1   **Carbon recovery in secondary forests: insights from three West African countries**

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13   **Abstract**

14   Despite the potential of secondary tropical forests to store and sequester substantial amounts of

15   carbon, little is known about their above-ground carbon (AGC) stocks and the factors affecting them,

16   especially in West Africa. This information is of key importance if the countries in this region want to

17   achieve their forest restoration and climate mitigation commitments. To fill in this gap, we

18   investigated how environmental and local management (e.g. remnant trees) factors influenced AGC

19   and tree species richness in secondary forests at seven sites across Guinea, Sierra Leone and Liberia.

20   We established 140 plots (20 x 50m) in fallows <15 years (20 plots per site) and sampled all trees ≥10

21   cm diameter following standardised protocols. We found that AGC stocks and tree species richness

22   increased with fallow age, but were highly variable across sites driven by both climatic and local

23   management practices. While drought stress negatively affected AGC, remnant trees had a positive

24   effect. AGC recovery rates ranged between 0.72 Mg C ha^{-1} y^{-1} (second driest site) and 13.76 Mg C ha^{-1}

25   y^{-1} (wettest site). Given its low cost, our findings highlight the potential of passive restoration in

26   secondary forests for carbon sequestration, particularly in wetter landscapes and areas with remnant

27   trees from prior land use.

28   **Keywords**

29   Forest growth, Species composition recovery, Tree diversity, Carbon sequestration, Tropical forests

30   **Research Highlights**

31   Above-ground carbon and tree species diversity increased with fallow age

32   Above-ground carbon recovered slower in drier compared to wetter sites

33   Remnant trees had a positive effect on above-ground carbon and species recovery

34   Previous estimates from Ivory Coast are not applicable to the countries we studied

35

1. Introduction

Secondary forests, those growing after the complete clearance of old-growth forests for agricultural purposes, are expanding across the tropics (Vancutsem et al., 2021). There is an increasing interest in such forests and their potential for climate change mitigation, biodiversity conservation and water cycling (Chazdon et al., 2016; Locatelli et al., 2015). For instance, most of the commitments in the Bonn Challenge, which aims to reforest 350 million hectares globally by 2030 -100 of which in Africa- (see Bonn Challenge 2020), are likely to be achieved through passive restoration by natural regrowth (Chazdon et al., 2016). The need to embrace secondary forests as a low-cost, nature-based solution to meet the United Nations' Sustainable Development Goals and the United Nations' Decade on Ecosystem Restoration goals (UNEA, 2019), has been highlighted (Poorter, et al., 2021a). Thus, it is of particular importance to accurately quantify the carbon accumulation rates in these recovering forests, and understand the factors that influence variation in such rates.

Several factors are known to affect forest recovery trajectories at different scales. Climate is an important factor at larger spatial scales (Chazdon et al., 2016; Poorter et al., 2016). In the Amazon, for instance, areas with the greatest seasonal moisture limitation and highest incoming shortwave radiation had slower recovery rates, indicating the role of drought stress in limiting forest recovery (Heinrich et al., 2021). In the Congo Basin, though, these drought-stress associated variables had more limited effects (Heinrich et al., 2023). This aligns with previous work on old-growth forests showing that forests in Central Africa are more resistant to climate extremes than in the Amazon and Borneo (Bennett et al., 2021), driven in part by more drought-adapted tree species in Central Africa (Zhou et al., 2014). However, it is unclear whether these limited climate effects also apply to the Upper Guinean forests of West Africa, as the pantropical study by Heinrich et al., (2023) did not include data from them. Responses may be different in the Upper Guinean forests as they are exposed to hotter temperatures on average than those in Central Africa which could exacerbate seasonal drought stress (Sullivan et al., 2020). Furthermore, this region has a strong south-north

61   climatic gradient, with forests changing from evergreen to semi-deciduous and then to dry forests in

62   just few hundred kilometres (White, 1983)

63   Connectivity between secondary forests and old-growth forests is also critical, as old-growth forests

64   serve as seed/propagule reservoirs and often constitute habitats for dispersing animals (Arroyo-

65   Rodríguez et al., 2017). At local scales, the duration and intensity of cultivation and subsequent

66   influences on soil fertility and the number of remnant trees (trees from the old-growth forest spared

