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## **Dynamics of biomass and nutrient accumulation in rubber (*Hevea brasiliensis*) plantations established on two soil types: Implications for nutrient management over the immature phase**

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1           **Dynamics of biomass and nutrient accumulation in rubber (*Hevea brasiliensis*)**  
2 **plantations established on two soil types: implications for nutrient management over**  
3 **the immature phase.**

4  
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## 18 I. Introduction

19

20 The rubber tree (*Hevea brasiliensis*) is the main source of natural rubber (NR). In order to  
21 meet the growing demand for NR, the area occupied by rubber plantations worldwide  
22 increased from 3.9 million ha in 1961 to 12.5 million ha in 2018 (FAO, 2020). The  
23 sustainability of latex production is a growing concern for the stakeholders of the NR value  
24 chain. Highly productive rubber plantations need to match the use of mineral fertilizers to the  
25 dynamics of the nutrient requirements of the trees, taking into account their availability in the  
26 soil (Vrignon-Brenas et al., 2019).

27 Although rubber trees are unproductive during the immature phase, from planting to about  
28 6 years old, this period is critical for the future latex yields and the profitability of the  
29 plantation. The immature phase can be divided into two periods with regard to tree  
30 phenology and growth. The juvenile phase (from planting to 2 years old) is characterized by  
31 fast vertical growth, while the maturation period (from 2 years old up to latex collection at 6  
32 years) is characterized by an acceleration of the radial growth of the stem (Compagnon,  
33 1986; Vrignon-Brenas et al., 2019). The immature phase ends when 50% of the trees reach  
34 a trunk girth of 50 cm 1 m from the ground. Rubber trees are then tapped for latex production  
35 until they reach 25 to 40 years old. Management practices in immature plantations therefore  
36 seek to maximize the growth of the trees to start latex collection as early as possible.

37 NPK fertilizers are commonly used to increase the growth of immature rubber trees  
38 (Abraham et al., 2015; Alle et al., 2015; Samarappuli, 2000a). In a recent review of the  
39 literature, Vrignon-Brenas et al. (2019) showed huge ranges of fertilizer applications, from 27  
40 to 697 kg ha<sup>-1</sup> yr<sup>-1</sup> for N, 29 to 326 kg ha<sup>-1</sup> yr<sup>-1</sup> for P and 14 to 232 kg ha<sup>-1</sup> yr<sup>-1</sup> for K, depending  
41 on local conditions. This review paper shows that most of these recommendations rely on  
42 local empirical experiences and that references on the dynamics of tree nutrient  
43 requirements over the immature phase are mostly old (Polinière and Van Brandt, 1964;  
44 Shorrocks, 1965a). Experience in fast-growing planted forests suggests that improving our  
45 knowledge of tree nutrient requirements throughout the early growth stages could help  
46 design more sustainable nutrient management plans for immature rubber plantations (Laclau  
47 et al., 2003; Laclau et al., 2010b). In tropical planted forests, nutrients accumulate differently  
48 throughout the rotation. N, P and K would seem to accumulate more during the early growth  
49 stage, while Ca and Mg accumulation is more linear throughout the lifespan of the plantation  
50 (Fernández-Moya et al., 2015). In the case of rubber trees, the consequences of fertilizer  
51 applications for the dynamics of nutrient accumulation in the trees has never been quantified  
52 over an entire rotation (35-40 years), as far as we are aware.

53 According to Vrignon-Brenas et al. (2019), logging residues ((i.e. trunks, branches, leaves,  
54 stumps and roots of the logged plantation) could be managed better to reduce the amounts

55 of fertilizers needed to address the problem of long-term fertility loss in rubber monocultures.  
56 Logging residues should be left on the soil surface after the clear-cutting of old stands. Even  
57 though no data are available for rubber plantations, the ways in which logging residue  
58 management affect tree growth have been abundantly studied in eucalyptus plantations. An  
59 isotopic study showed that logging residues provided 39% of tree N requirements over the  
60 first two years after planting in the Congo (Versini et al., 2014). In this sandy soil, a positive  
61 and strong relationship was established between the amount of logging residues left on site  
62 after harvesting and the aboveground biomass of eucalyptus trees at the end of the following  
63 rotation (Laclau et al., 2010a). Logging residue management practices particularly affect tree  
64 growth on low-fertility soils (Van Bich et al., 2019), and most rubber plantations are  
65 established on such soils.

66 The common practice in rubber cultivation is to burn or to export logging residues.  
67 Planters used to adopt these practices to limit the risk of root rot disease (Nandris et al.,  
68 1987), which can be a major constraint in rubber plantations (Ogbebor et al., 2013).  
69 However, the risk linked to root disease seems to be mainly observed over the first rotation  
70 of a rubber plantation, after conversion from forest. Burning or exporting residues is generally  
71 done nowadays for economic considerations. Residue burning remains the cheapest way of  
72 preparing land for large-scale plantations (Simorangkir, 2006). However, it was banned some  
73 decades ago in several countries for its adverse effects on air quality (Tomich et al., 1998)  
74 and nutrient losses through runoff and/or volatilization. The most common practice  
75 nowadays, in both industrial rubber plantations and smallholdings, is to export logging  
76 residues from plots to be used as timber, or for their heating value (Hytönen et al., 2019).  
77 Trunks, branches and stumps may be exported depending on the type of use, but leaves are  
78 generally left on site. Information on the nutrient stocks in tree components at the time of the  
79 clear-cut is therefore needed to assess the consequences of logging practices on soil  
80 nutrient depletion and on the amounts of nutrients available for the next rubber cycle.

81 Allometric equations are needed for an accurate estimation of the biomass and nutrient  
82 stocks in tree plantations (Picard et al., 2012). These equations link a predictive variable  
83 (biomass or nutrient stock of a given tree component) with an easily measurable  
84 dendrometric variable, such as tree height or trunk diameter. Many studies have already  
85 used allometric equations to estimate the biomass of rubber trees (Blagodatsky et al., 2016).  
86 However, to date, the dynamics of nutrient accumulation in tree components have never  
87 been studied over the complete cycle of a rubber plantation.

88 Our study set out to gain insights into the dynamics of nutrient accumulation over the  
89 complete plantation cycle of rubber trees growing in two regions with contrasting soil  
90 properties and fertilization practices. We focused on the following questions: (1) what are the  
91 consequences of contrasting management practices (for two clones planted on two soil

92 types) on nutrient accumulation in rubber trees? and (2) what is the impact of logging  
93 practices on the amounts of nutrients left on-site in logging residues at the clear-cutting of  
94 commercial rubber plantations?  
95

## 96 **II. Materials and methods**

### 97 **2.1 Study sites**

98  
99  
100 The study was carried out from October 2016 to January 2017 in two commercial rubber  
101 plantations located in Ivory Coast (Figure 1): the Toupah-Osrou plantation belonging to  
102 *Société Africaine des Plantations d'Hévéas* (SAPH), located in the South-East of the country  
103 (latitude 5°19'8.446"N, longitude 4°33'54.502"W, 54 m elevation) with 6,700 ha of rubber  
104 plantations, and *Société de Caoutchouc de Grand-Béréby* (SOGB), located in the  
105 South-West of the country (latitude 4°43'9.696"N, longitude 7°6'41.795"W, 34 m elevation)  
106 with 16,300 ha of rubber plantations. Both commercial plantations were established in the  
107 ecological zone of the rainforest, where a subequatorial climate suited to rubber tree  
108 cultivation prevailed. The rainfall regime in South Ivory Coast is divided into two rainy  
109 seasons, a major from May to July and a minor from October to November, and two dry  
110 seasons, from December to April and from August to September. Average annual rainfall  
111 from 2013 to 2018 was similar at SOGB (1674 mm) and SAPH (1718 mm). Mean monthly  
112 rainfall ranges from 40 to 451 mm at SAPH and from 48 to 581 mm at SOGB  
113 (Supplementary Figure 1).

