



**HAL**  
open science

## Life after fire - Long-term responses of 20 timber species in semi-deciduous forests of West Africa

Aka G.M. Elogne, Camille Piponiot, Irie Zo-Bi, Bienvenu Amani, Victor van  
der Meersch, Bruno Hérault

### ► To cite this version:

Aka G.M. Elogne, Camille Piponiot, Irie Zo-Bi, Bienvenu Amani, Victor van der Meersch, et al.. Life after fire - Long-term responses of 20 timber species in semi-deciduous forests of West Africa. *Forest Ecology and Management*, 2023, 538, pp.120977. 10.1016/j.foreco.2023.120977 . hal-04959548

**HAL Id: hal-04959548**

**<https://cnrs.hal.science/hal-04959548v1>**

Submitted on 21 Feb 2025

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Life after Fire - Long-term responses of 20 timber species in  
2 semi-deciduous forests of West Africa

3 Aka G.M. Elogne<sup>1</sup>, Camille Piponiot<sup>2,3</sup>, Irie C. Zo-Bi<sup>1</sup>, Bienvenu H. K. Amani<sup>4,5</sup>, Victor  
4 Van der Meersch<sup>6</sup>, and Bruno Hérault<sup>2,3,\*</sup>

5 <sup>1</sup>Institut National Polytechnique Félix Houphouët-Boigny (INP-HB), Yamoussoukro, Côte  
6 d'Ivoire

7 <sup>2</sup>CIRAD, UPR Forêts et Sociétés, F-34398 Montpellier, France

8 <sup>3</sup>Forêts et Sociétés, Univ Montpellier, CIRAD, Montpellier, France

9 <sup>4</sup>Université Félix Houphouët-Boigny, UFR Biosciences, Laboratoire de Botanique, Abidjan,  
10 Côte d'Ivoire

11 <sup>5</sup>Université Jean Lorougnon Guédé, Unité de Formation et de Recherche en Agroforesterie,  
12 BP 150, Daloa, Côte d'Ivoire

13 <sup>6</sup>CEFE, Université de Montpellier, CNRS, EPHE, IRD, Montpellier, France

14 \* author for correspondence [bruno.herault@cirad.fr](mailto:bruno.herault@cirad.fr)

15 March 22, 2023

16 **Abstract**

17 Understanding the response of commercial timber species to fire is fundamental to designing sustainable forest management  
18 strategies in West Africa. In this area of high deforestation for agriculture, semi-deciduous tropical forests have been reduced  
19 to a trickle in 50 years and are now subject not only to logging but also to increasingly frequent fires. This paper aims to study  
20 the long-term (37 years) demographic and growth responses of 20 timber species after a spatially heterogeneous fire in a West  
21 African semi-deciduous forest. We (i) inventoried, in 2020, 100 hectares of plots already established before the 1983 fire, (ii)  
22 built demographic and growth models, in a Bayesian framework, to estimate the vulnerability to fire of each species and (iii)  
23 linked this vulnerability to functional traits: wood density (WD) and bark thickness (BT). Our results show that most species  
24 have lower current abundances but higher growths in burnt areas than in fire-preserved areas. We identified three categories of  
25 vulnerability to fire: 1 non-vulnerable species, 16 species with vulnerable demography, and 3 highly vulnerable species. Species  
26 with high wood density or thin bark show higher demographic vulnerability to fire. Our results show that fire management  
27 is a top priority in West African semi-deciduous forests to maintain long-term populations of timber species and ultimately  
28 the forest industry. The differences in vulnerability observed, and the strong predictive power of the functional traits studied,  
29 should make it possible to (i) better define harvesting rates and adapt them to fire risk and (ii) better select commercial species  
30 to be promoted for reforestation or natural (assisted) regeneration.

31 **Keywords:** West Africa, fire, timberwood, wood density, bark thickness, semi-deciduous forest, vulnerability, bayesian modeling

## 32 Introduction

33 Tropical forests have a rich flora characterized by many commercial timber species with diverse and desirable  
34 timber properties. The economic value of these woods, in conjunction with an ever-increasing demand, has  
35 sometimes led foresters to overexploit this resource (Grogan et al., 2010) to the point of degrading the forests  
36 that harbor them (Hirschmugl et al., 2014). It is therefore necessary to consider promoting good management  
37 practices to ensure the sustainability of the economic resource, and that of the timber industry (Siry et al.,  
38 2005). Moreover, sustainable management of tropical timber resources must now be articulated with other  
39 challenges that forest managers face in the context of global change: extreme weather events, recurrent  
40 fires, biological invasions to name but a few (Barlow et al., 2016). In particular, with climate change and  
41 increasing forest degradation, the frequency and intensity of forest fires has increased dramatically in recent  
42 decades (Roux et al., 2022). Fire leads to rapid degradation of forest condition, with a positive feedback  
43 loop, related to the presence of large amounts of dead wood after fire, leading to more intense fires (Silvestrini  
44 et al., 2011), reduced potential for recovery of mature individual trees (Kinnaird and O'Brien, 1998) and  
45 irreparable loss of some valuable timber species (Slik et al., 2002).

46 In West Africa, the prevalence of forest fires is well documented (Dwomoh et al., 2019; Dwomoh and Wim-  
47 berly, 2017; Swaine, 1992). Some estimates report a 90% degradation of natural forests, mainly due to the  
48 populations who practice, for the most part, slash-and-burn agriculture (Brandt et al., 2017). In particular,  
49 in semi-deciduous forests, intermediate forests between the evergreen forests bordering the Gulf of Guinea in  
50 the South and the dry forests bordering the Sahelian belt in the North, the seasonal loss of the leaves seems  
51 to be a natural factor capable of increasing their flammability in the dry season (Borchert et al., 2002). In  
52 Côte d'Ivoire, these forests constitute a large proportion of the forest areas (Aubr'eville, 1949) and an im-  
53 portant timber resource, with a density of commercial timber trees of about 10 trees per hectare (Pirard et  
54 al., 2021). The prevalence of fire in West African semi-deciduous forests reduces the overall timber resource,  
55 which is already greatly reduced by the high level of deforestation (Barnes, 1990). Fire is therefore a major  
56 concern for forest managers in this semi-deciduous zone. Paradoxically, very little information is available  
57 on the response to fire of timber species in West African semi-deciduous forests.

58 Tropical forest dynamic depends mainly on (i) edaphic and climatic factors (Quesda et al., 2012) and (ii)  
59 human and natural disturbance (Herault and Piponiot, 2018). In particular, fire has a strong demographic  
60 impact on forest species with a change in (i) not only the abundance of populations but also (ii) the per-  
61 formance of surviving individuals (Murphy and Bowman, 2012). (i) Fire can destroy or damage all vital  
62 organs, from roots to foliage, resulting in a rapid increase in mortality (Chazdon, 2003), which can range  
63 from 25% to 80% of individuals per species within a semi-deciduous forest in West Africa (Bertault, 1992).  
64 (ii) Surviving trees may show reduced growth because of fire-induced foliage loss and injuries to vascular

65 tissues (Battipaglia, 2014). A decrease in reproductive functions in trees after fire events may also be ob-  
66 served (Hoffmann, 1998). On the other hand, fire can also have strong indirect impacts on the ecosystem  
67 composition and functioning, by creating large open spaces in forest canopy. Remaining trees may benefit  
68 from reduced competition for water, nutrients, and light. However, light-demanding pioneer species could be  
69 greatly favoured during post-fire generation, leading to an increase in competition that may be detrimental  
70 to the growth of surviving trees (Flores et al., 2011).

71 Survival, regeneration and growth of surviving trees after fire vary greatly between species. This variability  
72 in response is a function of, among other things, quantifiable characteristics, called functional traits, which  
73 can modulate the effect of fire on the demographic response of species. In particular, wood density and  
74 bark thickness have previously been identified as important functional traits in explaining differential tree  
75 mortality after fire (Brando et al., 2012). Bark thickness reduces heat transfer, acting as a shield against  
76 overheating (Pausas, 2015) and thus reducing tissue damage (Staver et al., 2019; Midgley et al., 2011).  
77 Other bark traits such as bark density and moisture content can also explain some variation in heat transfer,  
78 and thus affect post-fire tree mortality (Bauer et al., 2010). In contrast, the role of wood density on tree  
79 survival after fire is less well understood (Osazuwa-Peters et al., 2017), but has been hypothesized to be  
80 related to the rapid containment of fire-induced necrosis in species with higher wood density (Romero and  
81 Bolker, 2008). In addition, wood density plays an important role in many plant functions, *i.e.* investment  
82 in woody tissues, metabolic rates, mechanical support, water transport, etc... (Chave et al., 2009), and thus  
83 could be an indicator of plant life strategies that have different responses to fire damage (Paine et al., 2010).  
84 Investigating, or confirming, the links between functional traits and the responses of timber tree species to  
85 fire is therefore a major research priority for the semi-deciduous forests of West Africa. Doing so, functional  
86 traits may constitute proxies that make it possible to define which species to promote, or not, without having  
87 to wait decades to understand the long-term response of the dozens of commercial timber species of interest  
88 to bushfire.

89 In this work, we analysed the (i) demographic and (ii) growth responses after fire for 20 commercial timber  
90 species from the T'en'é experimental site, a semi-deciduous forest in Côte d'Ivoire. The interest of this site lies  
91 in the fact that, after having undergone silvicultural operations, it was traversed by a high intensity fire in  
92 1983 (3 days on site). Data were collected in 2020 on 9081 individual trees whose species contained at least  
93 8 individuals surviving the fire. Based on demographic and growth models, we estimated the vulnerability  
94 of each of these 20 commercial timber species. We then related this vulnerability to two functional traits  
95 often used as proxies in the literature, namely wood density and bark thickness. Specifically, we asked the  
96 following questions:

- 97 • What is the long-term demographic response of the 20 timber species studied?

