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# 1 24 years to start harvesting timber in West African cocoa agroforestry systems with spontaneous trees demonstrating clear advantages

Aimé K. Kouassi<sup>1</sup>, Irié C. Zo-Bi<sup>1</sup>, Bruno Hérault<sup>2,3</sup>, Isaac K. Konan<sup>4</sup>, Marie R. Dago<sup>1</sup>, Baptiste Lasbats<sup>5</sup>, Sylvain Schmitt<sup>2,3</sup>, Anny E. N'Guessan<sup>4</sup>, and Raphaël Aussenac<sup>6,3</sup>

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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

<sup>1</sup>UMRI SAPT, INPHB, Yamoussoukro, Côte d'Ivoire, <sup>2</sup>CIRAD, UPR Forêts et Sociétés, F-34398 Montpellier, France, <sup>3</sup>Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France, <sup>4</sup>Laboratoire de Botanique, Université Félix Houphouët-Boigny, Abidjan, Côte d'Ivoire, <sup>5</sup>ENS de Lyon, Lyon, France, <sup>6</sup>CIRAD, UPR Forêts et Sociétés, Yamoussoukro, Côte d'Ivoire

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## 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% of  
28 global cocoa production. These initiatives primarily aim to achieve sustainability and long-term  
29 stabilization of cocoa production (Carimentrand, 2020). By doing so, the establishment of new  
30 deforestation fronts to seek fertile soils would be avoided, thereby reducing pressure on the few  
31 remaining forests (Ruf et al., 2015).

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

46 are more subject to variations in temperature and humidity, influencing their mechanical struc-  
47 ture (Johnson et al., 2011). Improving knowledge on growth trajectories and tree architecture  
48 in agroforestry contexts is thus urgent to correctly quantify the productive potentials of timber  
49 trees.

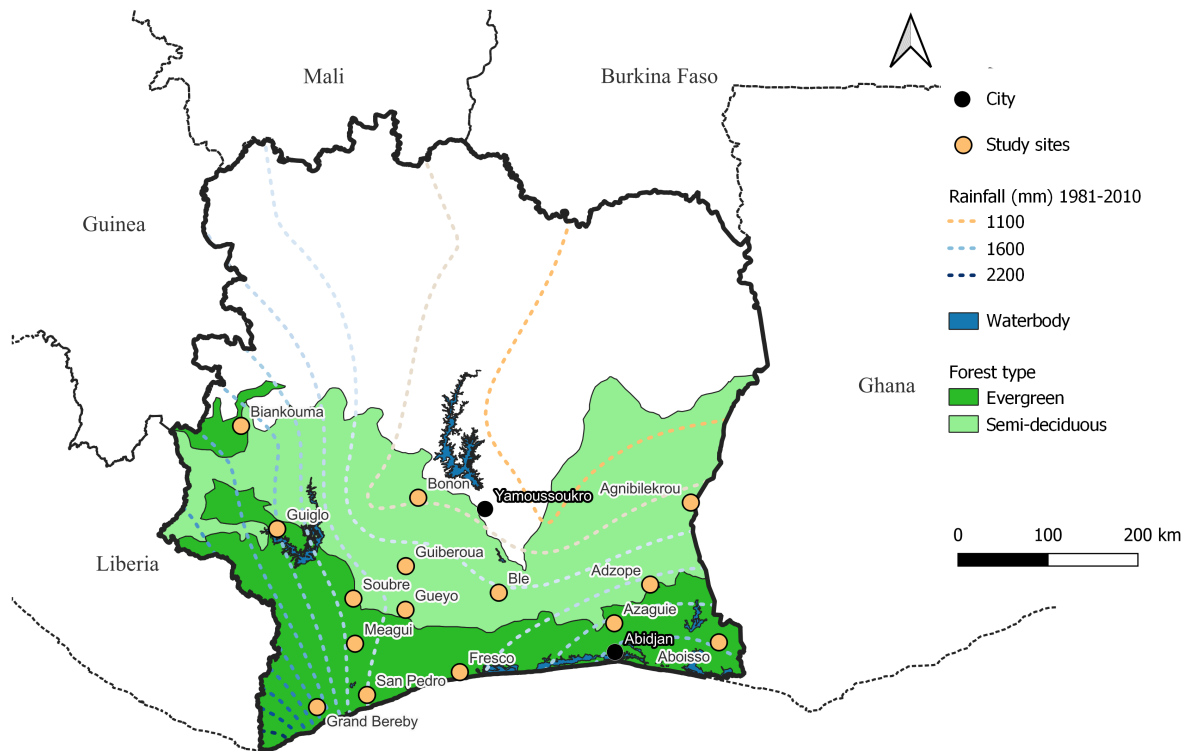
50 The actual implementation of agroforestry promotion activities often involves the massive distri-  
51 bution in cocoa fields, by industries and through cooperatives or development NGOs, of young  
52 trees raised in nurseries (IDH, 2021). However, recent results suggest that the survival rate and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

69 The main objective of our study is to assess the timber production potential of trees in cocoa  
70 agroforestry systems (AFS) in Côte d'Ivoire (West Africa). Specifically, we estimated the time  
71 required for trees to reach their minimum logging diameter (MLD) and the corresponding vol-  
72 ume at this stage. We also assessed the effect of the origin of the trees, be they from natural  
73 regeneration or (trans)plantation, on this production potential. To achieve these objectives, we  
74 (i) modelled the diameter growth of forest species identified as potentially suitable for wood  
75 production in cocoa AFS; (ii) established specific allometric models for trees in cocoa AFS to as-  
76 sess their volume when they reach their minimum logging diameter; (iii) evaluated the effect of  
77 spontaneous or (trans)planted origin of trees on their growth trajectories, allometry, and thus on  
78 their logging volume trajectories. The results of this study provide key indicators for establish-  
79 ing silvicultural management technical itineraries for associated trees in cocoa fields based on  
80 their actual performance, thereby encouraging decision-makers to better promote timber trees  
81 in cocoa fields.

## 82 Material and methods

### 83 Sampling design

84 *Study area.* Our study covers the cocoa production area of Côte d'Ivoire (Figure 1). This area is  
85 characterised by an annual precipitation gradient varying from 2 500 mm in the south to 1 100  
86 mm in the north, and by an average annual temperature of around 26.5°C. The area spans from  
87 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.

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

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

102 In this study, we only considered 23 tree species identified as potentially suitable for wood  
 103 production in cocoa AFS (Kouassi et al., 2023a). Also, here we only consider spontaneous and  
 104 (trans)planted trees excluding remnant trees. Remnant trees are expected to have different de-  
 105 velopment 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.cm<sup>3</sup>); WOOD USES from Prota4u; (\*) indicates exotic species (Aké-Assi, 2001).

