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

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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 trees can reach a 50 cm diameter (the smallest MLD) as early as 14 years old, and a bole height of up to 8.83 m at this diameter. Spontaneous trees grow 10% faster annually than (trans)planted trees, reaching their MLD up to 10 years earlier. For a given bole height, spontaneous trees have a 43% greater volume compared to (trans)planted trees, with a bole volume up to 0.71 m³ higher. 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

3 In a global context where the demand for tropical timber is constantly increasing (Chimeli et
4 al., 2012), natural forests, which provide the majority of this resource, are under unprecedented
5 pressure (FAO, 2020). In West Africa, this pressure is exacerbated by real estate development
6 (driven by high population growth) that fuels a very strong local demand for construction timber
7 (Uzu et al., 2022). This demand completely exceeds the supply capacities of production forests
8 (Louppe and Ouattara, 2013), in a context where over 80% of the original forest mass has been
9 lost in favor of agricultural development (Aleman et al., 2018; Traoré et al., 2024). Thus, it is
10 imperative to seek alternative sources of production to meet regional needs and uses and to en-
11 sure the sustainability of the timber sector and the people who depend on it (Tsanga et al., 2020).
12 Large-scale tree planting has long been seen as an ideal solution to meet the needs for tropical
13 timber. For example, 45% of the national commitments made under the Bonn Challenge, an in-
14 ternational goal aiming to restore 350 million hectares of land by 2030 (Verdone and Seidl, 2017),
15 involve multiplying tree plantations (Lewis et al., 2019). However, large-scale analyses show that
16 these projects, in addition to their high costs and lack of long-term funding (Brancalion and Holl,
17 2020), have often been much less successful than expected, or even outright failed (Brancalion
18 and Holl, 2020; Holl and Brancalion, 2020), and have also led to numerous territorial conflicts
19 (Gerber, 2011).

20 Multiple studies highlight the potential for timber production outside of natural forests and ded-
21 icated plantations. Two systems appear particularly promising in West Africa: secondary forests
22 from agricultural fallows (Doua-Bi et al., 2021) and agroforestry systems (Tschora and Cheru-
23 bini, 2020). Developing timber supply from these systems can represent a viable alternative to
24 help resolve the local timber deficit while (i) diversifying farmers' income sources (Kinyili et al.,
25 2020; Kouassi et al., 2023b) and (ii) ensuring more sustainable use of agricultural lands (Plieninger
26 et al., 2020). In this context, numerous agroforestry promotion initiatives have emerged in the
27 West African cocoa production area (Zo-Bi and Hérault, 2023), which accounts for nearly 70%
28 of global cocoa production. Cocoa agroforestry consists in cultivating cocoa trees under the
29 shade of larger trees. At low-to-intermediate shade levels, this practice can help reduce disease
30 prevalence, buffer climate extremes, mitigate climate change and conserve biodiversity, while
31 maintaining cocoa production levels (Blaser et al., 2018). Thus, the agroforestry promotion ini-
32 tiatives primarily aim to achieve sustainability and long-term stabilization of cocoa production
33 (Carimentrand, 2020). By doing so, the establishment of new deforestation fronts to seek fer-
34 tile soils would be avoided, thereby reducing pressure on the few remaining forests (Ruf et al.,
35 2015).

36 Despite all these agroforestry promotion activities, a significant limitation to the adoption of
37 agroforestry practices remains a lack of knowledge about the actual productive potential of tim-
38 ber trees in cocoa fields and thus about the added value these trees can generate for the farmer
39 (Sonwa et al., 2014). Indeed, while this productive potential is well known in natural forests (e.g.,
40 Zobi et al., 2009) or in dedicated plantations (e.g., Hérault et al., 2021; Hérault et al., 2020), it is
41 not transferable to cocoa fields where the biophysical environment is very different. There are
42 two main reasons for this: (i) the growth trajectories of trees in cocoa fields are unknown and
43 are expected to be very different in open, low-competition environments (cocoa fields) than in
44 high-competition forest environments (Rozendaal et al., 2020); (ii) allometric equations, neces-
45 sary for determining the commercial volumes of trees, should also be different from those used

46 in forests for several reasons. First, trees in cocoa fields receive more light and have more space
47 to extend their branches laterally, unlike trees in dense forests that grow vertically to access
48 light (Harja et al., 2012). Second, trees in cocoa fields are more exposed to wind, causing them
49 to develop sturdier trunks and more extensive root systems to remain stable (Ennos, 1997). Im-
50 proving knowledge on growth trajectories and tree architecture in agroforestry contexts is thus
51 urgent to correctly quantify the productive potentials of timber trees.

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

71 The main objective of our study is to assess the timber production potential of trees in cocoa
72 agroforestry systems (AFS) in Côte d'Ivoire (West Africa). Specifically, we estimated the time re-
73 quired for trees to reach their minimum logging diameter (MLD) and the corresponding volume
74 at this stage. MLD values used in this study are legally defined thresholds below which logging
75 is prohibited. These values correspond to the diameter at which approximately 80% of trees of
76 a given species reach a stage of abundant and regular fruiting (Sodefor, 2019). This criterion
77 ensures the sustainable renewal of tree populations. We also assessed the effect of the origin
78 of the trees, be they from natural regeneration or (trans)plantation, on this production potential.
79 To achieve these objectives, we (i) modelled the diameter growth of forest species identified as
80 potentially suitable for wood production in cocoa AFS; (ii) established specific allometric models
81 for trees in cocoa AFS to assess their volume when they reach their minimum logging diameter;
82 (iii) evaluated the effect of spontaneous or (trans)planted origin of trees on their growth trajec-
83 tories, allometry, and thus on their logging volume trajectories. The results of this study provide key
84 indicators for establishing silvicultural management technical itineraries for associated trees in
85 cocoa fields based on their actual performance, thereby encouraging decision-makers to better
86 promote timber trees in cocoa fields.

87

Material and methods

88 Sampling design

89 *Study area.* Our study covers the cocoa production area of Côte d'Ivoire (Figure 1). This area is
 90 characterised by an annual precipitation gradient varying from 2 500 mm in the south to 1 100
 91 mm in the north, and by an average annual temperature of around 26.5°C. The area spans from
 92 evergreen forests in the south to semi-deciduous forests in the north.