114 Soil types and topographical conditions are different between the two sites, with mainly  
115 flat areas (<5% slope) and deep yellow ferrallitic Arenosol soils derived from tertiary sands at  
116 SAPH, while the SOGB site is characterized by hilly areas (10-25% slope) and gravel-rich  
117 red Ferralsol soils developed from schist and basalt. The soil texture in the upper layers is  
118 loamy sand at SAPH with 9% of clay on average, and sandy loam at SOGB with 22% of clay.  
119 The soils are acidic at both sites with an average  $\text{pH}_{\text{H}_2\text{O}}$  of about 5 in the upper horizons  
120 (Table 1). Overall, soil chemical fertility is better at SOGB than at SAPH, with a higher cation  
121 exchange capacity (CEC), total N and total C contents.  
122

### 123 **2.2 Plot selection**

124  
125 Changes in nutrient stocks throughout the rotation of a rubber plantation were studied  
126 using a chronosequence approach with 4 stand ages at each site. Four plots representative  
127 of commercial plantations were inventoried at each site and for each of the 4 stand ages. We  
128 selected plots at the end of the juvenile phase (2 years after planting) and at the end of the  
129 immature period (5 years after planting). We then selected 20-year-old stands, which is in the

130 middle of the latex production period in most commercial plantations in this region. Lastly,  
131 stands at the end of the cultural cycle (just before clear-cut) were sampled at 40 years old at  
132 SAPH and 38 years old at SOGB. All the stands in these chronosequences were planted  
133 with the GT1 clone at SAPH and the PB217 clone at SOGB. These clones are widespread in  
134 rubber plantations all over the world. Many studies observed that commercial clones had not  
135 significant effect on biomass accumulation in the tree. In a study conducted in Ghana  
136 including clones PB217 and GT1, Wauters et al. (2008) showed that variable “*clone type*” did  
137 not bring any significant improvement in the robustness of models for carbon stock  
138 estimation. In the same line, Chaudhuri et al. (1995) and Shorrocks et al. (1965) did not  
139 found any significant differences between allometric equations of different rubber clones of  
140 the same ages.

141 An inventory (on 500 to 858 trees) and destructive sampling of trees representing the  
142 different diameter classes in the stand were carried out in one plot (called the reference plot)  
143 out of the four plots per age studied at each site (cf. section 4). In the other three plots (called  
144 the additional plots), an inventory of the stand was carried out on 80 to 200 trees. The  
145 additional and reference plots of a given age were located within a 10-km radius. In total for  
146 SAPH and SOGB, 32 plots were inventoried measuring tree girth and quantifying the  
147 percentage of missing trees.

148

### 149 **2.3 Crop management and stand characteristics**

150

151 At SAPH, the tree density at planting ranged from 476 to 555 trees ha<sup>-1</sup> (Table 2). At  
152 SOGB, all the plots were planted at a density of 500 trees ha<sup>-1</sup>, except the 38-year-old plots  
153 with 555 trees ha<sup>-1</sup>. Two different planting designs were used at SOGB, either simple rows or  
154 double rows. Double-row spacing consists of inter-rows of 3 m and 13 m, alternately, while  
155 the inter-row remains the same for simple-row planting. Our inventories showed that the  
156 planting design in simple or double rows had little influence on tree growth. The survival rate  
157 in both the additional and reference plots ranged from 98 to 56% at SOGB and from 99 to  
158 54% at the SAPH site. These survival rates were consistent with tree mortality rates due to  
159 wind damage and root diseases commonly observed throughout the entire rotation in  
160 commercial rubber tree plantations. The survival rate in the 5-year-old stand at SAPH (83%  
161 of living trees in the reference plot) was lower than expected at this age, due to a root  
162 infection caused by *Rigidoporus lignosus* that prevails in West Africa (Ogbebor et al., 2013) .

163 At each site, all the plots sampled at each age received the same amount of mineral  
164 fertilizers. At SAPH, fertilizers were only applied in the first three years after planting for a  
165 total amount of 101, 31 and 106 kg ha<sup>-1</sup> for N, P and K, respectively. At SOGB, fertilizers  
166 were systematically applied every year up to 5 years after planting for a total amount of 300,

167 61 and 250 kg ha<sup>-1</sup> for N, P and K, respectively. Over the mature phase, from 6 years  
168 onwards, fertilization was applied depending on the latex production at SOGB, while no  
169 fertilizer was applied at SAPH.

170 Chemical weeding was carried out 4 to 6 times per year in immature stands and once a  
171 year in mature stands, 1 metre either side of the planting row. *Pueraria phaseoloides* was  
172 used as a cover crop in the inter-row during the immature phase at both sites to prevent soil  
173 erosion and to improve soil nitrogen status.

174 In mature stands at both sites, trees were tapped every 4 days for latex collection, 6 days  
175 a week (Sunday excluded), either in half spiral cut tapped downward or in quarter spiral cut  
176 tapped upward. Given the confidential nature of latex production in both rubber estates,  
177 nutrient exports in latex could not be considered in the present study.

178

#### 179 **2.4 Biomass and nutrient stocks in trees**

180

181 In the 2-, 5- and 20-year-old plots, 6 trees were selected for destructive measurements  
182 from 6 classes of basal area (i.e. 1 tree per class). In the oldest plots, 10 trees were selected  
183 from 10 classes of basal area. In total, 56 trees were destructively sampled to determine the  
184 biomass and nutrient concentrations in each component.

185 For each sampled tree, the height and circumference were measured (1 m from the  
186 ground for immature stands and 1.7 m for mature stands). The aboveground section was  
187 separated into three components, namely trunk, branches and leaves. Branches were  
188 considered as ramifications below 5 cm in diameter and the trunk consisted of the main stem  
189 and all ramifications above 5 cm in diameter. Due to the difficulty in observing the root  
190 system, 3 out of 6 trees for the aboveground components were sampled in the 2, 5 and 20-  
191 year-old stands, while all trees were sampled, both aboveground and belowground, in the  
192 38-40 year-old plots (i.e. 10 trees). The stumps were uprooted down to a depth of 1 m and  
193 the lateral roots were sampled up to a diameter of 1 cm. The fresh weights of all the tree  
194 components were measured in the field. Subsamples of each component were collected and  
195 weighed for moisture content measurements. The samples were then oven dried (65°C) and  
196 crushed before chemical analyses. The P, K, Ca and Mg concentrations were determined  
197 using a spectrophotometer after digestion by hydrofluoric acid and double calcination. The N  
198 concentration was determined by the Kjeldahl method.

199

#### 200 **2.5 Allometric equations and data analysis**

201

202 We used log-transformed linear equations (Eq. 1) to investigate the relationship between  
203 the biomass of the tree components (leaves, trunk, branches and stump), or nutrient  
204 contents in each tree component, and a predictive variable:

$$205 \ln(y) = \ln(a) + b\ln(x) \quad (\text{Eq.1})$$

206 where  $y$  is the biomass or nutrient stock (kg tree<sup>-1</sup>),  $x$  the predictive variable,  $a$  the intercept  
207 coefficient, and  $b$  the scaling exponent.

208 To estimate the biomass and nutrient contents of each tree component, linear  
209 regressions were tested using diameter as the predictive variable. Diameter is the most  
210 commonly adopted predictive variable for biomass estimations in the case of the rubber tree  
211 (Wauters et al., 2008). Given the different clones and contrasting edaphic conditions  
212 between the study sites, the models were established at site level. The Akaike Information  
213 Criterion (AIC) and adjusted coefficient of determination (adj.  $R^2$ ) were used to select the  
214 best individual models. The model with the lowest AIC and highest adj.  $R^2$  was adopted. The  
215 selected models were applied to the stand inventory of both the reference and additional  
216 plots to assess the biomass and nutrient stock of each component.

217 The use of logarithmic equations might lead to an underestimation of the response  
218 variable  $y$  when converting  $\ln(y)$  to the untransformed scale  $y$ . To correct this bias, a  
219 correction factor (CF) was used for each allometric equation, as proposed by Baskerville  
220 (1972):

$$221 CF = \exp\left(\frac{RSE^2}{2}\right)$$

222 where RSE is the residual standard error of the model. The untransformed  $y$  was then  
223 obtained with the following equation:

$$224 y = e^a x^b + CF \quad (\text{Eq. 2})$$

225 For a given nutrient, the amount accumulated annually in the stand (expressed in kg ha<sup>-1</sup>  
226 yr<sup>-1</sup>) between the ages  $n-1$  and  $n$  were then estimated with the following equation:

$$227 NAR = \frac{\text{nutrient stock}(age_n) - \text{nutrient stock}(age_{n-1})}{age_n - age_{n-1}} \quad (\text{Eq. 3})$$

228 where NAR is the mean nutrient accumulation rate between age  $n-1$  and age  $n$ .

229 The statistical analysis and allometric equations were carried out using RStudio software  
230 (RStudio Inc, Version 1.1463). The effect of stand age on nutrient concentrations as well as  
231 the effect of logging residue management on nutrient removal were investigated using  
232 analysis of variance (ANOVA). The normality of the model residuals and homoscedasticity of  
233 variances' residuals were checked prior the ANOVA. In the case of significant effect ( $p <$   
234  $0.05$ ), Tukey HSD multiple comparisons of means (post-hoc test) was implemented, using  
235 the package *agricolae* (de Mendiburu, 2020).

236



### 237 III. Results

238

#### 239 3.1 Allometric equations

240

241 In total, 48 allometric equations were fitted at the two study sites (Supplementary Table  
242 1). They were used to predict the biomass and nutrient contents (N, P, K, Ca and Mg) in  
243 each tree component (leaves, branches, trunk and stump) from the stand inventories at each  
244 site. Figure 2 shows, as an example, the allometric equations developed to estimate the  
245 nitrogen contents in the tree components. The  $R^2$  value of the tree biomass models ranged  
246 from 0.83 to 0.98 at SAPH and from 0.56 to 0.98 at SOGB. On average, the models  
247 predicting tree nutrient stocks explained 86% and 75% of the variability at SAPH and SOGB,  
248 respectively.