67   during land clearing for farming) are known to be key factors for forest recovery trajectories (Amani

68   et al., 2021; Derroire et al., 2016). With increased duration and intensity (use of pesticides,

69   ploughing) of cultivation, soils are more depleted of both nutrients and propagules, hampering the

70   start of secondary succession (Amani et al., 2021). Remnant trees also determine forest recovery as

71   they modify local microclimate (e.g. shade, moisture) and attract dispersing animals like birds

72   (Derroire et al., 2016). furthermore,the functional identity of remnant trees is ~~also~~ important, with

73   nitrogen-fixing species potentially important as they increase the nutrient availability in the soil,

74   ultimately affecting biomass growth rates in the longer term (Lai et al., 2018).

75   Few studies have focused on forest recovery processes in West Africa (Amani et al., 2021). Recent

76   work from Ivory Coast has shown that above-ground carbon recovery rates in this country (2.1 Mg C

77   ha^{-1} y^{-1}) are much lower than in Tropical America (N'Guessan et al., 2019). However, such slow

78   recovery rates might not be representative for the whole West Africa region, because forested

79   landscapes in Ivory Coast are known to be so degraded that they support an extremely poor fauna

80   (Norris et al., 2010), and the lack of dispersal agents (e.g. birds, bats, monkeys) is believed to impede

81   secondary forest recovery trajectories, even in conditions of good forest connectivity (see Traoré et

82   al., 2024). Indeed, a rate of 4.9 Mg C ha^{-1} y^{-1} has been reported for young (<10 year) fallows in

83   eastern Sierra Leone (Cuni-Sanchez & Lindsell, 2016), while tree diversity increased rapidly in both

84   eastern Sierra Leone and forest clearings in Ghana (Swaine and Hall 1983). As highlighted by Poorter

85   et al. (2021b), we need to better understand how and why forest recovery varies across

86 environmental gradients and broad geographic scales, therefore it is necessary to conduct the study

87 across environmental gradients and broad geographic scales in the West Africa forest region.

88 This study, focused on seven sites in three countries (Guinea, Sierra Leone and Liberia), aims to

89 provide better understanding of forest recovery trajectories across the West Africa forest region.

90 We addressed the following research questions: (a) What are the relative rates of above-ground

91 carbon and tree diversity recovery in abandoned agricultural fields in West Africa? (b) What is the

92 relative influence of regional climatic and local variables (e.g. number of remnant trees) on these

93 recovery rates? (c) What lessons can be drawn for the management of secondary forests in West

94 Africa? We expect faster recovery rates in wetter sites compared to drier sites, and also faster for

95 patches with remnant trees compared to those without.

96 **2.Materials and Methods**

97 *2.1 Study sites*

98 The study was conducted in the secondary forests surrounding seven protected areas in Guinea

99 (Pinselli-Soyah-Sabouyah National Park and Massif du Ziama Biosphere Reserve), Sierra Leone

100 (Outamba-Kilimi National Park, Gola Rainforest National Park) and Liberia (Gola Forest National Park,

101 Wologizi-Wonegizi Nature Reserve, Sapo and Grebo Krahn National Park) (Fig. 1). These sites were

102 selected to represent an environmental gradient from drier (Pinselli and Outamba) to wetter (Sapo

103 and Grebo Krahn) sites, while also representing different farming practices at the local level (Table

104 1). In the drier sites of Pinselli and Outamba, the natural vegetation comprises dry forests and

105 savannas, while in the other sites the forests are evergreen lowland *terra firme*. Outside the

106 protected areas secondary forests of different ages and old-growth forests are distributed in patches

107 within the landscape due to the rotation between slash-and-burn agriculture and the fallowing for

108 forest regrowth.

