2021). This was also highlighted by Kearsley et al. (2013, 2017) for height-diameter relationships in the central Congo Basin.

We did not find evidence of any effect of forest type on tree survival or growth rates, while such differences are expected across forest types (Baker et al. 2003; Fayolle et al. 2016). It should be noted that we examined the growth and survival of several species together and, in most cases (97%), they were planted within their natural distribution range.

Do planting methods and species guilds affect plantation performance?

Different planting methods were expected to affect plantation performance (Catinot 1965a; Dupuy 1990; Zaou et al. 1998; Ilunga-Mulala et al. 2021). Our analyses revealed that it may influence mostly height and diameter growth, whereas survival could depend more on other factors, at least in the short-term (the average experiment duration was 12 years). The effect of planting method on tree growth depended on species guild (a significant interaction).

Pioneer species grow relatively rapidly in an open environment (Poorter et al. 2003; Schmitt et al. 2022). They indeed grew faster in height in degraded areas and in gaps than in understory plantations. This ranking slightly changed when considering diameter increment. Pioneer species grew faster in diameter in degraded areas than in gaps and in understorey plantations (Fig. 6). Hypothetically, the competition for light can be severe in gaps (Toledo-Aceves and Swaine 2008) and planted trees may allocate more resources into height increment than into diameter increment in such conditions (Cahill and Casper 2003; Poorter et al. 2003; Rozendaal et al. 2020). Different situations might, however, be found within gaps, depending on gap size and orientation (Makana and Thomas 2005; Ouédraogo et al. 2014) and plantation maintenance. In degraded sites, the presence of large trees may have limited the availability of light at the ground to a level that constrained the development of competitive vegetation, hence allowing the planted seedlings to grow fast in diameter. For example and, in line with previous results Doucet et al. (2016), *Distemonanthus benthamianus* Baill., *Lophira alata* Banks ex C. F. Gaertn., *Terminalia superba* Engl. & Diels and *Triplochiton scleroxylon* K. Schum. showed the highest diameter growth on degraded sites (Fig. 7).

For non-pioneer light-demanding species, height increments did not vary significantly across planting methods (Fig. 6a). However, diameter increments were larger in clear-cut areas than in gap, line and understorey plantations (Fig. 6b). Diameter increments were clearly higher than those usually found for mature trees in natural forests for some species (*Afzelia bipindensis* Harms, *Entandrophragma cylindricum* (Sprague) Sprague, *Entandrophragma utile*

(Dawe & Sprague) Sprague, *Khaya anthotheca* (Welw.) C.DC., *Lovoa trichilioides* Harms, *Mansonia altissima* (A.Chev.) A.Chev. and *Tarrietia utilis* (Sprague) Sprague), with averages ranging from 6.2 mm year^{-1} for *E. cylindricum* to 21.3 mm year^{-1} for *K. anthotheca*. In natural forests, diameter increments range between 2.1 mm year^{-1} for *A. bipindensis* and 6.2 mm year^{-1} for *E. utile* and *K. anthotheca* according to Ligot et al. (2022). Trees planted in degraded areas and with the regrowth method did not show significant differences in diameter growth with those planted in clear-cuts. Non-pioneer light-demanding species tolerate some shade and may thus be less sensitive to competition for light. Plantations in gaps had the poorest performance. Their growth was likely limited or affected by interspecific competition (herbaceous plants, lianas and other pioneer species) (Makana and Thomas 2005) with abundant soil seed bank e.g., *Macaranga spp.* (Zébaze et al. 2022). Plantations in gaps were monitored during a shorter period than for the other methods (average of 3.3 years for the gap plantings versus 12.1 years for the overall average) which could have affected our estimates.

We found that shade-tolerant species grew slowly in height and diameter when planted in gaps. The largest mean increments were observed in regrowth and degraded area plantations, but they were not significantly different to the increment observed with all planting methods but for plantation in gaps. These results are in line with the ecology of shade-tolerant species which generally grow slowly and are abundant in the understory (Hubau et al. 2019; Kengne et al. 2022). Nevertheless, better results might have been expected in understorey plantations and in line planting, but these methods seem poorly adapted for most species.