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

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

### 109 Modelling

110 We developed three models to assess the wood production potential of trees in cocoa AFS:  
 111 (i) a model describing the diameter growth trajectories of trees as a function of their age (Eq 2),  
 112 (ii) a model evaluating the relationship between tree diameter and bole height (Eq 4), and (iii) a  
 113 model assessing the commercial volume of trees as a function of their diameter and bole height  
 114 (Eq 5). Each model includes an origin effect to assess the differences between spontaneous and  
 115 (trans)planted trees. We estimated the model parameters in a Bayesian framework using Stan  
 116 (Carpenter et al., 2017; Stan Development Team et al., 2018) in the R environment (Team et al.,  
 117 2021). We provide the STAN code in Supplementary Information (Kouassi et al., 2024).

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

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

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

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

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

125 with

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

128 and where:

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

129 with:

- 130 •  $G_{max_s} \sim \mathcal{LN}(\log(G_{max}), \sigma_{gmax})$ : the species-specific maximum growth potential, follow-  
 131 ing a log-normal distribution with parameters  $G_{max}$  and  $\sigma_{gmax}$ .  $G_{max}$  represents the ex-  
 132 pected maximum growth potential for all species and  $\sigma_{gmax}$  the dispersion parameter.
- 133 •  $D_{opt_s} = \theta_d \cdot D_{max_s}$ : the species-specific diameter at which  $G_{max_s}$  is reached, defined as a  
 134 function of  $D_{max_s}$ , the maximum diameter observed for each species, weighted by  $\theta_d$ , a  
 135 parameter between 0 and 1.



- 136 •  $K_s = \theta_{k0} + \theta_k \cdot wd_s$ : the species-specific kurtosis coefficient defining the width of the  
137 growth curve, reflecting ontogenetic variation in growth potential.  $K_s$  is a linear function  
138 of species wood density  $wd_s$ , with parameters  $\theta_{k0}$  and  $\theta_k$ .
- 139 •  $\theta_{si} \sim \mathcal{LN}(\log(1), \sigma_{si})$ : a site effect following a log-normal distribution with parameters  
140  $\log(1)$  and  $\sigma_{si}$ . Site effects are therefore centred on 1 and dispersed according to  $\sigma_{si}$ .
- 141 •  $\theta_{origin}^O$ : an origin effect evaluating growth difference between spontaneous and (trans)planted  
142 trees. Practically, the origin variable (O) takes the value 1 for spontaneous trees and 0 for  
143 (trans)planted trees. Thus,  $\theta_{origin}^O$  represents the annual diameter growth rate advantage  
144 of spontaneous trees over (trans)planted trees.

145 We modelled the diameter growth trajectories with a subset of 959 trees (767 spontaneous  
146 and 192 (trans)planted) for which age and diameter data were available.

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

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

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

154 with:

- 155 •  $BH_{i,s}$ : the bole height of tree  $i$  of species  $s$ .
- 156 •  $DBH_{i,s}$ : the diameter at breast height of tree  $i$  of species  $s$ .
- 157 •  $\alpha$ : represents the asymptotic bole height.
- 158 •  $\beta$ : represents the diameter at which half the asymptotic height ( $\frac{BH_{i,s}}{2}$ ) is reached.
- 159 •  $\theta_s \sim \mathcal{LN}(\log(1), \sigma_s)$ : a species effect following a log-normal distribution with parameters  
160  $\log(1)$  and  $\sigma_s$ . Species effects are therefore centred on 1 and dispersed according to  $\sigma_s$ .
- 161 •  $\theta_{si} \sim \mathcal{LN}(\log(1), \sigma_{si})$ : a site effect following a log-normal distribution with parameters  
162  $\log(1)$  and  $\sigma_{si}$ . Site effects are therefore centred on 1 and dispersed according to  $\sigma_{si}$ .
- 163 •  $\theta_{origin}^O$ : an origin effect evaluating the difference in asymptotic bole height between spon-  
164 taneous and (trans)planted trees. Practically, the origin variable (O) takes the value 1 for  
165 spontaneous trees and 0 for (trans)planted trees. Thus,  $\theta_{origin}^O$  represents the advantage  
166 of spontaneous trees over (trans)planted trees in terms of asymptotic bole height.
- 167 •  $\sigma_h$ : the dispersion parameter of the log-normal distribution.

168 We modelled tree bole height with a subset of 1008 trees (806 spontaneous and 202 (trans)planted)  
169 for which diameter and bole height data were available.

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

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

173 with:

- 174 •  $BV_{i,s}$ : the bole volume of tree  $i$  of species  $s$ .
- 175 •  $DBH_{i,s}$ : the diameter at breast height of tree  $i$  of species  $s$ .
- 176 •  $BH_{i,s}$ : the bole height of tree  $i$  of species  $s$ .
- 177 •  $\alpha$ ,  $\beta$  et  $\gamma$ : parameters to be estimated.
- 178 •  $\theta_s \sim \mathcal{LN}(\log(1), \sigma_s)$ : a species effect following a log-normal distribution with parameters
- 179  $\log(1)$  and  $\sigma_s$ . Species effects are therefore centred on 1 and dispersed according to  $\sigma_s$ .
- 180 •  $\theta_{origin}^O$ : an origin effect evaluating the difference in bole volume between spontaneous and
- 181 (trans)planted trees. Practically, the origin variable (O) takes the value 1 for spontaneous
- 182 trees and 0 for (trans)planted trees. Thus,  $\theta_{origin}^O$  represents the advantage of spontaneous
- 183 trees over (trans)planted trees in terms of bole volume.
- 184 •  $\sigma_v$ : the dispersion parameter of the log-normal distribution.

185 We modelled bole volume with a subset of 155 trees (135 spontaneous and 20 (trans)planted)

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

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

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

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

190 these systems.

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

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

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

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

195  $BH_{i,s}$ .

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

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

198 (equation 4).

## 199 Results

### 200 Tree diameter growth

201 On average, species reach a diameter of 50 cm (smallest MLD value) in 33 years (Fig. 2).

202 The fastest growing species is *Ceiba pentandra* (FROMAGER), reaching 50 cm in 15 years. The

203 slowest growing species is *Piptadeniastrum africanum* (DABEMA) reaching the same diameter in

204 62 years.

205 The expected maximum annual growth potential ( $G_{max}$  in equation 3) for all species is  $10.1 \text{ cm.yr}^{-1}$ .

206 On average, the maximum annual growth potential occurs at an optimal diameter ( $D_{opt_s}$  in equa-

207 tion 3) of 0.5 cm. Species annual growth rates are therefore maximum for DBH smaller than 1 cm

208 and decrease as DBH increases.