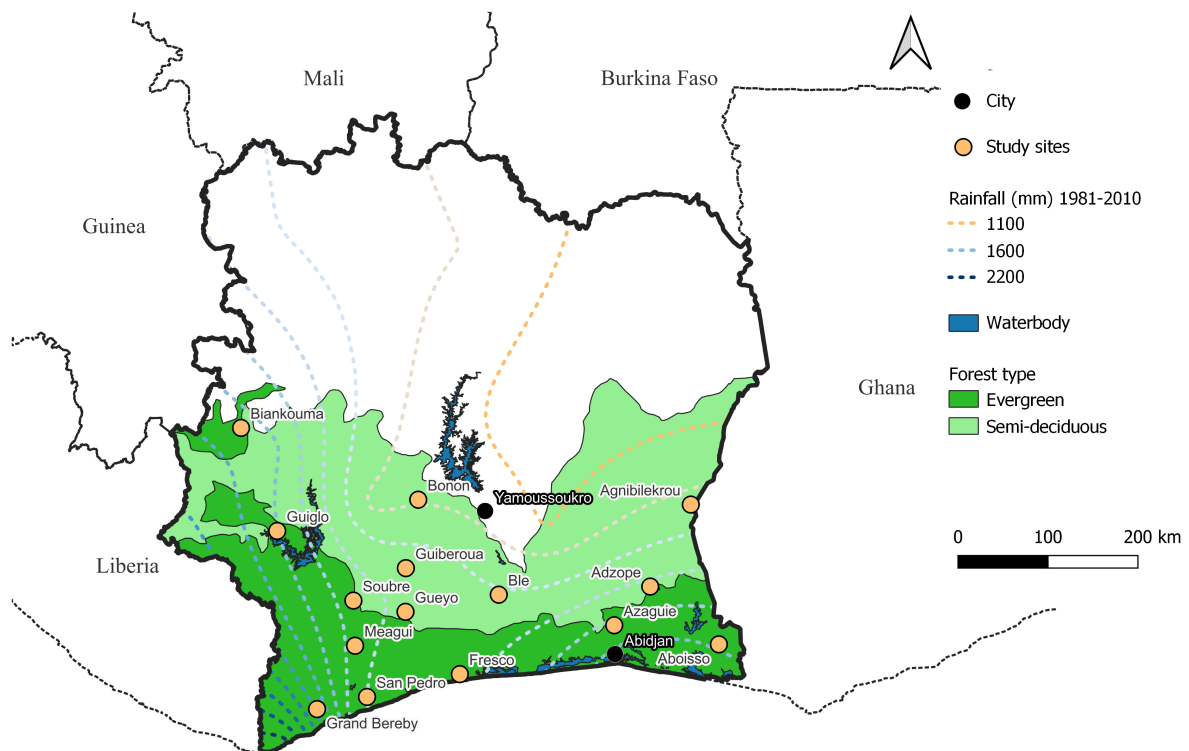


Figure 1 – Location of the 15 study sites across a gradient of climate and vegetation.

93 *Sampling plots.* A total of 150 plots were set up, grouped into 15 sites of 10 plots each. Each of
 94 these plots represents a management unit of the farmer or his manager. They range in size from
 95 0.3 to 5 ha and together cover 240.5 ha. Our sampling covers a gradient of structural complexity:
 96 from low tree density AFS with a single stratum to complex AFS with high tree density and
 97 multiple strata.

98 *Sampling data.* We carried out an exhaustive tree inventory in our plots between March 2021
 99 and November 2022. We measured the diameter at breast height (DBH) and bole height (BH) of
 100 all trees with a DBH of at least 10 cm. We identified trees to the species level following the Taxo-
 101 nomic Name Resolution Service as implemented in the R BIOMASS package (Réjou-Méchain et
 102 al., 2017). We also recorded their origin (remnant, spontaneous, or (trans)planted) based on the
 103 farmer's declaration. The farmer also provided the age of spontaneous and (trans)planted trees
 104 (the age of remnant trees being unknown). Finally, we measured successive diameters along the

105 bole (every meter) of a subset of 200 trees using a Bitterlich relascope to calculate their bole
106 volume.

107 A total of 11 999 trees belonging to 284 species were inventoried (a summary of this in-
108 ventory is presented in table S1 of the Supplementary Information; Kouassi et al. (2024)). In this
109 study, we only considered the species listed in the national list of timber species (Sodefor (2017);
110 table S1 of the Supplementary Information), or the species listed as commonly used by Ivorian
111 cocoa farmers for construction purposes (Dago et al. (in press); table S1 of the Supplementary
112 Information). Also, here we only consider spontaneous and (trans)planted trees excluding rem-
113 nant trees. Remnant trees are expected to have different development trajectories as they have
114 grown, at least in part, in a forest environment. Finally we only consider species with at least 5
115 individuals. Our dataset thus includes a total of 4634 trees belonging to 59 species, including
116 2530 spontaneous trees and 2104 (trans)planted trees.

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

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 (2005) (g.cm³); 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; (*) indicates exotic species (Aké-Assi, 2001).

Species name	Trade name	MLD	DBH	BH	AGE	WD	N _s	N _{tp}	WOOD USES
<i>Alstonia boonei</i>	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
<i>Amphimas pterocarpoides</i>	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
<i>Antiaris toxicaria</i>	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
<i>Bombax brevisuspe</i>	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
<i>Bombax buonopozense</i>	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
<i>Cedrela odorata*</i>	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
<i>Ceiba pentandra</i>	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
<i>Celtis zenkeri</i>	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
<i>Distemonanthus benthamianus</i>	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
<i>Entandrophragma angolense</i>	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
<i>Funtumia africana</i>	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
<i>Gmelina arborea*</i>	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
<i>Lannea welwitschii</i>	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
<i>Milicia excelsa</i>	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
<i>Milicia regia</i>	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
<i>Parkia bicolor</i>	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
<i>Petersianthus macrocarpus</i>	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
<i>Piptadeniastrum africanum</i>	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
<i>Pycnanthus angolensis</i>	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
<i>Ricinodendron heudelotii</i>	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
<i>Terminalia ivorensis</i>	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
<i>Terminalia superba</i>	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
<i>Zanthoxylum gillettii</i>	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

124 Modelling

125 We developed three models to assess the wood production potential of trees in cocoa AFS:
 126 (i) a model describing the diameter growth trajectories of trees as a function of their age (Eq
 127 2), (ii) a model evaluating the relationship between tree diameter and bole height (Eq 4), and
 128 (iii) a model assessing the commercial volume of trees as a function of their diameter and bole
 129 height (Eq 5). Each model includes an origin effect to assess the differences between sponta-
 130 neous and (trans)planted trees. We estimated the model parameters in a Bayesian framework
 131 using Stan (Carpenter et al., 2017; Stan Development Team et al., 2018) in the R environment (R
 132 Core Team, 2021). The Bayesian approach offers great flexibility and transparency in modeling
 133 complex phenomena and uncertainty. It makes it possible to incorporate prior knowledge (priors)
 134 and to obtain probability distributions (posteriors) for model parameters, from which credible in-
 135 tervals are derived. We provide the STAN code in Supplementary Information (Kouassi et al.,
 136 2024).

137 *Diameter growth model.* We base our analysis on the conceptual framework developed by Hérault
 138 et al. (2011) and Schmitt et al. (2023):

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

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

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

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

144 with

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

147 and where:

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

148 with:

- 149 • $G_{max_s} \sim \mathcal{LN}(\log(G_{max}), \sigma_{gmax})$: the species-specific maximum growth potential, follow-
 150 ing a log-normal distribution with parameters G_{max} and σ_{gmax} . G_{max} represents the ex-
 151 pected maximum growth potential for all species and σ_{gmax} the dispersion parameter.
- 152 • $D_{opt_s} = \theta_d \cdot D_{max_s}$: the species-specific diameter at which G_{max_s} is reached, defined as
 153 a function of D_{max_s} , the maximum diameter observed for each species, weighted by θ_d ,
 154 a parameter between 0 and 1. $\theta_d \sim \mathcal{LN}(\log(\mu_{\theta_d}), \sigma_{\theta_d})$ centred on μ_{θ_d} and dispersed
 155 according to σ_{θ_d} .