249

#### 250 3.2 Dynamics of stand biomass accumulation

251

252 Tree biomass was 8.6, 51.2, 169.7 and 213.2 t ha<sup>-1</sup> at 2, 5, 20 and 40 years after planting  
253 at SAPH, respectively. The dynamics of tree biomass accumulation were similar at SOGB  
254 with 12.0, 47.9, 164.1 and 255.6 t ha<sup>-1</sup> at 2, 5, 20 and 38 years after planting, respectively  
255 (Figure 3). The highest current annual increment in biomass occurred between 2 and 5 years  
256 after planting, with stand biomass increasing by 493% (14.2 t ha<sup>-1</sup> yr<sup>-1</sup>) at SAPH and by 299%  
257 (12.0 t ha<sup>-1</sup> yr<sup>-1</sup>) at SOGB. Tree biomass at 5 years old accounted for about 20% of the  
258 standing biomass at the end of the plantation cycle. The share of trunk biomass in the total  
259 tree biomass kept increasing as the tree aged: from 33% at 2 years old to 64% at the clear-  
260 cut age at SAPH (from 31% to 74%, respectively, at SOGB). Conversely, the share of foliage  
261 within the total tree biomass sharply decreased from 14% in 2-year-old stands to 2% at the  
262 clear-cut age at both sites. To a lesser extent than for foliage, the share of stump and  
263 branches in the total biomass decreased as the tree aged.

264

#### 265 3.3 Nutrient concentrations

266

267 Regardless of tree age, the average N, P, K, Ca and Mg concentrations in tree  
268 components decreased following the ranking: Leaf > Branch > Stump > Trunk (Table 3).  
269 Changes in nutrient concentrations with tree age were consistent for the two  
270 chronosequences. While N, P and K concentrations in the aboveground tree components  
271 decreased from 2 to 20 years after planting (except in the leaves at SOGB), surprisingly,  
272 these concentrations tended to increase from 20 to 40 years after planting in most of the tree

273 components. Calcium concentrations increased with tree age in the ligneous tree  
274 components at both sites. The consequences of tree aging for Mg concentrations were less  
275 clear. The between-tree variability of nutrient concentrations in the stumps was high, which  
276 led to few significant differences between stand ages.

277

### 278 **3.4 Dynamics of nutrient accumulation**

279

280 The dynamics of N, P and K accumulation showed that the immature phase (the first 6  
281 years after planting) was a period of intense nutrient uptake (Figure 4, Supplementary Figure  
282 2). While the first 5 years covered only 12% of the plantation cycle, the amounts of N, P and  
283 K accumulated in the 5-year-old stands accounted for 25 to 36% of the total amounts at the  
284 clear-cut. N, P and K contents in the trees at 5 years old amounted to 291, 51 and 130 kg ha<sup>-1</sup>,  
285 respectively, at SAPH and 230, 29, and 177 kg ha<sup>-1</sup> at SOGB. The trunk was the main sink  
286 for N, P and K at 5 years old at both sites and the share of the trunk in the total accumulation  
287 of N, P and K in the trees increased sharply up to the end of the cycle. Large amounts of N,  
288 P and K were also accumulated in the branches and the stump at 5 years old, but these tree  
289 components contained a small proportion of the total accumulation in the trees at the clear-  
290 cut. While the accumulation of N, P and K in the trees remained large over the first half of the  
291 latex production phase (from 6 to 20 years after planting) at both sites (except for P at  
292 SOGB), the N, P and K contents in the trees increased much less over the second half of the  
293 cycle, in particular at SAPH. Before the clear-cut, the stocks of N, P and K in the tree  
294 components amounted to 970, 189, and 366 kg ha<sup>-1</sup>, respectively, at SAPH and 908, 118 and  
295 628 kg ha<sup>-1</sup> at SOGB.

296 Unlike the sharp decrease in N, P and K accumulation as the trees aged, the dynamics of  
297 Ca accumulation continued steadily throughout the cycle (Figure 4). Only 15-17% of the total  
298 Ca content in the trees at the clear-cut was accumulated in 5-year-old stands (i.e. 163 kg ha<sup>-1</sup>  
299 at SAPH and 232 kg ha<sup>-1</sup> at SOGB). The accumulation pattern for Mg was intermediate  
300 between that of N, P and K, on the one hand, and that of Ca on the other hand  
301 (Supplementary Figure 2). Before the clear-cut, the amount of Ca accumulated in the trees  
302 was much higher at SOGB (1498 kg ha<sup>-1</sup>) than at SAPH (942 kg ha<sup>-1</sup>). The pattern was  
303 similar for Mg (374 kg ha<sup>-1</sup> at SOGB versus 256 kg ha<sup>-1</sup> at SAPH).

304 At both sites, the nutrient accumulation rates (NAR) in the trees peaked between 2 and 5  
305 years after planting, regardless of the nutrient (Figure 5). Over this period, the highest rate of  
306 accumulation was for N at SAPH (80 kg ha<sup>-1</sup> yr<sup>-1</sup>), while Ca was the nutrient most  
307 accumulated in the trees at SOGB (58 kg ha<sup>-1</sup> yr<sup>-1</sup>), closely followed by N (53 kg ha<sup>-1</sup> yr<sup>-1</sup>).

308 After 5 years old, the NAR of all the nutrients continued to decrease at both sites up to the  
309 end of the plantation cycle.

310

### 311 **3.5 Consequences of the fertilization regime for the immature phase**

312

313 From planting to 2 years old, the conventional NPK fertilization regimes in the rubber  
314 companies led to an input of nutrients to the soil that was much higher (from 30 to 167%)  
315 than the amounts accumulated in the trees (Table 2, Supplementary Table 3), except for Ca  
316 at SOGB (58 kg ha<sup>-1</sup> accumulated in trees vs 40 kg ha<sup>-1</sup> added through fertilization). The input  
317 of Mg to the soil through the addition of dolomite was 14 and 4 times higher than the  
318 amounts of Mg accumulated in the trees at SAPH and SOGB, respectively.

319 From 2 to 5 years after planting, the nutrient input to soil through fertilization at SAPH  
320 was 31, 9 and 34 kg ha<sup>-1</sup> of N, P and K, respectively. The accumulation of N, P and K in the  
321 trees over this period (240, 42 and 104 kg ha<sup>-1</sup>, respectively) was 8, 5 and 3 times higher  
322 than the amounts applied with fertilization (Table 2, Supplementary Table 3). Over the same  
323 period, the SOGB plots received 210, 43 and 173 kg ha<sup>-1</sup> of N, P, and K through fertilization,  
324 respectively. Unlike the plantations at SAPH, the inputs of N, P and K with fertilization  
325 exceeded the amounts accumulated in the trees during this period (161, 20 and 117 kg ha<sup>-1</sup>  
326 for N, P, and K, respectively).

327

## 328 **IV. Discussion**

329

### 330 **4.1 Biomass accumulation in rubber plantations**

331

332 The dynamics of biomass accumulation in our chronosequences were representative of  
333 highly productive rubber plantations worldwide. We found 14 references in the literature with  
334 estimates of biomass in rubber plantations, within the range of 2 to 40 years (Figure 6).  
335 Whilst the critical stage of biomass accumulation occurs over the early growth period, as  
336 shown in our study, there are very few references for immature stands (only 2 at 2 years old  
337 and 6 at 5 years old) compared with mature plantations. Some of the references (6 out of  
338 14), mostly the older ones, did not use an accurate method to estimate stand biomass, but  
339 simply multiplied the biomass of the sampled trees by the stocking density. Inaccurate  
340 estimates (not using allometric relationships) might account for stand biomass values much  
341 higher than those at SAPH and SOGB reported in some studies. The variability in stand  
342 biomass in the literature might also be attributable to factors directly influencing tree growth  
343 related to inherent environmental parameters, such as climate (Munasinghe et al., 2014;

344 Wauters et al., 2008), elevation (Yang et al., 2017), but also related to management  
345 practices such as the stocking density and planting design (Wauters et al., 2008).

346

#### 347 **4.2 Dynamics of nutrient accumulation in tree components**

348

349 Each plantation has its own fertilization schedule built on empirical experience and it was  
350 not possible to sample stands with the same fertilization at the two sites. We compared two  
351 situations representative of commercial plantations in this study (with two clones in two soil  
352 types and two fertilization regimes). Our experimental does not make it possible to  
353 disentangle the effect of the clone from the effects of soil types and fertilization regimes in  
354 the dynamics of nutrient accumulations in the trees at the two sites. However, despite these  
355 differences, the consistent dynamics of nutrient accumulation in the trees at the two sites are  
356 an important finding of our study.