- 98 • What is the long-term growth response of individuals that survived fire?  
99 • Are wood density and bark thickness good indicators of the vulnerability of timber species to fire in  
100 the semi-deciduous forests of West Africa?

101 In conclusion, we will draw the consequences of our results for the management of semi-deciduous tropical  
102 forests in West Africa, in the context of a general increase in the frequency of bush fires.

## 103 **Materials and Methods**

### 104 **Study Site**

105 The study was conducted in the state forest of T'en'é (6 ° 31'14 "N, 5 ° 28'44"W) located in Côte d'Ivoire.  
106 T'en'é is a semi-deciduous tropical forest of the Sudano-Guinean domain (Aubr'eville, 1949). The climate is  
107 sub-equatorial, characterised by low amplitudes of **monthly averaged temperatures** ranging from 25°C to  
108 30°C and rainfall varies considerably from month to month (Appendix). This zone has two dry seasons  
109 (December - February and July - August) and two wet seasons (March - June and September - November).  
110 The average annual temperature is 26.6°C. The relief of the T'en'é is made up of granitic plateaus at an  
111 altitude of between 260 and 320 m. The soils are ferralitic (more or less desaturated) or hydromorphic with  
112 pseudogley species (Bertault, 1992).

113 The T'en'é experiment was set up in 1978, covering 400 ha of natural forest divided into 25 plots of 16 ha  
114 each (4 ha of inventoried area and 12 hectares of buffer zone around, silvicultural treatments applied over the  
115 entire plot, *i.e.* inventoried + buffer areas). The first objective of the experiment was to study the effects of  
116 forestry on stand dynamics. To do this, among the 25 plots, 10 were logged, 5 thinned and 10 were conserved  
117 as control plots (Table 1). The felling of trees was carried out on the basis of the diameter threshold values  
118 authorized in Côte d'Ivoire. These differ from one species to another. And, the tree felling process within a  
119 plot was stopped once the desired logging intensity was reached. Then, all the logged trees were removed in  
120 a way that minimized the damage caused to the forest. **The thinning was carried out by a chemical method  
121 using an arboricide. Once the arboricide was sprayed into notches made in the trees to be killed, they were  
122 left in the plots until they died and decayed by gradually breaking down.**

123  
124 In the long dry season of 1983 (Appendix), a forest fire burnt the experiment for several days. The burnt  
125 surfaces varied from 12 to 87%, with on average 54% of individual tree mortality (Bertault, 1992). This  
126 variability depends on the forestry treatment. On average, the fire was twice more **extensive** in thinned plots  
127 (63%) and logged plots (57%) than in control plots (29%) (Table 1). In control plots, the fire was shorter  
128 (ground layer fire) while the fire lasted several days in logged or thinned plots (**high flame fire**). This is  
129 related to the presence of more dead wood from devitalization (thinned plots), and of logging debris (logged

plots). Several other small fires occurred in the area over the next 37 years. During all these years, the vigilance of the forestry agents has prevented these fires from reaching the T'en'e plots, except for the one in 2016, 33 years later. This one had slight sparse damage in the undergrowth and was of incomparably low intensity in comparison to that of 1983.

## Data collection

The data were collected in 1978, *i.e.* before the logging interventions and in 2020, 37 years later. All timber trees with diameter at breast height (DBH)  $\geq 10$  cm were mapped and their diameters were measured with a forestry tape. In our study, we focused on the 20 commercial timber species that had at least 8 individuals.ha<sup>-1</sup> three years after the major fire of 1983 (Table 2).

## Response variables

- *N*: the number of trees of a given commercial timber species per hectare (Individuals. ha<sup>-1</sup>) in 2020.
- *AGR*: the absolute diameter growth rate (mm.year<sup>-1</sup>) at breast height of the 662 trees surviving the 1983 fire and that could be retrieved from the plots in 2020 (Table 2).

## Covariates

- *Fire*: The percentage of the plot surface that was burnt in 1983. This percentage was computed from the 1983 field maps of burnt areas (Bertault, 1992).
- *Disturb*: An estimate of the disturbance induced by the pre-fire silvicultural treatment estimated as the percentage of removed basal area either by logging or by thinning (H'erault and Piponiot, 2018).
- *InitDens*: The 1978 (pre-logging, pre-thinning and pre-fire) initial density of the studied commercial timber species (Bertault, 1992). The purpose of this variable is to control for differences in initial densities of the number of individuals per species between plots due to differences in the local environment (soil, topography) and/or to an aggregated distribution due to limited dispersion.

All covariates were centered and scaled before being included in the data analyses.

## Functional Traits

- **Wood density** (WD) was computed with the BIOMASS package (R'ejou-M'echain et al., 2017). Species-level means were assigned using the Global Wood Density database as retrieved in the package.
- **Bark thickness** (BT) was measured from bark samples taken in the field. To this end, we first randomly selected between 3 and 5 adult trees per species (DBH > 30 cm). Then, we collected at breast height and measured the bark thickness from 3 pieces (4\*4cm square which does not depend on cracks or splits) per tree with a caliper. Finally, we calculated the average of measures per species. All

162 native datas are available on request in the TRY database (DatasetID 546, <https://www.try-db.org>).

## 163 **Data analysis**

### 164 **Demographic response**

165 In order to predict the long-term demographic response, we designed a model in which the density of trees  
166  $N$  of a timber species  $s$  in a plot  $p$  follows a Poisson probability distribution:

$$167 N_{s,p} \sim P(\lambda_{s,p})$$

168 where  $N_{s,p}$  is the observed tree density (tree.ha<sup>-1</sup>) in 2020 and  $\lambda_{s,p}$ , the parameter of the Poisson distribution  
169 for species  $s$  in plot  $p$ . Because  $\lambda_{s,p}$  are defined on  $\mathbf{R}^+$ , we introduced the studied covariates in the model  
170 through an exponential function:

$$171 \lambda_{s,p} = \exp(\beta_{o,s} + \beta_{fir,s} \cdot Fire_p + \beta_{trt,s} \cdot Disturb_p + \beta_{id,s} \cdot InitDens_{s,p})$$

172 with

$$173 \beta_{o,s} \sim \log N(\log(\beta_o), \sigma_{\beta_o})$$

$$174 \beta_{fir,s} \sim N(\beta_{fir}, \sigma_{\beta_{fir}})$$

$$175 \beta_{trt,s} \sim N(\beta_{trt}, \sigma_{\beta_{trt}})$$

$$176 \beta_{id,s} \sim N(\beta_{id}, \sigma_{\beta_{id}})$$

177 where  $\beta_{o,s}$  are species-specific parameters denoting demographic performance (*i.e* the value that controls  
178 the Poisson distribution when covariates are equal to zero) that follow a lognormal distribution given that  
179 they are defined on  $\mathbf{R}^+$ .  $\beta_{fir,s}$  and  $\beta_{trt,s}$  are respectively the species responses to the fire and disturbance  
180 intensities and  $\beta_{id,s}$  the species-specific tree density before the fire.

### 181 **Growth response**

182 In order to predict the absolute growth rate (AGR), we parameterized an existing ontogenic growth  
183 model (Herault et al., 2011). We inferred AGR within a lognormal law because AGR is always positive:

$$184 AGR_{i,s,p} \sim \log N \left( \log \left( \theta_{o,s} + \theta_{fir,s} \cdot Fire_p + \theta_{trt,s} \cdot Disturb_p \right) \cdot \exp \left( - \frac{\log \left( \frac{DBH_i - g_s}{\theta_{dbh} \cdot DBH_s} \right)}{\theta_{wd} \cdot WD_s} \right) \cdot \sigma^2 \right)$$

185 with

$$186 \theta_{o,s} \sim \log N(\log(\theta_o), \sigma_{\theta_o})$$

$$187 \theta_{fir,s} \sim N(\theta_{fir}, \sigma_{\theta_{fir}})$$

$$188 \theta_{trt,s} \sim N(\theta_{trt}, \sigma_{\theta_{trt}})$$



189 where  $AGR_{i,s,p}$  was the annual absolute growth rate of an individual tree  $i$  from a species  $s$  in plot  $p$  and  $\theta_{o,s}$   
 190 are the species-specific maximum growth values (*i.e.* when covariates are equal to zero) that follow a log-  
 191 normal distribution given that they are defined on  $\mathbf{R}^+$ .  $\theta_{fir,s}$  and  $\theta_{trt,s}$  are the species-specific parameters  
 192 associated, respectively, with the effects of the fire and the disturbance intensities.  $\theta_{dbh}$  and  $\theta_{wd}$  are the model  
 193 parameters that multiply, respectively, the 95<sup>th</sup> percentile of the species DBH distribution  $DBH^{95}$  and the  
 194 wood density  $WD$  in order to predict, respectively, the diameter at maximum growth and the kurtosis of  
 195 the growth model (H´erault et al., 2011).

## 196 **Assessing Vulnerability**

197 We defined the vulnerability of a given species as the opposite of their responses to fire ( $-\beta_{fir,s}$  or  $-\theta_{fir,s}$ ).  
 198 Thus, if the response is positive, then the species is non-vulnerable, and if the response is negative, then the  
 199 species is vulnerable. We classified the timber species according to their long-term demographic and growth  
 200 responses to fire :

- 201 • Non-vulnerable :  $\beta_{fir,s}$  and  $\theta_{fir,s} \geq 0$
- 202 • Vulnerable Demography :  $\beta_{fir,s} < 0$  and  $\theta_{fir,s} \geq 0$
- 203 • Vulnerable Growth :  $\beta_{fir,s} \geq 0$  and  $\theta_{fir,s} < 0$
- 204 • Highly-vulnerable :  $\beta_{fir,s}$  and  $\theta_{fir,s} < 0$

## 205 **Using wood density and bark thickness as vulnerability proxy**

206 To assess whether species vulnerability can be predicted from the functional traits of wood density and bark  
 207 thickness, we assumed a linear relationship between vulnerability and trait values. The predictive quality  
 208 has been estimated using the coefficient of determination and the value of the slope of the linear regression.