209 Species annual growth rates (AGR) at DBH = 10 cm range from  $2.1 \text{ cm.yr}^{-1}$  to  $6 \text{ cm.yr}^{-1}$ , with

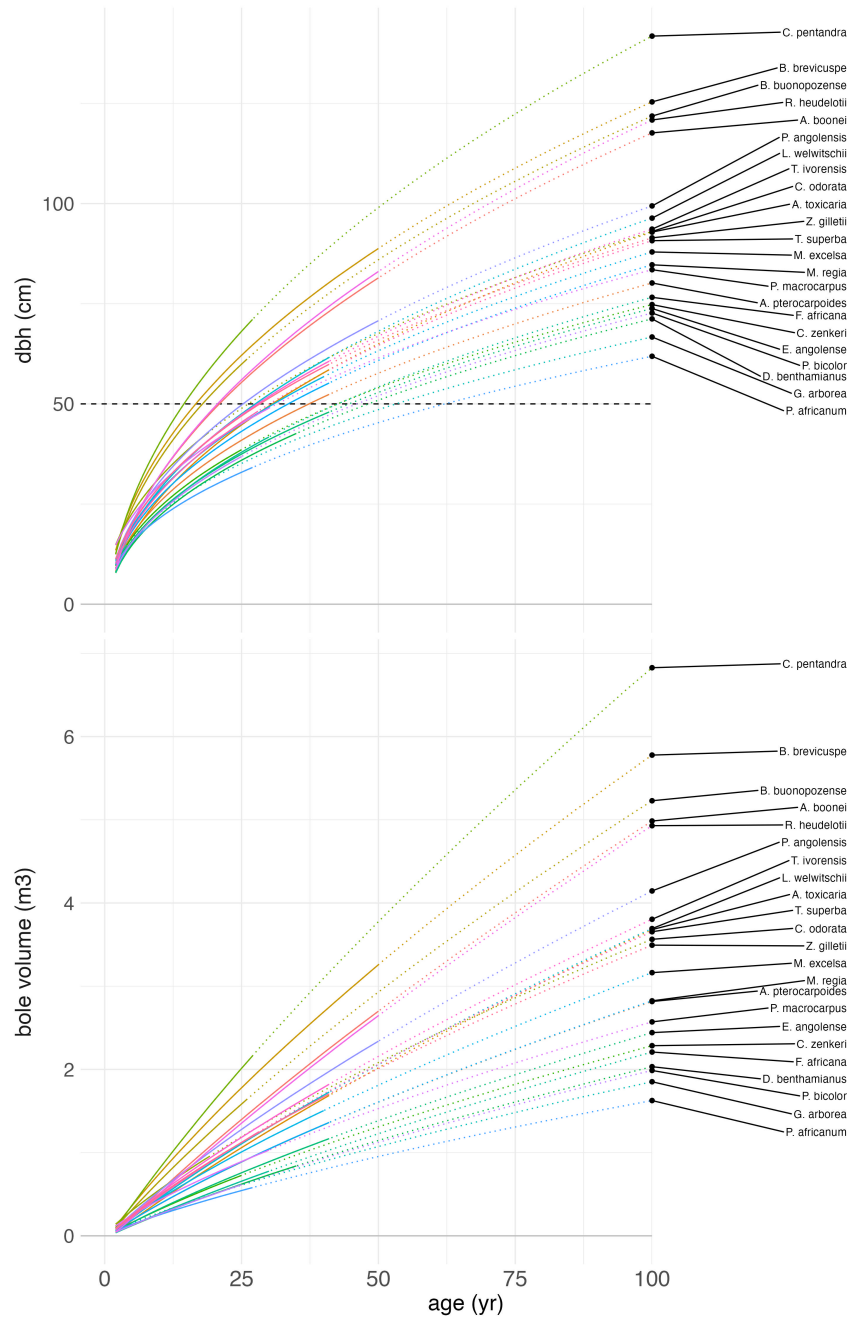
210 an average of  $3.5 \text{ cm.yr}^{-1}$ . At DBH = 70 cm, species AGR range from  $0.2 \text{ cm.yr}^{-1}$  to  $1.5 \text{ cm.yr}^{-1}$ ,

211 with an average of  $0.6 \text{ cm.yr}^{-1}$ . Maximum values at 10 and 70 cm DBH are reached by *Ceiba pen-*

212 *tandra* (FROMAGER), while minimum values are reached by *Piptadeniastrum africanum* (DABEMA).

213 The model parameter values and their credibility intervals are presented from table S1 to table

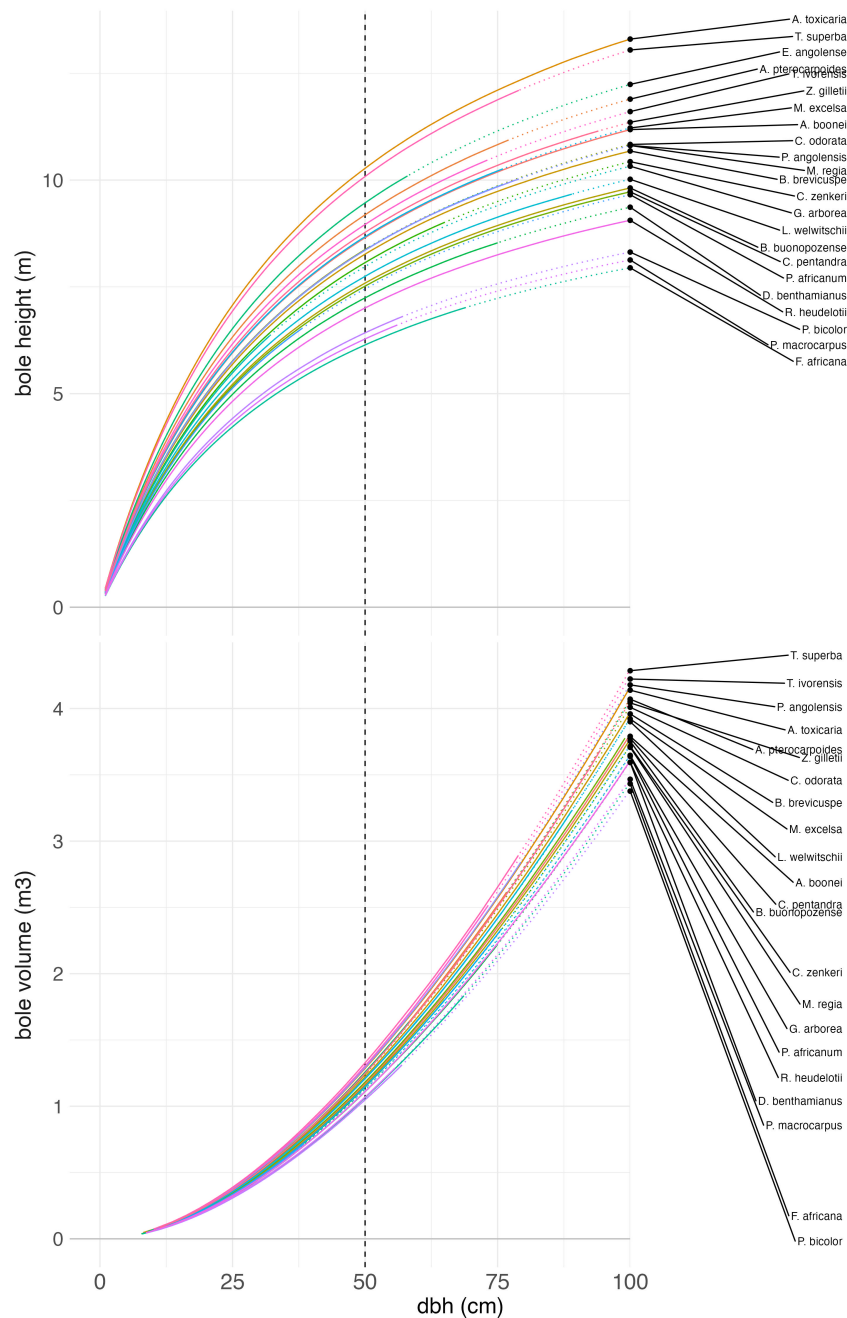
214 S5 of the Supplementary Information (Kouassi et al., 2024).