357 A large proportion of the N, P and K stocks in the trees at the clear-cut was accumulated  
358 over the early growth stage while Ca and Mg accumulation occurred linearly as the rubber  
359 tree aged. We showed that the rate of nutrient and biomass accumulation peaked very early  
360 after planting (between 2 and 5 years old). The dynamics of biomass accumulation in rubber  
361 tree components were characterized by a decrease in the share of leaf biomass and an  
362 increase in the share of trunk biomass within the total tree biomass as the plantation aged,  
363 thereby following the general trend for woody species (Miller, 1995). The fast N, P and K  
364 accumulation during early growth could be explained by the early development of nutrient-  
365 rich components, such as leaves and fine roots (not quantified in our study). The early  
366 growth stage of trees is indeed characterized by the maximum production of these two  
367 components acquiring the resources to achieve early dominance (Miller, 1995).

368 However, after the stand achieves its maximum leaf area, competition for light promotes  
369 the development of the trunk and branches, while the crown biomass is merely maintained or  
370 even decreases, as observed in our study. The trunk and branches, characterized by high  
371 Ca and Mg concentrations, became the main nutrient sinks. As the share of foliage in total  
372 tree biomass was less, N, P and K accumulation decreased and, conversely, Ca and Mg  
373 continued to accumulate, with the share of the trunk and branches becoming greater in the  
374 total tree biomass. In addition, mechanisms linked to nutrient retranslocations are largely  
375 involved in such nutrient accumulation dynamics. Rubber tree is a deciduous tree species  
376 that starts shedding its leaves from 4-5 years after planting. Leaf senescence leads to  
377 nutrient retranslocations from dying leaves to woody components, such as the trunk and  
378 branches. In rubber trees, approximately 50% of N, P and K from leaves is retranslocated to  
379 other tree components (Li et al., 2016). The strong biomass accumulation in the trunk and  
380 stump throughout the rotation with little internal remobilisation of Ca and Mg, as shown in

381 other woody species (Santos et al., 2017; Sette et al., 2013), probably leads to more regular  
382 accumulation throughout the cycle.

383 To our knowledge, the only study dealing with the dynamics of nutrient accumulation  
384 throughout the life span of a rubber plantation is Shorrocks (1965b). Our data on nutrient  
385 stocks were much lower than the latter study for all the sampling ages, e.g. for N stocks in 2-  
386 year-old stands, 51 kg N ha<sup>-1</sup> at SAPH vs 72 kg ha<sup>-1</sup> in Shorrocks (1965b), and at the clear-  
387 cut age, 970 kg N ha<sup>-1</sup> at SAPH vs 1779 kg ha<sup>-1</sup> in Shorrocks (1965b). These differences  
388 might be attributable to different methods of calculation, as detailed in section 4.1. The  
389 tendency regarding nutrient accumulation within the stand in Shorrocks (1965b) is in line with  
390 other studies carried out in fast-growing tree species for N and P (high accumulation over the  
391 early growth period) as well as Ca (linear accumulation). However, the accumulation of K  
392 was linear in Shorrocks (1965b), while most of the Mg accumulation occurred over the early  
393 growth period. The nutrient accumulation pattern in our study was consistent with other  
394 tropical tree species, such as teak in Central America (Fernández-Moya et al., 2015) and  
395 eucalyptus in Brazil (Sette et al., 2013). In other eucalypt plantations in the Congo, N, K and  
396 Ca followed the same dynamics as in our study, while a different pattern for Mg and P might  
397 reflect site-specific conditions with high soil P contents (Mareschal et al., 2011) and very low  
398 Mg bioavailability (Laclau et al., 2000).

399

#### 400 **4.3 Influence of the fertilization regime and soil conditions on nutrient** 401 **accumulation in trees**

402

403 The much larger amounts of fertilizer applied at SOGB than at SAPH did not necessarily  
404 increase nutrient accumulation in all the tree components. The dynamics of nutrient  
405 accumulation in trees showed two contrasting behaviours. The influence of nutrient  
406 bioavailability (in the soil and fertilizer inputs) on accumulation in the trees was weak for N,  
407 while the amounts of P, K, Ca and Mg accumulated in the trees at the end of the cycle  
408 reflected their bioavailability, either as exchangeable elements in the soil, or added as  
409 fertilizer. A meta-analysis for tropical tree species in planted forests highlighted a similar  
410 pattern, with phosphorus use efficiency to produce biomass that was much more variable  
411 than nitrogen use efficiency (Inagaki and Tange, 2014) (Figure 7). The latter study suggested  
412 that the accumulation of phosphorus in tree biomass depends more on soil conditions than  
413 on genetic factors, unlike nitrogen accumulation, as demonstrated by Fyllas et al. (2009). For  
414 Ca and Mg, a linear relationship between the accumulation of both nutrients in the trunk of  
415 eucalypt trees and soil Ca and Mg availability was shown for 45 stands in Brazil (Rocha et  
416 al., 2019). Research on plant physiology demonstrated that available P, K, Ca and Mg  
417 uptake rates - and consequently the concentration of these nutrients in the plant tissues -

418 continue to increase with an increase in the nutrient level in the soil solution (Gregory, 1996).  
419 This is consistent with the dynamics of accumulation in rubber trees in our study: the more P,  
420 K, Ca and Mg were available in the soil, the more these nutrients were taken up and  
421 accumulated in the trees.

422 We found that despite higher N and P fertilization at SOGB, the SAPH stands  
423 accumulated more of these two nutrients at 5, 20 and 40 years old. As the tree aged, the  
424 dependence of nutrient accumulation on soil nutrient availability and fertilization seemed to  
425 decrease, which may be due to alternative mechanisms. Firstly, it was demonstrated that  
426 biomass increments in nutrient-poor soils depends greatly on nutrient cycling from litter. In a  
427 study on poor Amazonian soils, Grau et al. (2017) demonstrated that N, P and K contents in  
428 the litter were positively correlated with the quadratic diameter. They hypothesized that  
429 nutrient uptake from litter could reduce the dependence of trees on soil nutrients in the  
430 context of nutrient-poor soils (Vitousek, 1984). In a 25-year-old rubber plantation in Ivory  
431 Coast, annual returns through litter fall amounted to 5.1 Mg ha<sup>-1</sup> yr<sup>-1</sup> (N'Dri et al., 2018). Litter  
432 decomposition results in substantial nutrient fluxes, which are decisive for the productivity of  
433 rubber plantations (Gréggio et al., 2008; Jessy et al., 2009). Further studies are needed for  
434 rubber trees to ascertain to what extent the nutrients released from leaf decomposition  
435 participate in nutrient accumulation within tree biomass.

436 Secondly, nutrient retranslocation increases with tree aging (Millard and Grelet, 2010)  
437 and this mechanism supplies a considerable amount of nutrients for tree growth. In an old  
438 Corsican pine plantation, it was shown that 50% of N and 68% of K was supplied through  
439 retranslocation for new growth, as opposed to 16% and 24%, respectively, in young  
440 plantations (Miller, 1995). For nutrient cycling from litter, retranslocation has been suggested  
441 as a plausible mechanism for reducing the dependency of tree growth on direct nutrient  
442 uptake in a context of poor-nutrient soils (Grau et al., 2017; Sardans and Peñuelas, 2015).  
443 There are very few studies dealing with nutrient retranslocations in rubber trees in the  
444 literature and further research is needed to quantify the amounts of nutrients retranslocated  
445 in different contexts of soil nutrient availability. Lastly, the higher N and P accumulation in the  
446 SAPH stands beyond 5 years old compared with SOGB suggested that other sources of  
447 nutrients (in addition to fertilizers) met the nutrient requirements of the trees. Among other  
448 things, atmospheric N fixation by the cover crop (Clermont-Dauphin et al., 2005), wet and dry  
449 deposits (Shorrocks, 1965a), mineralisation of soil organic matter and decomposition of tree  
450 residues from the previous crop cycle (Yew, 2001) play important roles in tree nutrition. This  
451 emphasises the need to take into account the overall nutrient inputs and outputs in the soil,  
452 as well as the stocks of bioavailable nutrients and the dynamics of tree requirements, to  
453 design appropriate fertilization programmes (Ranger and Turpault, 1999). However, the  
454 biogeochemical cycles of nutrients are still poorly documented in rubber plantations, which is

455 a considerable hindrance for establishing relevant fertilization regimes throughout the life  
456 span of rubber trees (Vrignon-Brenas et al., 2019).

457

#### 458 **4.4 Consequences for managing logging residues**

459

460 Exports of residues for timber use only concerned the trunk (scenario 1, Table 4), while  
461 both the trunk and the branches were harvested for heating use (scenario 2, Table 4). These  
462 two residue management are the most implemented in rubber plantations and led to  
463 considerable exports of nutrients: between 42 and 88% of the nutrient stocks in the trees  
464 were removed depending on the nutrient and the site (Table 4).

