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24 years to start harvesting timber in West African cocoa agroforestry systems with spontaneous trees demonstrating clear advantages

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Abstract

In West Africa, where over 80% of original forests have been lost to agriculture, finding alternative timber sources is critical for regional needs and sustainability. The widespread development of agroforestry could be a promising source of timber wood, but the production potential of trees in agricultural fields cannot be directly transferred from natural forests or dedicated plantations due to different biophysical environments. Our study assesses the timber production potential of trees in 150 cocoa agroforestry systems (AFS) in Côte d'Ivoire. To achieve this, we: (i) modelled the diameter growth of forest tree species with timber potential in cocoa AFS; (ii) developed specific allometric models for trees in cocoa AFS to estimate their volume at minimum logging diameter (MLD); and (iii) evaluated the effect of tree origin (natural regeneration vs. plantation) on growth trajectories, allometry, and bole volumes. Our results show that, on average, species reach a 50 cm diameter (the smallest MLD) in 33 years, with an average bole height of 8.1 m at this diameter. Depending on species identity, trees reach MLD between 24 and 93 years. Spontaneous trees grow 10% faster annually than (trans)planted trees, reaching MLD 3.7 years earlier on average. For a given bole height, spontaneous trees are 41% larger in volume than (trans)planted trees. These findings highlight that natural regeneration is a more efficient and effective strategy than plantation for renewing trees in cocoa AFS. Natural regeneration results in higher growth rates and greater timber volumes compared to planting. Therefore, natural regeneration shows great potential for (i) sustainable forestry management in agroforestry systems and (ii) significantly contributing to meeting regional timber demands.

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

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2 Introduction

In a global context where the demand for tropical timber is constantly increasing (Chimeli et 3 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 5 (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 7 (Louppe and Ouattara, 2013), in a context where over 80% of the original forest mass has been lost in favor 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 en-10 sure the sustainability of the timber sector and the people who depend on it (Tsanga et al., 2020). 11 Large-scale tree planting has long been seen as an ideal solution to meet the needs for tropical 12 timber. For example, 45% of the national commitments made under the Bonn Challenge, an in-13 ternational goal aiming to restore 350 million hectares of land by 2030 (Verdone and Seidl, 2017), 14 involve multiplying tree plantations (Lewis et al., 2019). However, large-scale analyses show that 15 these projects, in addition to their high costs and lack of long-term funding (Brancalion and Holl, 16 2020), have often been much less successful than expected, or even outright failed (Brancalion 17 and Holl, 2020; Holl and Brancalion, 2020), and have also led to numerous territorial conflicts 18 (Gerber, 2011). 19 Multiple studies highlight the potential for timber production outside of natural forests and ded-20 icated plantations. Two systems appear particularly promising in West Africa: secondary forests 21 from agricultural fallows (Doua-Bi et al., 2021) and agroforestry systems (Tschora and Cheru-22 bini, 2020). Developing timber supply from these systems can represent a viable alternative to 23 help resolve the local timber deficit while (i) diversifying farmers' income sources (Kinyili et al., 24 2020; Kouassi et al., 2023b) and (ii) ensuring more sustainable use of agricultural lands (Plieninger 25 et al., 2020). In this context, numerous agroforestry promotion initiatives have emerged in the 26 West African cocoa production area (Zo-Bi and Hérault, 2023), which accounts for nearly 70% of 27 global cocoa production. These initiatives primarily aim to achieve sustainability and long-term 28 stabilization of cocoa production (Carimentrand, 2020). By doing so, the establishment of new 29 deforestation fronts to seek fertile soils would be avoided, thereby reducing pressure on the few 30 remaining forests (Ruf et al., 2015). 31 Despite all these agroforestry promotion activities, a significant limitation to the adoption of 32 agroforestry practices remains a lack of knowledge about the actual productive potential of tim-33 ber trees in cocoa fields and thus about the added value these trees can generate for the farmer 34 (Sonwa et al., 2014). Indeed, while this productive potential is well known in natural forests (e.g., 35 Zobi et al., 2009) or in dedicated plantations (e.g., Hérault et al., 2021; Hérault et al., 2020), it is 36 not transferable to cocoa fields where the biophysical environment is very different. There are 37 two main reasons for this: (i) the growth trajectories of trees in cocoa fields are unknown and are 38 expected to be very different in open, low-competition environments (cocoa fields) than in high-39 competition forest environments (Rozendaal et al., 2020); (ii) allometric equations, necessary for 40 determining the commercial volumes of trees, should also be different from those used in forests 41 for several reasons. First, trees in cocoa fields receive more light and have more space to extend 42 their branches laterally, unlike trees in dense forests that grow vertically to access light (Harja 43 et al., 2012). Second, trees in cocoa fields are more exposed to wind, causing them to develop 44 sturdier trunks and more extensive root systems to remain stable (Ennos, 1997). Finally, trees 45