- 156 • $K_s = \theta_k \cdot wd_s$: the species-specific kurtosis coefficient defining the width of the growth
157 curve, reflecting ontogenetic variation in growth potential. K_s is a linear function of
158 species wood density wd_s , with parameters θ_k . $\theta_k \sim \mathcal{LN}(\log(\mu_{\theta_k}), \sigma_{\theta_k})$ centred on μ_{θ_k}
159 and dispersed according to σ_{θ_k} .
- 160 • $\theta_{si} \sim \mathcal{LN}(\log(1), \sigma_{si})$: a site effect following a log-normal distribution with parameters
161 $\log(1)$ and σ_{si} . Site effects are therefore centred on 1 and dispersed according to σ_{si} .
- 162 • θ_{origin}^O : an origin effect evaluating growth difference between spontaneous and (trans)planted
163 trees. Practically, the origin variable (O) takes the value 1 for spontaneous trees and 0 for
164 (trans)planted trees. Thus, θ_{origin}^O represents the annual diameter growth rate advantage
165 of spontaneous trees over (trans)planted trees.

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

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

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

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

175 with:

- 176 • $BH_{i,s}$: the bole height of tree i of species s .
- 177 • $DBH_{i,s}$: the diameter at breast height of tree i of species s .
- 178 • α : represents the asymptotic bole height.
- 179 • β : represents the diameter at which half the asymptotic height ($\frac{BH_{i,s}}{2}$) is reached.
- 180 • $\theta_s \sim \mathcal{LN}(\log(1), \sigma_s)$: a species effect following a log-normal distribution with parameters
181 $\log(1)$ and σ_s . Species effects are therefore centred on 1 and dispersed according to σ_s .
- 182 • $\theta_{si} \sim \mathcal{LN}(\log(1), \sigma_{si})$: a site effect following a log-normal distribution with parameters
183 $\log(1)$ and σ_{si} . Site effects are therefore centred on 1 and dispersed according to σ_{si} .
- 184 • θ_{origin}^O : an origin effect evaluating the difference in asymptotic bole height between spon-
185 taneous and (trans)planted trees. Practically, the origin variable (O) takes the value 1 for
186 spontaneous trees and 0 for (trans)planted trees. Thus, θ_{origin}^O represents the advantage
187 of spontaneous trees over (trans)planted trees in terms of asymptotic bole height.
- 188 • σ_h : the dispersion parameter of the log-normal distribution.

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

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

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

194 with:

- 195 • $BV_{i,s}$: the bole volume of tree i of species s .
- 196 • $DBH_{i,s}$: the diameter at breast height of tree i of species s .
- 197 • $BH_{i,s}$: the bole height of tree i of species s .
- 198 • α , β et γ : parameters to be estimated.
- 199 • $\theta_s \sim \mathcal{LN}(\log(1), \sigma_s)$: a species effect following a log-normal distribution with parameters
- 200 $\log(1)$ and σ_s . Species effects are therefore centred on 1 and dispersed according to σ_s .
- 201 • θ_{origin}^O : an origin effect evaluating the difference in bole volume between spontaneous and
- 202 (trans)planted trees. Practically, the origin variable (O) takes the value 1 for spontaneous
- 203 trees and 0 for (trans)planted trees. Thus, θ_{origin}^O represents the advantage of spontaneous
- 204 trees over (trans)planted trees in terms of bole volume.
- 205 • σ_v : the dispersion parameter of the log-normal distribution.

206 We modelled bole volume with a subset of 200 trees (176 spontaneous and 24 (trans)planted)

207 for which bole volume, diameter and bole height data were available. These trees were selected

208 in the field for their remarkable commercial quality: bole height of at least 5 m and good health

209 and conformation (Kouassi et al., 2023a). This subset is therefore not representative of all trees

210 in cocoa AFS, but rather allows to evaluate the bole volumes that can be reached by trees in

211 these systems.

212 We used this model to predict the bole volume of spontaneous and (trans)planted trees as

213 a function of age (up to age 100). For that, we predicted $DBH_{i,s}$ as a function of age using our

214 diameter growth model (equation 2), then $BH_{i,s}$ as a function of the predicted $DBH_{i,s}$ using our

215 bole height model (equation 4), and finally the bole volume using these predicted $DBH_{i,s}$ and

216 $BH_{i,s}$.

217 We also used this model to predict the bole volume of spontaneous and (trans)planted trees

218 as a function of DBH (up to DBH = 100 cm). We predicted $BH_{i,s}$ using our bole height model

219 (equation 4).

220

Results

221 In this section, we present the results obtained for the 23 species identified as the most suit-

222 able for timber production, as previously mentioned. The parameter values and credible intervals

223 for all 59 species considered in this study are provided in Tables S3 to S12 of the Supplementary

224 Information (Kouassi et al., 2024).

Tree diameter growth

226 On average, the 23 species we focus on reach a diameter of 50 cm (smallest MLD value) in 36

227 years (Fig. 2). The fastest growing species is *Ceiba pentandra* (FROMAGER), reaching 50 cm in 14

228 years. The slowest growing species is *Distemonanthus benthamianus* (MOVINGUI) reaching the

229 same diameter in 79 years. The expected maximum annual growth potential (G_{max} in equation

230 3) for all species is 8.74 cm.yr⁻¹. On average, the maximum annual growth potential occurs at

231 an optimal diameter (D_{opt_s} in equation 3) of 0.87 cm. In general, species annual growth rates are

232 therefore maximum for DBH smaller than 1 cm and decrease as DBH increases.

233 Species annual growth rates (AGR) at DBH = 10 cm range from 2.28 cm.yr⁻¹ for *Piptadenias-*
 234 *trum africanum* (DABEMA) to 6.57 cm.yr⁻¹ for *Bombax brevicuspe* (KONDROTI), with an average
 235 of 3.87 cm.yr⁻¹. At DBH = 70 cm, species AGR range from 0.13 cm.yr⁻¹ for *Distemonanthus*
 236 *benthamianus* (MOVINGUI) to 1.73 cm.yr⁻¹ for *Ceiba pentandra* (FROMAGER), with an average
 237 of 0.61 cm.an⁻¹. The model parameter values and their credible intervals are presented from
 238 table S3 to table S7 of the Supplementary Information, including the parameter values for the
 239 36 additional timber species (Kouassi et al., 2024).