465 In agreement with meta-analyses in forest areas (Achat et al., 2015; Wan et al., 2018),  
466 our study suggested that leaving logging residues on site could enhance the growth of  
467 replanted trees over the next rotation, especially in low-fertility soils. In rubber plantations,  
468 logging residues are commonly harvested for economic benefits, either as timber  
469 (Shigematsu et al., 2013), or as firewood for their heating value (Hytönen et al., 2019).  
470 Exporting off-site the large nutrient stocks contained in logging residues might negatively  
471 affect soil fertility (Watson, 1964; Webster, 1989) and the sustainability of future rotations  
472 established on nutrient-poor soils, as shown in tropical forest plantations (Laclau et al.,  
473 2010a; Legout et al., 2020; Versini et al., 2014). In addition to nutrient exports, the removal of  
474 logging residues can reduce C stocks in the topsoil, which can affect soil biological activity  
475 and the long-term sustainability of tropical plantations. Recent studies in Brazil and the  
476 Congo showed that the removal of harvest residues over 2-3 rotations in tropical eucalypt  
477 plantations can reduce C stocks in the topsoil (0-5 cm layer) by 40-50% (Epron et al., 2015;  
478 Rocha et al., 2018). Removing logging residues decreased the enzyme activities and  
479 catabolic potential of the soil microbial community in a Brazilian Ferralsol, suggesting that  
480 exporting all the logging residues could be harmful to soil health in tropical plantations  
481 (Maillard et al., 2019).

482 The amounts of nutrients exported off-site if the whole tree was harvested (scenario 4,  
483 Table 4) were greater than the total amounts applied as fertilisation over the cycle in both  
484 companies. In this scenario at SAPH, where fertilizer applications stopped 3 years after  
485 planting, the stocks of N, P, K, Ca and Mg exported accounted for 120-960% of the nutrient  
486 input through fertilization. At SOGB, the amount of nutrient removed after exporting residues  
487 in scenario 4 accounted for 193-1126% of N, P, K, Ca and Mg fertilization applied from  
488 planting to 5 years old. At the clear-cut stage, the N, P and K exported via logging residues  
489 accounted for 44-99% of N, P and K fertilization applied over the entire plantation cycle.

490 The ability of rubber trees to take up the nutrients released during residue decomposition  
491 is still poorly understood. While the decomposition of logging residues is rapid in rubber

492 plantations, the nutrient accumulation rates show that tree requirements are not linear over  
493 the immature phase, with higher demand between 2 and 5 years after planting. Few studies  
494 have dealt with the dynamics of nutrient releases throughout the decomposition of logging  
495 residues in rubber plantations. Yew (2001) provided some primary information regarding the  
496 decay time for different tree components, but that study did not provide precise  
497 decomposition kinetics making it possible to quantify nutrient releases. In eucalypt  
498 plantations, while some studies in Brazil showed that immobilisation within logging residues  
499 could postpone the release of nutrients relative to tree nutrient needs (Ferreira et al., 2016;  
500 Rocha et al., 2016), an isotopic study in the Congo showed that approximately 40% of the N  
501 content in 2-year-old eucalyptus trees was derived from the labelled logging residues (Versini  
502 et al., 2014). Further studies quantifying the release of nutrients in different types of logging  
503 residues, as well as the dynamics of soil exploration by fine roots after replanting, are  
504 needed to help improve nutrient management practices after replanting in immature rubber  
505 plantations.

506

## 507 **V. Conclusion**

508

509 Our study shows consistent dynamics of nutrient accumulation throughout the growth of  
510 rubber trees in plantations established at two sites with two clones and contrasting  
511 fertilization practices. Nutrient accumulation rate peaked between 2 and 5 years after  
512 planting. While 25 to 36% of the stocks of N, P and K in the trees at the clear-cut stage were  
513 already accumulated at 5 years old, the accumulation of Ca was steady over the entire cycle  
514 of 40 years and the behaviour was intermediate for Mg. After the immature phase, recycling  
515 processes in addition to an increasing proportion of the trunk (with low concentrations of N,  
516 P, K) in total biomass, could account for the accumulation dynamics observed. Our study  
517 shows that logging practices can greatly influence the amounts of nutrients left on-site at the  
518 clear-cut stage, which could greatly influence soil fertility for the next rotation. The amount of  
519 nutrients removed in the case of whole-tree harvesting could account for 120-960% and 44-  
520 99% of the fertilization input over the entire rotation at SAPH and SOGB respectively.  
521 However, knowledge gaps need to be investigated to design more sustainable nutrient  
522 management strategies in immature rubber plantations. A precise assessment of nutrient  
523 input-output budgets over the immature phase is needed to improve the current fertilizer  
524 programmes. Information on the kinetics of nutrient release from logging residues is also  
525 needed to assess to what extent logging residues could replace fertilizers in the first years  
526 after planting.

527



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534

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538

539 **Conflict of interests**

540 The authors declare that they have no conflict of interests.

541

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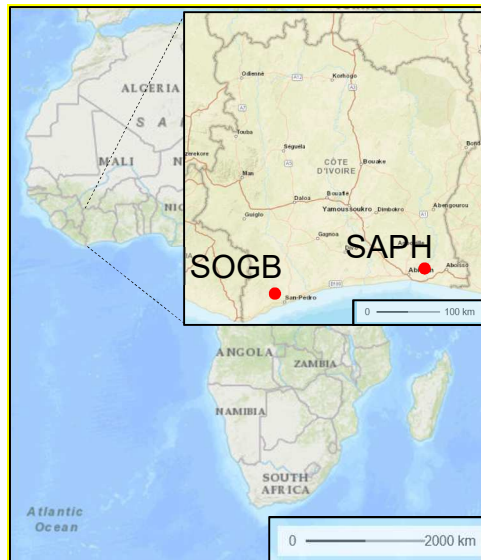


Figure 1: Map of Ivory Coast showing the geographical location of the study sites.

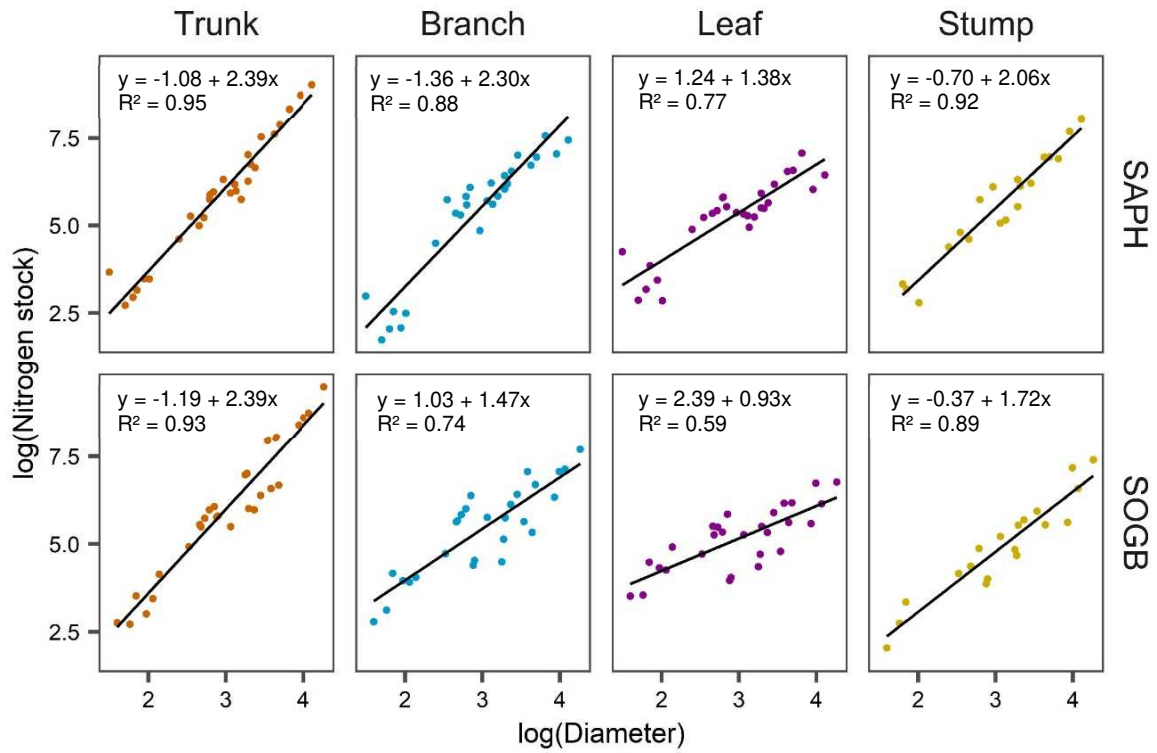


Figure 2: Log-transformed relationships between tree nitrogen stock ( $\text{g tree}^{-1}$ ) and tree diameter (cm) within tree components at SAPH and SOGB. At each site,  $n=28$  for branches, leaves and trunk;  $n=19$  for stumps.