## 209 **Results**

### 210 **Demographic response**

211 Fire and silvicultural treatments affect the demography of most species (Table 3). The effects of fire on  
 212 demography show 19 species with negative responses ( $\beta_{fir,s} < 0$ ) with most of them significantly affected.  
 213 There is only one positive response, Eho *Ricinodendron heudelotii*, but the value is very close to zero. In  
 214 terms of response to disturbance, there are 14 species with negative response ( $\beta_{trt,s} < 0$ ) and 6 species with  
 215 positive response ( $\beta_{trt,s} > 0$ ). All in all, the demographic responses to fire are much more pronounced (14  
 216 species with  $|\beta_{fir,s}| > 0.1$ ) than the responses to the disturbance (1 species only with  $|\beta_{trt,s}| > 0.1$ ).

217

## 218 **Growth response**

219 Out of 20, 17 species have positive responses to fire ( $\theta_{fir,s} > 0$ ) while 3 only showed negative responses  
220 ( $\theta_{fir,s} < 0$ ). However, these three species (Kotibe *Nesogordonia papavifera*, Asan *Celtis zenkeri*, Sapelli *En-*  
221 *tandrophragma cylindricum*) have extremely negative parameter values ( $\theta_{fir,s} < -0.25$ ), *i.e.* their growths  
222 are highly affected by fire. In terms of silvicultural treatment, there were 6 species with negative responses  
223 ( $\theta_{trt,s} < 0$ ) and 14 species with a positive responses ( $\theta_{trt,s} > 0$ ). All in all, the growth responses to fire  
224 are more pronounced (16 species with  $|\theta_{fir,s}| > 0.1$ ) than the responses to the disturbance (8 species only  
225 with  $|\theta_{trt,s}| > 0.1$ ).

226

## 227 **Vulnerability assessment**

228 The 20 investigated into 3 categories of vulnerability (Figure 1):

- 229 • 1 non-vulnerable species
- 230 • 16 species that have a vulnerable demography
- 231 • 3 species that are highly-vulnerable

232 The only non-vulnerable species corresponds to a demographic response to fire very close to zero. Among  
233 the highly-vulnerable species, Asan (*Celtis zenkeri*) has the highest demographic vulnerability while Kotibe  
234 (*Nesogordonia papavifera*) has the highest growth vulnerability. Remarkably enough, no species falls into  
235 the “Vulnerable Growth” group.

## 236 **Functional traits and vulnerability to fire**

237 In our study, wood density and bark thickness are relatively well linked to demography and growth vulner-  
238 ability (figure 2):

- 239 • A positive link between wood density and species vulnerability to fire
- 240 • A negative link between bark thickness and species vulnerability to fire

241 More specifically, we found that wood density and bark thickness were significantly associated with demo-  
242 graphic vulnerability (*i.e.* the change in species abundances after fire) but not significantly with species’  
243 growth vulnerability to fire (Figure 2). In other words, post-fire species abundance increased in species with  
244 lower wood density and thicker bark.

## 245 **Discussion**

246 Overall, our results show that fire causes more damage to long-term demography than to the growth of  
247 the commercial timber species studied (Table 3). Surprisingly, it appears that the presence of fire boosted  
248 the growth of surviving individuals. This means that the ecological conditions, in the broad biotic and  
249 abiotic sense, of the site were certainly modified sufficiently to prevent the recruitment of the timber species  
250 impacted by fire (Cochrane, 2003). These changes may involve soils (Stoof et al., 2010), fauna (Haslem et  
251 al., 2010) or microclimate (Didham and Lawton, 1999). Our classification of species into three vulnerability  
252 groups showed that, in the end, only one species out of 20 was not vulnerable and that the overwhelming  
253 majority of species are demographically vulnerable. This demographic vulnerability (i.e., change in number  
254 of trees after fire) was significantly correlated with both wood density and bark thickness. This demonstrates  
255 that these two functional traits can be useful proxies for predicting how timber species will respond to fire.  
256 We focused in this study on the fire long term impacts, but species vulnerability to drought and insect pests  
257 could also explain the observed differences in the long-term responses of trees. We were not able to investigate  
258 these effects, since annual tree growth surveys and insect damage monitoring are lacking. However, as the  
259 1983 forest fire was unusually extensive and devastating (more than 16.000 hectares burnt in the department  
260 where the T'en'e forest is located, Bertault 1992), we might expect that it was the main factor impacting  
261 demography and growth in the study period.

### 262 **A high demographic vulnerability of timber species to fire**

263 The reasons for the overall high demographic vulnerability of species to fire are multiple. However, our field  
264 observations and results suggest that these negative responses are related to two key steps in the demographic  
265 dynamics of forest stands: (i) death of surviving trees over time, and (ii) limited regeneration of the targeted  
266 timber species.

267 First, fire-induced mortality effectively reduced species abundance after the fire. Three years after the fire and  
268 on the same system, immediate mortality ranged from 25% to 80% depending on the species (Bertault, 1992).  
269 Fire can also have long-lasting effects, causing long-term mortality that would not be observed in the first few  
270 years after the fire. Indeed, the reduction in species abundance may preferentially expose remaining isolated  
271 trees because these trees are the last sources of food for insects and other primary consumers (Engstrom,  
272 2010). Furthermore, when fire weakens the defense and nutritional systems of trees, they become highly  
273 vulnerable to these same insects and other pathogens (van Lierop et al., 2015).

274 Second, with respect to limiting species regeneration, it should first be noted that the immediate ability of  
275 species to regenerate (regardless of resprouting) is first related to the quality of the seed bank (H'erault and  
276 Hiernaux, 2004), which has possibly been greatly affected by fire. If the seed bank is failing, then this regen-

277 eration depends on the number of seeds produced by surviving trees, their dispersal and germination (Keeley  
278 and Fotheringham, 2000). In the semi-deciduous zone of West Africa, it has already been shown that, after  
279 agriculture, species regeneration is related to the number of remnant trees (Doua-Bi et al., 2021). How-  
280 ever, this important role of remnant trees in post-cultivation successions (N'Guessan et al., 2019; Amani et  
281 al., 2021; Amani et al., 2022) may be hampered in our situation by the very specific effects of fire on the  
282 ecosystem. Indeed, it is quite possible that fruiting and flowering of tropical trees in the vicinity of burned  
283 areas may be reduced due to the stress experienced by surviving trees (Kinnaid and O'Brien, 1998). On  
284 the other hand, one of the barriers to regeneration could be the high sunlight entry into the understory that  
285 favored the rapid recolonization of burned areas by Marantaceae and Zingiberaceae plants which prevent the  
286 regeneration of forest species because of their important root mat (Swaine, 1992).

287 Finally, the presence of *Ricinodendron heudelotii* (Eho) among the non-vulnerable species shows, neverthe-  
288 less, that post-fire conditions may be appropriate for the demographic development of some timber species.  
289 This could be because Eho is a pioneer species whose seedlings require light to develop (Amissah, 2014).

### 290 **Overall a positive growth response of timber species to fire**

291 Overall, the growth response for 17 of the 20 species studied showed that fire improved their diametric  
292 increase (Fig 1). This gain is of interest as these timber species are of significant economic interest in West  
293 Africa (Lewis, 2005). However, in order to assess the combined effect of demographic losses and individual  
294 growth gain on overall forest production, it would be necessary in future work to combine the two effects in  
295 a forest simulator to make an integrated assessment (Aubry-Kientz et al., 2015; Aubry-Kientz et al., 2019).

296 The effects of fire on tropical tree growth can vary depending on the forest type and the fire regime, i.e. its  
297 seasonality, return frequency and intensity (Staal et al., 2018). The reasons for the overall growth gain in  
298 our case are likely to be twofold:

- 299 • By causing significant mortality on the site, the 1983 fire greatly reduced competition, which may have  
300 increased the long-term growth of surviving trees in the same way that forest thinnings improve growth  
301 through increased availability of light, water and nutrients (Herault et al., 2010).
- 302 • Fire acts as a rapid mineralisation agent that releases nutrients instantly, unlike natural decomposition  
303 processes that can take decades (H' erault et al., 2010). This ultra-fast mineralisation provides surviving  
304 trees with essential nutrients (Grau et al., 2017; Urbina et al., 2021) that are easily absorbed by their  
305 roots (Bauters et al., 2022) and boost their growth for several years (Soong et al., 2020).

306 Fire can also limit the growth of trees of 3 species (see Fig 1), and this has to be related to the autoecology of  
307 these species. Indeed, in forests of the semi-deciduous zone of West Africa, savannah and humid forest species  
308 can coexist. It is common for savannah species, due to their long coevolution with fire, to have a productivity

309 favoured by fire (Werner, 2005) whereas tree growth is reduced by fire for rainforest species (Murphy et al.,  
310 2010). This is typically the case for our 3 vulnerable species (*i.e.* kotibe, asan, sapelli, see Fig 1) which  
311 are at their distribution margins in the semi-deciduous forest and which are otherwise very abundant in the  
312 Central African rainforests. For these species, high-intensity fires could slow growth by keeping the tree in a  
313 shrubby state and contributing to stem deformation as well as by changing the relative allocation of growth  
314 from the stem to other organs such as roots, leaves and the defence system (N'Dri et al., 2012; N'Dri et al.,  
315 2013).

