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Tree growth in West African cocoa agroforestry systems: high timber yields and superior performance of natural regeneration

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Abstract

Key message Cocoa agroforestry systems (AFS) in West Africa represent an underexplored yet promising source of timber. Within these systems, species can reach a 50-cm diameter as early as 14 years of age. Naturally regenerated trees grow 10% faster than planted ones and develop a 43% greater bole volume. These findings underscore the high timber potential of cocoa AFS and confirm natural regeneration as a superior strategy for tree renewal and wood production.

Context In West Africa, where over 80% of original forests have been converted to agriculture, finding alternative timber sources is essential. Agroforestry, prevalent across the region, offers a potential solution.

Aims This study assesses the timber production potential of trees in cocoa agroforestry systems in Côte d'Ivoire.

Methods In 150 cocoa agroforestry plots, we (i) modelled the diameter growth of forest tree species; (ii) developed specific allometric models for cocoa AFS; and (iii) evaluated the effect of tree origin (natural regeneration vs. plantation) on growth trajectories, allometry, and bole volume.

Results Trees can reach a diameter of 50 cm as early as 14 years of age, and a bole height of up to 8.83 m at this diameter. Naturally regenerated trees grow 10% faster annually than planted trees, reaching their minimum logging diameter up to 10 years earlier, and have a 43% greater bole volume.

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Conclusion Natural regeneration is a more effective strategy than planting for tree renewal in cocoa AFS, providing faster growth, greater timber volumes, and significant potential for sustainable forestry management and meeting regional timber demands.

Keywords Timber wood, Growth trajectories, Silvicultural management, Natural regeneration, Cocoa agroforestry, West Africa

1 Introduction

In a global context where the demand for tropical timber is constantly increasing (Chimeli et al. 2012), natural forests, which provide the majority of this resource, are under unprecedented pressure (FAO 2020). In West Africa, this pressure is exacerbated by real estate development (driven by high population growth) that fuels a very strong local demand for construction timber (Uzu et al. 2022). This demand completely exceeds the supply capacities of production forests (Louppe and Ouattara 2013), in a context where over 80% of the original forest mass has been lost in favour of agricultural development (Aleman et al. 2018; Traoré et al. 2024). Thus, it is imperative to seek alternative sources of production to meet regional needs and uses and to ensure the sustainability of the timber sector and the people who depend on it (Tsanga et al. 2020). Large-scale tree planting has long been seen as an ideal solution to meet the needs for tropical timber. For example, 45% of the national commitments made under the Bonn Challenge, an international goal aiming to restore 350 million hectares of land by 2030 (Verdone and Seidl 2017), involve multiplying tree plantations (Lewis et al. 2019). However, large-scale analyses show that these projects, in addition to their high costs and lack of long-term funding (Brancalion and Holl 2020), have often been much less successful than expected, or even outright failed (Brancalion and Holl 2020; Holl and Brancalion 2020), and have also led to numerous territorial conflicts (Gerber 2011).

Multiple studies highlight the potential for timber production outside of natural forests and dedicated plantations. Two systems appear particularly promising in West Africa: secondary forests from agricultural fallows (Doua-Bi et al. 2021) and agroforestry systems (Tschora and Cherubini 2020). Developing timber supply from these systems can represent a viable alternative to help resolve the local timber deficit while (i) diversifying farmers' income sources (Kinyili et al. 2020; Kouassi et al. 2023a) and (ii) ensuring more sustainable use of agricultural lands (Plieninger et al. 2020). In this context, numerous agroforestry promotion initiatives have emerged in the West African cocoa production area (Zo-Bi and Hérault 2023), which accounts for nearly 70% of global cocoa production. Cocoa agroforestry consists in cultivating cocoa trees under the shade of larger trees. At low-to-intermediate shade levels, this practice can help reduce disease prevalence, buffer climate extremes, mitigate climate change and conserve biodiversity, while maintaining cocoa production levels (Blaser et al. 2018). Thus, the agroforestry promotion initiatives primarily aim to achieve sustainability and long-term stabilization of cocoa production (Carimentrand 2020). By doing so, the establishment of new deforestation fronts to seek fertile soils would be avoided, thereby reducing pressure on the few remaining forests (Ruf et al. 2015).

Despite all these agroforestry promotion activities, a significant limitation to the adoption of agroforestry practices remains a lack of knowledge about the actual productive potential of timber trees in cocoa fields and thus about the added value these trees can generate for the farmer (Sonwa et al. 2014). Indeed, while this productive potential is well known in natural forests (e.g., Zobi et al. (2009)) or in dedicated plantations (e.g., Hérault et al. (2020, 2021)), it is not transferable to cocoa fields where the biophysical environment is very different. There are two main reasons for this: (i) the growth trajectories of trees in cocoa fields are unknown and are expected to be very different in open, low-competition environments (cocoa fields) than in high-competition forest environments (Rozendaal et al. 2020; ii) allometric equations, necessary for determining the commercial volumes of trees, should also be different from those used in forests for several reasons. First, trees in cocoa fields receive more light and have more space to extend their branches laterally, unlike trees in dense forests that grow vertically to access light (Harja et al. 2012). Second, trees in cocoa fields are more exposed to wind, causing them to develop sturdier trunks and more extensive root systems to remain stable (Ennos 1997). Improving knowledge on growth trajectories and tree architecture in agroforestry contexts is thus urgent to correctly quantify the productive potentials of timber trees.

The actual implementation of agroforestry promotion activities often involves the massive distribution in cocoa fields, by industries and through cooperatives or development NGOs, of young trees raised in nurseries (IDH 2021). However, recent results suggest that the survival rate and growth performance of these planted trees are low and that the natural regeneration of these same tree species in the fields could offer much better performance for forest cover restoration (Kouassi et al. 2023a; Sanial et al. 2023). Indeed, planted trees, initially raised under controlled nursery conditions, seem less adapted once transplanted into the natural environment and less competitive than spontaneous recruits, making them more vulnerable to various stresses (Preece et al. 2023). On the other hand, naturally regenerated trees are subjected from the start to intense selection pressure exerted by the local environment and the farmers themselves. This selection pressure favours, among the hundreds or thousands of seedlings germinating each year in the fields, the best-adapted and most performant individuals over time (Sanial 2019). Naturally regenerated trees are thus recognized for their more vigorous growth compared to planted trees, due to their strong adaptation to the local parcel conditions (Werden et al. 2018), which also improves their long-term survival capacities (Aubry-Kientz et al. 2015). In conclusion, while the shock effect of planting seems evident in the early stages of tree development, improving our knowledge on the long-term consequences of choosing a "reforestation" technical itinerary, i.e., planting or natural regeneration, is necessary to determine which timber production strategy is most optimal.