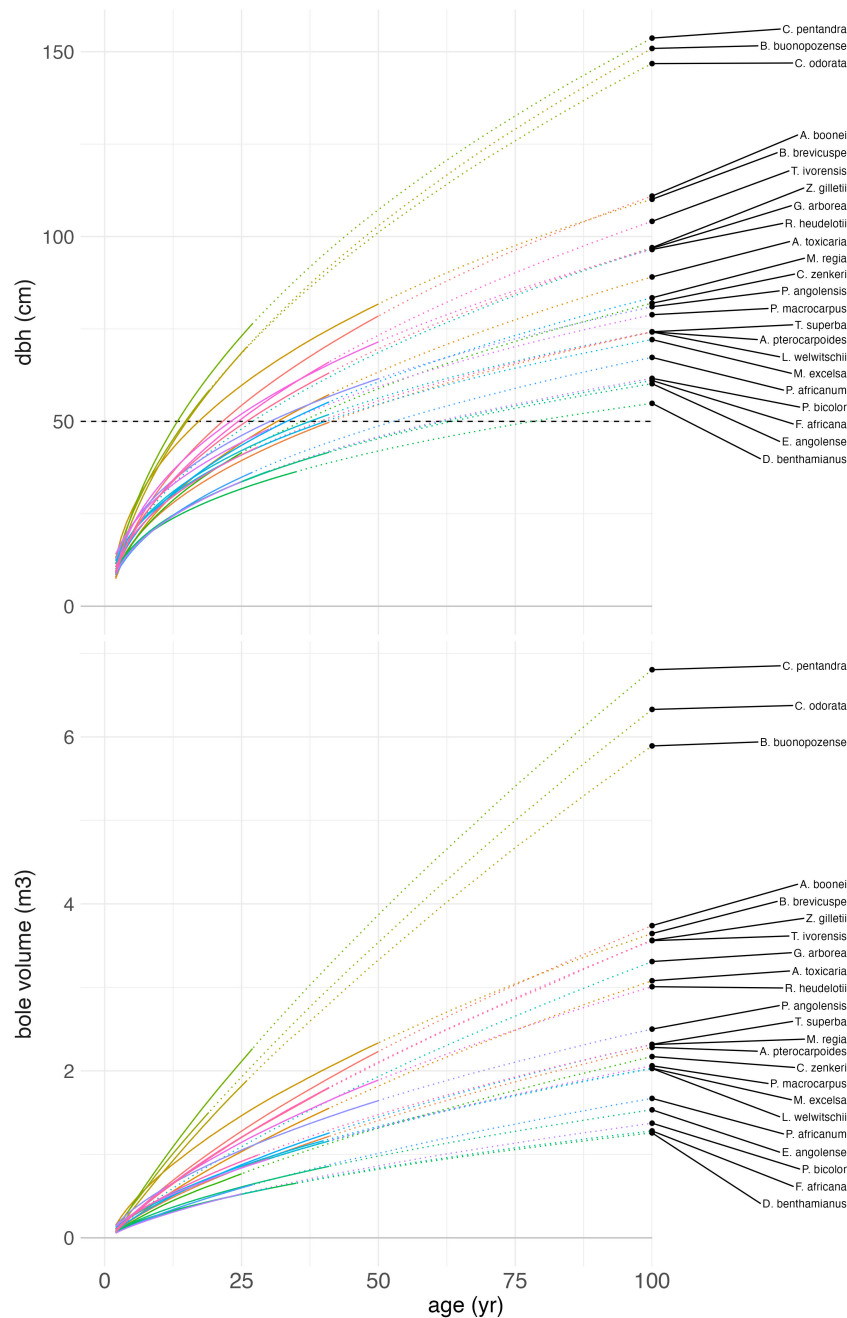


Figure 2 – Diameter growth and bole volume trajectories of our 23 tree species. Full lines stop at the maximum age recorded for each species. Dotted lines extend predictions to age 100. Here we present the trajectories predicted for spontaneous trees.

240 **Diameter - bole height relationship**

241 At 50 cm in DBH (smallest MLD value), the trees reach an average bole height of 6.75 m (Fig.
 242 3), ranging from 4.33 m to 8.83 m. The predicted tree asymptotic bole height (α in equation 4) is
 243 6.75 m. The species effect θ_s ranges from 0.80 (i.e. -20%) to 1.64 (i.e. +64%). Maximun values at
 244 50 cm DBH are reached by *Antiaris toxicaria* (AKO), while minimun values are reached by *Parkia*
 245 *bicolor* (LO). The model parameter values and their credible intervals are presented from table
 246 S8 to table S10 of the Supplementary Information, including the parameter values for the 36
 247 additional timber species (Kouassi et al., 2024).

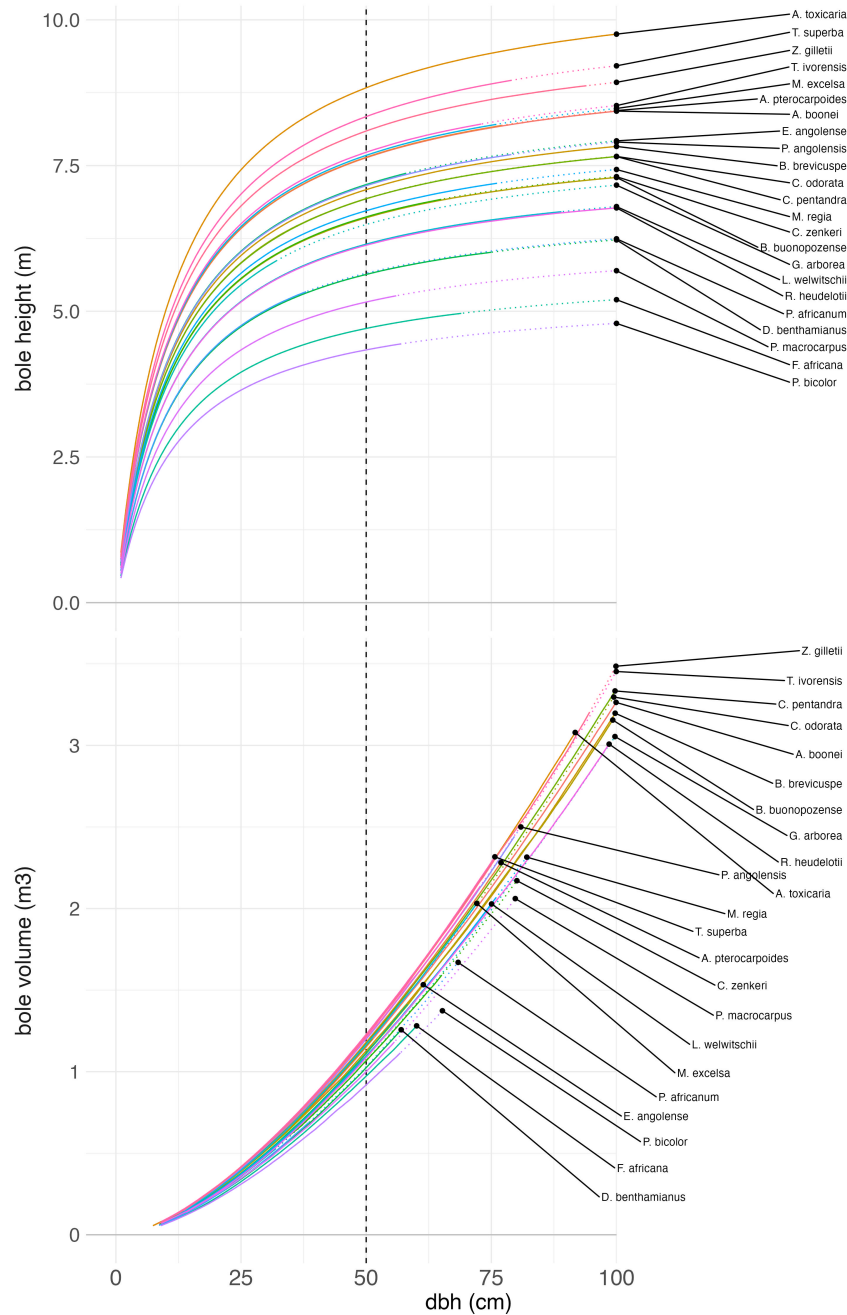


Figure 3 – Diameter - bole height and diameter - bole volume relationships for our 23 tree species. Full lines stop at the maximum DBH observed for each species. Dotted lines extend the predictions to a DBH of 100 cm or an age of 100 years. Here we present the relationships predicted for spontaneous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

248 Wood production potential of trees

249 At age 25 (a commonly used logging age in forest plantations), trees reach a mean bole vol-
 250 ume of 1.04 m³ (Fig. 2). The fastest growing species is *Ceiba pentandra* (FROMAGER), which
 251 reaches 2.11 m³, corresponding to an anhydrous wood mass of 630 kg, at age 25. The slow-
 252 est growing species, *Distemonanthus benthamianus* (MOVINGUI) and *Funtumia africana* (POUO),
 253 reach 0.52 m³, corresponding to an anhydrous wood mass of 300 kg and 200 kg, respectively,
 254 at the same age.