109 *2.2 Vegetation sampling*

110   In each study area we sampled 20 plots of 20 m x 50 m (total number of plots =140). To capture

111   spatial variation, we sampled two young (5-7 years) and two old (10-15 years) fallows in five

112   different villages per study site. Fallow age was determined by local farmers from each village. We

113   chose these two fallow categories as younger still had open canopy while the older had closed

114   canopies. Within each plot, we recorded tree diameter at 1.3 m along the stem from the ground (or

115   above buttresses if present) of each tree ≥10 cm diameter, following RAINFOR protocols

116   (http://www.rainfor.org/). We choose a 10-diameter threshold as smaller stems contribute little to

117   plot-level above-ground biomass, as shown for different forest types in nearby Togo (Atsri et al.,

118   2020). Stems were identified to species where possible by a professional botanist (co-author

119   M.N.S.), and samples of unidentified trees were collected for identification at either and Institut de

120   Recherche Agronomique de Guinea in Seredou (Guinea), the Herbaria of Njala University (Sierra

121   Leone) or Forestry Training institute (Liberia). Families and species names follow the African Plant

122   Database (http://africanplantdatabase.ch). The final dataset consists of 5,247 stems, of which 95.8

123   % were identified to species, 99.73 % to genus and 99.86 % to family. Data collection took place

124   between October 2022 and April 2023.

125   ***2.3 Aboveground carbon stocks and species composition***

126   For each tree we used Chave et al. (2014) equation to estimate above-ground biomass (AGB), which

127   includes tree diameter (D), wood mass density (ρ) and tree height (H), and is as follows: AGB =

128    $0.0559(\rho D^2 H)$. The best taxonomic match wood density of each stem was extracted from a global

129   database (Chave et al., 2009, Zanne et al. 2009) following (Lewis et al., 2009). For tree height, we

130   built site-level allometric models to predict height (H) from tree diameter (D) using measurements of

131   tree height in adjacent old-growth forests at each site (Sullivan et al., 2018). We compared Weibull,

132   Michalis-Menten and log-log model forms, and selected the Weibull model form [H= a (1−exp(−bD^c)),

133   where a, b and c are estimated parameters and D is diameter at breast height] as it was consistently

134   the best or occasionally second best (lowest root mean square error between predicted and

135   observed height) at each site, and we wanted to use a consistent model form across sites for

136 consistency of cross-site comparisons. Above-ground biomass was then summed across stems in

137 each plot, and converted to above-ground carbon (AGC) stocks using a carbon fraction of 0.456

138 (Martin et al., 2018). For each plot we computed AGC including and excluding remnant trees.

139 Following Cuni-Sanchez & Lindsell. (2016), stems from non-pioneer species with annual growth >3

140 cm year^{-1} (minimum annual growth rates calculated by dividing tree diameter by fallow age) were

141 considered remnant trees. For each plot we also calculated AGC recovery rate (slope of the

142 regression relationship between carbon stocks and fallow age, in Mg C ha^{-1} y^{-1}), tree species richness

143 (number of tree species per plot), proportion of N-fixing stems (all stems) and proportion of N-fixing

144 remnant trees. We assigned species as N-fixing or not according to (Sprent, 2009) and (Diabate et al.,

145 2005). Overall, 19 species in the dataset were found to be N-fixers (see Table S1). To have an

146 indication of differences in tree community composition across sites studied, we also quantified the

147 three most abundant species (in terms of number of stems) in young and old fallows with and

148 without remnant trees at each study site.

149 **2.4 Climatic and landscape data**

150 We extracted monthly precipitation at each plot location from the Worldclim V2 database (Fick &

151 Hijmans, 2017), and used this to calculate maximum cumulative water deficit (MCWD). Starting from

152 the wettest month at each location, we calculated the difference between monthly precipitation and

153 evapotranspiration, taking a figure of 100mm for the latter following (Malhi et al., 2013). If

154 precipitation exceeded evapotranspiration, the excess was assumed to have run off so there was a

155 net balance of zero, while if evapotranspiration exceeded precipitation there would be a negative

156 water balance. This water balance was used as the starting point for the next month, to which the

157 monthly precipitation was added, and the monthly evapotranspiration subtracted. This process was

158 repeated iteratively across the year, and the lowest value was taken as a measure of maximum water

159 deficit. For ease of interpretation, we then switched the sign, so higher MCWD values indicate

160 greater water deficits. We also extracted the average maximum annual temperature and average

161 annual shortwave radiation from Worldclim V2 (see Table 1), but these were not further included in

162 analysis because they were strongly correlated with MCWD (i.e. all sites were on a gradient from hot,

163 sunny and dry to cooler, wetter and cloudier).