**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.

### 215 Diameter - bole height relationship

216 At 50 cm in DBH (smallest MLD value), the trees reach an average bole height of 8.1 m (Fig.  
 217 3), ranging from 6.1 m for *Funtumia africana* (POUO) to 10.3 m for *Antiaris toxicaria* (AKO). The  
 218 predicted tree asymptotic bole height ( $\alpha$  in equation 4) is 14.9 m. The species effect  $\theta_s$  ranges  
 219 from 0.76 (i.e. -24%) for *Funtumia africana* (POUO) to 1.28 (i.e. +28%) *Antiaris toxicaria* (AKO).  
 220 The model parameter values and their credibility intervals are presented from table S6 to table  
 221 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.

222 **Wood production potential of trees**



223 At age 25 (a commonly used logging age in forest plantations), trees reach a mean bole volume  
 224 of 1.1 m<sup>3</sup> (Fig. 2). The fastest growing species is *Ceiba pentandra* (FROMAGER), reaching 2 m<sup>3</sup>  
 225 at age 25. The slowest growing species is *Piptadeniastrum africanum* (DABEMA) reaching 0.6 m<sup>3</sup>  
 226 at the same age.

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

229 On average, trees reach their MLD at 42.7 years of age (Fig. 4). *Bombax brevicuspe* (KON-  
 230 DROTI) reaches its MLD first at the age of 24 while *Piptadeniastrum africanum* (DABEMA) reaches  
 231 its MLD last at the age of 93. At their MLD, trees have on average a volume of 1.5 m<sup>3</sup>. *Parkia bi-*  
 232 *color* (LO), with 1 m<sup>3</sup>, has the smallest volume, while *Ceiba pentandra* (FROMAGER), with 2.6 m<sup>3</sup>,  
 233 has the largest volume.

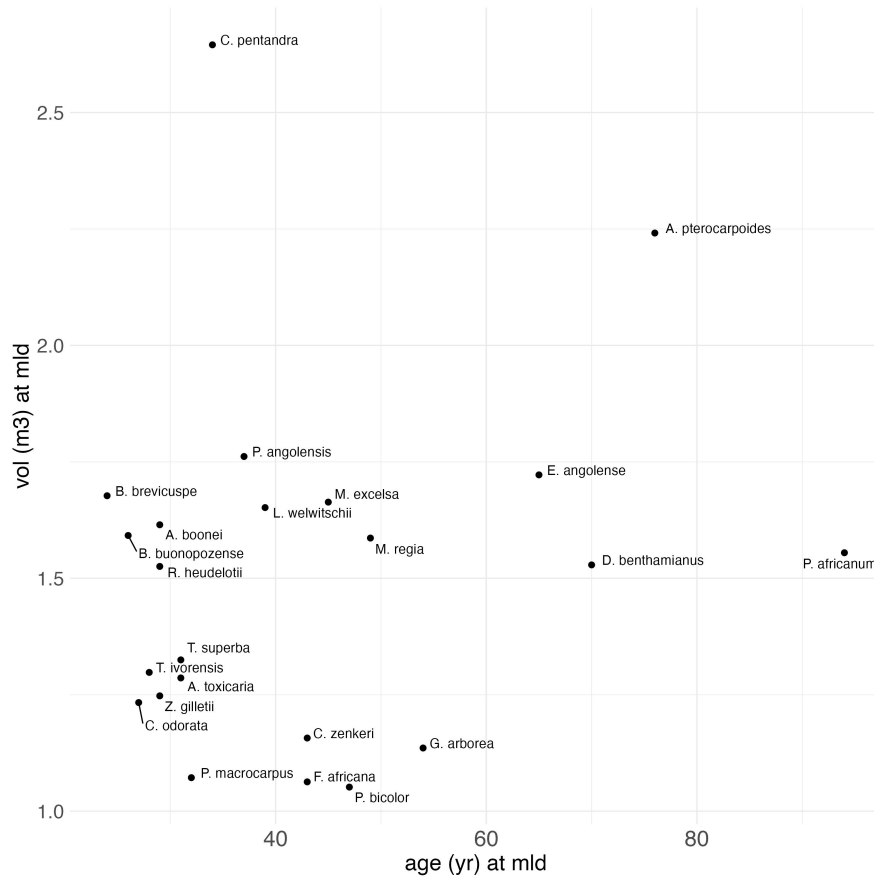


Figure 4 – Bole volume and age at minimum logging diameter for our 23 species.

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

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

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

### 239 Effect of trees' origin on their wood production potential

240 In our diameter growth model (equation 3)  $\theta_o = 1.1$ . This means that the annual growth rate  
 241 of spontaneous trees is 10% higher than that of (trans)planted trees. As a consequence, sponta-  
 242 neous trees reach their MLD 3.7 years earlier than (trans)planted trees (Fig. 5) on average. This  
 243 advantage of spontaneous trees over (trans)planted trees ranges from 2 years for *Bombax bre-*  
 244 *vicuspe* (KONDROTI), *Ricinodendron heudeloti* (EHO), *Cedrela Odorata* (CEDRELA) and *Terminalia*  
 245 *superba* (FRAKE) to 8 years for *Amphimas pterocarpoides*.

246 In our bole volume model (equation 5)  $\theta_o = 1.41$ . This means that for a given diameter and  
 247 a given bole height, spontaneous trees are 41% larger in volume than (trans)planted trees. As a  
 248 consequence, spontaneous trees reach a higher bole volume of 0.4 m<sup>3</sup> on average as compared  
 249 to spontaneous trees (Fig 5). This advantage in volume ranges from 0.3 m<sup>3</sup> for *Parkia bicolor* (LO)  
 250 to 0.7 m<sup>3</sup> for *Ceiba pentandra* (FROMAGER).