255 At 50 cm DBH (smallest MLD value), tree bole volume ranges from 0.94 to 1.24 m³ (Fig. 3).
 256 These volumes increase to reach 3.11 to 3.53 m³ for trees 100 cm in diameter.

257 On average, trees reach their MLD at 44.82 years of age (Fig. 4). *Cedrela odorata* (CEDRELA)
 258 reaches its MLD first at the age of 15 while *Entandrophragma angolense* (TIAMA) reaches its
 259 MLD last at the age of 100. At their MLD, trees have on average a volume of 1.37 m³. *Parkia*
 260 *bicolor* (LO), with 0.92 m³, has the smallest volume, while *Ceiba pentandra* (FROMAGER), with
 261 2.36 m³, has the largest volume. The evaluation of our bole volume model (equation 5) provides
 262 the following allometric equation adapted to predict the bole volume of trees in cocoa AFS:

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

263 With $\theta_o = 1.43$ for spontaneous trees and $\theta_o = 1$ for a (trans)planted trees (see next section
 264 about the effect of tree origin). The model parameter values and their credible intervals are
 265 presented from table S11 to table S12 of the Supplementary Information, while the relationship
 266 between predicted and measured bole volumes is presented in Figure S1 (Kouassi et al., 2024).

267 Effect of trees' origin on their wood production potential

268 In our diameter growth model (equation 3) $\theta_o = 1.10$. This means that the annual growth rate
 269 of spontaneous trees is 10% higher than that of (trans)planted trees. As a consequence, spon-
 270 taneous trees reach their MLD 4.76 years earlier than (trans)planted trees (Fig. 5) on average.
 271 This advantage of spontaneous trees over (trans)planted trees ranges from 2 years for *Bombax*
 272 *buonopozense* (OBA/KAPOKIER) and *Cedrela Odorata* (CEDRELA) to 10 years for *Amphimas pte-*
 273 *rocarpoides* (LATI).

274 In our bole volume model (equation 5) $\theta_o = 1.43$. This means that for a given diameter and
 275 a given bole height, spontaneous trees are 43% larger in volume than (trans)planted trees. As a
 276 consequence, spontaneous trees reach a higher bole volume of 0.43 m³ on average as compared
 277 to spontaneous trees (Fig 5). This advantage in volume ranges from 0.29 m³ for *Funtumia africana*
 278 (POUO) and *Parkia bicolor* (LO) to 0.71 m³ for *Ceiba pentandra* (FROMAGER).

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

281 Discussion

282 To our knowledge, this study is the first to assess the diameter growth and the wood produc-
 283 tion potential of trees in West African cocoa AFS. Our results show that trees can reach their
 284 MLD as early as 15 years of age for bole volumes greater than 0.92 m³. Our results also show
 285 that spontaneous trees have a clear advantage over transplanted trees: they can reach their MLD
 286 up to 10 years earlier and produce up to 0.71 m³ more over the same period.

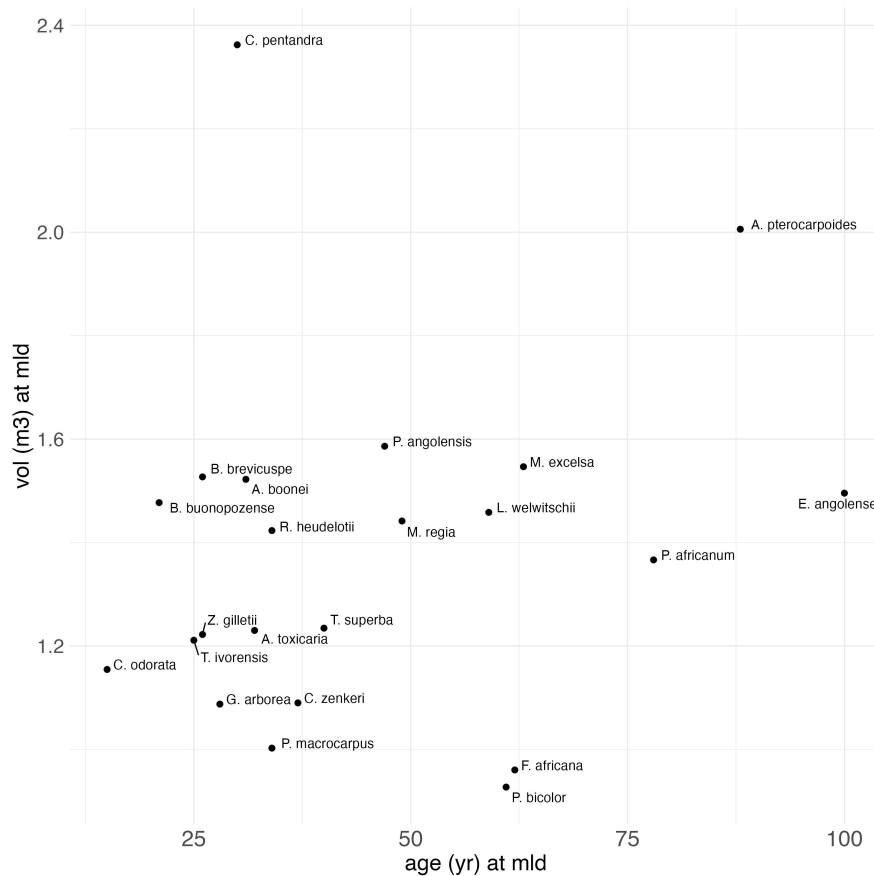


Figure 4 – Bole volume and age at minimum logging diameter for our 23 species. *Distemonanthus benthamianus* (MOVINGUI) is not represented as it does not reach its MLD within 100 years.

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

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

299 The faster growth of trees in cocoa AFS could be due to the greater availability of light in
 300 these systems than in forests or plantations (Pillet et al., 2018). This greater availability of light
 301 could lead trees to invest more in their diameter growth once they have emerged from the co-
 302 coa canopy (Ek, 1974; King, 1981). Our results show maximum annual growth rates from the
 303 very first years ($G_{max} = 8.74$ cm.yr⁻¹ for a mean $D_{opt_s} = 0.87$ cm), which is in line with the
 304 hypothesis of a priority given to diameter growth. In contrast, in forests and plantations, closed
 305 systems where competition for light is strong, growth in height could be favoured (Ammer, 2003;