164 To have an indicator of potential forest connectivity in the study areas, we estimated forest cover in a

165 4-km buffer around the villages sampled, using the Hansen Global Forest Change (v1.11) dataset

166 (Hansen et al., 2013). We expect that the extent of forest in the local area will provide some

167 indication of propagule pressure and habitat for forest-associated seed dispersers (Selwyn et al.,

168 2023), but note that these could also be influenced by the spatial configuration of forest. We

169 subtracted forest loss (up to 2022) from the tree cover map for the year 2000 (considering canopy

170 closure greater than 30%). While we cannot determine the age of forests, this method ensures that

171 only forest that has remained for at least 22 years is included. Only patches greater than 0.5 hectares

172 (FAO definition of forest) were considered. Google Earth Engine and QGIS 3.34.6 were used to extract

173 spatial data on forest cover.

174 ***2.5 Data analysis***

175 We assessed variation in i) AGC stocks (all stems) and ii) AGC stocks (excluding remnant trees)

176 between sites and with fallow age using linear mixed effects models, with site identity as a random

177 effect. Age was included as a random intercept, permitting variation in stand age effects between

178 sites. AGC stocks were log-transformed to meet model assumptions of normality of residuals and

179 homogeneity of variances across fitted values. P values were obtained using Satterthwaite's

180 approximation. This analysis was repeated for tree species richness (all stems). For tree species

181 richness (excluding remnant trees), we used generalised linear mixed effects models with a Poisson

182 error distribution as the response variable was an integer count.

183 We assessed how site-level variation in AGC stocks and tree species richness related to MCWD using

184 linear and Poisson generalised linear (respectively) models with fallow age, MCWD and their

185 interaction as explanatory variables. To further investigate within-site variation in our response

186 variables, we used the mixed-effects modelling framework described above with age now treated as

187   a continuous variable rather than grouped into age classes, and RT density, % N-fixers (all stems), and

188   their two-way interactions with fallow age also included as explanatory variables. Alternative models

189   with remnant trees density replaced with N-fixer remnant tree density were considered but were

190   less well supported (ΔAIC > 20). The potential for the effect of remnant trees to be non-linear (e.g.

191   facilitation at low densities switching to inhibition at high densities) was assessed by adding a

192   polynomial term for remnant trees, but this model was less well supported than the linear-term only

193   model (ΔAIC = 5.6). Finally, we assessed whether MCWD influenced the effect of remnant trees by

194   adding a two-way interaction between MCWD and remnant trees' density into the above mixed

195   effects models. As forest cover was quite similar across the sites studied (see Table 1), we did not

196   include this as an explanatory variable in the analyses. In highly forested landscapes of DRC,

197   surrounding forest cover did not influence AGC recovery rates in young secondary forests (Moonen

198   et al., 2019).

199   All data analysis was conducted in R version 4.2.2 (R Core Team 2022), with the raster package

200   (Hijmans, 2023) used to process spatial environmental variables, the BIOMASS package (Rejou-

201   Mechain et al., 2017) used to estimate above-ground carbon stocks, the lme4 package (Bates et al.,

202   2015) used to fit mixed effects models, and the lmerTest package (Kuznetsova et al., 2017) used to

203   obtain P values from mixed effects models.

204   **3.Results**

205   ***3.1 AGC stocks***

206   Across sites older fallows contained significantly more AGC (mixed effects model: t = 3.5, df = 6.0, P =

207   0.013 for all stems, t = 19.8, df=50.2, P<0.001 excluding RT), but this difference was less pronounced

208   in drier sites (Fig. 2, a-b). Mean AGC estimates (all stems) for old fallows ranged between 21.1 Mg C

209   ha^{-1} (Pinselli, driest) and 125.9 Mg C ha^{-1} (Sapo, wettest) while AGC recovery rates were 0.72 Mg C ha^{-1}

210   ^{1} y^{-1} (Outamba, second driest) and 13.76 Mg C ha^{-1} y^{-1} (Sapo, wettest). Mean AGC estimates (all

211   stems) for young fallows ranged from 13.6 Mg C ha^{-1} (Wonegizi, third wettest) to 35.1 Mg C ha^{-1}

212   (Gola-L, second wettest).