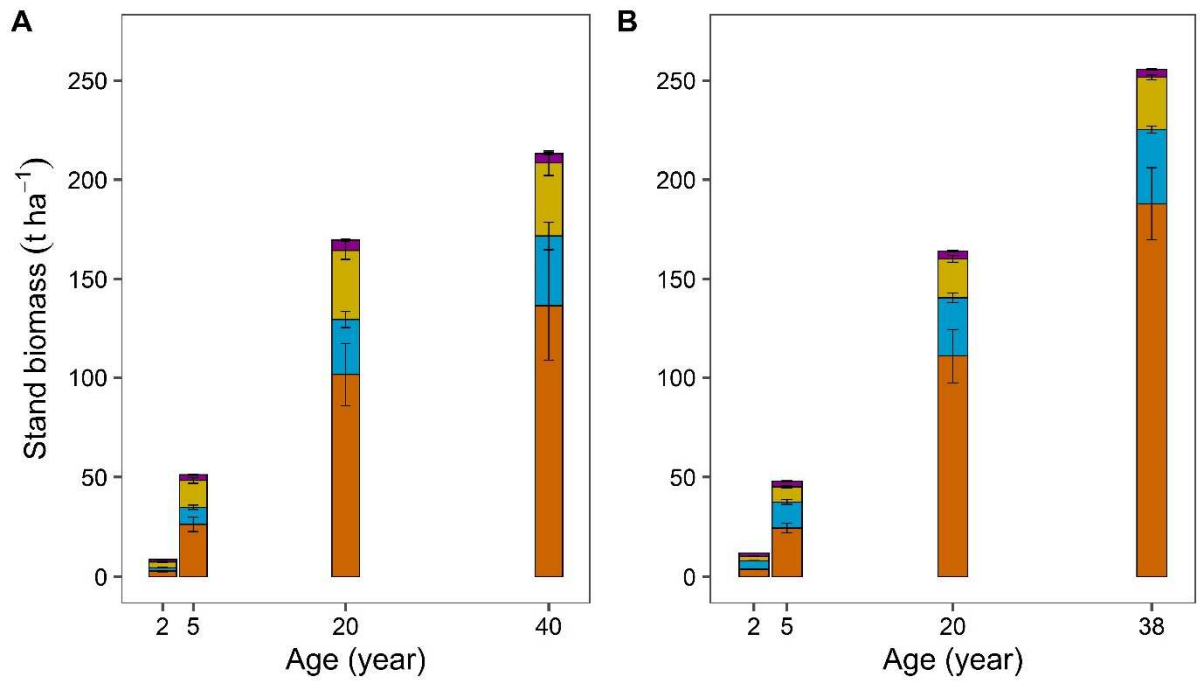


Figure 3: Dynamics of biomass accumulation (t ha<sup>-1</sup>) within tree components throughout the chronosequence at SAPH (A) and SOGB (B) obtained from the allometric equations. Standard deviations between the inventoried stands are indicated for each tree component (n=4).

Caption:





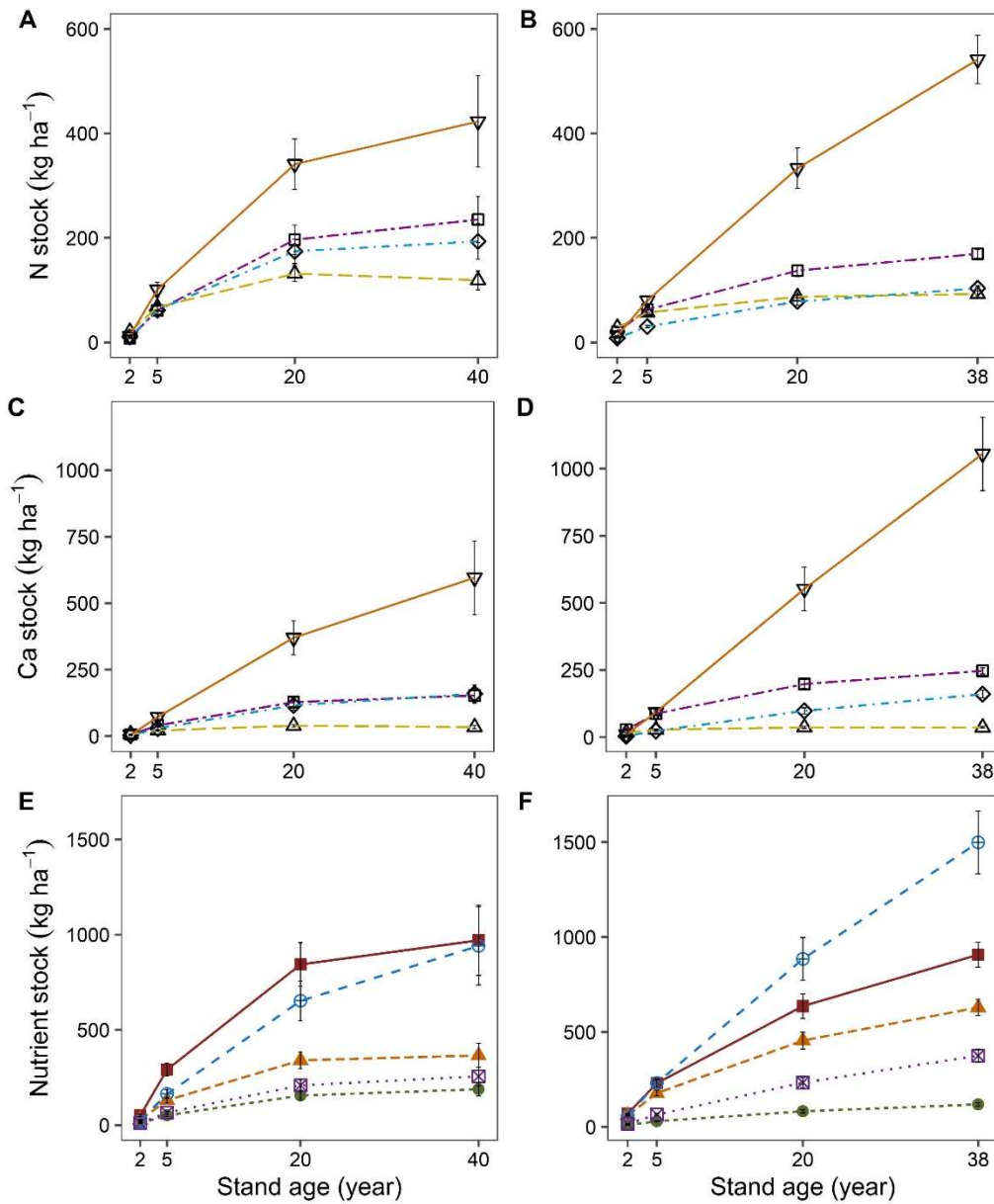


Figure 4: Dynamics of nutrient accumulation (in kg ha<sup>-1</sup>) for nitrogen at SAPH (A) and SOGB (B), calcium at SAPH (C) and SOGB (D) within tree components and in the whole tree at SAPH (E) and SOGB (F), throughout the chronosequence (n=4). Results were obtained from the allometric equations.

Caption Figure 5.A, B, C, D

- Branch
- △ Leaf
- ◇ Stump
- ▽ Trunk

Caption Figure 5.E, F

- N
- P
- ▲ K
- ⊕ Ca
- ⊠ Mg

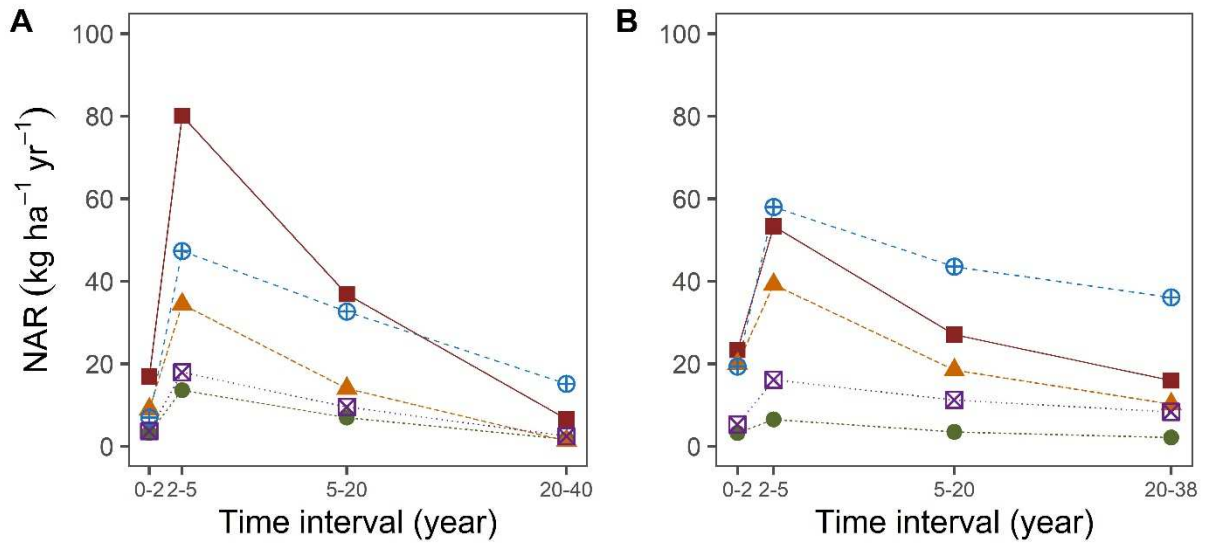


Figure 5: Nutrient accumulation rates (NAR, expressed in  $\text{kg ha}^{-1} \text{yr}^{-1}$ ) within stands throughout the chronosequence at SAPH (A) and SOGB (B).