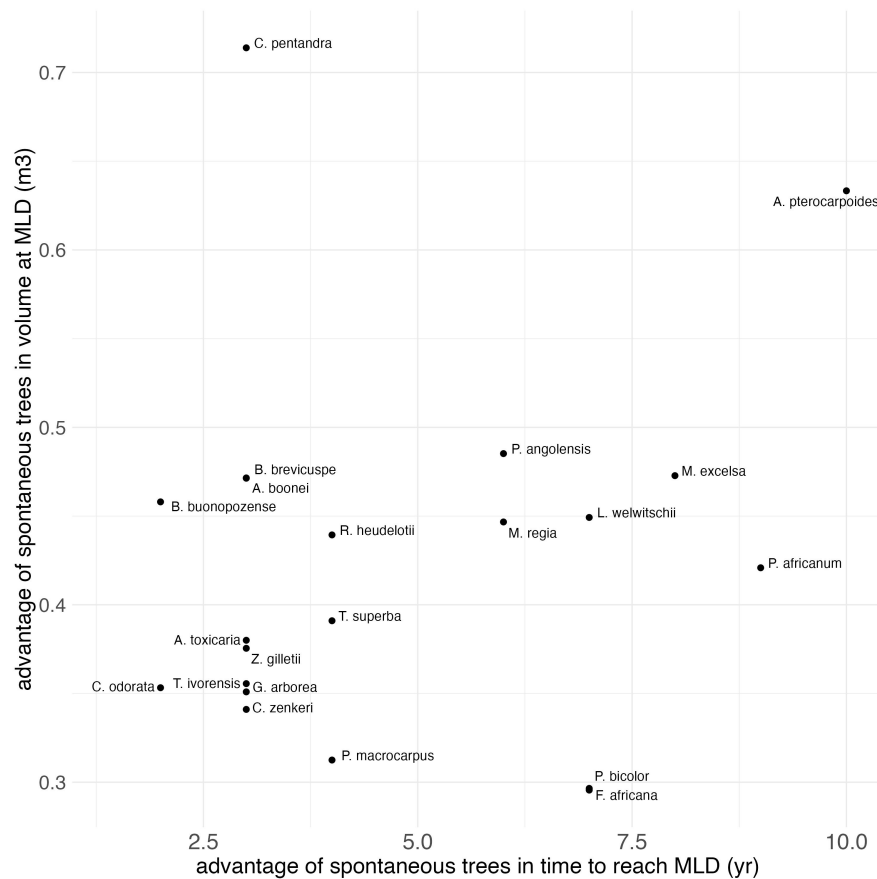


Figure 5 – Advantage of spontaneous trees over (trans)planted trees in time to reach their MLD and in volume at MLD. *Distemonanthus benthamianus* (MOVINGUI) is not represented as it does not reach its MLD within 100 years. *Entandrophragma angolense* (TIAMA) is also excluded because, although spontaneous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

306 Prévosto and Balandier, 2007), to the expanse of diameter growth (Falster and Westoby, 2003,
 307 2005). Prioritizing diameter growth also enhances tree stability and resilience to wind, especially
 308 in resource-limited environments. As a result, trees tend to develop more conical boles rather
 309 than perfectly cylindrical ones, as evidenced by the low values of the volume model parameters
 310 ($\beta = 1.45$ and $\gamma = 0.43$, compared to the expected $\beta = 2$ and $\gamma = 1$). These parameters indicate
 311 that as trees grow larger, their shape becomes increasingly conical, reinforcing the hypothesis of
 312 prioritized diameter growth in AFS.

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

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

327 **A lower wood production potential than in managed cocoa AFS**

328 The wood production potential we found for trees in West African cocoa AFS proved to
329 be lower than reported in other regions. Indeed, in Honduras for instance, trees can reach a
330 volume of 0.60 to 2.40 m³ in 18 years (Ramírez-Argueta et al., 2022) while we predict a bole
331 volume ranging from 0.41 to 1.56 m³ at this age. Similarly, in Brasil, trees can reach a volume of
332 1.90 m³ at age 20 (Gama-Rodrigues et al., 2021) while we predict a volume ranging from 0.45
333 to 1.73 m³ at this age. This difference could be attributed to the implementation of silvicultural
334 practices (plantation of fast-growing species, thinning, pruning) in both Honduras and Brazil,
335 whereas there is little or no tree management in Côte d'Ivoire. Our results are in line with this
336 hypothesis. Indeed, although trees in Honduras grow faster in volume, trees in Côte d'Ivoire grow
337 much faster in diameter: it only takes 5 to 15 years for trees in Côte d'Ivoire to reach a DBH of
338 25 cm while this DBH is reached in 13 to 18 years in Honduras. This suggest trees in Honduras
339 have greater bole heights which can be attributed to pruning.

340 **A clear advantage of spontaneous trees over (trans)planted trees**

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

352 On the other hand, we found no difference between spontaneous and (trans)planted trees
353 with regard to their diameter - bole height relationship. This is an expected outcome as self-
354 pruning is controlled by light availability (Koike, 1989; Mäkelä, 1997; Sorrensen-Cothorn et al.,
355 1993). Both spontaneous and (trans)planted trees are therefore expected to maintain their lower
356 branches at the same height, i.e. once above the cocoa canopy.

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

358 Our results show a high variability in the wood production potential of trees depending on
359 species (Fig. 2). This variability could be explained by differences in species ecology. In an addi-
360 tional analysis (see Fig.S1 in Supplementary Information provided by Kouassi et al., 2024), we
361 found tree bole volume predicted at age 25 is negatively correlated to wood density. This indi-
362 cates species with low wood density tend to grow faster than species with high wood density.
363 This result is consistent with previous findings showing a negative correlation between wood

364 density and growth speed in most biomes; species with low wood density having generally a
365 low ability to tolerate competition and a low competitive effect on their neighbours (Kunstler
366 et al., 2016).

367 **Implication for tree management in cocoa AFS**

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

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

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

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393 pertise to meet West African cocoa production development challenges. It brings together many
394 partners jointly striving to place people and the environment at the core of tomorrow's cocoa
395 production.