The main objective of our study was to assess the timber production potential of trees in cocoa agroforestry systems (AFS) in Côte d'Ivoire (West Africa). Specifically, we estimated the time required for trees to reach their minimum logging diameter (MLD) and the corresponding volume at this stage. MLD values used in this study are legally defined thresholds below which logging is prohibited. These values correspond to the diameter at which approximately 80% of trees of a given species reach a stage of abundant and regular fruiting (Sodefor, 2017). This criterion ensures the sustainable renewal of tree populations. We also assessed the effect of the origin of the trees, be they from natural regeneration or (trans) plantation, on this production potential. To achieve these objectives, we (i) modelled the diameter growth of forest species identified as potentially suitable for wood production in cocoa AFS; (ii) established specific allometric models for trees in cocoa AFS to assess their volume when they reach their minimum logging diameter; and (iii) evaluated the effect of spontaneous or (trans)planted origin of trees on their growth trajectories, allometry, and thus on their logging volume trajectories. The results of this study provide key indicators for establishing silvicultural management technical itineraries for associated trees in cocoa AFS based on their actual performance, thereby encouraging decision-makers to better promote timber trees associated to cocoa production.

2 Material and methods

2.1 Sampling design

2.1.1 Study area

Our study covers the cocoa production area of Côte d'Ivoire (Fig. 1). This area is characterised by an annual precipitation gradient varying from 2500 mm in the south to 1100 mm in the north, and by an average annual temperature of around 26.5 °C. The area spans from evergreen forests in the south to semi-deciduous forests in the north.

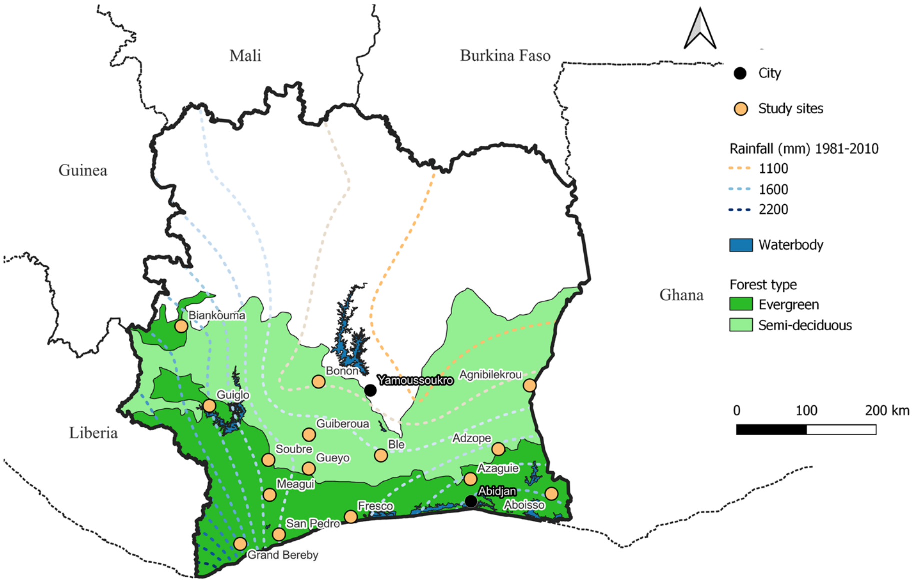

Fig. 1 Location of the 15 study sites across a gradient of climate and vegetation in central and southern Côte d'Ivoire

2.1.2 Sampling plots

A total of 150 plots were set up, grouped into 15 sites of 10 plots each. Each of these plots represents a management unit of the farmer or his manager. They range in size from 0.3 to 5 ha and together cover 240.5 ha. Our sampling covers a gradient of structural complexity: from low tree density AFS with a single stratum to complex AFS with high tree density and multiple strata.

2.1.3 Sampling data

We carried out an exhaustive tree inventory in our plots between March 2021 and November 2022. We measured the diameter at breast height (DBH) and bole height (BH) of all trees with a DBH of at least 10 cm. We identified trees to the species level following the Taxonomic Name Resolution Service as implemented in the R BIOMASS package (Réjou-Méchain et al. 2017). We also recorded their origin based on farmer declarations as remnant (pre-existing before cocoa farm conversion), spontaneous (naturally regenerated), or (trans)planted (intentionally planted or transplanted). The farmer also provided the age of spontaneous and (trans)planted trees (the age of remnant trees being unknown). Finally, we measured successive diameters along the bole (every metre) of a subset of 200 trees using a Bitterlisch relascope to calculate their bole volume.

A total of 11,999 trees belonging to 284 species were inventoried (a summary of this inventory is presented in Table S1; Kouassi et al. (2024)). In this study, we only considered the species listed in the national list of timber species (Sodefor 2017), or the species listed as commonly used by Ivorian cocoa farmers for construction purposes (Dago et al. 2025); Table S1 in Kouassi et al. 2024). Also, here we only consider spontaneous and (trans)planted trees while excluding remnant trees. Remnant trees are expected to have different development trajectories as they have grown, at least in part, in a forest environment. This approach ensures our analysis focuses solely on trees that developed entirely within cocoa agroforestry conditions, free from prior forest influence. Finally, we only consider species with at least 5 individuals. Our dataset thus includes a total of 4634 trees belonging to 59 species, including 2530 spontaneous trees and 2104 (trans) planted trees.

For the sake of clarity and simplicity, we focus in the main text on presenting the analyses and results for 23 species identified as the most suitable for timber production in cocoa agroforestry systems (Kouassi et al. 2023b). These species were identified based on their good cylindricity, straightness, and overall health, key indicators of high-quality commercial timber. A summary of the dendrometric characteristics of these 23 species is presented in Table 1. A summary of the dendrometric characteristics of the other 36 species is presented in Table S2 of Kouassi et al. (2024).

2.2 Modelling

We developed three models to assess the wood production potential of trees in cocoa agroforestry systems, using the sampled trees as the basis for parameter estimation. Rather than constructing separate models for each species, we incorporated species effects directly into specific model parameters to account for interspecific variation within a unified framework. Specifically, we modelled (i) diameter growth trajectories of trees as a function of their age (Eq. 2), (ii) the relationship between tree diameter and bole height (Eq. 4), and (iii) commercial volume of trees as a function of their diameter and bole height (Eq. 5). Each model includes an origin effect to assess the differences between spontaneous and (trans) planted trees. We estimated the model parameters in a Bayesian framework using Stan (Stan Development Team C et al. 2018; Carpenter et al. 2017) in the R environment (R Core Team 2021). The Bayesian approach offers great flexibility and transparency in modelling complex phenomena and uncertainty. It makes it possible to incorporate prior knowledge (priors) and to obtain probability distributions (posteriors) for model parameters, from which credible intervals are derived. We provide the STAN code in Kouassi et al (2024).

2.2.1 Diameter growth model

We base our analysis on the conceptual framework developed by Hérault et al. (2011) and Schmitt et al. (2023):

The diameter of an individual tree i of species s at age a can be calculated as the sum of its initial diameter at age 1 $DBH_{(i,s,1)}$ plus the sum of all annual growth rates (AGR) from age 1 to age $a - 1$:

$$DBH_{i,s,a} = DBH_{i,s,1} + \sum_{y=1}^{y=a-1} AGR_{i,s,y} \tag{1}$$

Using our field data, we modelled the diameter growth trajectories of trees as a function of their age as follows:

$$DBH_{i,s,a} \sim \mathcal{LN}\left(log\left(DBH_{i,s,1} + \sum_{y=1}^{y=a-1} AGR_{i,s,y}\right), \sigma_g\right) \tag{2}$$

with

- $DBH_{(i,s,1)}$: the initial diameter, set to 1 cm, assuming farmers notice trees from this size.
- σ_g: the dispersion parameter of the log-normal distribution.