are more subject to variations in temperature and humidity, influencing their mechanical structure (Johnson et al., 2011). 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 distri-50 bution in cocoa fields, by industries and through cooperatives or development NGOs, of young 51 trees raised in nurseries (IDH, 2021). However, recent results suggest that the survival rate and 52 growth performance of these planted trees are low and that the natural regeneration of these 53 same tree species in the fields could offer much better performance for forest cover restoration 54 (Kouassi et al., 2023a; Sanial et al., 2023). Indeed, planted trees, initially raised under controlled 55 nursery conditions, seem less adapted once transplanted into the natural environment and less 56 competitive than spontaneous recruits, making them more vulnerable to various stresses (Preece 57 et al., 2023). On the other hand, naturally regenerated trees are subjected from the start to in-58 tense selection pressure exerted by the local environment and the farmers themselves. This 59 selection pressure favors, among the hundreds or thousands of seedlings germinating each year 60 in the fields, the best-adapted and most performant individuals over time (Sanial, 2019). Natu-61 rally regenerated trees are thus recognized for their more vigorous growth compared to planted 62 trees, due to their strong adaptation to the local parcel conditions (Werden et al., 2018), which 63 also improves their long-term survival capacities (Aubry-Kientz et al., 2015). In conclusion, while 64 the shock effect of planting seems evident in the early stages of tree development, improving 65 our knowledge on the long-term consequences of choosing a "reforestation" technical itinerary, 66 i.e., planting or natural regeneration, is necessary to determine which timber production strategy 67 is most optimal. 68

The main objective of our study is 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. 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; (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 fields based on their actual performance, thereby encouraging decision-makers to better promote timber trees in cocoa fields.

Material and methods

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Study area. Our study covers the cocoa production area of Côte d'Ivoire (Figure 1). This area is
 characterised by an annual precipitation gradient varying from 2 500 mm in the south to 1 100
 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.

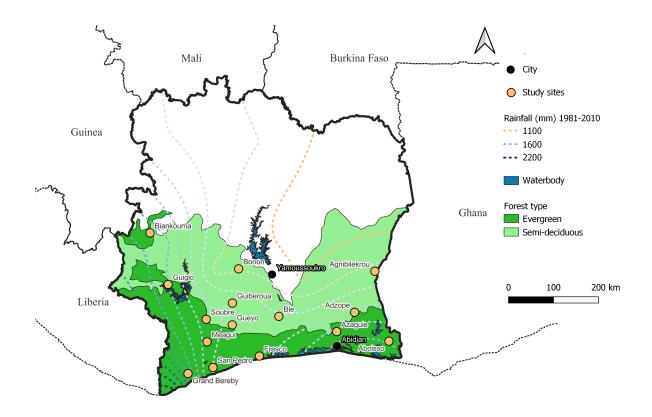


Figure 1 - Location of the 15 study sites across a gradient of climate and vegetation.

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.

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 (remnant, spontaneous or (trans)planted) based on the farmer's declaration. 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 trees using a Bitterlisch relascope in order to calculated their bole volume.

In this study, we only considered 23 tree species identified as potentially suitable for wood production in cocoa AFS (Kouassi et al., 2023a). Also, here we only consider spontaneous and (trans)planted trees excluding remnant trees. Remnant trees are expected to have different development trajectories as they have grown, at least in part, in a forest environment.

Table 1 – Summary of the dendrometric characteristics and uses of the wood of the 23 studied species. 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); N: total number of trees; WD: wood density from (Chave, 2005) (g.cm³); WOOD USES from Prota4u; (*) indicates exotic species (Aké-Assi, 2001).