396 **Conflict of interest disclosure**

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

399 **Data, script, code, and supplementary information availability**

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

References

402

- 403 Aké-Assi L (2001). *Flore de la Côte d'Ivoire: catalogue systématique, biogéographie et écologie*. Genève,
404 Suisse: Conservatoire et Jardin Botanique de Genève.
- 405 Alder D (1989). *Natural forest increment, growth and yield*. In: *Ghana Forest Inventory seminar pro-*
406 *ceedings*. ODA (UK)/FD (Ghana), Forest Planning Unit, pp. 47–58.
- 407 Aleman JC, Jarzyna MA, Staver AC (2018). *Forest extent and deforestation in tropical Africa since*
408 *1900*. *Nature ecology & evolution* **2**, 26–33.
- 409 Ammer C (2003). *Growth and biomass partitioning of Fagus sylvatica L. and Quercus robur L. seedlings*
410 *in response to shading and small changes in the R/FR-ratio of radiation*. *Annals of Forest Science*
411 **60**, 163–171.
- 412 Aubry-Kientz M, Rossi V, Boreux JJ, Hérault B (2015). *A joint individual-based model coupling*
413 *growth and mortality reveals that tree vigor is a key component of tropical forest dynamics*. *Ecology*
414 *and evolution* **5**, 2457–2465.
- 415 Zo-Bi IC, Hérault B (2023). *Fostering agroforestry? Lessons from the Republic of Côte d'Ivoire: English*
416 *version*. *BOIS & FORETS DES TROPIQUES* **356**, 99–104.
- 417 Blaser WJ, Oppong J, Hart SP, Landolt J, Yeboah E, Six J (2018). *Climate-smart sustainable agri-*
418 *culture in low-to-intermediate shade agroforests*. *Nature Sustainability* **1**, 234–239.
- 419 Blaser-Hart WJ, Hart SP, Oppong J, Kyereh D, Yeboah E, Six J (2021). *The effectiveness of cocoa*
420 *agroforests depends on shade-tree canopy height*. *Agriculture, Ecosystems & Environment* **322**,
421 107676.
- 422 Brancalion PH, Holl KD (2020). *Guidance for successful tree planting initiatives*. *Journal of Applied*
423 *Ecology* **57**, 2349–2361.
- 424 Brown N (2004). *SILVICULTURE| Natural Regeneration of Tropical Rain Forests*.
- 425 Carimentrand A (2020). *Cacao. Etat des lieux sur la déforestation et les standards de durabilité*.
- 426 Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker MA, Guo J,
427 Li P, Riddell A (2017). *Stan: A probabilistic programming language*. *Journal of statistical software*
428 **76**.
- 429 Chave J (2005). *Measuring wood density for tropical forest trees. A field manual for the CTFs sites*.
430 *Université Paul Sabatier, Toulouse, France*.
- 431 Chimeli AB, Boyd RG, Adams DM (2012). *International timber markets and tropical deforestation:*
432 *the evidence from prices*. *Applied Economics* **44**, 1303–1314.
- 433 Dago MR, Zo-Bi IC, Konan IK, Kouassi AK, Guei S, Jagoret P, N'Guessan AE, Sanial E, Tankam C,
434 Traoré S, et al. (in press). *What motivates West African cocoa farmers to value trees? Taking the*
435 *4 W approach to the heart of the field*. *People and Nature*.
- 436 Doua-Bi GY, Zo-Bi IC, Amani BH, Elogne AG, N'dja JK, N'Guessan AE, Hérault B (2021). *Tak-*
437 *ing advantage of natural regeneration potential in secondary forests to recover commercial tree*
438 *resources in Côte d'Ivoire*. *Forest Ecology and Management* **493**, 119240.
- 439 Durrieu de Madron L, Favrichon V, Dupuy B, Bar Hen A, Houde L, Maître HF (1998a). *Crois-*
440 *sance et productivité en forêt dense humide : bilan des expérimentations dans le dispositif d'Irobo -*
441 *Côte d'Ivoire (1978-1990)*. Tech. rep. Campus International de Baillarguet, Montpellier, France:
442 CIRAD-Forêt.

- 443 Durrieu de Madron L, Favrichon V, Dupuy B, Bar Hen A, Houde L, Maître HF (1998b). *Croissance et productivité en forêt dense humide : bilan des expérimentations dans le dispositif de Mopri - Côte d'Ivoire (1978 -1992)*. Tech. rep. Campus International de Baillarguet, Montpellier, France: CIRAD-Forêt.
- 447 Ek AR (1974). *Dimensional relationships of forest and open grown trees in-Wisconsin*. Forestry research notes.
- 449 Ennos A (1997). *Wind as an ecological factor*. *Trends in Ecology & Evolution* **12**, 108–111.
- 450 Esche L, Schneider M, Milz J, Armengot L (2023). *The role of shade tree pruning in cocoa agroforestry systems: agronomic and economic benefits*. *Agroforestry Systems* **97**, 175–185.
- 452 Falster DS, Westoby M (2003). *Plant height and evolutionary games*. *Trends in ecology & evolution* **18**, 337–343.
- 454 Falster DS, Westoby M (2005). *Tradeoffs between height growth rate, stem persistence and maximum height among plant species in a post-fire succession*. *Oikos* **111**, 57–66.
- 456 FAO (2020). *Évaluation des ressources forestières mondiales 2020*.
- 457 Fritts HC, Shatz DJ (1975). *Selecting and characterizing tree-ring chronologies for dendroclimatic analysis*.
- 459 Gama-Rodrigues AC, Müller MW, Gama-Rodrigues EF, Mendes FAT (2021). *Cacao-based agroforestry systems in the Atlantic Forest and Amazon Biomes: an ecoregional analysis of land use*. *Agricultural Systems* **194**, 103270.
- 462 Gerber JF (2011). *Conflicts over industrial tree plantations in the South: Who, how and why?* *Global Environmental Change* **21**, 165–176.
- 464 Harja D, Vincent G, Mulia R, Noordwijk M (2012). *Tree shape plasticity in relation to crown exposure*. *Trees* **26**, 1275–1285.
- 466 Hérault B, Ahoba A, Amani B, Benedet F, Coulibaly B, Doua-Bi Y, Ehouman E, Koffi T, Koffi-Konan J, Konaté I, Kouassi A, Louppe D, N'Guessan A, Ouattara N, Tieoulé F, Wourro F, Zo-Bi I (2021). *Plantations forestières innovantes, promouvoir les plantations en mélange pour sécuriser la production de bois d'œuvre et le maintien des services écosystémiques, Rapport technique final du projet Forestinnov*. Tech. rep. FIRCA-FCIAD, p. XX.
- 471 Hérault B, Bachelot B, Poorter L, Rossi V, Bongers F, Chave J, Paine CT, Wagner F, Baraloto C (2011). *Functional traits shape ontogenetic growth trajectories of rain forest tree species*. *Journal of ecology* **99**, 1431–1440.
- 474 Hérault B, N'guessan AK, Ahoba A, Bénédet F, Coulibaly B, Doua-Bi Y, Koffi T, Koffi-Konan JC, Konaté I, Tiéoulé F, et al. (2020). *The long-term performance of 35 tree species of sudanian West Africa in pure and mixed plantings*. *Forest ecology and management* **468**, 118171.
- 477 Holl KD, Brancalion PH (2020). *Tree planting is not a simple solution*. *Science* **368**, 580–581.
- 478 Huang S, Titus SJ, Wiens DP (1992). *Comparison of nonlinear height-diameter functions for major Alberta tree species*. *Canadian Journal of Forest Research* **22**, 1297–1304.
- 480 IDH (2021). *The Cocoa & Forest Initiative: Annual Report*. 35p, Abidjan, Côte d'Ivoire.
- 481 King D (1981). *Tree dimensions: maximizing the rate of height growth in dense stands*. *Oecologia* **51**, 351–356.
- 483 Kinyili B, Ndunda E, Kitur E (2020). *Influence of Agroforestry on Rural Income and Livelihood of Smallholder Farmers in the Semi-Arid Region of Sub Saharan Africa*. *Journal of tropical forestry and environment* **10**.