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

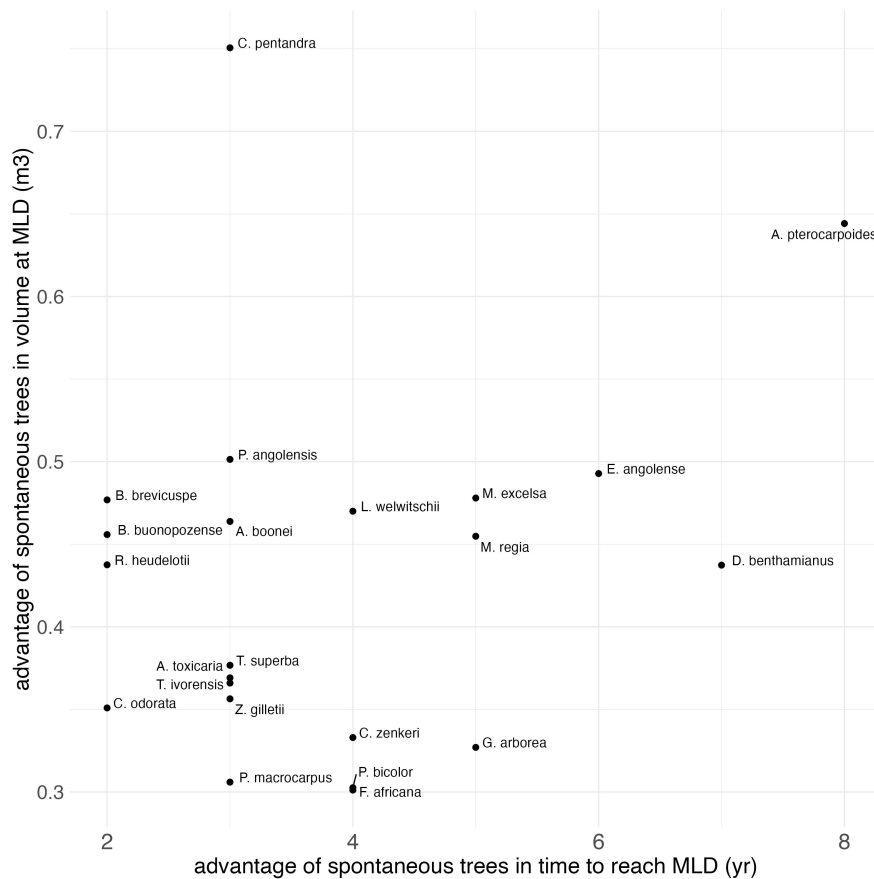


Figure 5 – Advantage of spontaneous trees over (trans)planted trees in time to reach their MLD and in volume at MLD.

253

### Discussion

254 To our knowledge, this study is the first to assess the diameter growth and the wood produc-  
 255 tion potential of trees in West African cocoa AFS. Our results show that trees can reach their  
 256 MLD as early as 24 years of age for bole volumes greater than 1m<sup>3</sup>. Our results also show that  
 257 spontaneous trees have a clear advantage over transplanted trees: they can reach their MLD up  
 258 to 8 years earlier and produce up to 0.7 m<sup>3</sup> more over the same period.

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

260 Our results suggest trees can achieve greater annual growth rates in cocoa AFS than in forests  
 261 or plantations. Indeed, for trees with diameters ranging from 10 to 70 cm, we predict growth  
 262 rates varying from 0.2 to 6 cm.yr<sup>-1</sup>. In comparison, the average annual growth rates recorded in  
 263 West African forests for trees of the same size are at the lower end of this range. In Côte d'Ivoire,

264 Durrieu de Madron et al. (1998a) and Durrieu de Madron et al. (1998b) found an average annual  
 265 growth rate of 0.27 cm.yr<sup>-1</sup> for an evergreen forest and of 0.29 cm.yr<sup>-1</sup> for a semi-deciduous  
 266 forest, respectively. In Ghana, Alder (1989) found average annual growth rates ranging from 0.8  
 267 to 1 cm.yr<sup>-1</sup> for pioneer species and ranging from 0.4 to 0.5 cm.yr<sup>-1</sup> for shade-tolerant species.  
 268 Similarly, in plantations in Côte d'Ivoire, Hérault et al. (2021) reported more than 35 years were  
 269 needed to reach 50 cm in diameter, whereas we found only 15 years are needed in cocoa AFS.

270 The faster growth of trees in cocoa AFS could be due to the greater availability of light in  
 271 these systems than in forests or plantations (Pillet et al., 2018). This greater availability of light  
 272 could lead trees to invest more in their diameter growth once they have emerged from the co-  
 273 coa canopy (Ek, 1974; King, 1981). Our results show maximum annual growth rates from the  
 274 very first years ( $G_{max} = 10.1$  cm.yr<sup>-1</sup> for a mean  $D_{opt_s} = 0.5$  cm), which is in line with the  
 275 hypothesis of a priority given to diameter growth. In contrast, in forests and plantations, closed  
 276 systems where competition for light is strong, growth in height could be favoured (Ammer, 2003;  
 277 Prévosto and Balandier, 2007), to the expense of diameter growth (Falster and Westoby, 2003,  
 278 2005).

279 We therefore expect trees in forests or plantations to take longer to reach the same diameter  
 280 than trees in cocoa AFS. However, for a same diameter, we expect trees in forests or plantations  
 281 to have a greater bole volume than trees in cocoa AFS, due to their greater height. As a conse-  
 282 quence of the exponential relationship between diameter and volume, the larger the trees, the  
 283 greater this difference in volume. This is supported by our results. Indeed, we found trees in  
 284 cocoa AFS can reach 1.4 m<sup>3</sup> at 50 cm DBH while in Côte d'Ivoire, Hérault et al. (2021) found  
 285 trees in plantation can reach about 2.5 m<sup>3</sup> at the same DBH. At 100 cm DBH, we found trees  
 286 in cocoa AFS could reach 4.4 m<sup>3</sup> while at this size, trees in plantation can reach a much higher  
 287 volume of over 15 m<sup>3</sup>.