### 316 **Use of wood density and bark thickness as proxies for the long-term species** 317 **responses to fire**

318 Wood density and bark thickness have shown good predictive abilities for long-term demographic responses  
319 but quite poor predictive power for growth response (Fig 2). Although wood density and bark thickness  
320 could be interesting proxies to predict the effect of fire on species abundance, we were only able to explain  
321 a portion of the variance observed in these responses. Furthermore, at the tree level, there is a great deal of  
322 intraspecific variability in these trait values (Siefert et al., 2015), which may also explain the variability in  
323 observed responses.

324 Wood density is commonly used as a key functional trait that is related to many metabolic and demographic  
325 processes, including tree growth (H'erault et al., 2011; Mirabel et al., 2020; Mirabel et al., 2021), mortality  
326 (Aubry-Kientz et al., 2013), metabolic maintenance (Larjavaara and Muller-Landau, 2010) and resistance  
327 to disturbances such as drought and fire (Brando et al., 2012). In this study, wood density had no significant  
328 effect on species growth vulnerability to fire, but species with higher wood density had smaller increases in  
329 abundance after fire. This might seem to contradict previous results showing that species with higher wood  
330 density generally have lower mortality rates after fire (Brando et al., 2012). However, changes in post-fire  
331 species abundance are the result not only of tree survival in the fire, but also of recruitment of new individuals.  
332 Higher post-fire abundances of low-density species could therefore be explained by high recruitment rates  
333 of pioneer species at low wood densities. Unfortunately, our data do not distinguish between the effects of  
334 recruitment and survival on species abundance.

335 Bark is a very important tree functional trait in the West African context as it protects the trees from many  
336 external stresses (Amahowe et al., 2018). In terms of demographic vulnerability, the negative relationship  
337 between bark thickness and vulnerability is very consistent with the behaviour of thick-barked species in  
338 neotropical forests which are less affected by fire than thin-barked species (Brando et al., 2012). Bark  
339 thickness can therefore be used as a proxy of the long-term demographic vulnerability in West Africa. In  
340 addition, it is sometimes argued that bark thickness is also strongly related to tree growth after fire, by  
341 keeping the vascular cambium in optimal conditions for xylem production (Paine et al., 2010). However,

342 when the link between growth and bark thickness is specifically looked at, it is much less clear or even  
343 non-existent (Wagner et al., 2014). Our results therefore tend to confirm that bark protects the tree at the  
344 time of fire occurrence, preventing death, but has little influence on the post-fire growth of these survivors.

### 345 **Implications for sustainable forest management**

346 From our work, most timber species are vulnerable from a demographic point of view (Fig. 2) so that only  
347 very long (more than a century) recovery periods between fires would be able to reconstitute exploitable  
348 stocks. In a context where fire frequency will increase in relation to ongoing climate change and the increasing  
349 population, it is less and less likely that these recovery periods necessary can be respected and this clearly  
350 poses a problem of sustainability of the resource. The problem needs to be addressed respectively at the  
351 level of (i) fire management in forest areas and (ii) conservation of commercial timber species.

- 352 • The fire management strategy must first consist of raising awareness among the population on how to  
353 control their use of fire for agriculture and hunting. For example, it has been shown that the use of  
354 early (not late) fires, lit just before the start of the dry season to clear the undergrowth of combustible  
355 biomass, can limit their impacts on standing tree stands (Dereix and N'Guessan, 1976). Secondly, in  
356 order to reduce the accumulation of flammable material in the forest (Cardil et al., 2020), woody debris  
357 resulting from natural thinning or silvicultural activities should be valorised.
- 358 • As the demography of the studied species is strongly affected by fire, more intensive monitoring of the  
359 condition of the stands after a fire should be carried out and management plans should be adapted  
360 immediately. In particular, the exploitation of the most vulnerable species (Kotibe, Sapelli and Asan)  
361 should be avoided in forests that have suffered fires in recent decades. In critical situations, this  
362 could lead to more interventionist approaches by carrying out reforestation campaigns using native  
363 species (H'erault et al., 2020) or by putting in place means to protect natural regeneration (Doua-Bi  
364 et al., 2021). The species promoted will be chosen according to their susceptibility to resist/ benefit  
365 from fire in order to increase the success rate in the very long term.

366 West Africa is in the midst of a major transformation from a predominantly forested to a predominantly  
367 agricultural landscape in 50 years (Norris et al., 2010). In this context, a major issue is and will be the  
368 management of fires and burnt forest areas. One might have thought, *a priori*, that the long coevolution  
369 between fires and semi-deciduous forests would have made most species resilient. Our results show that this  
370 is not the case; the recovery of commercial timber tree populations after fire takes decades so that dedicated  
371 management measures are urgently needed for semi-deciduous forests. The survival in the wild of many  
372 species typical of this area is clearly at stake.

## Acknowledgements

The R'éVaT'en'é project is funded by the Education and Research Ministry of Côte d'Ivoire, as part of the Debt Reduction-Development Contracts (C2Ds) managed by IRD.

## References

- Amahowe, I.O., Gaoue, O.G., Natta, A.K., Piponiot, C., Zobi, I.C., H'erault, B., 2018. Functional traits partially mediate the effects of chronic anthropogenic disturbance on the growth of a tropical tree. *AoB Plants* 10. <https://doi.org/10.1093/aobpla/ply036>
- Amani, B.H.K., N'Guessan, A.E., der Meersch, V.V., Derroire, G., Piponiot, C., Elogne, A.G.M., Traor'é, K., N'Dja, J.K., H'erault, B., 2022. Lessons from a regional analysis of forest recovery trajectories in West Africa. *Environmental Research Letters* 17, 115005. <https://doi.org/10.1088/1748-9326/ac9b4f>
- Amani, B.H.K., N'Guessan, A.E., Derroire, G., N'dja, J.K., Elogne, A.G.M., Traor'é, K., Zo-Bi, I.C., H'erault, B., 2021. The potential of secondary forests to restore biodiversity of the lost forests in semi-deciduous West Africa. *Biological Conservation* 259, 109154. <https://doi.org/10.1016/j.biocon.2021.109154>
- Amissah, L., 2014. Functional traits, drought performance, and the distribution of tree species in tropical forests of Ghana (PhD thesis). Wageningen University.
- Aubry-Kientz, M., H'erault, B., Ayotte-Trépanier, C., Baraloto, C., Rossi, V., 2013. Toward trait-based mortality models for tropical forests. *PLoS One* 8, e63678. <https://doi.org/10.1371/journal.pone.0063678>
- Aubry-Kientz, M., Rossi, V., Boreux, J.J., H'erault, B., 2015. A joint individual-based model coupling growth and mortality reveals that tree vigor is a key component of tropical forest dynamics.. *Ecol Evol* 5, 2457–65. <https://doi.org/10.1002/ece3.1532>
- Aubry-Kientz, M., Rossi, V., Cornu, G., Wagner, F., H'erault, B., 2019. Temperature rising would slow down tropical forest dynamic in the Guiana Shield. *Sci Rep* 9, 10235. <https://doi.org/10.1038/s41598-019-46597-8>
- Aubr'eville, A., 1949. *Climats : forêts et désertification de l'Afrique tropicale*. Société d'éditions géographiques, maritimes et coloniales. Paris.
- Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R.M., Thomson, J.R., de Barros Ferraz, S.F., Louzada, J., Oliveira, V.H.F., Parry, L., de Castro Solar, R.R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., de Oliveira Jr, R.C., Jr, C.M.S., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A.,

403 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*  
404 535, 144–147. <https://doi.org/10.1038/nature18326>

405 Barnes, R.F.W., 1990. Deforestation trends in tropical Africa. *African Journal of Ecology* 28, 161–173.  
406 <https://doi.org/10.1111/j.1365-2028.1990.tb01150.x>

407 Battipaglia, G., De Micco, V., Fournier, T., Aronne, G., Carcaillet, C., 2014. Isotopic and anatomical  
408 signals for interpreting fire-related responses in *Pinus halepensis*. *Trees* 28, 1095–1104. [https://doi.org/](https://doi.org/10.1007/s00468-014-1020-3)  
409 [10.1007/s00468-014-1020-3](https://doi.org/10.1007/s00468-014-1020-3)

410 Bauer, G., Speck, T., Blömer, J., Bertling, J., Speck, O., 2010. Insulation capability of the bark of trees with  
411 different fire adaptation. *Journal of Materials Science* 45, 5950–5959. [https://doi.org/10.1007/s10853-](https://doi.org/10.1007/s10853-010-4680-4)  
412 [010-4680-4](https://doi.org/10.1007/s10853-010-4680-4)

413 Bauters, M., Grau, O., Doetterl, S., Heineman, K.D., Dalling, J.W., Prada, C.M., Griepentrog, M., Malhi, Y.,  
414 Riutta, T., Scalon, M., Oliveras, I., Inagawa, T., Majalap, N., Beeckman, H., den Bulcke, J.V., Perring, M.P.,  
415 Dourdain, A., H´erault, B., Vermeir, P., Makelele, I.A., Fernández, P.R., Sardans, J., Peñuelas, J., Janssens,  
416 I.A., 2022. Tropical wood stores substantial amounts of nutrients but we have limited understanding why.  
417 *Biotropica* 54, 596–606. <https://doi.org/10.1111/btp.13069>

418 Bertault, J.-G., 1992. Etude de L'effet du Feu en Forêt Semi-décidue de Côte d'Ivoire au sein d'un Dispositif  
419 d'expérimentation sylvicole. Université Nancy 1. <https://agritrop.cirad.fr/333030/1/ID333030.pdf>