Tree growth and survival depends on tree ontogeny or its origin and development (Boyden et al. 2009; Hérault et al. 2011). Mortality rates were higher in young plantations (<7 years old) regardless of species guild (Fig. 3). In fact, mortality likely occurs when canopy gaps close (Beckage and Clark 2003) and depending on gap size, it might happen six to 11 years after plantation establishment (Neves et al. 2019). The survival of planted seedlings depends also on plantation maintenance that removes competing vegetation. This improves the performance of species regardless of planting methods, particularly in gaps (Doucet et al. 2009; Ouédraogo et al. 2014). Our results suggest that maintenance is especially required during the first seven years, which is in agreement with Catinot (1965b) and Dupuy (1990). This duration of maintenance can, however, be difficult to achieve in logging gaps, as roads are often closed after logging.

Degraded areas appeared suitable for all species guilds, while gaps may be suitable mostly for pioneer species. This general statement should nevertheless be questioned, considering species ecology and local conditions. In our analyses, species were grouped in guilds but their physiology can significantly differ (van Kuijk et al. 2008), and species of the same guild might show different performance (Hardt Ferreira dos Santos and Ferreira 2020). In addition, within the various planting methods, different treatments (e.g., seed sources, planting density and composition and clearing) were carried out. For the regrowth method in particular, planting densities varied greatly, reaching up to 1000 trees ha^{-1} (Ngueguim et al. 2016).

Do wood density, dispersal mode and leaf phenology affect plantation performance?

Traits such as wood density, dispersal mode and leaf phenology could be good predictors of species performance in plantations (Martínez-Garza et al. 2013) although such relationships are not always evident (Chapman et al. 2008; Doucet et al. 2016), even under controlled conditions (Bloor and Grubb 2003).

According to our findings, only wood density might be considered as a good proxy of species performance. Diameter increment was negatively correlated with density ($r = -0.34$, $P < 0.001$; Fig. 8). This observation has also been reported in natural forests (Gray et al. 2019; Rozendaal et al. 2020) with fast-growing species generally producing wood of low density (Asanok et al. 2013).

Dispersal mode is considered a critical factor for species establishment (Marques and Oliveira 2008; Zébazé et al. 2023), but its influence on plantation performance remains unclear. We found no significant relationship between dispersal mode, tree survival and height growth in plantations. An effect of seed dispersal was nevertheless noted on diameter growth, with unassisted species growing slightly faster ($t = 2.6$, $P < 0.05$; Table S4). Seed dispersal thus appeared as a trait that is not well-related to tree growth, confirming observations carried out in natural forests (Ouédraogo et al. 2018).

Leaf phenology affects water capture during dry seasons (Williams et al. 1997) and deciduous species generally grow faster than evergreen species (Baker et al. 2003; Poorter et al. 2005; Chi et al. 2015). Nevertheless, such an effect could not be found in this study perhaps because of the limited number of study species (89) and number of observations. Such an effect might only be identified at a latter ontogeny stage.

Bias and limitations of this study

Our methodological approach did not weigh the results of the publications according to the number of observations or dispersion values around the mean. However, it does provide a broad view of the results of different plantation experiments according to site conditions, planting methods, plantation age and species traits. The results of this study only relate to the sites that have been described in the literature (Table S1). Caution should be exercised before applying them to other areas. Several other sources of variabilities can be detected when conducting studies with original data. As we have seen, the large variability in survival and growth is site-specific. Plantation maintenance and thinning may explain a large proportion of the variability in performance between species. However, they were not considered in this paper.

Conclusion and research perspectives

This review highlights that an appropriate correspondence between species, site and planting method is essential to ensure the survival and growth of seedlings. Overall, plantations in degraded areas and in clear-cuts as well plantations with the regrowth method showed good results. In contrast, plantations in the understory or line planting provided limited results and should not be recommended except perhaps for shade-tolerant species. Pioneer species could be planted in gaps but may result in smaller diameters than with the other methods. Planting in gaps is however, unfavourable for shade-tolerant species. Moreover, our review may make possible silvicultural decision-making in prioritizing species for reforestation, as species with high survival rates and large diameter increments can easily be identified (Fig. S2). Our results also support Doucet et al. (2016) and Latterini et al. (2023) that future research should continue comparing the performance of species planted with different methods in neighbouring sites. Further studies should also compare plantation performance by using a standard protocol over a longer period (at least up to 25 years). Finally, studies of the effect of maintenance techniques on tree performance are crucial. This would determine the best method of thinning to increase individual tree growth and produce high-quality wood.

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