- 486 Köhl M, Magnussen S, Marchetti M, et al. (2006). *Sampling methods, remote sensing and GIS mul-*
487 *tiresource forest inventory*. Vol. 2. Springer.
- 488 Koike F (1989). *Foliage-crown development and interaction in Quercus gilva and Q. acuta*. *The Jour-*
489 *nal of Ecology*, 92–111.
- 490 Kouassi AK, Zo-Bi IC, Hérault B, Konan IK, Dago MR, Lasbats B, Schmitt S, N'Guessan AE, Aussenac
491 R (2024). *Data and Supplementary Information: timber resource dynamics in West African cocoa*
492 *agroforestry systems (Version 0.1.1)*. <https://doi.org/10.5281/zenodo.12581454>.
- 493 Kouassi AK, Zo-Bi IC, Aussenac R, Kouamé IK, Dago MR, N'guessan AE, Jagoret P, Hérault B
494 (2023a). *The great mistake of plantation programs in cocoa agroforests—Let's bet on natural re-*
495 *generation to sustainably provide timber wood*. *Trees, Forests and People* **12**, 100386.
- 496 Kouassi JL, Diby L, Konan D, Kouassi A, Bene Y, Kouamé C (2023b). *Drivers of cocoa agroforestry*
497 *adoption by smallholder farmers around the Taï National Park in southwestern Côte d'Ivoire*. *Sci-*
498 *entific Reports* **13**, 14309.
- 499 Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M,
500 Vieilledent G, Wright SJ, et al. (2016). *Plant functional traits have globally consistent effects on*
501 *competition*. *Nature* **529**, 204–207.
- 502 Lewis SL, Wheeler CE, Mitchard ET, Koch A (2019). *Restoring natural forests is the best way to*
503 *remove atmospheric carbon*.
- 504 Louppe D, Ouattara N (2013). *Etude sur l'exploitation forestière et les contraintes d'une gestion*
505 *durable des forêts dans le domaine rural en Côte d'Ivoire*.
- 506 Magnussen S, Reed D (2004). *Modeling for estimation and monitoring. Knowledge reference for*
507 *national forest assessments* **111**.
- 508 Mäkelä A (1997). *A carbon balance model of growth and self-pruning in trees based on structural*
509 *relationships*. *Forest Science* **43**, 7–24.
- 510 Molto Q, Hérault B, Boreux JJ, Daullet M, Rousteau A, Rossi V (2014). *Predicting tree heights for*
511 *biomass estimates in tropical forests—a test from French Guiana*. *Biogeosciences* **11**, 3121–3130.
- 512 Notaro M, Collado C, Depas JK, Dumovil D, Denis AJ, Deheuvels O, Tixier P, Gary C (2021). *The*
513 *spatial distribution and height of associated crops influence cocoa tree productivity in complex*
514 *agroforestry systems*. *Agronomy for Sustainable Development* **41**, 60.
- 515 Pillet M, Joetzier E, Belmin C, Chave J, Ciais P, Dourdain A, Evans M, Hérault B, Luysaert S, Poul-
516 ter B (2018). *Disentangling competitive vs. climatic drivers of tropical forest mortality*. *Journal of*
517 *Ecology* **106**, 1165–1179.
- 518 Plieninger T, Muñoz-Rojas J, Buck LE, Scherr SJ (2020). *Agroforestry for sustainable landscape*
519 *management*. *Sustainability Science* **15**, 1255–1266.
- 520 Preece ND, Oosterzee P, Lawes MJ (2023). *Reforestation success can be enhanced by improving*
521 *tree planting methods*. *Journal of environmental management* **336**, 117645.
- 522 Prévosto B, Balandier P (2007). *Influence of nurse birch and Scots pine seedlings on early aerial*
523 *development of European beech seedlings in an open-field plantation of Central France*. *Forestry*
524 **80**, 253–264.
- 525 R Core Team (2021). *R: A language and environment for statistical computing*. Version 4.0.0. Vienna,
526 Austria. URL: <https://www.R-project.org/>.
- 527 Ramírez-Argueta O, Orozco-Aguilar L, Dubón AD, Díaz FJ, Sánchez J, Casanoves F (2022). *Tim-*
528 *ber growth, cacao yields, and financial revenues in a long-term experiment of cacao agroforestry*
529 *systems in northern Honduras*. *Frontiers in Sustainable Food Systems* **6**, 434.

- 530 Réjou-Méchain M, Tanguy A, Pioniot C, Chave J, Hérault B (2017). *biomass: an r package for*
531 *estimating above-ground biomass and its uncertainty in tropical forests. Methods in Ecology and*
532 *Evolution* **8**, 1163–1167.
- 533 Rozendaal DM, Phillips OL, Lewis SL, Affum-Baffoe K, Alvarez-Davila E, Andrade A, Aragão
534 LE, Araujo-Murakami A, Baker TR, Bánki O, et al. (2020). *Competition influences tree growth,*
535 *but not mortality, across environmental gradients in Amazonia and tropical Africa. Ecology* **101**,
536 e03052.
- 537 Ruf F, Schroth G, Doffangui K (2015). *Climate change, cocoa migrations and deforestation in West*
538 *Africa: What does the past tell us about the future? Sustainability Science* **10**, 101–111.
- 539 Sanial E (2019). *A la recherche de l'ombre, géographie des systèmes agroforestiers émergents en ca-*
540 *caoculture ivoirienne post-forestière*. PhD thesis. Lyon.
- 541 Sanial E, Ruf F, Louppe D, Mietton M, Hérault B (2023). *Local farmers shape ecosystem service*
542 *provisioning in West African cocoa agroforests. Agroforestry Systems* **97**, 401–414.
- 543 Schmitt S, Hérault B, Derroire G (2023). *High intraspecific growth variability despite strong evolu-*
544 *tionary legacy in an Amazonian forest. Ecology letters*.
- 545 Sodefor (2017). *Règles de sylviculture et d'exploitation du bois en zone de forêt dense de Côte d'Ivoire,*
546 *Version définitive*. Abidjan, Côte d'Ivoire: Sodefor, p. 58.
- 547 Sonwa DJ, Weise SF, Schroth G, Janssens MJ, Shapiro HY (2014). *Plant diversity management in*
548 *cocoa agroforestry systems in West and Central Africa—effects of markets and household needs.*
549 *Agroforestry systems* **88**, 1021–1034.
- 550 Sorrensen-Cothorn KA, Ford ED, Sprugel DG (1993). *A model of competition incorporating plastic-*
551 *ity through modular foliage and crown development. Ecological Monographs* **63**, 277–304.
- 552 Stan Development Team C et al. (2018). *RStan: the R interface to Stan. R package version 2*.
- 553 Traoré S, Zo-Bi IC, Pioniot C, Aussenac R, Hérault B (2024). *Fragmentation is the main driver*
554 *of residual forest aboveground biomass in West African low forest-high deforestation landscapes.*
555 *Trees, Forests and People* **15**, 100477.
- 556 Tsanga R, Cerutti PO, Essiane E (2020). *Demandes en bois et produits dérivés dans les marchés*
557 *publics en Côte d'Ivoire*.
- 558 Tschora H, Cherubini F (2020). *Co-benefits and trade-offs of agroforestry for climate change mitiga-*
559 *tion and other sustainability goals in West Africa. Global Ecology and Conservation* **22**, e00919.
- 560 Uzu J, Bettinger P, Siry J, Mei B (2022). *Timber business in West Africa: a review and outlook. Inter-*
561 *national Forestry Review* **24**, 240–256.
- 562 Verdone M, Seidl A (2017). *Time, space, place, and the Bonn Challenge global forest restoration*
563 *target. Restoration ecology* **25**, 903–911.
- 564 Waring RH, Pitman GB (1985). *Modifying lodgepole pine stands to change susceptibility to mountain*
565 *pine beetle attack. Ecology* **66**, 889–897.
- 566 Werden LK, Alvarado J P, Zarges S, Calderón M E, Schilling EM, Gutiérrez L M, Powers JS (2018).
567 *Using soil amendments and plant functional traits to select native tropical dry forest species for*
568 *the restoration of degraded Vertisols. Journal of Applied Ecology* **55**, 1019–1028.
- 569 Wunder J, Brzeziecki B, Żybura H, Reineking B, Bigler C, Bugmann H (2008). *Growth–mortality re-*
570 *lationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged*
571 *European forests. Oikos* **117**, 815–828.
- 572 Zobi C, Chessel D, Kadio A, Pascal J (2009). *Détermination des paramètres influents de la dy-*
573 *namique des forêts naturelles ivoiriennes. Agronomie Africaine* **21**.