213   AGC stocks (all stems) showed a significantly negative relationship with MCWD (t = 3.3, df = 10, P =

214   0.009), which was more pronounced in older fallows than younger fallows (Fig. 3a). The MCWD-age

215   interaction was not statistically significant for AGC stocks excluding remnant trees (t = 1.0, df=10, P =

216   0.323), but absolute differences were modelled to be greater in wetter sites because of back

217   transforming long-scale predictions (Fig. 3b). Within-site variation in AGC stocks increased with

218   fallow age and with number of remnant trees (Fig. 4, Table S2). When remnant trees were excluded

219   from AGC calculations, there was a significant interaction between age and number of remnant

220   trees, meaning that older fallows with more remnant trees had higher AGC stocks in non-remnant

221   trees than fallows with fewer remnant trees (Fig. 4b, Table S2).

222   ***3.2 Tree diversity and composition***

223   Across sites older fallows contained significantly more tree species (Poisson mixed effects models, z =

224   5.2 and 6.8 for all stems or excluding remnant trees respectively, df= 135, P<0.001), but this

225   difference was again less pronounced in drier sites (Fig. 2, c-d). Tree species richness (all stems)

226   showed a significantly negative relationship with MCWD (t=2.6, df = 10, P = 0.026), which was more

227   pronounced in older fallows than younger fallows (Fig. 3c). Tree species richness (excluding remnant

228   trees) also showed a significantly negative relationship with MCWD (t = 2.3, df = 10, P = 0.048) (Fig.

229   3d). As for AGC, within-site variation in tree species richness increased with fallow age and with

230   number of remnant trees (Fig. 4c-d, Table S2). In terms of tree composition, most abundant species

231   varied across sites, especially between the two driest sites (Pinselli and Outamba) and the others

232   (Table 2). Except in these two driest sites, rapidly-growing pioneer species (such as *Musanga*

233   *cecropioides* and *Macaranga* spp.) were more abundant in plots without remnant trees while long-

234   lived pioneer species (*Funtumia* and *Albizia* spp.) were more abundant in plots with remnant trees

235   (see Table 2).

236   At site level there was positive relationship between tree diversity (mean tree species richness) and

237   AGC change (slope = 1.43, SE = 0.43, t = 3.37, df = 5, P = 0.020), but this is probably because both

238   were related to a moisture gradient. AGC stocks also increased with tree diversity (slope with log

239 carbon = 0.106, SE = 0.010, t = 11.0, df= 138, P < 0.001). When all stems were considered, there was

240 a marginally non-significant interaction between fallow age and the proportion of N-fixers (P = 0.056,

241 Table S2), with an initially negative effect of N-fixer dominance in young fallows reversing to be

242 positive in old fallows. N-fixer dominance (with regard to % of stems) varied considerably across

243 sites, from 2.4% to 35% (Pinselli and Ziama respectively, see Table 2).

244 **4.Discussion**

245 ***4.1 AGC stocks***

246 We found that AGC stocks of 10-15-year fallows ranged from 21 to 126 Mg C ha^{-1} across the

247 landscapes studied (including remnant trees, see Fig. 2), with rates of recovery influenced by both

248 regional climatic factors and by local scale factors. Our results add to the evidence that water

249 availability is a key constraint on AGC recovery of tropical forests (Fig. 3). This pattern has been well

250 documented in tropical American forests (Chazdon et al., 2016; Heinrich et al., 2021), but was found

251 to be weaker in Central African forests, potentially due to the inherent drought resistance of African

252 tropical forest tree communities (Heinrich et al., 2023). By sampling of the hotter and drier Upper

253 Guinean forests, our results show that West African tropical forests do show a pronounced biomass

254 recovery response to water availability. Our results also showed that the effect of water availability

255 was not limited to AGC recovery, as tree species richness of secondary forests was also lower when

256 water availability was most limited. The support our study provides for the role of water availability

257 limiting forest recovery in West Africa has implications for biome-wide predictions of forest recovery,

258 as water availability, together with other climate variables, could be used to predict secondary forest

259 recovery. The sensitivity of secondary forests to water availability also has implications for the

260 temporal sustainability of forest restoration in climates that have the potential to become drier in the

261 future.