Table 1 Summary of the dendrometric characteristics and uses of the wood of the 23 species we focus on. MLD, minimum logging diameter (cm); DBH: mean [min, max] diameter at breast height (cm); BH, mean [min, max] bole height (m); AGE, mean [min, max] tree age (year); WD, wood density from Chave et al. (2009) (g.cm^3); N_s, total number of spontaneous trees; N_tp, total number of (trans) planted trees; WOOD USES, T, timber, S, slicing, RP, Rotary peeling, from Prota4u; an asterisk indicates exotic species (Aké-Assi 2001)

Species name	Trade name	MLD	DBH	BH	AGE	WD	N_s	N_tp	WOOD USES
Alstonia boonei De Wild.	EMIEN	60	47.9 [11.0, 143.0]	9.2 [2.0, 34.0]	19.2 [3.0, 50.0]	0.32	47	1	T, S, RP
Amphimas pterocarpoides Harms	LATI	70	30.5 [10.0, 77.0]	8.1 [0.9, 29.0]	14.6 [1.0, 41.0]	0.62	57	0	T
Antiaris toxicaria (J.F.Gmel.) Lesch.	AKO	50	30.9 [10.0, 101.0]	7.9 [1.5, 23.0]	13.1 [2.0, 41.0]	0.38	93	1	T
Bombax brevicuspe Sprague	KONDROTI	60	44.3 [23.0, 109.0]	9.0 [4.5, 28.0]	15.8 [4.0, 50.0]	0.41	10	0	RP
Bombax buonopozense P.Beauv.	OBA/KAPOKIER	60	48.6 [11.7, 100.0]	7.3 [1.8, 15.0]	13.9 [3.0, 26.0]	0.32	19	3	T, S, RP
*Cedrela odorata L.**	CEDRELA*	50	29.6 [10.0, 51.4]	5.9 [2.0, 10.0]	7.5 [3.0, 19.0]	0.45	0	10	T, S, RP
Ceiba pentandra (L.) Gaertn.	FROMAGER	80	45.0 [10.9, 140.0]	7.2 [1.5, 25.0]	10.4 [1.0, 27.0]	0.31	43	3	RP
Celtis zenkeri Engl.	ASAN	50	38.4 [10.2, 65.2]	9.6 [1.0, 23.0]	16.4 [3.0, 25.0]	0.61	10	0	T
Distemonanthus benthamianus Baill.	MOVINGUI	60	28.1 [11.0, 75.0]	5.2 [1.3, 11.0]	15.0 [5.0, 35.0]	0.60	17	0	S
Entandrophragma angolense C.DC.	TIAMA	60	23.1 [10.3, 58.3]	8.9 [1.3, 20.0]	12.7 [4.0, 41.0]	0.48	49	0	T, S, RP
Funtumia africana (Benth.) Stapf	POUO	50	26.1 [10.1, 69.0]	5.0 [0.8, 15.0]	13.0 [3.0, 30.0]	0.42	45	0	RP
*Gmelina arborea Roxb.**	GMELINA*	50	18.7 [10.0, 32.7]	5.0 [2.2, 6.0]	3.6 [2.0, 4.0]	0.43	0	10	T, RP
Lannea welwitschii (Hiern) Engl.	LOLOTI	60	30.2 [14.0, 89.0]	6.6 [1.3, 20.0]	11.4 [3.0, 41.0]	0.41	34	2	S
Milicia excelsa (Welw.) C.C.Berg	IROKO BLANC	60	34.7 [10.8, 76.0]	8.8 [1.7, 21.0]	16.4 [2.0, 40.0]	0.57	67	9	T, S
Milicia regia (A.Chev.) C.C.Berg	IROKO ROUGE	60	28.6 [14.9, 76.0]	6.2 [3.0, 14.0]	11.8 [3.0, 41.0]	0.56	21	1	T, S
Parkia bicolor A.Chev.	LO	50	21.4 [10.4, 57.0]	3.4 [1.4, 9.0]	9.9 [5.0, 25.0]	0.46	5	4	T, S
Petersianthus macrocarpus (P.Beauv.) Liben	ABALE	50	36.5 [16.2, 56.0]	6.0 [2.0, 17.0]	15.5 [4.0, 30.0]	0.68	16	0	S
Piptadeniastrum africanum (Hook.f.) Brenan	DABEMA	60	24.5 [10.0, 38.6]	5.8 [2.3, 8.0]	12.8 [5.0, 27.0]	0.61	13	0	T
Pycnanthus angolensis (Welw.) Warb.	ILOMBA	60	39.4 [10.2, 79.9]	8.2 [3.0, 21.5]	18.6 [3.0, 50.0]	0.41	77	0	T, RP
Ricinodendron heudelotii (Baill.) Pierre ex Heckel	EHO/APKI	60	45.5 [11.6, 141.0]	6.5 [1.9, 20.0]	17.0 [3.0, 50.0]	0.21	31	19	RP
Terminalia ivorensis A.Chev.	FRAMIRE	50	35.4 [10.8, 73.2]	8.8 [2.1, 34.0]	14.9 [3.0, 41.0]	0.44	20	9	T, RP
Terminalia superba Engl. & Diels	FRAKE	50	26.4 [10.0, 79.0]	7.3 [1.0, 20.0]	9.4 [2.0, 28.0]	0.46	81	120	T, S
Zanthoxylum gilletii (De Wild.) P.G.Waterman	BAHE	50	50.0 [17.0, 94.6]	10.0 [1.8, 18.0]	23.2 [7.0, 41.0]	0.69	12	0	T, S

and where:

$$AGR_{i,s,y} = \theta_{si} \cdot \theta^{O}_{origin} \cdot G_{max_s} \cdot \exp\left(-\frac{1}{2}\left(\frac{\log\left(\frac{DBH_{i,s,y}}{D_{opt_s}}\right)}{K_s}\right)^2\right) \qquad (3)$$

with:

- $G_{max_s} \sim \mathcal{LN}(\log(G_{max}), \sigma_{gmax})$: the species-specific maximum growth potential, following a log-normal distribution with parameters G_{max} and σ_{gmax}. G_{max} represents the expected maximum growth potential for all species and σ_{gmax} the dispersion parameter.
- $D_{opt_s} = \theta_d \cdot D_{max_s}$: the species-specific diameter at which G_{max_s} is reached, defined as a function of D_{max_s}, the maximum diameter observed for each species, weighted by θ_d, a parameter between 0 and 1. $\theta_d \sim \mathcal{LN}\left(\log(\mu_{\theta_d}), \sigma_{\theta_d}\right)$ centred on μ_{θ_d} and dispersed according to σ_{θ_d}.
- $K_s = \theta_k \cdot wd_s$: the species-specific kurtosis coefficient defining the width of the growth curve, reflecting ontogenetic variation in growth potential. K_s is a linear function of species wood density wd_s, with parameters θ_k. $\theta_k \sim \mathcal{LN}\left(\log(\mu_{\theta_k}), \sigma_{\theta_k}\right)$ centred on μ_{θ_k} and dispersed according to σ_{θ_k}.
- $\theta_{si} \sim \mathcal{LN}(\log(1), \sigma_{si})$: a site effect following a log-normal distribution with parameters $log(1)$ and σ_{si}. Site effects are therefore centred on 1 and dispersed according to σ_{si}.
- θ^{O}_{origin}: an origin effect evaluating growth difference between spontaneous and (trans)planted trees. Practically, the origin variable (O) takes the value 1 for spontaneous trees and 0 for (trans)planted trees. Thus, θ^{O}_{origin} represents the annual diameter growth rate advantage of spontaneous trees over (trans) planted trees.

We modelled the diameter growth trajectories with a set of 4634 trees (2530 spontaneous and 2104 (trans) planted) for which age and diameter data were available.

We used this model to predict diameter as a function of age (up to age = 100), both for spontaneous and (trans) planted trees. We also recorded species annual growth rate (AGR) at diameter 10 cm and 70 cm for comparison with measurements taken in forests in the same region (see Discussion section).

2.2.2 Bole height model

We modelled the bole height of individual trees as a function of their diameter using a Michaelis-Menten model, which is commonly applied in ecology for height-diameter relationships (Molto et al. 2014; Huang et al. 1992). Our model is specified as:

$$BH_{\mathrm{i,s}} \sim \mathcal{LN}\left(\log\left(\theta_s \cdot \theta_{si} \cdot \theta^{O}_{origin} \cdot \frac{\alpha \cdot DBH_{\mathrm{i,s}}}{\beta + DBH_{\mathrm{i,s}}}\right), \sigma_h\right) \tag{4}$$

with:

- $BH_{i,s}$: the bole height of tree i of species s.
- $DBH_{i,s}$: the diameter at breast height of tree i of species s.
- α: represents the asymptotic bole height.
- β: represents the diameter at which half the asymptotic height $\left(\frac{BH_{\mathrm{i,s}}}{2}\right)$ is reached.
- $\theta_s \sim \mathcal{LN}(\log(1), \sigma_s)$: a species effect following a log-normal distribution with parameters $log(1)$ and σ_s. Species effects are therefore centred on 1 and dispersed according to σ_s.
- $\theta_{si} \sim \mathcal{LN}(\log(1), \sigma_{si})$: a site effect following a log-normal distribution with parameters $log(1)$ and σ_{si}. Site effects are therefore centred on 1 and dispersed according to σ_{si}.
- θ^{O}_{origin}: an origin effect evaluating the difference in asymptotic bole height between spontaneous and (trans)planted trees. Practically, the origin variable (O) takes the value 1 for spontaneous trees and 0 for (trans)planted trees. Thus, θ^{O}_{origin} represents the advantage of spontaneous trees over (trans)planted trees in terms of asymptotic bole height.
- σ_h: the dispersion parameter of the log-normal distribution.

We modelled tree bole height with a set of 4882 trees (2629 spontaneous and 2253 (trans)planted) for which diameter and bole height data were available.

2.2.3 Bole volume model

We modelled the bole volume of an individual tree i of species s as a function of its diameter at breast height (DBH) and bole height (BH) (Köhl et al. 2006; Magnussen and Reed 2004). Our model is given by:

$$BV_{i,s} \sim \mathcal{LN}\left(log\left(\theta_s \cdot \theta^{O}_{origin} \cdot \alpha \cdot DBH^{\beta}_{i,s} \cdot BH^{\gamma}_{i,s}\right), \sigma_v\right) \tag{5}$$

with:

- $BV_{i,s}$: the bole volume of tree i of species s.
- $DBH_{i,s}$: the diameter at breast height of tree i of species s.
- $BH_{i,s}$: the bole height of tree i of species s.
- α, β et γ: parameters to be estimated.
- $\theta_s \sim \mathcal{LN}(\log(1), \sigma_s)$: a species effect following a log-normal distribution with parameters $log(1)$ and σ_s. Species effects are therefore centred on 1 and dispersed according to σ_s.
- θ^{O}_{origin}: an origin effect evaluating the difference in bole volume between spontaneous and (trans)planted trees. Practically, the origin variable (O) takes the value 1 for spontaneous trees and 0 for (trans)planted trees. Thus, θ^{O}_{origin} represents the advantage of spontaneous trees over (trans)planted trees in terms of bole volume.
- σ_v: the dispersion parameter of the log-normal distribution.

We modelled bole volume with a subset of 200 trees (176 spontaneous and 24 (trans)planted) for which bole volume, diameter and bole height data were available. These trees were selected in the field for there remarkable commercial quality: bole height of at least 5 m and good health and conformation (Kouassi et al. 2023b). This subset is therefore not representative of all trees in cocoa AFS, but rather allows to evaluate the bole volumes that can be reached by trees in these systems.

We used this model to predict the bole volume of spontaneous and (trans)planted trees as a function of age (up to age 100). For that, we predicted $DBH_{i,s}$ as a function of age using our diameter growth model (Eq. 2), then $BH_{i,s}$ as a function of the predicted $DBH_{i,s}$ using our bole height model (Eq. 4), and finally the bole volume using these predicted $DBH_{i,s}$ and $BH_{i,s}$.

We also used this model to predict the bole volume of spontaneous and (trans)planted trees as a function of DBH (up to DBH = 100 cm). We predicted $BH_{i,s}$ using our bole height model (Eq. 4).

3 Results

In this section, we presented the results obtained for the 23 species identified as the most suitable for timber production, as previously mentioned. The parameter values and credible intervals for all 59 species considered in this study were provided in Tables S3 to S12 of the Supplementary Information (Kouassi et al. 2024).