Species name	Trade name	MLD	DBH	ВН	AGE	WD	N	WOOD USES
Alstonia boonei	EMIEN	60	47.9 [11.0, 143.0]	9.2 [2.0, 34.0]	19.2 [3.0, 50.0]	0.3	48	timber, slicing, unwinding
Amphimas pterocarpoides	LATI	70	30.5 [10.0, 77.0]	8.1 [0.9, 29.0]	14.6 [1.0, 41.0]	0.6	57	timber
Antiaris toxicaria	AKO	50	30.9 [10.0, 101.0]	7.9 [1.5, 23.0]	13.1 [2.0, 41.0]	0.4	94	timber
Bombax brevicuspe	KONDROTI	60	44.3 [23.0, 109.0]	9.0 [4.5, 28.0]	15.8 [4.0, 50.0]	0.4	10	unwinding
Bombax buonopozense	OBA/KAPOKIER	60	48.6 [11.7, 100.0]	7.3 [1.8, 15.0]	13.9 [3.0, 26.0]	0.3	22	timber, slicing, unwinding
Cedrela odorata*	CEDRELA*	50	29.6 [10.0, 51.4]	5.9 [2.0, 10.0]	7.5 [3.0, 19.0]	0.4	10	timber, slicing, unwinding
Ceiba pentandra	FROMAGER	80	45.0 [10.9, 140.0]	7.2 [1.5, 25.0]	10.4 [1.0, 27.0]	0.3	46	unwinding
Celtis zenkeri	ASAN	50	38.4 [10.2, 65.2]	9.6 [1.0, 23.0]	16.4 [3.0, 25.0]	0.6	10	timber
Distemonanthus benthamianus	MOVINGUI	60	28.1 [11.0, 75.0]	5.2 [1.3, 11.0]	15.0 [5.0, 35.0]	0.6	17	slicing
Entandrophragma angolense	TIAMA	60	23.1 [10.3, 58.3]	8.9 [1.3, 20.0]	12.7 [4.0, 41.0]	0.5	49	timber, slicing, unwinding
Funtumia africana	POUO	50	26.1 [10.1, 69.0]	5.0 [0.8, 15.0]	13.0 [3.0, 30.0]	0.4	45	unwinding
Gmelina arborea*	GMELINA*	50	18.7 [10.0, 32.7]	5.0 [2.2, 6.0]	3.6 [2.0, 4.0]	0.4	10	timber, unwinding
Lannea welwitschii	LOLOTI	60	30.2 [14.0, 89.0]	6.6 [1.3, 20.0]	11.4 [3.0, 41.0]	0.4	36	slicing
Milicia excelsa	IROKO BLANC	60	34.7 [10.8, 76.0]	8.8 [1.7, 21.0]	16.4 [2.0, 40.0]	0.6	76	timber, slicing
Milicia regia	IROKO ROUGE	60	28.6 [14.9, 76.0]	6.2 [3.0, 14.0]	11.8 [3.0, 41.0]	0.6	22	timber, slicing
Parkia bicolor	LO	50	21.4 [10.4, 57.0]	3.4 [1.4, 9.0]	9.9 [5.0, 25.0]	0.5	9	timber, slicing
Petersianthus macrocarpus	ABALE	50	36.5 [16.2, 56.0]	6.0 [2.0, 17.0]	15.5 [4.0, 30.0]	0.7	16	slicing
Piptadeniastrum africanum	DABEMA	60	24.5 [10.0, 38.6]	5.8 [2.3, 8.0]	12.8 [5.0, 27.0]	0.6	13	timber
Pycnanthus angolensis	ILOMBA	60	39.4 [10.2, 79.9]	8.2 [3.0, 21.5]	18.6 [3.0, 50.0]	0.4	77	timber, unwinding
Ricinodendron heudelotii	EHO	60	45.5 [11.6, 141.0]	6.4 [1.9, 20.0]	17.0 [3.0, 50.0]	0.2	50	unwinding
Terminalia ivorensis	FRAMIRE	50	35.4 [10.8, 73.2]	8.8 [2.1, 34.0]	14.9 [3.0, 41.0]	0.4	29	timber, unwinding
Terminalia superba	FRAKE	50	26.4 [10.0, 79.0]	7.3 [1.0, 20.0]	9.4 [2.0, 28.0]	0.5	201	timber, slicing
Zanthoxylum gilletii	BAHE	50	50.0 [17.0, 94.6]	10.0 [1.8, 18.0]	23.2 [7.0, 41.0]	0.7	12	timber, slicing

Our dataset thus includes a total of 1008 trees, including 806 spontaneous trees and 202 (trans)planted trees. A summary of the dendrometric characteristics of the 23 studied species is presented in table 1.