### 288 **A lower wood production potential than in managed cocoa AFS**

289 The wood production potential we found for trees in West African cocoa AFS proved to be  
 290 lower than reported in other regions. Indeed, in Honduras for instance, trees can reach a volume  
 291 of 0.6 to 2.4 m<sup>3</sup> in 18 years (Ramírez-Argueta et al., 2022) while we predict a bole volume ranging  
 292 from 0.4 to 1.5 m<sup>3</sup> at this age. Similarly, in Brasil, trees can reach a volume of 1.9 m<sup>3</sup> at age 20  
 293 (Gama-Rodrigues et al., 2021) while we predict a volume ranging from 0.5 to 1.6 m<sup>3</sup> at this age.  
 294 This difference could be attributed to the implementation of silvicultural practices (plantation of  
 295 fast-growing species, thinning, pruning) in both Honduras and Brazil, whereas there is little or no  
 296 tree management in Côte d'Ivoire. Our results are in line with this hypothesis. Indeed, although  
 297 trees in Honduras grow faster in volume, trees in Côte d'Ivoire grow much faster in diameter: it  
 298 only takes 5 to 14 years for trees in Côte d'Ivoire to reach a DBH of 25 cm while this DBH is  
 299 reached in 13 to 18 years in Honduras. This suggest trees in Honduras have greater bole heights  
 300 which can be attributed to pruning.

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

302 Our results show that spontaneous trees have an annual growth rate 10% higher than (trans)planted  
 303 trees and a bole volume 41% greater for a same diameter. This latter result indicates spontaneous  
 304 trees have a more cylindrical bole than (trans)planted trees. These better performances of spon-  
 305 taneous trees could be due to the fact that, having remained in the same environment, they



306 could have a more extensive root system, more efficient at absorbing water and nutrients (Wer-  
307 den et al., 2018). In contrast, transplanted trees experience disturbances in their root systems  
308 when moved to a new environment, negatively impacting their growth (Brown, 2004; Werden  
309 et al., 2018). In addition, spontaneous trees, having remained in the same environment, could pri-  
310 oritise resource allocation to growth, unlike (trans)planted trees, which could allocate resources  
311 preferentially to defence and reproduction (Fritts and Shatz, 1975; Waring and Pitman, 1985;  
312 Wunder et al., 2008).

313 On the other hand, we found no difference between spontaneous and (trans)planted trees  
314 with regard to their diameter - bole height relationship. This is an expected outcome as self-  
315 pruning is controlled by light availability (Koike, 1989; Mäkelä, 1997; Sorrensen-Cothorn et al.,  
316 1993). Both spontaneous and (trans)planted trees are therefore expected to maintain their lower  
317 branches at the same height, i.e. once above the cocoa canopy.


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

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

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

### 331 **Implication for tree management in cocoa AFS**

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

343 Besides  our results show trees in West African cocoa AFS have low bole height. This sug-  
344 gest pruning could be an effective lever for improving wood production. Indeed, by increasing  
345 the bole height, this operation increases tree commercial volume. The cocoa sector should help  
346 implement strategies to support pruning in cocoa AFS, as farmers alone may not be able to cover  
347 the additional costs on their own (Esche et al., 2023).



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

352

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357 partners jointly striving to place people and the environment at the core of tomorrow's cocoa  
358 production.

359

### Conflict of interest disclosure

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

362

### Data, script, code, and supplementary information availability

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

365

### References

- 366 Aké-Assi L (2001). *Flore de la Côte d'Ivoire: catalogue systématique, biogéographie et écologie*. Genève,  
367 Suisse: Conservatoire et Jardin Botanique de Genève.
- 368 Alder D (1989). *Natural forest increment, growth and yield*. In: *Ghana Forest Inventory seminar pro-*  
369 *ceedings*. ODA (UK)/FD (Ghana), Forest Planning Unit, pp. 47–58.
- 370 Aleman JC, Jarzyna MA, Staver AC (2018). *Forest extent and deforestation in tropical Africa since*  
371 *1900*. *Nature ecology & evolution* **2**, 26–33.
- 372 Ammer C (2003). *Growth and biomass partitioning of Fagus sylvatica L. and Quercus robur L. seedlings*  
373 *in response to shading and small changes in the R/FR-ratio of radiation*. *Annals of Forest Science*  
374 **60**, 163–171.
- 375 Aubry-Kientz M, Rossi V, Boreux JJ, Hérault B (2015). *A joint individual-based model coupling*  
376 *growth and mortality reveals that tree vigor is a key component of tropical forest dynamics*. *Ecology*  
377 *and evolution* **5**, 2457–2465.
- 378 Zo-Bi IC, Hérault B (2023). *Fostering agroforestry? Lessons from the Republic of Côte d'Ivoire: English*  
379 *version*. *BOIS & FORETS DES TROPIQUES* **356**, 99–104.
- 380 Blaser WJ, Oppong J, Hart SP, Landolt J, Yeboah E, Six J (2018). *Climate-smart sustainable agri-*  
381 *culture in low-to-intermediate shade agroforests*. *Nature Sustainability* **1**, 234–239.
- 382 Blaser-Hart WJ, Hart SP, Oppong J, Kyereh D, Yeboah E, Six J (2021). *The effectiveness of cocoa*  
383 *agroforests depends on shade-tree canopy height*. *Agriculture, Ecosystems & Environment* **322**,  
384 107676.
- 385 Brancalion PH, Holl KD (2020). *Guidance for successful tree planting initiatives*. *Journal of Applied*  
386 *Ecology* **57**, 2349–2361.
- 387 Brown N (2004). *SILVICULTURE| Natural Regeneration of Tropical Rain Forests*.