262 Our results also provide support for the role of remnant trees in determining AGC recovery and

263 species richness of non-remnant trees (see Fig. 4). This is consistent with previous research in West

264 Africa (e.g. Amani et al.,2022; Cuni-Sanchez & Lindsell, 2016), but extends this research by showing

265 that effects persist over a broad climate gradient, and provides further support for their effect on

266 tree species richness (Sandor & Chazdon, 2014). The positive relationship between the number of

267 remnant trees and the AGC and tree species richness of newly established trees is consistent with

268 remnant trees facilitating the establishment of other trees (i.e. facilitated succession sensu Connell &

269 Slatyer, 1977, e.g. by modifying the local microclimate through shading), or could also arise through

270 remnant trees attracting seed dispersers (Guevara et al., 1986).

271 Within a West African context, we found some differences between our results and patterns of forest

272 recovery from previous work. Our AGC estimates are greater than those reported for Ivory Coast: e.g.

273 below 20 Mg C ha^{-1} were recorded for 10-year fallows in several sites across that country (Amani et

274 al., 2022) while 22.1 Mg C ha^{-1} were recorded for 20-year fallows in the south-east (N'Guessan et al.,

275 2019). This would be consistent with the higher forest degradation and lack of dispersing agents in

276 Ivory Coast limiting forest recovery there relative to our study areas. Our AGC estimates are within

277 those reported for similar-aged fallows elsewhere in the Congo Basin (see Table 3), although our

278 estimates from our wettest site are slightly greater, probably because of larger number of trees left

279 when land clearing in Sapo.

280 In terms of recovery rates, estimated rates ranged between 0.7 and 13.7 Mg C ha^{-1} y^{-1} across the

281 landscapes studied, also being greater in wetter sites. Our findings differ from those from Ivory

282 Coast, where AGC recovered faster in the drier northern region (compared to central or southern

283 regions) and authors linked it lower competition between understory annual herbaceous plants and

284 tree seedlings in that region (compared to central/southern regions with perennial herbaceous

285 plants) (Amani et al., 2022). In all our study sites, given high canopy cover, perennial herbaceous

286 plants were rare in the understory (M.S. Pers. Obs. 2024), which is very different from the situation

287 reported in Ivory Coast. Another possible explanation of differences in AGC recovery rates between

288 Ivory Coast and our study is crop(s) cultivated and farming practices. N'Guessan et al. (2019) showed

289 lower AGC recovery rates for abandoned rice fields compared to yam, cassava or maize abandoned

290   fields, which were all grown in mostly monocropping systems. In our study sites, though,

291   polycropping is the norm (as shown in Table 1).

292   AGC recovery estimates in our wetter sites are much greater than estimates from elsewhere in

293   tropical Africa, probably because of larger number of trees left when land clearing. For instance, 1.98

294   Mg C ha^{-1} year^{-1} have been reported for the Congo Basin (Heinrich et al., 2023), while 3.2 Mg C ha^{-1}

295   year^{-1} has been reported for Kenya (Ojoatre et al., 2024). Previous work from Cameroon also

296   reported relatively high rates which range from 3.9 Mg C/ha^{-1}year^{-1} (see Njomgang et al., 2011) to 9.4

297   Mg C ha^{-1} year^{-1} (see Kotto-Same et al., 1997) . Most likely greater number and sizes of remnant

298   trees left when land clearing in our wetter sites explain these differences, although local soil

299   properties – which we did not investigate in this study- might also be of importance.

300   **4.2 Tree diversity and composition**

301   Tree diversity and composition were also highly variable across the landscapes studied, modulated

302   by climate (MWCD) and remnant trees (Fig. 3-4), with higher diversity in wetter sites and in plots

303   with remnant trees. Our results support previous work from southern Sierra Leone (Cuni-Sanchez &

304   Lindsell, 2016) showing that rapidly growing pioneer species such as *Musanga cecropioides, or*

305   *Macaranga* spp. are more abundant in plots without remnant trees while long-lived pioneer species

306   are more abundant in plots with remnant trees, indicating that remnant tree presence shortened

307   fallow tree species' composition recovery. In a certain way, remnant trees facilitated the

308   establishment of the 'second stage' of the succession with abundant longer-lived pioneers like *Albizia*

309   or *Funtumia* spp., skipping the 'first stage' of the short-lived *Musanga cecropioides* . Results from