109 Modelling

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We developed three models to assess the wood production potential of trees in cocoa AFS:

(i) a model describing the diameter growth trajectories of trees as a function of their age (Eq 2),

(ii) a model evaluating the relationship between tree diameter and bole height (Eq 4), and (iii) a

model assessing the 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

(Carpenter et al., 2017; Stan Development Team et al., 2018) in the R environment (Team et al.,

2021). We provide the STAN code in Supplementary Information (Kouassi et al., 2024).

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:

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

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

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

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

and where:

(3)
$$AGR_{i,s,y} = \theta_{si} \cdot \theta_{origin}^{O} \cdot G_{max_{s}} \cdot \exp\left(-\frac{1}{2} \left(\frac{\log\left(\frac{DBH_{i,s,y}}{D_{opt_{s}}}\right)}{K_{s}}\right)^{2}\right)$$

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.

• $K_s = \theta_{k0} + \theta_k \cdot wd_s$: 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_{k0} and 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_{origin}^O : 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_{origin}^O represents the annual diameter growth rate advantage of spontaneous trees over (trans)planted trees.

We modelled the diameter growth trajectories with a subset of 959 trees (767 spontaneous and 192 (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.

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 (Huang et al., 1992; Molto et al., 2014). Our model is specified as:

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

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 $(\frac{BH_{i,s}}{2})$ 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_{origin}^O : 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_{origin}^O 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 subset of 1008 trees (806 spontaneous and 202 (trans)planted) for which diameter and bole height data were available.

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:

(5)
$$BV_{i,s} \sim \mathcal{LN}(log(\theta_s \cdot \theta_{origin}^O \cdot \alpha \cdot DBH_{i,s}^\beta \cdot BH_{i,s}^\gamma), \sigma_v)$$

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_{origin}^O : 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_{origin}^O 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 155 trees (135 spontaneous and 20 (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., 2023a). 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 (equation 2, then $BH_{i,s}$ as a function of the predicted $DBH_{i,s}$ using our bole height model (equation 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 (equation 4).

199 Results

Tree diameter growth

On average, species reach a diameter of 50 cm (smallest MLD value) in 33 years (Fig. 2). The fastest growing species is *Ceiba pentandra* (FROMAGER), reaching 50 cm in 15 years. The slowest growing species is *Piptadeniastrum africanum* (DABEMA) reaching the same diameter in 62 years.

The expected maximum annual growth potential (G_{max} in equation 3) for all species is 10.1 cm.yr⁻¹. On average, the maximum annual growth potential occurs at an optimal diameter (D_{opt_s} in equation 3) of 0.5 cm. Species annual growth rates are therefore maximum for DBH smaller than 1 cm and decrease as DBH increases.

Species annual growth rates (AGR) at DBH = 10 cm range from 2.1 cm.yr^{-1} to 6 cm.yr^{-1} , with an average of 3.5 cm.yr^{-1} . At DBH = 70 cm, species AGR range from 0.2 cm.yr^{-1} to 1.5 cm.yr^{-1} , with an average of 0.6 cm.an^{-1} . Maximum values at 10 and 70 cm DBH are reached by *Ceiba pentandra* (FROMAGER), while minimum values are reached by *Piptadeniastrum africanum* (DABEMA). The model parameter values and their credibility intervals are presented from table S1 to table S5 of the Supplementary Information (Kouassi et al., 2024).

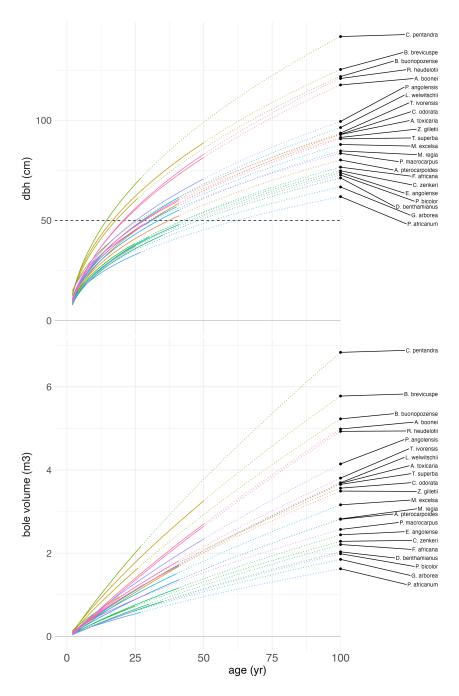


Figure 2 – Diameter growth and bole volume trajectories of our 23 tree species. Full lines stop at the maximum age recorded for each species. Dotted lines extend predictions to age 100. Here we present the trajectories predicted for spontaneous trees.