420 Borchert, R., Rivera, G., Hagnauer, W., 2002. Modification of Vegetative Phenology in a Tropical Semi-  
421 deciduous Forest by Abnormal Drought and Rain. *Biotropica* 34, 27–39. [https://doi.org/10.1111/j.](https://doi.org/10.1111/j.1744-7429.2002.tb00239.x)  
422 [1744-7429.2002.tb00239.x](https://doi.org/10.1111/j.1744-7429.2002.tb00239.x)

423 Brando, P.M., Nepstad, D.C., Balch, J.K., Bolker, B., Christman, M.C., Coe, M., Putz, F.E., 2012. Fire-  
424 induced tree mortality in a neotropical forest: the roles of bark traits tree size, wood density and fire behavior.  
425 *Global Change Biology* 18, 630–641. <https://doi.org/10.1111/j.1365-2486.2011.02533.x>

426 Brandt, M., Rasmussen, K., Peñuelas, J., Tian, F., Schurgers, G., Verger, A., Mertz, O., Palmer, J.R.B.,  
427 Fensholt, R., 2017. Human population growth offsets climate-driven increase in woody vegetation in sub-  
428 Saharan Africa. *Nature Ecology & Evolution* 1. <https://doi.org/10.1038/s41559-017-0081>

429 Cardil, A., de-Miguel, S., Silva, C.A., Reich, P.B., Calkin, D., Brancalion, P.H.S., Vibrans, A.C., Gamarra,  
430 J.G.P., Zhou, M., Pijanowski, B.C., Hui, C., Crowther, T.W., H´erault, B., Piotto, D., Salas-Eljatib, C.,  
431 Broadbent, E.N., Zambrano, A.M.A., Picard, N., Aragão, L.E.O.C., Bastin, J.-F., Routh, D., van den  
432 Hoogen, J., Peri, P.L., Liang, J., 2020. Recent deforestation drove the spike in Amazonian fires. *Environ-*  
433 *mental Research Letters* 15, 121003. <https://doi.org/10.1088/1748-9326/abcac7>



- 434 Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., Zanne, A. E., 2009. Towards a worldwide  
435 wood economics spectrum. *Ecology letters* 12, 351-366. [https://doi.org/10.1111/j.1461-0248.2009.](https://doi.org/10.1111/j.1461-0248.2009.01285.x)  
436 [01285.x](https://doi.org/10.1111/j.1461-0248.2009.01285.x)
- 437 Chazdon, R.L., 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspec-*  
438 *tives in Plant Ecology Evolution and Systematics* 6, 51-71. <https://doi.org/10.1078/1433-8319-00042>
- 439 Cochrane, M.A., 2003. Fire science for rainforests. *Nature* 421, 913-919. [https://doi.org/10.1038/](https://doi.org/10.1038/nature01437)  
440 [nature01437](https://doi.org/10.1038/nature01437)
- 441 Dereix, C., N'Guessan, A., 1976. Etude de l'action des feux de brousse sur la v'eg'etation, les parcelles feux  
442 de Kokond'ekro - R'esultats apr`es 40 ans de traitement. Centre Technique Forestier Tropical de C'ote d'Ivoire.
- 443 Didham, R.K., Lawton, J.H., 1999. Edge structure determines the magnitude of changes in microclimate and  
444 vegetation structure in tropical forest fragments. *Biotropica* 31, 17-30. [https://doi.org/10.1111/j.1744-](https://doi.org/10.1111/j.1744-7429.1999.tb00113.x)  
445 [7429.1999.tb00113.x](https://doi.org/10.1111/j.1744-7429.1999.tb00113.x)
- 446 Doua-Bi, G.Y.A., Zo-Bi, I.C., Amani, B.H.K., Elogne, A.G.M., N'dja, J.K., N'Guessan, A.E., H'erault, B.,  
447 2021. Taking advantage of natural regeneration potential in secondary forests to recover commercial tree  
448 resources in C'ote d'Ivoire. *Forest Ecology and Management* 493, 119240. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.foreco.2021.119240)  
449 [foreco.2021.119240](https://doi.org/10.1016/j.foreco.2021.119240)
- 450 Dwomoh, F., Wimberly, M., 2017. Fire regimes and their drivers in the Upper Guinean region of West  
451 Africa. *Remote Sensing* 9, 1117. <https://doi.org/10.3390/rs9111117>
- 452 Dwomoh, F.K., Wimberly, M.C., 2017. Fire regimes and forest resilience: alternative vegetation states in the  
453 West African tropics. *Landscape Ecology* 32, 1849-1865. <https://doi.org/10.1007/s10980-017-0553-4>
- 454 Dwomoh, F.K., Wimberly, M.C., Cochrane, M.A., Numata, I., 2019. Forest degradation promotes fire  
455 during drought in moist tropical forests of Ghana. *Forest Ecology and Management* 440, 158-168. [https:](https://doi.org/10.1016/j.foreco.2019.03.014)  
456 [//doi.org/10.1016/j.foreco.2019.03.014](https://doi.org/10.1016/j.foreco.2019.03.014)
- 457 Engstrom, R.T., 2010. First-order fire effects on animals: review and recommendations. *Fire Ecology* 6,  
458 115-130. <https://doi.org/10.4996/fireecology.0601115>
- 459 Fine, P.V.A., 2002. The invasibility of tropical forests by exotic plants. *Journal of Tropical Ecology* 18,  
460 687-705. <https://doi.org/10.1017/s0266467402002456>
- 461 Flores, C., Bounds, D.L., Ruby, D.E., 2011. Does prescribed fire benefit wetland vegetation?. *Wetlands* 31,  
462 35-44. <https://doi.org/10.1007/s13157-010-0131-x>
- 463 Grau, O., Peñuelas, J., Ferry, B., Freycon, V., Blanc, L., Desprez, M., Baraloto, C., Chave, J., Descroix, L.,

- 464 Dourdain, A., Guitet, S., Janssens, I.A., Sardans, J., H´erault, B., 2017. Nutrient-cycling mechanisms other  
465 than the direct absorption from soil may control forest structure and dynamics in poor Amazonian soils.  
466 Scientific Reports 7. <https://doi.org/10.1038/srep45017>
- 467 Grogan, J., Blundell, A.G., Landis, R.M., Youatt, A., Gullison, R.E., Martinez, M., Kómetter, R., Lentini,  
468 M., Rice, R.E., 2010. Over-harvesting driven by consumer demand leads to population decline: big-leaf  
469 mahogany in South America. Conservation Letters 3, 12–20. [https://doi.org/10.1111/j.1755-263x.  
470 2009.00082.x](https://doi.org/10.1111/j.1755-263x.2009.00082.x)
- 471 Haslem, A., Kelly, L.T., Nimmo, D.G., Watson, S.J., Kenny, S.A., Taylor, R.S., Avitabile, S.C., Callister,  
472 K.E., Spence-Bailey, L.M., Clarke, M.F., Bennett, A.F., 2010. Habitat or fuel? Implications of long-term  
473 post-fire dynamics for the development of key resources for fauna and fire. Journal of Applied Ecology 48,  
474 247–256. <https://doi.org/10.1111/j.1365-2664.2010.01906.x>
- 475 Herault, B., Ouallet, J., Blanc, L., Wagner, F., Baraloto, C., 2010. Growth responses of neotropical trees  
476 to logging gaps. Journal of Applied Ecology 47, 821–831. [https://doi.org/10.1111/j.1365-2664.2010.  
477 01826.x](https://doi.org/10.1111/j.1365-2664.2010.01826.x)
- 478 Hirschmugl, M., Steinegger, M., Gallaun, H., Schardt, M., 2014. Mapping forest degradation due to selective  
479 logging by means of time series analysis: case studies in Central Africa. Remote Sensing 6, 756–775.  
480 <https://doi.org/10.3390/rs6010756>
- 481 Hoffmann, W.A., 1998. Post-burn reproduction of woody plants in a neotropical savanna: the relative  
482 importance of sexual and vegetative reproduction. Journal of Applied Ecology 35, 422–433. [https://doi.  
483 org/10.1046/j.1365-2664.1998.00321.x](https://doi.org/10.1046/j.1365-2664.1998.00321.x)
- 484 H´erault, B., Bachelot, B., Poorter, L., Rossi, V., Bongers, F., Chave, J., Paine, C.E.T., Wagner, F., Baraloto,  
485 C., 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species. Journal of  
486 Ecology 99, 1431–1440. <https://doi.org/10.1111/j.1365-2745.2011.01883.x>
- 487 H´erault, B., Beauch`ene, J., Muller, F., Wagner, F., Baraloto, C., Blanc, L., Martin, J.-M., 2010. Modeling  
488 decay rates of dead wood in a neotropical forest. Oecologia 164, 243–251. [https://doi.org/10.1007/  
489 s00442-010-1602-8](https://doi.org/10.1007/s00442-010-1602-8)
- 490 H´erault, B., Hiernaux, P., 2004. Soil seed bank and vegetation dynamics in Sahelian fallows the impact of  
491 past cropping and current grazing treatments. Journal of Tropical Ecology 20, 683–691. [https://doi.org/  
492 10.1017/s0266467404001786](https://doi.org/10.1017/s0266467404001786)
- 493 H´erault, B., N’Guessan, A.K., Ouattara, N., Ahoba, A., B´en´edet, F., Coulibaly, B., Doua-Bi, Y., Koffi,  
494 T., Koffi-Konan, J.-C., Konat´e, I., Ti´eoul´e, F., Wourro, F., Zo-Bi, I.C., Louppe, D., 2020. The long-term

495 performance of 35 tree species of sudanian West Africa in pure and mixed plantings. *Forest Ecology and*  
496 *Management* 468, 118171. <https://doi.org/10.1016/j.foreco.2020.118171>