Caption:

- N
- P
- ▲ K
- ⊕ Ca
- ⊠ Mg

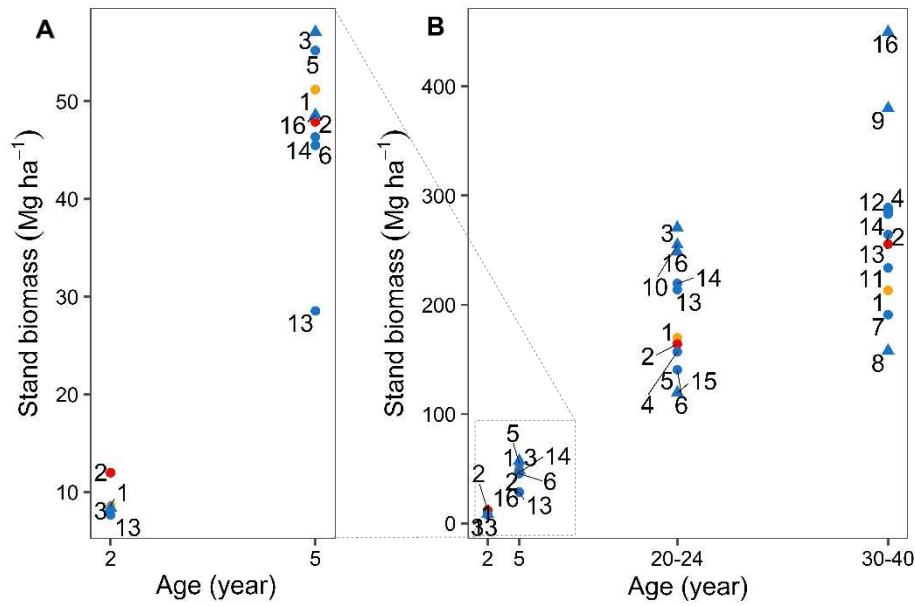


Figure 6: Dynamics of biomass accumulation in rubber stands according to 14 references plus our 2 study sites focusing on early growth (A) or on the whole cycle (B). Circles refer to studies using allometric equations to estimate stand biomass. Triangles refer to studies that estimated stand biomass by multiplying the biomass of the sampled trees by the stocking density. (1) SAPH; (2) SOGB; (3) Shorrocks (1965); (4) Hytönen et al. (2018); (5) Khamyong et al. (2011); (6) Yang et al. (2017); (7) Munasinghe et al. (2014); (8) Yew (2001); (9) Polinière and Van Brandt (1964); (10) Sivanadyan et al. (1995); (11) Méndez et al. (2012); (12) Brahma et al. (2018); (13) Wauters et al. (2008); (14) Petsri et al. (2013); (15) Zhang et al. (2016); (16) Samarappuli (1996).

Caption:

- Allometric equation
- ▲ Other method
  
- SAPH
- SOGB
- Reference data

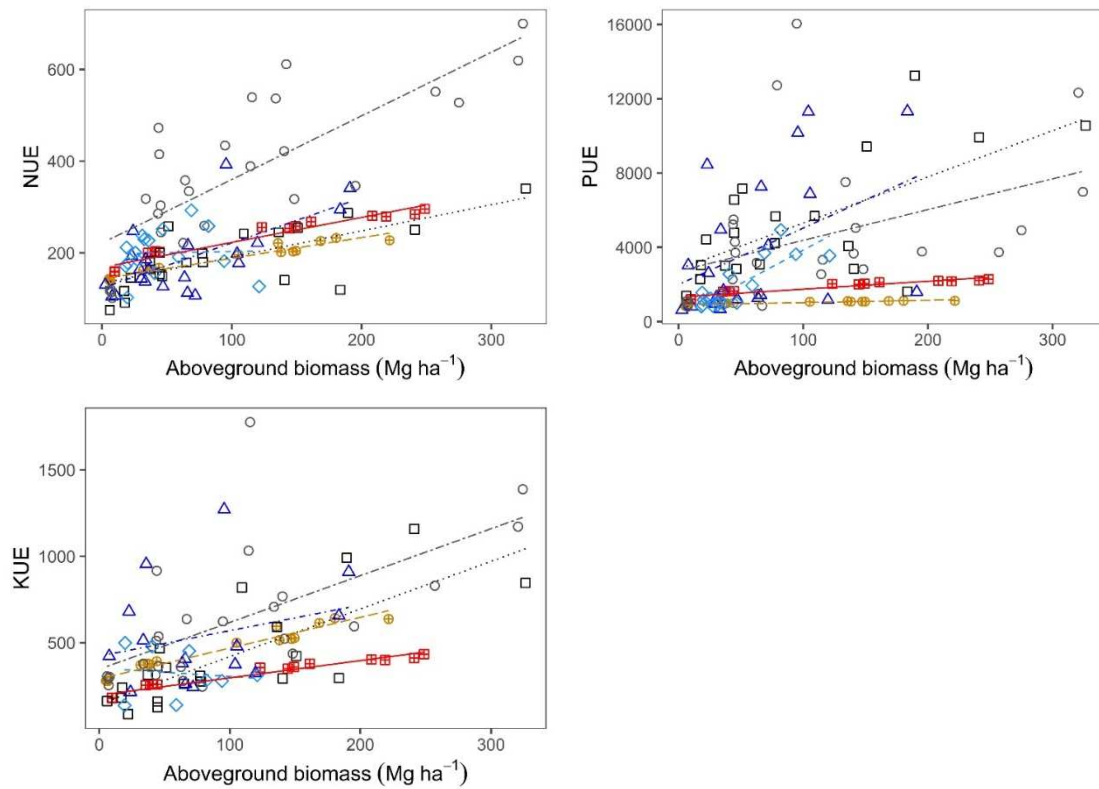


Figure 7: Relationships between aboveground biomass and nitrogen use efficiency (NUE), phosphorus use efficiency (PUE) and potassium use efficiency (KUE) at the SAPH and SOGB sites compared to four reference trees from Inagaki and Tange (2014): *Eucalyptus*, *Acacia*, other non-nitrogen fixing broadleaved trees (ONNFB) and  $N_2$  fixing trees excluding *Acacia*.

Caption:

- Acacia trees
- Eucalyptus trees
- △  $N_2$  fixing trees ex. Acacia
- ◇ ONNFB trees
- SAPH
- SOGB

Table 1: Main soil characteristics in the upper layers (0-30 cm) in the reference plots of the chronosequence at SAPH and SOGB.

Site	Plot age (yr)	pH (H <sub>2</sub> O) <sup>a</sup>	Total C <sup>b</sup> (%)	Total N <sup>b</sup>	P <sup>c</sup> (ppm)	K <sup>d</sup> (cmol kg <sup>-1</sup> )	Ca <sup>d</sup>	Mg <sup>d</sup>	Clay (%)	Silt	Sand
SAPH	2	4.7	0.79	0.05	1.9	0.03	0.43	0.17	9.0	5.0	83.7
	5	5.8	0.99	0.05	3.6	0.02	1.57	0.26	6.5	13.8	79.0
	20	4.8	1.35	0.10	1.3	0.03	0.22	0.17	10.4	12.0	79.2
	40	4.3	0.76	0.06	8.7	0.02	0.25	0.06	10.3	2.1	87.4
SOGB	2	4.9	0.97	0.06	2.9	0.05	0.65	0.35	23.8	27.9	47.5
	5	5.7	0.84	0.07	2.7	0.07	3.89	0.63	25.4	12.4	60.1
	20	4.9	1.33	0.10	2.5	0.04	0.56	0.22	19.1	11.4	66.9
	38	4.7	1.08	0.09	5.4	0.04	0.30	0.12	19.0	15.3	65.9

<sup>a</sup> ratio 1:5

<sup>b</sup> by elemental analyser (FlashSmart™, ThermoFisher)

<sup>c</sup> ion exchange resin method, after extraction and dosage to vanado-molybdate

<sup>d</sup> ammonium acetate method (pH 7)

Table 2: Main characteristics of the stands studied in the two chronosequences, at SAPH and SOGB. Standard deviation among the 3 additional plots are indicated for survival rates, circumferences and tree density at planting.