Diameter - bole height relationship

At 50 cm in DBH (smallest MLD value), the trees reach an average bole height of 8.1 m (Fig. 3), ranging from 6.1 m for *Funtumia africana* (POUO) to 10.3 m for *Antiaris toxicaria* (AKO). The predicted tree asymptotic bole height (α in equation 4) is 14.9 m. The species effect θ_s ranges from 0.76 (i.e. -24%) for *Funtumia africana* (POUO) to 1.28 (i.e. +28%) *Antiaris toxicaria* (AKO). The model parameter values and their credibility intervals are presented from table S6 to table S8 of the Supplementary Information (Kouassi et al., 2024).

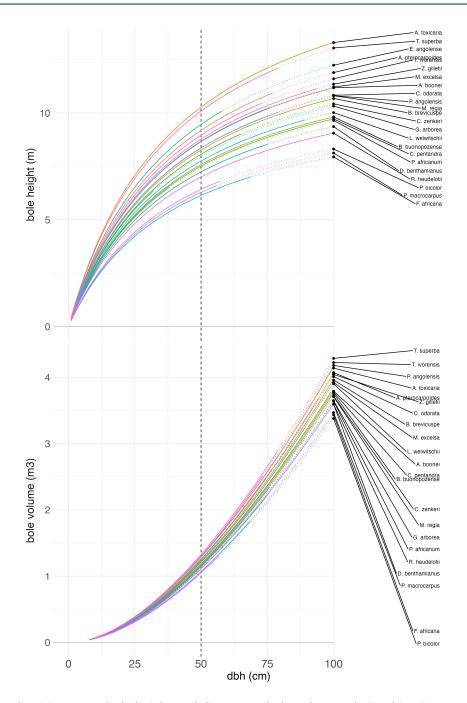


Figure 3 – Diameter - bole height and diameter - bole volume relationships for our 23 tree species. Full lines stop at the maximum DBH observed for each species. Dotted lines extend predictions to DBH = 100 cm. Here we present the relationships predicted for spontaneous trees.

Wood production potential of trees

At age 25 (a commonly used logging age in forest plantations), trees reach a mean bole volume of 1.1 m³ (Fig. 2). The fastest growing species is *Ceiba pentandra* (FROMAGER), reaching 2 m³ at age 25. The slowest growing species is *Piptadeniastrum africanum* (DABEMA) reaching 0.6 m³ at the same age.

At 50 cm DBH (smallest MLD value), tree bole volume ranges from 1.1 to 1.4 m³ (Fig. 3). These volumes increase to reach 3.4 to 4.4 m³ for trees 100 cm in diameter.

On average, trees reach their MLD at 42.7 years of age (Fig. 4). Bombax brevicuspe (KON-DROTI) reaches its MLD first at the age of 24 while Piptadeniastrum africanum (DABEMA) reaches its MLD last at the age of 93. At their MLD, trees have on average a volume of 1.5 m³. Parkia bicolor (LO), with 1 m³, has the smallest volume, while Ceiba pentandra (FROMAGER), with 2.6 m³, has the largest volume.

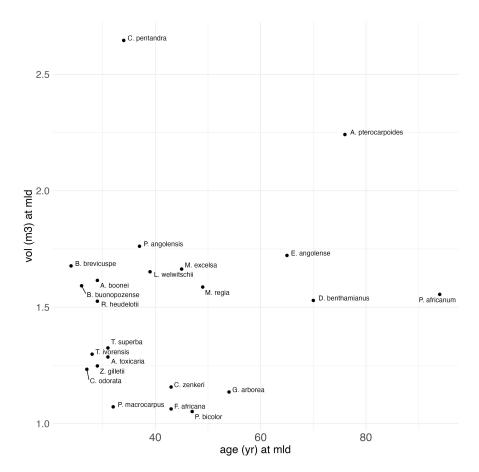


Figure 4 - Bole volume and age at minimum logging diameter for our 23 species.

The evaluation of our bole volume model (equation 5) provides the following allometric equation adapted to predict the bole volume of trees in cocoa AFS:

(6)
$$BV = \theta_0 \cdot 1.05 \cdot DBH^{1.54} \cdot BH^{0.42}$$

With $\theta_o = 1.41$ for spontaneous trees and $\theta_o = 1$ for a (trans)planted trees (see next section about the effect of tree origin). The model parameter values and their credibility intervals are presented from table S9 to table S11 of the Supplementary Information (Kouassi et al., 2024).