497 H´erault, B., Pioniot, C., 2018. Key drivers of ecosystem recovery after disturbance in a neotropical forest.  
498 *Forest Ecosystems* 5. <https://doi.org/10.1186/s40663-017-0126-7>

499 Keeley, J.E., Fotheringham, C.J., 2000. Role of fire in regeneration from seed., in: *Seeds: the Ecology of*  
500 *Regeneration in Plant Communities*. CABI, pp. 311–330. [https://doi.org/10.1079/9780851994321.](https://doi.org/10.1079/9780851994321.0311)  
501 0311

502 Kinnaird, M.F., O'Brien, T.G., 1998. Ecological Effects of Wildfire on Lowland Rainforest in Sumatra.  
503 *Conservation Biology* 12, 954–956. <https://doi.org/10.1046/j.1523-1739.1998.00005.x>

504 Kouassi, J.-L., Wandan, N., Mbow, C., 2020. Exploring wildfire occurrence: local farmers' perceptions and  
505 adaptation strategies in Central Côte d'Ivoire, West Africa. *Journal of Sustainable Forestry* 41, 173–192.  
506 <https://doi.org/10.1080/10549811.2020.1845744>

507 Larjavaara, M., Muller-Landau, H. C. 2010. Rethinking the value of high wood density. *Functional Ecology*,  
508 701–705. <https://doi.org/10.1111/j.1365-2435.2010.01698.x>

509 Lewis, S.L., 2005. Tropical forests and the changing earth system. *Philosophical Transactions of the Royal*  
510 *Society B: Biological Sciences* 361, 195–210. <https://doi.org/10.1098/rstb.2005.1711>

511 Midgley, J.J., Kruger, L.M., Skelton, R., 2011. How do fires kill plants? The hydraulic death hypothesis  
512 and Cape Proteaceae “fire-resisters”. *South African Journal of Botany* 77, 381–386. [https://doi.org/10.](https://doi.org/10.1016/j.sajb.2010.10.001)  
513 1016/j.sajb.2010.10.001

514 Mirabel, A., H´erault, B., Marcon, E., 2020. Diverging taxonomic and functional trajectories following  
515 disturbance in a Neotropical forest. *Science of The Total Environment* 720, 137397. [https://doi.org/10.](https://doi.org/10.1016/j.scitotenv.2020.137397)  
516 1016/j.scitotenv.2020.137397

517 Mirabel, A., Marcon, E., H´erault, B., 2021. 30 Years of postdisturbance recruitment in a Neotropical forest.  
518 *Ecology and Evolution* 11, 14448–14458. <https://doi.org/10.1002/ece3.7634>

519 Murphy, B.P., Bowman, D.M.J.S., 2012. What controls the distribution of tropical forest and savanna?.  
520 *Ecology Letters* 15, 748–758. <https://doi.org/10.1111/j.1461-0248.2012.01771.x>

521 Murphy, B.P., Russell-Smith, J., Prior, L.D., 2010. Frequent fires reduce tree growth in northern Australian  
522 savannas: implications for tree demography and carbon sequestration. *Global Change Biology* 16, 331–343.  
523 <https://doi.org/10.1111/j.1365-2486.2009.01933.x>

524 N'Dri, A.B., Gignoux, J., Barot, S., Konat´e, S., Demb´el´e, A., Werner, P.A., 2013. The dynamics of hollowing

525 in annually burnt savanna trees and its effect on adult tree mortality. *Plant Ecology* 215, 27–37. <https://doi.org/10.1007/s11258-013-0276-9>

526

527 N'Dri, A.B., Gignoux, J., Dembele, A., Konate, S., 2012. Short term effects of fire intensity and fire regime  
528 on vegetation dynamic in a tropical humid savanna (Lamto, central Cote d'Ivoire). *Natural Science* 04,  
529 1056–1064. <https://doi.org/10.4236/ns.2012.412134>

530 Norris, K., Asase, A., Collen, B., Gockowski, J., Mason, J., Phalan, B., Wade, A., 2010. Biodiversity in  
531 a forest-agriculture mosaic – The changing face of West African rainforests. *Biological Conservation* 143,  
532 2341–2350. <https://doi.org/10.1016/j.biocon.2009.12.032>

533 N'Guessan, A.E., N'dja, J.K., Yao, O.N., Amani, B.H.K., Gouli, R.G.Z., Piponiot, C., Zo-Bi, I.C., H´erault,  
534 B., 2019. Drivers of biomass recovery in a secondary forested landscape of West Africa. *Forest Ecology and*  
535 *Management* 433, 325–331. <https://doi.org/10.1016/j.foreco.2018.11.021>

536 Osazuwa-Peters, O.L., Wright, S.J., Zanne, A.E., 2017. Linking wood traits to vital rates in tropical rain-  
537 forest trees: Insights from comparing sapling and adult wood. *American Journal of Botany* 104, 1464–1473.  
538 <https://doi.org/10.3732/ajb.1700242>

539 Paine, C.E.T., Stahl, C., Courtois, E.A., Patiño, S., Sarmiento, C., Baraloto, C., 2010. Functional ex-  
540 planations for variation in bark thickness in tropical rain forest trees. *Functional Ecology* 24, 1202–1210.  
541 <https://doi.org/10.1111/j.1365-2435.2010.01736.x>

542 Pausas, J.G., 2015. Bark thickness and fire regime. *Functional Ecology* 29, 315–327. [https://doi.org/10.](https://doi.org/10.1111/1365-2435.12372)  
543 [1111/1365-2435.12372](https://doi.org/10.1111/1365-2435.12372)

544 Pirard, R., Cuny, P., Plancheron, F., Rageade, M., Leclercq, P.E., 2021. Inventaire Forestier et Faunique  
545 National (IFFN). ONF International.

546 Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manr´iquez, G., Harms, K.E., Licona,  
547 J.C., Mart´inez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Pena-Claros, M., Webb, C.O., Wright, I.J.,  
548 2008. Are functional traits good predictors of demographic rates? Evidence from five neotropical forests.  
549 *Ecology* 89, 1908–1920. <https://doi.org/10.1890/07-0207.1>

550 Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., ... Lloyd, J.,  
551 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate.  
552 *Biogeosciences* 9, 2203–2246. <https://doi.org/10.5194/bg-9-2203-2012>

553 Romero, C., Bolker, B.M., 2008. Effects of stem anatomical and structural traits on responses to stem  
554 damage: an experimental study in the Bolivian Amazon. *Canadian Journal of Forest Research* 38, 611–618.  
555 <https://doi.org/10.1139/x07-205>

556 Roux, R.L., Wagner, F., Blanc, L., Betbeder, J., Gond, V., Dessard, H., Funatzu, B., Bourgoïn, C., Cornu,  
557 G., Herault, B., Montfort, F., Sist, P., Begue, A., Dubreuil, V., Laurent, F., Messner, F., Hasan, A.F., Arvor,  
558 D., 2022. How wildfires increase sensitivity of Amazon forests to droughts. *Environmental Research Letters*  
559 17, 044031. <https://doi.org/10.1088/1748-9326/ac5b3d>

560 R´ejou-M´echain, M., Tanguy, A., Piponiot, C., Chave, J., H´erault, B., 2017. biomass : an r package for  
561 estimating above-ground biomass and its uncertainty in tropical forests. *Methods in Ecology and Evolution*  
562 8, 1163–1167. <https://doi.org/10.1111/2041-210x.12753>

563 Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., ... Wardle, D. A., 2015.  
564 A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology*  
565 *Letters* 18, 1406–1419. <https://doi.org/10.1111/ele.12508>

566 Silvestrini, R.A., Soares-Filho, B.S., Nepstad, D., Coe, M., Rodrigues, H., Assun ç ˜ao, R., 2011. Simulating  
567 fire regimes in the Amazon in response to climate change and deforestation. *Ecological Applications* 21,  
568 1573–1590. <https://doi.org/10.1890/10-0827.1>

569 Siry, J.P., Cubbage, F.W., Ahmed, M.R., 2005. Sustainable forest management: global trends and opportu-  
570 nities. *Forest Policy and Economics* 7, 551–561. <https://doi.org/10.1016/j.forpol.2003.09.003>

571 Slik, J.W.F., Verburg, R.W., Keßler, P.J.A., 2002. Effects of fire and selective logging on the tree species  
572 composition of lowland dipterocarp forest in East Kalimantan, Indonesia. *Biodiversity and Conservation* 11,  
573 85–98. <https://doi.org/10.1023/a:1014036129075>

574 Soong, J.L., Janssens, I.A., Grau, O., Margalef, O., Stahl, C., Langenhove, L.V., Urbina, I., Chave, J.,  
575 Dourdain, A., Ferry, B., Freycon, V., Herault, B., Sardans, J., Peñuelas, J., Verbruggen, E., 2020. Soil  
576 properties explain tree growth and mortality but not biomass, across phosphorus-depleted tropical forests.  
577 *Scientific Reports* 10. <https://doi.org/10.1038/s41598-020-58913-8>

578 Staal, A., Nes, E.H., Hantson, S., Holmgren, M., Dekker, S.C., Pueyo, S., Xu, C., Scheffer, M., 2018.  
579 Resilience of tropical tree cover: The roles of climate fire, and herbivory. *Global Change Biology* 24,  
580 5096–5109. <https://doi.org/10.1111/gcb.14408>

581 Staver, A.C., Brando, P.M., Barlow, J., Morton, D.C., Paine, C.E.T., Malhi, Y., Murakami, A.A., Pasquel,  
582 J., 2019. Thinner bark increases sensitivity of wetter Amazonian tropical forests to fire. *Ecology Letters* 23,  
583 99–106. <https://doi.org/10.1111/ele.13409>