- 388 Carimentrand A (2020). *Cacao. Etat des lieux sur la déforestation et les standards de durabilité*.
- 389 Carpenter B, Gelman A, Hoffman MD, Lee D, Goodrich B, Betancourt M, Brubaker MA, Guo J,  
390 Li P, Riddell A (2017). *Stan: A probabilistic programming language*. *Journal of statistical software*  
391 **76**.
- 392 Chave J (2005). *Measuring wood density for tropical forest trees. A field manual for the CTFs sites*.  
393 *Universite Paul Sabatier, Toulouse, France*.
- 394 Chimeli AB, Boyd RG, Adams DM (2012). *International timber markets and tropical deforestation:*  
395 *the evidence from prices*. *Applied Economics* **44**, 1303–1314.
- 396 Doua-Bi GY, Zo-Bi IC, Amani BH, Elogne AG, N'dja JK, N'Guessan AE, Hérault B (2021). *Tak-*  
397 *ing advantage of natural regeneration potential in secondary forests to recover commercial tree*  
398 *resources in Côte d'Ivoire*. *Forest Ecology and Management* **493**, 119240.
- 399 Durrieu de Madron L, Favrichon V, Dupuy B, Bar Hen A, Houde L, Maître HF (1998a). *Crois-*  
400 *sance et productivité en forêt dense humide : bilan des expérimentations dans le dispositif d'Irobo -*  
401 *Côte d'Ivoire (1978-1990)*. Tech. rep. Campus International de Baillarguet, Montpellier, France:  
402 CIRAD-Forêt.
- 403 Durrieu de Madron L, Favrichon V, Dupuy B, Bar Hen A, Houde L, Maître HF (1998b). *Crois-*  
404 *sance et productivité en forêt dense humide : bilan des expérimentations dans le dispositif de Mo-*  
405 *pri - Côte d'Ivoire (1978 -1992)*. Tech. rep. Campus International de Baillarguet, Montpellier,  
406 France: CIRAD-Forêt.
- 407 Ek AR (1974). *Dimensional relationships of forest and open grown trees in-Wisconsin*. *Forestry re-*  
408 *search notes*.
- 409 Ennos A (1997). *Wind as an ecological factor*. *Trends in Ecology & Evolution* **12**, 108–111.
- 410 Esche L, Schneider M, Milz J, Armengot L (2023). *The role of shade tree pruning in cocoa agro-*  
411 *forestry systems: agronomic and economic benefits*. *Agroforestry Systems* **97**, 175–185.
- 412 Falster DS, Westoby M (2003). *Plant height and evolutionary games*. *Trends in ecology & evolution*  
413 **18**, 337–343.
- 414 Falster DS, Westoby M (2005). *Tradeoffs between height growth rate, stem persistence and maxi-*  
415 *mum height among plant species in a post-fire succession*. *Oikos* **111**, 57–66.
- 416 FAO (2020). *Évaluation des ressources forestières mondiales 2020*.
- 417 Fritts HC, Shatz DJ (1975). *Selecting and characterizing tree-ring chronologies for dendroclimatic*  
418 *analysis*.
- 419 Gama-Rodrigues AC, Müller MW, Gama-Rodrigues EF, Mendes FAT (2021). *Cacao-based agro-*  
420 *forestry systems in the Atlantic Forest and Amazon Biomes: an ecoregional analysis of land use*.  
421 *Agricultural Systems* **194**, 103270.
- 422 Gerber JF (2011). *Conflicts over industrial tree plantations in the South: Who, how and why?* *Global*  
423 *Environmental Change* **21**, 165–176.
- 424 Harja D, Vincent G, Mulia R, Noordwijk M (2012). *Tree shape plasticity in relation to crown exposure*.  
425 *Trees* **26**, 1275–1285.
- 426 Hérault B, Ahoba A, Amani B, Benedet F, Coulibaly B, Doua-Bi Y, Ehouman E, Koffi T, Koffi-  
427 Konan J, Konaté I, Kouassi A, Louppe D, N'Guessan A, Ouattara N, Tieoulé F, Wourro F, Zo-Bi  
428 I (2021). *Plantations forestières innovantes, promouvoir les plantations en mélange pour sécuriser*  
429 *la production de bois d'œuvre et le maintien des services écosystémiques, Rapport technique final*  
430 *du projet Forestinnov*. Tech. rep. FIRCA-FCIAD, p. XX.

- 431 Hérault B, Bachelot B, Poorter L, Rossi V, Bongers F, Chave J, Paine CT, Wagner F, Baraloto C  
432 (2011). *Functional traits shape ontogenetic growth trajectories of rain forest tree species*. *Journal*  
433 *of ecology* **99**, 1431–1440.
- 434 Hérault B, N'guessan AK, Ahoba A, Bénédet F, Coulibaly B, Doua-Bi Y, Koffi T, Koffi-Konan JC,  
435 Konaté I, Tiéoulé F, et al. (2020). *The long-term performance of 35 tree species of sudanian West*  
436 *Africa in pure and mixed plantings*. *Forest ecology and management* **468**, 118171.
- 437 Holl KD, Brancalion PH (2020). *Tree planting is not a simple solution*. *Science* **368**, 580–581.
- 438 Huang S, Titus SJ, Wiens DP (1992). *Comparison of nonlinear height–diameter functions for major*  
439 *Alberta tree species*. *Canadian Journal of Forest Research* **22**, 1297–1304.
- 440 IDH (2021). *The Cocoa & Forest Initiative: Annual Report*. 35p, Abidjan, Côte d'Ivoire.
- 441 Johnson DM, McCulloh KA, Reinhardt K (2011). *The earliest stages of tree growth: development,*  
442 *physiology and impacts of microclimate. Size-and age-related changes in tree structure and func-*  
443 *tion*, 65–87.
- 444 King D (1981). *Tree dimensions: maximizing the rate of height growth in dense stands*. *Oecologia* **51**,  
445 351–356.
- 446 Kinyili B, Ndunda E, Kitur E (2020). *Influence of Agroforestry on Rural Income and Livelihood of*  
447 *Smallholder Farmers in the Semi-Arid Region of Sub Saharan Africa*. *Journal of tropical forestry*  
448 *and environment* **10**.
- 449 Köhl M, Magnussen S, Marchetti M, et al. (2006). *Sampling methods, remote sensing and GIS mul-*  
450 *tiresource forest inventory*. Vol. 2. Springer.
- 451 Koike F (1989). *Foliage-crown development and interaction in Quercus gilva and Q. acuta*. *The Jour-*  
452 *nal of Ecology*, 92–111.
- 453 Kouassi AK, Zo-Bi IC, Hérault B, Konan IK, Dago MR, Lasbats B, Schmitt S, N'Guessan AE, Aussenac  
454 R (2024). *Data and Supplementary Information: timber resource dynamics in West African cocoa*  
455 *agroforestry systems (Version 0.1.1)*. <https://doi.org/10.5281/zenodo.12581454>.
- 456 Kouassi AK, Zo-Bi IC, Aussenac R, Kouamé IK, Dago MR, N'guessan AE, Jagoret P, Hérault B  
457 (2023a). *The great mistake of plantation programs in cocoa agroforests—Let's bet on natural re-*  
458 *generation to sustainably provide timber wood*. *Trees, Forests and People* **12**, 100386.
- 459 Kouassi JL, Diby L, Konan D, Kouassi A, Bene Y, Kouamé C (2023b). *Drivers of cocoa agroforestry*  
460 *adoption by smallholder farmers around the Taï National Park in southwestern Côte d'Ivoire*. *Sci-*  
461 *entific Reports* **13**, 14309.
- 462 Kunstler G, Falster D, Coomes DA, Hui F, Kooyman RM, Laughlin DC, Poorter L, Vanderwel M,  
463 Vieilledent G, Wright SJ, et al. (2016). *Plant functional traits have globally consistent effects on*  
464 *competition*. *Nature* **529**, 204–207.
- 465 Lewis SL, Wheeler CE, Mitchard ET, Koch A (2019). *Restoring natural forests is the best way to*  
466 *remove atmospheric carbon*.
- 467 Louppe D, Ouattara N (2013). *Etude sur l'exploitation forestière et les contraintes d'une gestion*  
468 *durable des forêts dans le domaine rural en Côte d'Ivoire*.
- 469 Magnussen S, Reed D (2004). *Modeling for estimation and monitoring. Knowledge reference for*  
470 *national forest assessments* **111**.
- 471 Mäkelä A (1997). *A carbon balance model of growth and self-pruning in trees based on structural*  
472 *relationships*. *Forest Science* **43**, 7–24.
- 473 Molto Q, Hérault B, Boreux JJ, Daullet M, Rousteau A, Rossi V (2014). *Predicting tree heights for*  
474 *biomass estimates in tropical forests—a test from French Guiana*. *Biogeosciences* **11**, 3121–3130.