3.1 Tree diameter growth

On average, the 23 species we focused on reached a diameter of 50 cm (smallest MLD value) in 36 years (Fig. 2). The fastest growing species was *Ceiba pentandra*,

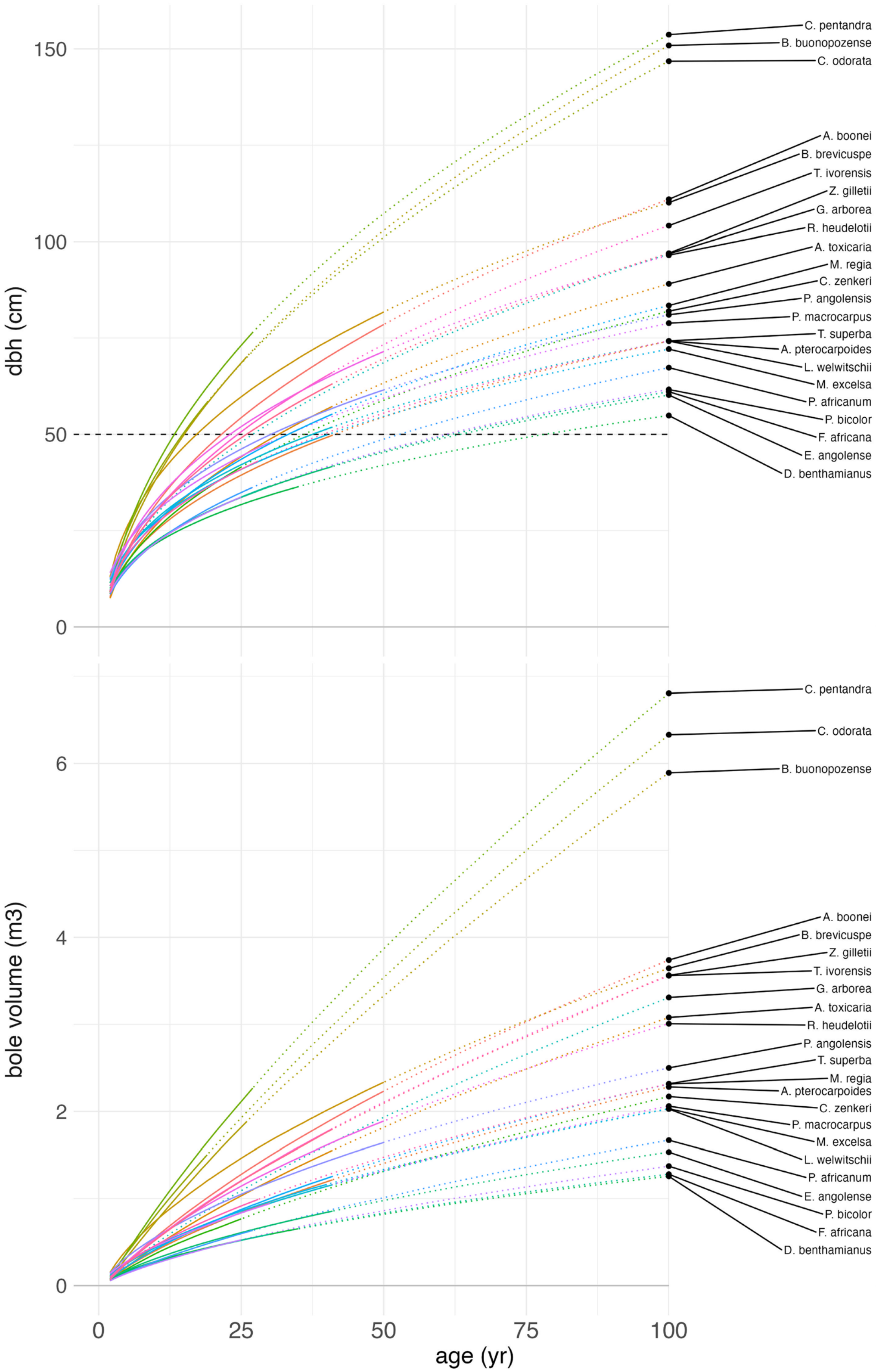

Fig. 2 Diameter growth and bole volume trajectories of our 23 tree species. Full lines stop at the maximum age recorded for each species. Dotted lines extend predictions to age 100. Here, we present the trajectories predicted for spontaneous trees

reaching 50 cm in 14 years. The slowest growing species was *Distemonanthus benthamianus*, reaching the same diameter in 79 years. The expected maximum annual growth potential (G_{max} in Eq. 3) for all species was 8.74 cm year^{-1}. On average, the maximum annual growth potential occurred at an optimal diameter (D_{opt_s} in Eq. 3) of 0.87 cm. In general, species annual growth rates were therefore maximum for DBH smaller than 1 cm and decreased as DBH increased.

Species annual growth rates (AGR) at DBH = 10 cm ranged from 2.28 cm year^{-1} for *Piptadeniastrum africanum* to 6.57 cm.yr^{-1} for *Bombax brevicuspe*, with an average of 3.87 cm year^{-1}. At DBH = 70 cm, species AGR ranged from 0.13 cm year^{-1} for *Distemonanthus benthamianus* to 1.73 cm.yr^{-1} for *Ceiba pentandra*, with an average of 0.61 cm year^{-1}. The model parameter values and their credible intervals, including the parameter values for the 36 additional timber species are presented from Table S3 to Table S7 in Kouassi et al. (2024).

3.2 Diameter-bole height relationship

At 50 cm in DBH (smallest MLD value), the trees reached an average bole height of 6.75 m (Fig. 3), ranging from 4.33 m to 8.83 m. The predicted tree asymptotic bole height (α in Eq. 4) was 6.75 m. The species effect θ_s ranged from 0.80 (i.e. −20%) to 1.64 (i.e. +64%). Maximum values at 50 cm DBH were reached by *Antiaris toxicaria*, while minimum values were reached by *Parkia bicolor*. The model parameter values and their credible intervals, including the parameter values for the 36 additional timber species are presented in tables S8 to S10 of Kouassi et al. (2024).

3.3 Wood production potential of trees

At age 25 (a commonly used logging age in forest plantations), trees reached a mean bole volume of 1.04 m^3 (Fig. 2). The fastest growing species was *Ceiba pentandra*, which reached 2.11 m^3, corresponding to an anhydrous wood mass of 630 kg, at age 25. The slowest growing species, *Distemonanthus benthamianus* and *Funtumia africana*, reached 0.52 m^3, corresponding to an anhydrous wood mass of 300 kg and 200 kg, respectively, at the same age.

At 50 cm DBH (smallest MLD value), tree bole volume ranged from 0.94 to 1.24 m^3 (Fig. 3). These volumes increased to reach 3.11 to 3.53 m^3 for trees 100 cm in diameter.

On average, trees reached their MLD at 44.82 years of age (Fig. 4). *Cedrela odorata* reached its MLD first at the age of 15, while *Entandrophragma angolense* reached its MLD last at the age of 100. At their MLD, trees had on average a volume of 1.37 m^3. *Parkia bicolor*, with 0.92 m^3, had the smallest volume, while *Ceiba pentandra*, with 2.36 m^3, had the largest volume. The evaluation of our bole volume model (Eq. 5) provided the following allometric equation adapted to predict the bole volume of trees in cocoa AFS:

$$BV = \theta_o \cdot 0.95 \cdot DBH^{1.45} \cdot BH^{0.43} \qquad (6)$$

With $\theta_o = 1.43$ for spontaneous trees and $\theta_o = 1$ for (trans)planted trees (see the next section about the effect of tree origin). The model parameter values and their credible intervals are presented in Table S11 to Table S12, and is presented in Fig. S1 of Kouassi et al. (2024).