584 Stoof, C.R., Wesseling, J.G., Ritsema, C.J., 2010. Effects of fire and ash on soil water retention. *Geoderma*  
585 159, 276–285. <https://doi.org/10.1016/j.geoderma.2010.08.002>

586 Swaine, M.D., 1992. Characteristics of dry forest in West Africa and the influence of fire. *Journal of*

587 Vegetation Science 3, 365–374. <https://doi.org/10.2307/3235762>

588 Urbina, I., Grau, O., Sardans, J., Margalef, O., Peguero, G., Asensio, D., LLusià, J., Ogaya, R., Gargallo-  
589 Garriga, A., Langenhove, L.V., Verryckt, L.T., Courtois, E.A., Stahl, C., Soong, J.L., Chave, J., H´erault,  
590 B., Janssens, I.A., Sayer, E., Peñuelas, J., 2021. High foliar K and P resorption efficiencies in old-growth  
591 tropical forests growing on nutrient-poor soils. *Ecology and Evolution* 11, 8969–8982. [https://doi.org/](https://doi.org/10.1002/ece3.7734)  
592 [10.1002/ece3.7734](https://doi.org/10.1002/ece3.7734)

593 Wagner, F., Rossi, V., Baraloto, C., Bonal, D., Stahl, C., H´erault, B., 2014. Are Commonly Measured  
594 Functional Traits Involved in Tropical Tree Responses to Climate?. *International Journal of Ecology* 2014,  
595 1–10. <https://doi.org/10.1155/2014/389409>

596 Werner, P.A., 2005. Impact of feral water buffalo and fire on growth and survival of mature savanna trees:  
597 An experimental field study in Kakadu National Park northern Australia. *Austral Ecology* 30, 625–647.  
598 <https://doi.org/10.1111/j.1442-9993.2005.01491.x>

599 van Lierop, P., Lindquist, E., Sathyapala, S., Franceschini, G., 2015. Global forest area disturbance from  
600 fire insect pests, diseases and severe weather events. *Forest Ecology and Management* 352, 78–88. [https:](https://doi.org/10.1016/j.foreco.2015.06.010)  
601 [//doi.org/10.1016/j.foreco.2015.06.010](https://doi.org/10.1016/j.foreco.2015.06.010)

602 **Tables**

Table 1: List of sampled plots with the forestry treatment type, the percentage of basal area removed by the forestry treatment and the percentage of burnt area.

Plot Number	Treatment	% Basal Area Removed	% Surface Burnt
1	thinning	29	64
2	control	0	31
3	control	0	39
4	logging	16	66
5	control	0	32
6	logging	27	47
7	logging	21	52
8	control	0	13
9	thinning	35	62
10	logging	29	73
11	thinning	29	85
12	logging	16	41
13	control	0	31
14	control	0	34
15	control	0	46
16	logging	26	73
17	control	0	37
18	logging	43	35
19	thinning	36	52
20	logging	43	87
21	logging	31	19
22	logging	27	74
23	control	0	12
24	thinning	32	50
25	control	0	13

Table 2: List of the studied timber species with Commercial Names in french,  $N_{20}$  the total number of individuals in the site in 2020,  $DBH_{20}$  the tree diameter range (minimum - maximum),  $WD$  the wood density [minimum - maximum],  $BT$  the bark thickness and  $AGR$  the average growth rate by species.

Family	Species	Commercial name	$N_{20}$	$DBH_{20}$ (cm)	$WD$ (g/cm <sup>3</sup> )	$BT$ (mm)	$AGR$ (mm/yr)
Anacardiaceae	<i>Lannea welwitschii</i>	Loloti	432	15 - 150	0.40 [0.33-0.47]	7.30	4.50
Apocynaceae	<i>Alstonia boonei</i>	Emien	66	22 - 150	0.32 [0.25-0.39]	5.46	3.38
Bombacaceae	<i>Ceiba pentandra</i>	Fromager	1006	20 - 140	0.30 [0.23-0.37]	21.03	10.63
Caesalpiniaceae	<i>Guibourtia ehie</i>	Amazakou´e	42	16 - 65	0.71 [0.64-0.78]	8.50	4.35
Euphorbiaceae	<i>Ricinodendron heudelotii</i>	Eho	944	17 - 154	0.21 [0.14-0.28]	8.26	7.39
Flacourtiaceae	<i>Scottellia coriacea</i>	Akossika	100	15 - 90	0.56 [0.47-0.65]	5.60	1.95
Meliaceae	<i>Entandrophragma cylindricum</i>	Sapelli	86	14 - 90	0.57 [0.50-0.64]	5.73	2.68
Moraceae	<i>Morus mesozygia</i>	Difou	62	11 - 58	0.72 [0.65-0.79]	4.72	1.59
Sapotaceae	<i>Aningeria altissima</i>	Aniegr´e blanc	48	18 - 111	0.51 [0.31-0.71]	6.25	2.59
Sapotaceae	<i>Gambeya africana</i>	Akatio	142	15 - 90	0.52 [0.38-0.66]	4.68	3.63
Sterculiaceae	<i>Eribroma oblogum</i>	Bi	446	18 - 65	0.64 [0.57-0.71]	9.90	3.11
Sterculiaceae	<i>Mansonia altissima</i>	Bete	1074	29 - 70	0.56 [0.49-0.63]	12.97	2.57
Sterculiaceae	<i>Nesogordonia papaverifera</i>	Kotibe	1049	15 - 250	0.64 [0.57-0.71]	5.43	2.38
Sterculiaceae	<i>Pterygota macrocarpa</i>	Koto	280	25 - 110	0.49 [0.42-0.56]	12.45	4.28
Sterculiaceae	<i>Sterculia rhinopetala</i>	Lotofa	616	12 - 90	0.67 [0.60-0.74]	11.98	2.91
Sterculiaceae	<i>Triplochiton scleroxylon</i>	Samba	1076	23 - 110	0.33 [0.26-0.40]	8.12	6.22
Ulmaceae	<i>Celtis mildbraedii</i>	Ba	860	11 - 116	0.62 [0.55-0.69]	3.89	2.25
Ulmaceae	<i>Celtis zenkeri</i>	Asan	523	18 - 105	0.61 [0.54-0.68]	4.98	3.19
Ulmaceae	<i>Holoptelea grandis</i>	Kekele	149	20 - 110	0.59 [0.52-0.66]	5.08	8.33
Ulmaceae	<i>Celtis aldofi-friderici</i>	Lohonf´e	80	23 - 86	0.57 [0.48-0.66]	10.69	4.34



Table 3: Species-specific responses to fire and disturbance. Values are the posterior mean of a given parameter.  $\beta_{fir,s}$  is the species demographic response to fire,  $\beta_{trt,s}$  the species demographic response to silvicultural treatments,  $\theta_{fir,s}$  is the species growth response to fire and  $\theta_{trt,s}$  the species growth response to silvicultural treatments. Values with a \* are significantly different from 0 ( $P < 0.05$ )

Species	$\beta_{fir,s}$	$\beta_{trt,s}$	$\theta_{fir,s}$	$\theta_{trt,s}$
<i>Aningeria altissima</i>	-0.094	+0.026	+0.311	+0.123
<i>Gambeya africana</i>	-0.174*	-0.074	+0.197	+0.024
<i>Scottellia coriacea</i>	-0.219*	-0.079	+0.079	+0.220
<i>Guibourtia ehie</i>	-0.163	-0.051	+0.273	+0.099
<i>Celtis zenkeri</i>	-0.322*	-0.034	-0.514	+0.001
<i>Celtis mildbraedii</i>	-0.181*	-0.091	+0.054	-0.031
<i>Mansonia altissima</i>	-0.017	+0.066	+0.134	+0.004
<i>Eribroma oblogum</i>	-0.156*	-0.023	+0.677	-0.019
<i>Morus mesozygia</i>	-0.165	-0.048	+0.553*	-0.310
<i>Ricinodendron heudelotii</i>	+0.011	+0.043	+0.275	+0.099
<i>Alstonia boonei</i>	-0.145	-0.003	+0.182	+0.265
<i>Ceiba pentandra</i>	-0.051	+0.025	+0.270	+0.120
<i>Holoptelea grandis</i>	-0.173	-0.106	+0.157	+0.103
<i>Nesogordonia papaverifera</i>	-0.163*	-0.041	-0.943	-0.041
<i>Pterygota macrocarpa</i>	-0.124	+0.031	+0.153	-0.050
<i>Celtis aldofi-friderici</i>	-0.108	-0.037	+0.124	+0.084
<i>Lannea welwitschii</i>	-0.162*	-0.077	+0.481	+0.213
<i>Sterculia rhinopetala</i>	-0.053	-0.056	+0.091	-0.018
<i>Triplochiton scleroxylon</i>	-0.059	+0.028	+0.093	+0.112
<i>Entandrophragma cylindricum</i>	-0.168	-0.049	-0.261	+0.083