- 475 Notaro M, Collado C, Depas JK, Dumovil D, Denis AJ, Deheuvels O, Tixier P, Gary C (2021). *The*  
476 *spatial distribution and height of associated crops influence cocoa tree productivity in complex*  
477 *agroforestry systems*. *Agronomy for Sustainable Development* **41**, 60.
- 478 Pillet M, Joetzier E, Belmin C, Chave J, Ciaï P, Dourdain A, Evans M, Hérault B, Luysaert S, Poul-  
479 *ter B* (2018). *Disentangling competitive vs. climatic drivers of tropical forest mortality*. *Journal of*  
480 *Ecology* **106**, 1165–1179.
- 481 Plieninger T, Muñoz-Rojas J, Buck LE, Scherr SJ (2020). *Agroforestry for sustainable landscape*  
482 *management*. *Sustainability Science* **15**, 1255–1266.
- 483 Preece ND, Oosterzee P, Lawes MJ (2023). *Reforestation success can be enhanced by improving*  
484 *tree planting methods*. *Journal of environmental management* **336**, 117645.
- 485 Prévosto B, Balandier P (2007). *Influence of nurse birch and Scots pine seedlings on early aerial*  
486 *development of European beech seedlings in an open-field plantation of Central France*. *Forestry*  
487 **80**, 253–264.
- 488 Ramírez-Argueta O, Orozco-Aguilar L, Dubón AD, Díaz FJ, Sánchez J, Casanoves F (2022). *Tim-*  
489 *ber growth, cacao yields, and financial revenues in a long-term experiment of cacao agroforestry*  
490 *systems in northern Honduras*. *Frontiers in Sustainable Food Systems* **6**, 434.
- 491 Réjou-Méchain M, Tanguy A, Piponiot C, Chave J, Hérault B (2017). *biomass: an r package for*  
492 *estimating above-ground biomass and its uncertainty in tropical forests*. *Methods in Ecology and*  
493 *Evolution* **8**, 1163–1167.
- 494 Rozendaal DM, Phillips OL, Lewis SL, Affum-Baffoe K, Alvarez-Davila E, Andrade A, Aragão  
495 LE, Araujo-Murakami A, Baker TR, Bánki O, et al. (2020). *Competition influences tree growth,*  
496 *but not mortality, across environmental gradients in Amazonia and tropical Africa*. *Ecology* **101**,  
497 e03052.
- 498 Ruf F, Schroth G, Doffangui K (2015). *Climate change, cocoa migrations and deforestation in West*  
499 *Africa: What does the past tell us about the future?* *Sustainability Science* **10**, 101–111.
- 500 Sanial E (2019). *A la recherche de l'ombre, géographie des systèmes agroforestiers émergents en ca-*  
501 *caoculture ivoirienne post-forestière*. PhD thesis. Lyon.
- 502 Sanial E, Ruf F, Louppe D, Mietton M, Hérault B (2023). *Local farmers shape ecosystem service*  
503 *provisioning in West African cocoa agroforests*. *Agroforestry Systems* **97**, 401–414.
- 504 Schmitt S, Hérault B, Derroire G (2023). *High intraspecific growth variability despite strong evolu-*  
505 *tionary legacy in an Amazonian forest*. *Ecology letters*.
- 506 Sonwa DJ, Weise SF, Schroth G, Janssens MJ, Shapiro HY (2014). *Plant diversity management in*  
507 *cocoa agroforestry systems in West and Central Africa—effects of markets and household needs*.  
508 *Agroforestry systems* **88**, 1021–1034.
- 509 Sorrensen-Cothorn KA, Ford ED, Sprugel DG (1993). *A model of competition incorporating plastic-*  
510 *ity through modular foliage and crown development*. *Ecological Monographs* **63**, 277–304.
- 511 Stan Development Team C et al. (2018). *RStan: the R interface to Stan*. R package version 2.
- 512 Team RC et al. (2021). *R: A language and environment for statistical computing*. Vienna, Austria: R  
513 *Foundation for Statistical Computing*; 2020.
- 514 Traoré S, Zo-Bi IC, Piponiot C, Aussenac R, Hérault B (2024). *Fragmentation is the main driver*  
515 *of residual forest aboveground biomass in West African low forest-high deforestation landscapes*.  
516 *Trees, Forests and People* **15**, 100477.
- 517 Tsanga R, Cerutti PO, Essiane E (2020). *Demandes en bois et produits dérivés dans les marchés*  
518 *publics en Côte d'Ivoire*.

- 519 Tschora H, Cherubini F (2020). *Co-benefits and trade-offs of agroforestry for climate change mitiga-*  
520 *tion and other sustainability goals in West Africa. Global Ecology and Conservation* **22**, e00919.
- 521 Uzu J, Bettinger P, Siry J, Mei B (2022). *Timber business in West Africa: a review and outlook. Inter-*  
522 *national Forestry Review* **24**, 240–256.
- 523 Vallejos J, Moya R, Serrano R (2015). *Effects of thinning on diameter, heartwood, density and drying*  
524 *defects of Gmelina arborea. Maderas. Ciencia y tecnología* **17**, 365–372.
- 525 Verdone M, Seidl A (2017). *Time, space, place, and the Bonn Challenge global forest restoration*  
526 *target. Restoration ecology* **25**, 903–911.
- 527 Waring RH, Pitman GB (1985). *Modifying lodgepole pine stands to change susceptibility to mountain*  
528 *pine beetle attack. Ecology* **66**, 889–897.
- 529 Werden LK, Alvarado J P, Zarges S, Calderón M E, Schilling EM, Gutiérrez L M, Powers JS (2018).  
530 *Using soil amendments and plant functional traits to select native tropical dry forest species for*  
531 *the restoration of degraded Vertisols. Journal of Applied Ecology* **55**, 1019–1028.
- 532 Wunder J, Brzeziecki B, Żybura H, Reineking B, Bigler C, Bugmann H (2008). *Growth–mortality re-*  
533 *lationships as indicators of life-history strategies: a comparison of nine tree species in unmanaged*  
534 *European forests. Oikos* **117**, 815–828.
- 535 Zobi C, Chessel D, Kadio A, Pascal J (2009). *Détermination des paramètres influents de la dy-*  
536 *namique des forêts naturelles ivoiriennes. Agronomie Africaine* **21**.