Effect of trees' origin on their wood production potential

In our diameter growth model (equation 3) $\theta_o=1.1$. 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 3.7 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 brevicuspe* (KONDROTI), *Ricinodendron heudeloti* (EHO), *Cedrela Odorata* (CEDRELA) and *Terminalia superba* (FRAKE) to 8 years for *Amphimas pterocarpoides*.

In our bole volume model (equation 5) $\theta_o = 1.41$. This means that for a given diameter and a given bole height, spontaneous trees are 41% larger in volume than (trans)planted trees. As a consequence, spontaneous trees reach a higher bole volume of 0.4 m³ on average as compared to spontaneous trees (Fig 5). This advantage in volume ranges from 0.3 m³ for *Parkia bicolor* (LO) to 0.7 m³ for *Ceiba pentandra* (FROMAGER).

Finally, in our bole height model (equation 4) $\theta_o = 0.99$ suggesting differences between spontaneous and (trans)planted trees are negligible as for their diameter - height relationship.

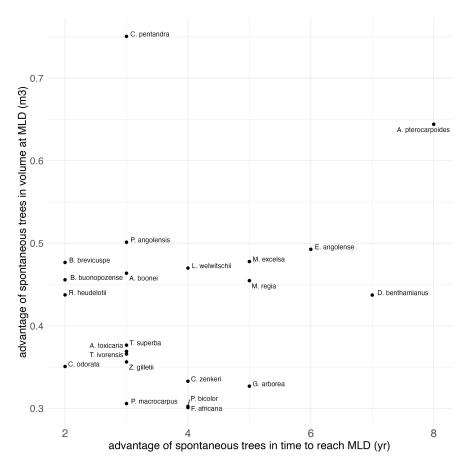


Figure 5 – Advantage of spontaneous trees over (trans)planted trees in time to reach their MLD and in volume at MLD.

253 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 24 years of age for bole volumes greater than 1m³. Our results also show that spontaneous trees have a clear advantage over transplanted trees: they can reach their MLD up to 8 years earlier and produce up to 0.7 m³ more over the same period.

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 0.2 to 6 cm.yr $^{-1}$. 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) and Durrieu de Madron et al. (1998b) found an average annual growth rate of 0.27 cm.yr⁻¹ for an evergreen forest and of 0.29 cm.yr⁻¹ for a semi-deciduous forest, respectively. In Ghana, Alder (1989) found average annual growth rates ranging from 0.8 to 1 cm.yr⁻¹ for pioneer species and ranging from 0.4 to 0.5 cm.yr⁻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 or plantations (Pillet et al., 2018). This greater availability of light could lead trees to invest more in their diameter growth once they have emerged from the cocoa canopy (Ek, 1974; King, 1981). Our results show maximum annual growth rates from the very first years ($Gmax = 10.1 \text{ cm.yr}^{-1}$ for a mean $D_{opt_s} = 0.5 \text{ cm}$), which is in line with the hypothesis of a priority given to diameter growth. 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).

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 exponential 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 1.4 m³ at 50 cm DBH while in Côte d'Ivoire, Hérault et al. (2021) found trees in plantation can reach about 2.5 m³ at the same DBH. At 100 cm DBH, we found trees in cocoa AFS could reach 4.4 m³ while at this size, trees in plantation can reach a much higher volume of over 15 m³.

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 0.6 to 2.4 m³ in 18 years (Ramírez-Argueta et al., 2022) while we predict a bole volume ranging from 0.4 to 1.5 m³ at this age. Similarly, in Brasil, trees can reach a volume of 1.9 m³ at age 20 (Gama-Rodrigues et al., 2021) while we predict a volume ranging from 0.5 to 1.6 m³ 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 14 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.

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 41% 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 (Fritts and Shatz, 1975; Waring and Pitman, 1985; Wunder et al., 2008).

On the other hand, we found no difference between spontaneous and (transp)lanted 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.

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 Supplementary Information provided by 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).

Our results show a poor performance of *Gmelina arborea* despite its reputation for remarkable growth (Vallejos et al., 2015). This result could be an artefact due to our sampling. In fact, we only observed 10 individuals of this species and all were no more than 4 years old.

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 suggest pruning could be an effective lever for improving wood production. Indeed, by increasing the bole height, this operation increases tree commercial volume. 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.

352 Fundings

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Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

Data, script, code, and supplementary information availability

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

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