3.4 Effect of trees' origin on their wood production potential

In our diameter growth model (Eq. 3), $\theta_o = 1.10$. This means that the annual growth rate of spontaneous trees is 10% higher than that of (trans)planted trees. As a consequence, spontaneous trees reach their MLD 4.76 years earlier than (trans)planted trees (Fig. 5) on average. This advantage of spontaneous trees over (trans) planted trees ranges from 2 years for *Bombax buonopozense* and *Cedrela Odorata* to 10 years for *Amphimas pterocarpoides*.

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In our bole volume model (Eq. 5), $\theta_o = 1.43$. This meant that for a given diameter and a given bole height, spontaneous trees were 43% larger in volume than (trans) planted trees. As a consequence, spontaneous trees reached a higher bole volume of 0.43 m^3 on average as compared to (trans)planted trees (Fig. 5). This advantage in volume ranged from 0.29 m^3 for *Funtumia africana* and *Parkia bicolor* to 0.71 m^3 for *Ceiba pentandra*.

Finally, in our bole height model (Eq. 4), $\theta_o = 1$, indicating no difference in the diameter-height relationship between spontaneous and (trans)planted trees.

4 Discussion

To our knowledge, this study is the first to assess the diameter growth and the wood production potential of trees in West African cocoa AFS. Our results show that trees can reach their MLD as early as 15 years of age for bole volumes greater than 0.92 m^3. Our results also show

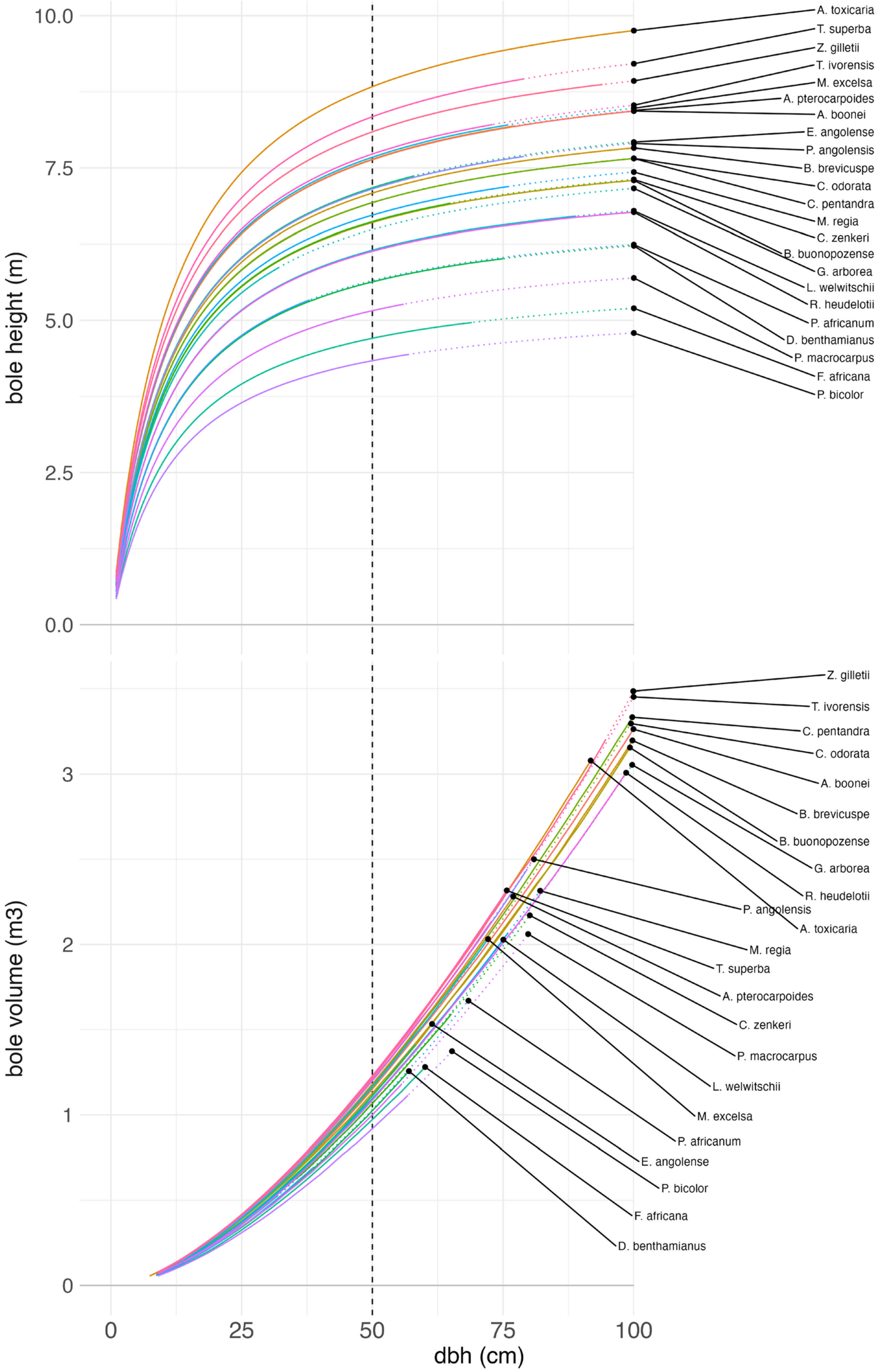

Fig. 3 Diameter-bole height and diameter-bole volume relationships for our 23 tree species. Full lines stop at the maximum DBH observed for each species. Dotted lines extend the predictions to a DBH of 100 cm or an age of 100 years. Here we present the relationships predicted for spontaneous trees