603 **Figures**

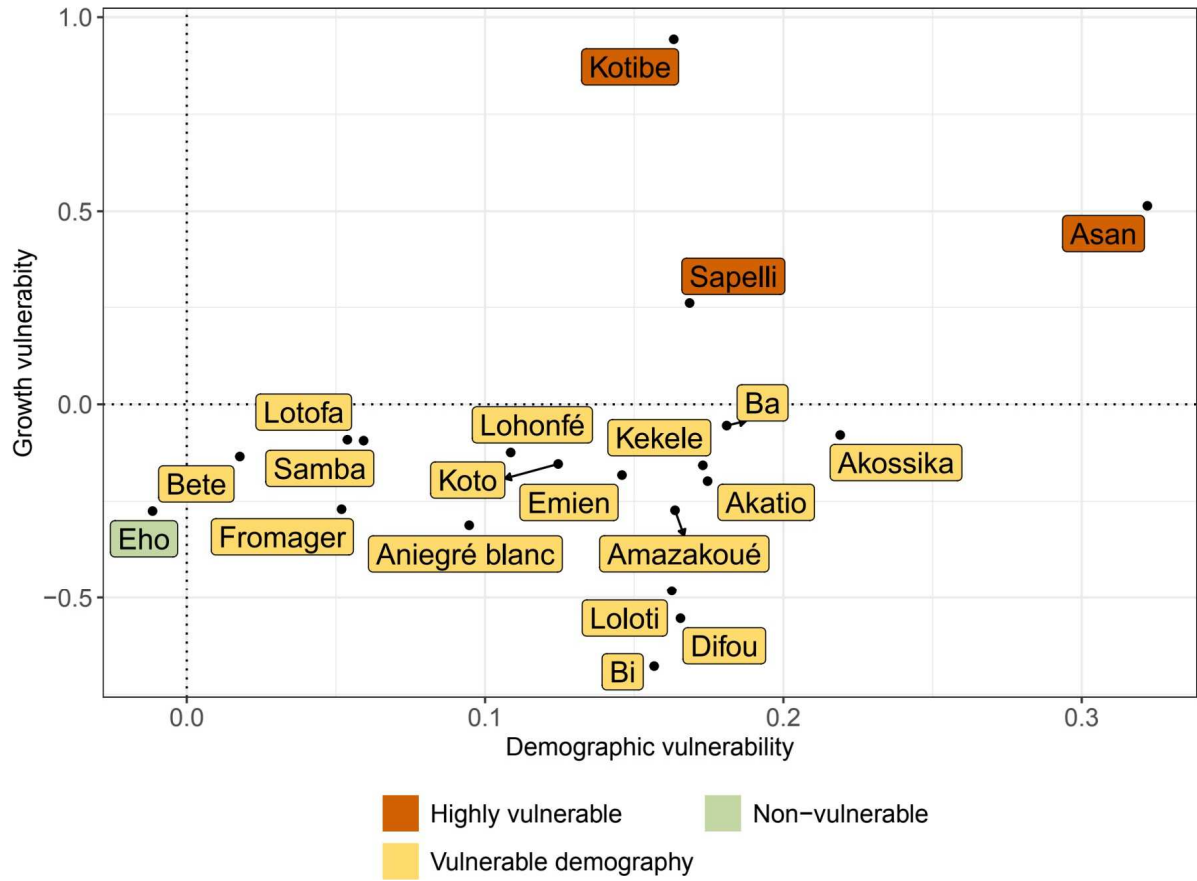


Figure 1: Long-term vulnerability (demography and growth) to fire for 20 commercial timber species from the T'en'é semi-deciduous forest, West Africa.

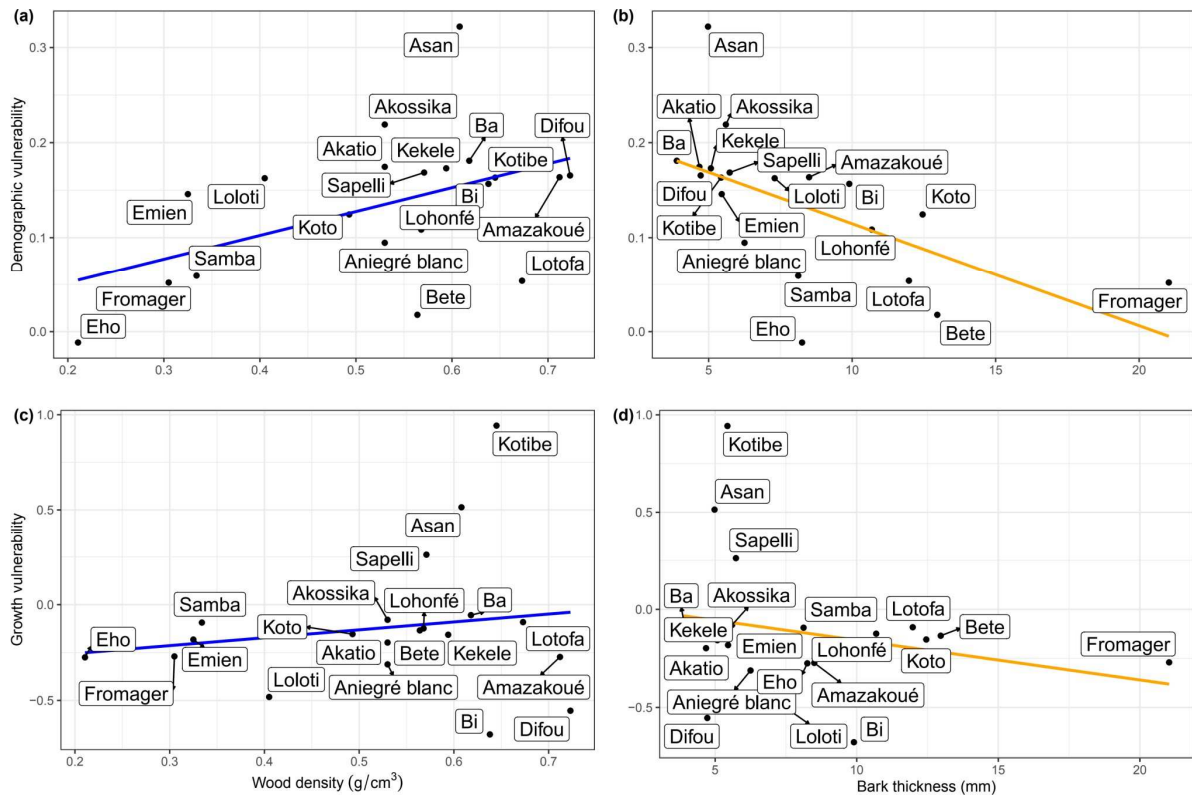


Figure 2: Species vulnerability vs wood density (a, c) and bark thickness (b, d). Dots are species. The blue line represents the linear link between wood density and fire-vulnerabilities in terms of demography ( $R^2 = 0.47$ , slope = 0.25 and  $P = 0.03$ ) and growth ( $R^2 = 0.16$ , slope = 0.41 and  $P = 0.48$ ); while the orange line shows the linear link between bark thickness and fire-vulnerabilities in terms of demography ( $R^2 = 0.59$ , slope = -0.01 and  $P = 0.006$ ) and growth ( $R^2 = 0.23$ , slope = -0.02 and  $P = 0.32$ ).

604 **Appendix**

Table 4: List of the number of individuals per studied species, subdivided into 1978 and 2020 ad each of the years divided into control, thinned and logged.

Species	Commercial Name	1978 Control	1978 Logging	1978 Thinning	2020 Control	2020 Logging	2020 Thinning
<i>Aningeria altissima</i>	Aniegr´e blanc	105	95	32	4	4	0
<i>Gambeya africana</i>	Akatio	475	309	264	43	57	40
<i>Scottellia coriacea</i>	Akossika	309	257	141	60	19	2
<i>Guibourtia ehie</i>	Amazakou´e	123	84	60	9	4	5
<i>Celtis zenkeri</i>	Asan	285	214	9	43	18	17
<i>Celtis mildbraedii</i>	Ba	2433	1977	1393	670	475	243
<i>Mansonia altissima</i>	Bete	184	161	105	346	459	308
<i>Eribroma oblongum</i>	Bi	363	217	120	310	164	126
<i>Morus mesozygia</i>	Difou	158	142	106	26	25	10
<i>Ricinodendron heudelotii</i>	Eho	220	281	173	306	363	231
<i>Alstonia boonei</i>	Emien	42	41	8	29	26	5
<i>Ceiba pentandra</i>	Fromager	63	52	35	360	483	193
<i>Holoptelea grandis</i>	Kekele	48	35	6	78	38	13
<i>Nesogordonia papaverifera</i>	Kotibe	847	693	466	530	362	198
<i>Pterygota macrocarpa</i>	Koto	26	67	32	92	123	57
<i>Celtis aldophi-friderici</i>	Lohonf´e	480	381	214	23	5	6
<i>Lannea welwitschii</i>	Loloti	81	90	0	259	126	61
<i>Sterculia rhinopetala</i>	Lotofa	985	823	385	312	200	81
<i>Triplochiton scleroxylon</i>	Samba	593	601	243	378	441	162
<i>Entandrophragma cylindricum</i>	Sapelli	110	84	63	40	27	12

Table 5: Seasonal rainfall statistics (mm) at the T'en'e station, Côte d'Ivoire

Year	Long dry (Dec-Feb)	Long wet (March-June)	Short dry (July-August)	Short wet (Sept-Nov)
1983	60	737	45	267
1984	97	715	191	175
1985	60	412	297	301
1986	56	473	67	294
1987	204	514	158	197
1988	38	460	121	303
1989	66	313	318	403
1990	184	615	71	395
1991	39	548	228	239
1992	73	382	12	295
1993	56	444	55	292
1994	84	183	58	144
1995	5	391	37	172
1996	101	94	89	195
1997	8	364	20	202
1998	40	637	79	330
2000	109	155	53	207
2001	7	425	116	167
2002	105	583	109	93
2003	56	387	110	303
2004	110	519	129	424
2005	230	443	99	317
2006	76	690	72	349
2007	69	563	214	167
2008	129	508	252	424
2009	163	948	81	162
2010	216	655	176	348
2011	125	329	106	488
2012	92	598	80	411
2013	187	728	86	439
2014	254	884	131	390
2015	178	807	146	315
2016	86	860	191	244