Site	Plot type	Age (yr)	Survival rate (%)	Mean circumference (cm)	Density at planting (tree ha <sup>-1</sup> )	Tree spacing (m) and planting design	N-P-K-Ca-Mg added since planting (kg ha <sup>-1</sup> )
SAPH	Reference	2	94	18.1	555	6x3 (SR <sup>a</sup> )	70-22-72-82-155
	Additional	2	99 ± 1	17.3 ± 1.2	555 ± 0	6x3 (SR)	70-22-72-82-155
	Reference	5	83	43.1	555	6x3 (SR)	101-31-106-113-214
	Additional	5	90 ± 4	46.0 ± 2.2	555 ± 0	6x3 (SR)	101-31-106-113-214
	Reference	20	87	72.3	476	6x3.5 (SR)	101-31-106-113-214
	Additional	20	87 ± 4	78.3 ± 1.7	555 ± 0	6x3 (SR)	101-31-106-113-214
	Reference	40	66	101.6	500	8x2.5 (SR)	101-31-106-113-214
	Additional	40	54 ± 1	98.0 ± 2.9	511 ± 19	5-8x2.5-4 (SR)	101-31-106-113-214
SOGB	Reference	2	98	19.0	500	8x2.5 (SR)	90-18-76-40-61
	Additional	2	95 ± 0	19.4 ± 0.4	500 ± 0	13-3x2.5 (DR <sup>b</sup> )	90-18-76-40-61
	Reference	5	98	44.7	500	13-3x2.5 (DR)	300-61-250-133-205
	Additional	5	89 ± 3	43.8 ± 1.8	500 ± 0	13-3x2.5 (DR)	300-61-250-133-205
	Reference	20	79	85.0	500	13-3x2.5 (DR)	570-151-520-133-205
	Additional	20	74 ± 12	86.0 ± 8.3	500 ± 0	13-3x2.5 (DR)	570-151-520-133-205
	Reference	38	63	103.7	500	8x2.5 (SR)	917-267-867-133-205
	Additional	38	56 ± 6	111.9 ± 7.3	555 ± 0	6x3 (SR)	917-267-867-133-205

<sup>a</sup> single-row planting

<sup>b</sup> double-row planting

Table 3: Nutrient concentrations in tree components depending on the site and stand age (standard deviations are given in brackets). Different letters indicate significant differences between stand ages at the same site (Tukey post-hoc test with  $p < 0.05$ ).

Site	Stand age (yr)	Tree component	Nutrient concentration (%)				
			N	P	K	Ca	Mg
SAPH	2	Trunk	0.54 (0.06) a	0.09 (0.01)	0.27 (0.07) a	0.08 (0.01) b	0.10 (0.02) ab
	5		0.40 (0.06) b	0.07 (0.02)	0.17 (0.03) b	0.09 (0.02) b	0.10 (0.02) ab
	20		0.19 (0.03) c	0.06 (0.01)	0.07 (0.01) c	0.11 (0.01) b	0.07 (0.01) b
	40		0.38 (0.06) b	0.08 (0.03)	0.18 (0.03) b	0.59 (0.21) a	0.13 (0.04) a
SOGB	2	Trunk	0.32 (0.03) a	0.04 (0.00) b	0.30 (0.02) a	0.12 (0.04) b	0.12 (0.01) b
	5		0.35 (0.04) a	0.04 (0.01) b	0.24 (0.03) b	0.11 (0.02) b	0.10 (0.02) b
	20		0.22 (0.03) b	0.03 (0.00) c	0.17 (0.02) c	0.24 (0.05) b	0.10 (0.02) b
	38		0.34 (0.06) a	0.05 (0.01) a	0.24 (0.03) b	0.90 (0.33) a	0.16 (0.03) a
SAPH	2	Branch	1.13 (0.13) a	0.21 (0.01) a	0.79 (0.28) a	0.66 (0.20) a	0.19 (0.03) a
	5		0.70 (0.12) b	0.13 (0.03) b	0.27 (0.11) b	0.41 (0.16) b	0.14 (0.04) b
	20		0.31 (0.07) c	0.08 (0.02) c	0.10 (0.03) b	0.19 (0.03) c	0.07 (0.01) c
	40		1.07 (0.18) a	0.18 (0.03) a	0.30 (0.07) b	0.59 (0.13) ab	0.12 (0.03) b
SOGB	2	Branch	0.54 (0.03) a	0.08 (0.01) a	0.69 (0.15) a	0.71 (0.20) ab	0.14 (0.02) a
	5		0.58 (0.04) a	0.07 (0.01) ab	0.61 (0.11) a	0.54 (0.12) ab	0.11 (0.00) b
	20		0.29 (0.03) b	0.04 (0.01) b	0.27 (0.09) b	0.35 (0.10) b	0.07 (0.02) c
	38		0.55 (0.15) a	0.07 (0.03) a	0.27 (0.12) b	0.86 (0.33) a	0.13 (0.02) ab
SAPH	2	Leaf	3.2 (0.21) a	0.28 (0.04)	1.06 (0.15) a	1.12 (0.08) a	0.33 (0.05) b
	5		2.94 (0.21) ab	0.26 (0.04)	0.85 (0.18) ab	1.13 (0.21) a	0.42 (0.02) a
	20		2.34 (0.19) b	0.28 (0.08)	0.51 (0.07) c	0.74 (0.09) b	0.36 (0.08) ab
	40		3.00 (0.56) a	0.25 (0.06)	0.76 (0.16) b	0.72 (0.15) b	0.25 (0.05) c
SOGB	2	Leaf	2.28 (0.19) b	0.17 (0.02) ab	1.13 (0.15) b	1.53 (0.37) a	0.27 (0.02)
	5		2.65 (0.23) a	0.19 (0.01) ab	1.00 (0.20) b	1.36 (0.16) a	0.32 (0.03)
	20		2.68 (0.18) a	0.20 (0.01) a	1.45 (0.10) a	0.90 (0.14) b	0.30 (0.06)
	38		2.48 (0.20) ab	0.16 (0.04) b	0.70 (0.20) c	0.97 (0.15) b	0.31 (0.05)
SAPH	2	Root	0.53 (0.02)	0.12 (0.01)	0.25 (0.02) ab	0.14 (0.03)	0.11 (0.01)
	5		0.49 (0.17)	0.10 (0.03)	0.38 (0.13) a	0.23 (0.08)	0.10 (0.04)
	20		0.31 (0.01)	0.09 (0.01)	0.10 (0.02) b	0.14 (0.05)	0.12 (0.03)
	40		0.63 (0.22)	0.09 (0.03)	0.28 (0.10) ab	0.63 (0.46)	0.18 (0.09)
SOGB	2	Root	0.44 (0.02)	0.06 (0.01)	0.35 (0.02)	0.22 (0.08) b	0.09 (0.02)
	5		0.52 (0.04)	0.07 (0.02)	0.32 (0.12)	0.16 (0.02) b	0.11 (0.01)
	20		0.35 (0.02)	0.05 (0.01)	0.20 (0.01)	0.29 (0.06) b	0.16 (0.01)
	38		0.40 (0.09)	0.06 (0.02)	0.31 (0.15)	0.85 (0.38) a	0.31 (0.13)

Table 4: Nutrient removal in different harvesting scenarios (in kg ha<sup>-1</sup>) estimated from the allometric equations. The percentage of total nutrient accumulation in the trees removed by harvesting is given in brackets. Different letters indicate significant differences between scenarios at the same site (Tukey post-hoc test with  $p < 0.05$ ).

Site	Scenario	Nutrient removal (kg ha <sup>-1</sup> )				
		N	P	K	Ca	Mg
SAPH	1. Trunk only exported	423 c (42%)	103 b (52%)	186 c (48%)	596 (60%)	149 b (58%)
	2. Trunk and branches exported	658 bc (68%)	147 ab (73%)	254 bc (69%)	749 (78%)	184 ab (72%)
	3. Trunk, branches and stump exported	851 ab (88%)	177 a (94%)	337 ab (92%)	908 (96%)	243 a (95%)
	4. Whole tree exported (including stump)	970 a (100%)	188 a (100%)	366 a (100%)	942 (100%)	256 a (100%)
SOGB	1. Trunk only exported	541 c (61%)	75 c (64%)	418 c (66%)	1055 b (72%)	257 b (69%)
	2. Trunk and branches exported	732 b (79%)	97 b (82%)	524 b (83%)	1302 ab (88%)	297 b (80%)
	3. Trunk, branches and stump exported	815 ab (90%)	112 a (95%)	597 a (95%)	1462 a (98%)	363 a (97%)
	4. Whole tree exported (including stump)	908 a (100%)	118 a (100%)	628 a (100%)	1498 a (100%)	375 a (100%)