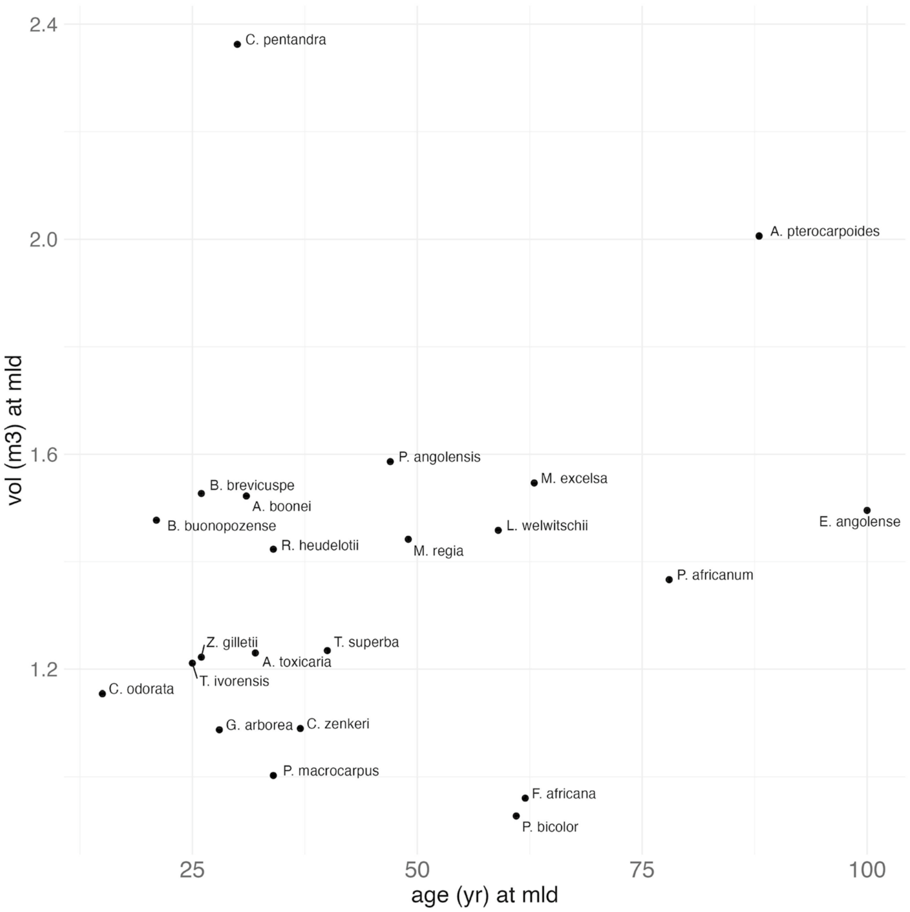

Fig. 4 Bole volume and age at minimum logging diameter for our 23 species. *Distemonanthus benthamianus* is not represented as it does not reach its MLD within 100 years

that spontaneous trees have a clear advantage over transplanted trees: they can reach their MLD up to 10 years earlier and produce up to 0.71 m^3 more over the same period.

4.1 A faster diameter growth in cocoa AFS than in forests or plantations, but a lower bole volume

Our results suggest trees can achieve greater annual growth rates in cocoa AFS than in forests or plantations. Indeed, for trees with diameters ranging from 10 to 70 cm, we predict growth rates varying from 0.13 to 6.57 cm $year^{-1}$. In comparison, the average annual growth rates recorded in West African forests for trees of the same size are at the lower end of this range. In Côte d'Ivoire, Durrieu de Madron et al. (1998a, 1998b) found an average annual growth rate of 0.27 cm $year^{-1}$ for an evergreen forest and of 0.29 cm $year^{-1}$ for a semi-deciduous forest, respectively. In Ghana, Alder (1989) found average annual growth rates ranging from 0.80 to 1 cm $year^{-1}$ for pioneer species and ranging from 0.40 to 0.50 cm $year^{-1}$ for shade-tolerant species. Similarly, in plantations in Côte d'Ivoire, Hérault et al. (2021) reported more than 35 years were needed to reach 50 cm in diameter, whereas we found only 15 years are needed in cocoa AFS.

The faster growth of trees in cocoa AFS could be due to the greater availability of light in these systems than in forests (Pillet et al. 2018) or plantations. This greater availability of light could lead trees to invest more in their diameter growth once they have emerged from the cocoa canopy (Rutishauser et al. 2016; Ek 1974; King 1981). Besides light, stronger wind exposure in open-canopy agroforestry systems may cause trees to develop sturdier trunks due to wind stress. This could also contribute to the faster diameter growth in these systems (Jaouen et al. 2010; Ennos 1997). Our results show maximum annual growth rates from the very first years ($Gmax = 8.74$ cm $year^{-1}$ for a mean $D_{opt_s} = 0.87$ cm), which is in line with the hypothesis of a priority given to diameter growth.

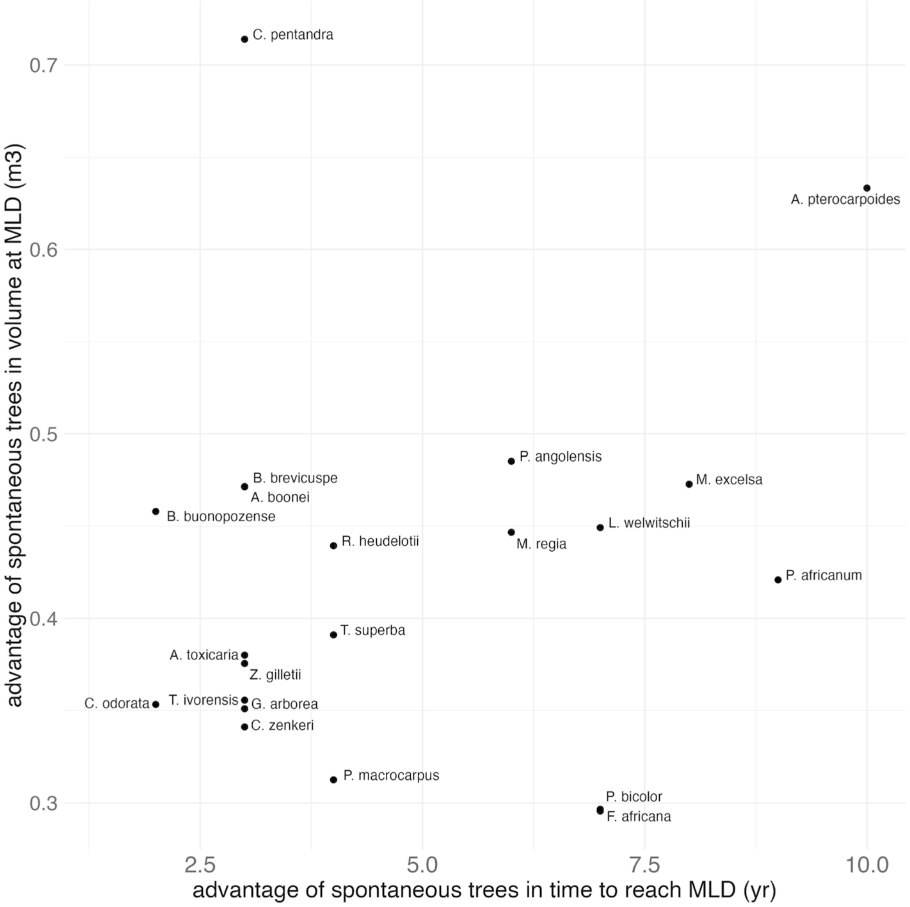

Fig. 5 Advantage of spontaneous trees over (trans)planted trees in time to reach their MLD and in volume at MLD. *Distemonanthus benthamianus* is not represented as it does not reach its MLD within 100 years. *Entandrophragma angolense* is also excluded because, although spontaneous trees reach their MLD within 100 years, planted trees do not, making it impossible to calculate the advantages in age and volume

In contrast, in forests and plantations, closed systems where competition for light is strong, growth in height could be favoured (Ammer 2003; Prévosto and Balandier 2007), to the expanse of diameter growth (Falster and Westoby 2003, 2005). Prioritizing diameter growth also enhances tree stability and resilience to wind, especially in resource-limited environments. As a result, trees tend to develop more conical boles rather than perfectly cylindrical ones, as evidenced by the low values of the volume model parameters ($\beta = 1.45$ and $\gamma = 0.43$, compared to the expected $\beta = 2$ and $\gamma = 1$). These parameters indicate that as trees grow larger, their shape becomes increasingly conical, reinforcing the hypothesis of prioritized diameter growth in AFS.

We therefore expect trees in forests or plantations to take longer to reach the same diameter than trees in cocoa AFS. However, for a same diameter, we expect trees in forests or plantations to have a greater bole volume than trees in cocoa AFS, due to their greater height. As a consequence of the power relationship between diameter and volume, the larger the trees, the greater this difference in volume. This is supported by our results. Indeed, we found trees in cocoa AFS can reach 1.25 m^3 at 50 cm DBH while in Côte d'Ivoire, Hérault et al. (2021) found trees in plantation can reach about 2.50 m^3 at the same DBH. At 100 cm DBH, we found trees in cocoa AFS could reach 3.53 m^3 while at this size, trees in plantation can reach a much higher volume of over 15 m^3.

The rapid diameter growth we observed in AFS could limit heartwood formation, which could affect wood quality in certain species. However, we currently lack the data to test this hypothesis. More generally, the quality of wood from cocoa AFS has yet to be assessed. Future studies could explore the link between growth rate and wood quality, as well as investigate the typical defects of wood in AFS and their impact on commercial value.

Finally, while our models are based on a robust dataset (4634 trees), predictions for greater ages (> 83 years) and dimensions (> 143 cm in DBH) rely on inferred growth patterns rather than direct observations. These extrapolations should be interpreted with caution, and further validation with additional data particularly for older and larger trees is needed.

4.2 A lower wood production potential than in managed cocoa AFS

The wood production potential we found for trees in West African cocoa AFS proved to be lower than reported in other regions. Indeed, in Honduras for instance, trees can reach a volume of 0.60 to 2.40 m^3 in 18 years (Ramírez-Argueta et al. 2022) while we predict a bole volume ranging from 0.41 to 1.56 m^3 at this age. Similarly, in Brazil, trees can reach a volume of 1.90 m^3 at age 20 (Gama-Rodrigues et al. 2021) while we predict a volume ranging from 0.45 to 1.73 m^3 at this age. This difference could be attributed to the implementation of silvicultural practices (plantation of fast-growing species, thinning, pruning) in both Honduras and Brazil, whereas there is little or no tree management in Côte d'Ivoire. Our results are in line with this hypothesis. Indeed, although trees in Honduras grow faster in volume, trees in Côte d'Ivoire grow much faster in diameter: it only takes 5 to 15 years for trees in Côte d'Ivoire to reach a DBH of 25 cm while this DBH is reached in 13 to 18 years in Honduras. This suggest trees in Honduras have greater bole heights which can be attributed to pruning.

4.3 A clear advantage of spontaneous trees over (trans)planted trees

Our results show that spontaneous trees have an annual growth rate 10% higher than (trans)planted trees and a bole volume 43% greater for a same diameter. This latter result indicates spontaneous trees have a more cylindrical bole than (trans)planted trees. These better performances of spontaneous trees could be due to the fact that, having remained in the same environment, they could have a more extensive root system, more efficient at absorbing water and nutrients (Werden et al. 2018). In contrast, transplanted trees experience disturbances in their root systems when moved to a new environment, negatively impacting their growth (Brown 2004; Werden et al. 2018). In addition, spontaneous trees, having remained in the same environment, could prioritise resource allocation to growth, unlike (trans)planted trees, which could allocate resources preferentially to defence and reproduction (Waring and Pitman 1985; Wunder et al. 2008; Fritts and Shatz 1975).

On the other hand, we found no difference between spontaneous and (trans)planted trees with regard to their diameter-bole height relationship. This is an expected outcome as self-pruning is controlled by light availability (Koike 1989; Mäkelä 1997; Sorrensen-Cothern et al. 1993). Both spontaneous and (trans)planted trees are therefore expected to maintain their lower branches at the same height, i.e., once above the cocoa canopy.

Finally, we acknowledge that species composition differs across origins, with some species common to all (27), while others are exclusively planted (2) or naturally regenerated (30). To account for these differences and sampling variability, our model includes both origin and species effects. This approach helps control for species composition differences and reduces bias in estimating the origin effect.

4.4 A high variability in species wood production potential due to differences in their ecology

Our results show a high variability in the wood production potential of trees depending on species (Fig. 2). This variability could be explained by differences in species ecology. In an additional analysis (see Fig. S1 in Kouassi et al. (2024)), we found tree bole volume predicted at age 25 is negatively correlated to wood density. This indicates species with low wood density tend to grow faster than species with high wood density. This result is consistent with previous findings showing a negative correlation between wood density and growth speed in most biomes; species with low wood density having generally a low ability to tolerate competition and a low competitive effect on their neighbours (Kunstler et al. 2016).

4.5 Implication for tree management in cocoa AFS

The promotion of timber species in cocoa fields is crucial for the development of agroforestry, both for the sustainability of cocoa production and for the diversification of farmers' incomes (Blaser-Hart et al. 2021; Notaro et al. 2021). Understanding the dynamics of wood production is therefore vital to develop management strategies maximising cocoa production as well as wood production, carbon sequestration, biodiversity, etc. In this study, we provide fundamental elements for developing a silviculture adapted for West African cocoa AFS. In particular, we estimated the time required for trees to reach their minimum logging diameter (MLD). This information can be used to define silvicultural cycles. We also provide allometric equations adapted to West African cocoa AFS to estimate bole volume. These equations can be used to assess tree commercial volumes and help estimate carbon stocks. Finally, our results suggest that natural regeneration is a more effective strategy than planting for renewing trees in cocoa AFS.

Besides, our results show trees in West African cocoa AFS have low bole height. This suggests pruning could be an effective lever for improving wood production. Indeed, by removing lower branches at an early stage, pruning helps prevent defects in the wood, which increases the commercially valuable length of the bole. The cocoa sector should help implement strategies to support pruning in cocoa AFS, as farmers alone may not be able to cover the additional costs on their own (Esche et al. 2023).

Wood production in cocoa AFS inevitably leads to shading, which, beyond a certain threshold, can be detrimental to cocoa production (Blaser et al. 2018). Further research should therefore investigate the link between wood production and shading to identify the best trade-off between wood and cocoa production.

Authors' contributions

Conceptualization: A.K.K., R.A., I.C.Z., and B.H.; methodology: A.K.K., R.A., I.C.Z., B.H., B.L., and S.S.; formal analysis and investigation: A.K.K., R.A., I.C.Z., B.H., B.L., and S.S.; writing—original draft preparation: A.K.K., B.H., and R.A.; writing—review and editing: A.K.K., R.A., I.C.Z., B.H., I.K.K., M.R.D., B.L., S.S., and A.E.N.; funding acquisition: I.C.Z. and B.H.; resources: A.K.K., R.A., I.C.Z., B.H., I.K.K., and M.R.D.; supervision: R.A., I.C.Z., and B.H.

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Data availability

Data, code, and supplementary information are available online (Kouassi et al. 2024, https://zenodo.org/doi/10.5281/zenodo.12581453).

Declarations

Competing interests

The authors declare no competing interests.

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