310   secondary forests in Ivory Coast have highlighted that tree diversity recovers faster than composition

311   or AGC (Amani et al., 2022), with no details on species recorded, so we were unable to compare our

312   results with theirs. In Yangambi in DRC, *Musanga cecropioides* and *Albizia adianthifolia* were also

313   amongst the three most abundant tree species in 5–10-year fallows (Mangaza et al., 2022), indicating

314   what would be a mix of the first and second stage of the succession as we describe here in West

315   Africa.

316   When considering tree diversity effects on AGC, we found a weak positive relationship between tree

317   diversity and AGC recovery, but this is likely to be driven by moisture effects rather than niche

318   complementarity as both AGC and tree species richness increased along the gradient of moisture

319   availability. Other studies on secondary forests have found that tree species diversity alone was not a

320   good predictor of AGC change over time. For example, in secondary forests in Mexico, forest age-

321   mediated effects on stand structural changes and species composition were better predictors of AGC

322   than the changes in tree diversity during succession (Aryal et al., 2024). In South Africa, niche

323   complementarity between canopy, sub-canopy, and emergent tree species explained the

324   relationships between stand diversity and biomass storage (Mensah et al., 2018).

325   With regard to N-fixer effects on AGC recovery, we found limited effects. N-fixation tends to be

326   common in early stages of the forest recovery succession – as there is abundant light and trees can

327   easily provide carbohydrates to their nitrogen-fixing symbionts (Batterman et al., 2013). But it

328   declines over time as light availability in the stand drops (Matsuo et al., 2021), and nitrogen fixation

329   becomes too costly (Battmerman et al., 2013). In DRC, a decrease in abundance of pioneer species

330   and an increase in N-fixing species early in succession of secondary was observed after repeated

331   clearing (Bauters et al., 2021). It is possible differences in clearing cycles or local soil properties, such

332   asPhosphorous or other Cations being more limiting than N in some sites, explain some of the

333   differences observed across the seven sites we studied, factors which should be considered in future

334   research. Future research focusing on tree diversity or composition should also consider using a

335   smaller tree diameter threshold, as trees <10cm diameter might not be major contributors to plot-

336   level AGC, but can be important components of forest composition and diversity (e.g. (Atsri et al.,

337   2020).

338   ***4.3 Implications of the findings***

339   What specific lessons can be drawn for the management of secondary forests in West Africa? First,

340   our findings show that previous work on trajectories of secondary forest recovery in Ivory Coast (a

341   country characterised by high forest degradation, see Traoré et al. 2024) is not applicable to

342   secondary forests found in Guinea, Sierra Leone or Liberia. Second, our findings also show that AGC

343   recovery is highly variable in these countries, driven by both regional climate (e.g. MWCD) and local

344   farming practices (e.g. remnant trees). Therefore, insights into local contexts should be gathered

345   before making any decision on their management. We recommend the consideration of MCWD

346   instead of other climatic variables such as annual rainfall or precipitation seasonality (used by e.g.

347   Amani et al. 2022; Traoré et al. 2024), as this variable has been shown to be more meaningful in

348   tropical forest contexts (Sullivan et al., 2020), including in the study of secondary forests (Heinrich et

349   al., 2021, 2023).

350   Overall, our findings also highlight the potential role of passive restoration of secondary forests for

351   carbon sequestration in most of the West African landscapes we studied, except in driest sites, where

352   active restoration might be needed. Apart from helping contribute to these countries' restoration

353   commitments in the Bonn Challenge (see Bonn Challenge 2020), secondary forests are likely to gain

354   importance to local communities, as old-growth forests continue to disappear. In fact, a complete

355   loss of old-growth forest before 2100 has been predicted for Guinea and Sierra Leone under a

356   business-as-usual scenario, including inside protected areas (see, Vieilledent et al., 2022). Notably,

357   for secondary forests to be left to continue recovering and sequestering carbon, local farmers would

358   need to change their farming practices from slash-and-burn to permanent farming, in which case

359   both external support and training would be needed. As secondary forests remain a source of

360   important ecosystem services to local communities, such as wild edible fruits and medicinal

361   plants(Cuni-Sanchez et al. in press), continued access to these important ecosystem services should

362   be ensured, even if carbon sequestration is a management priority at regional or national level.
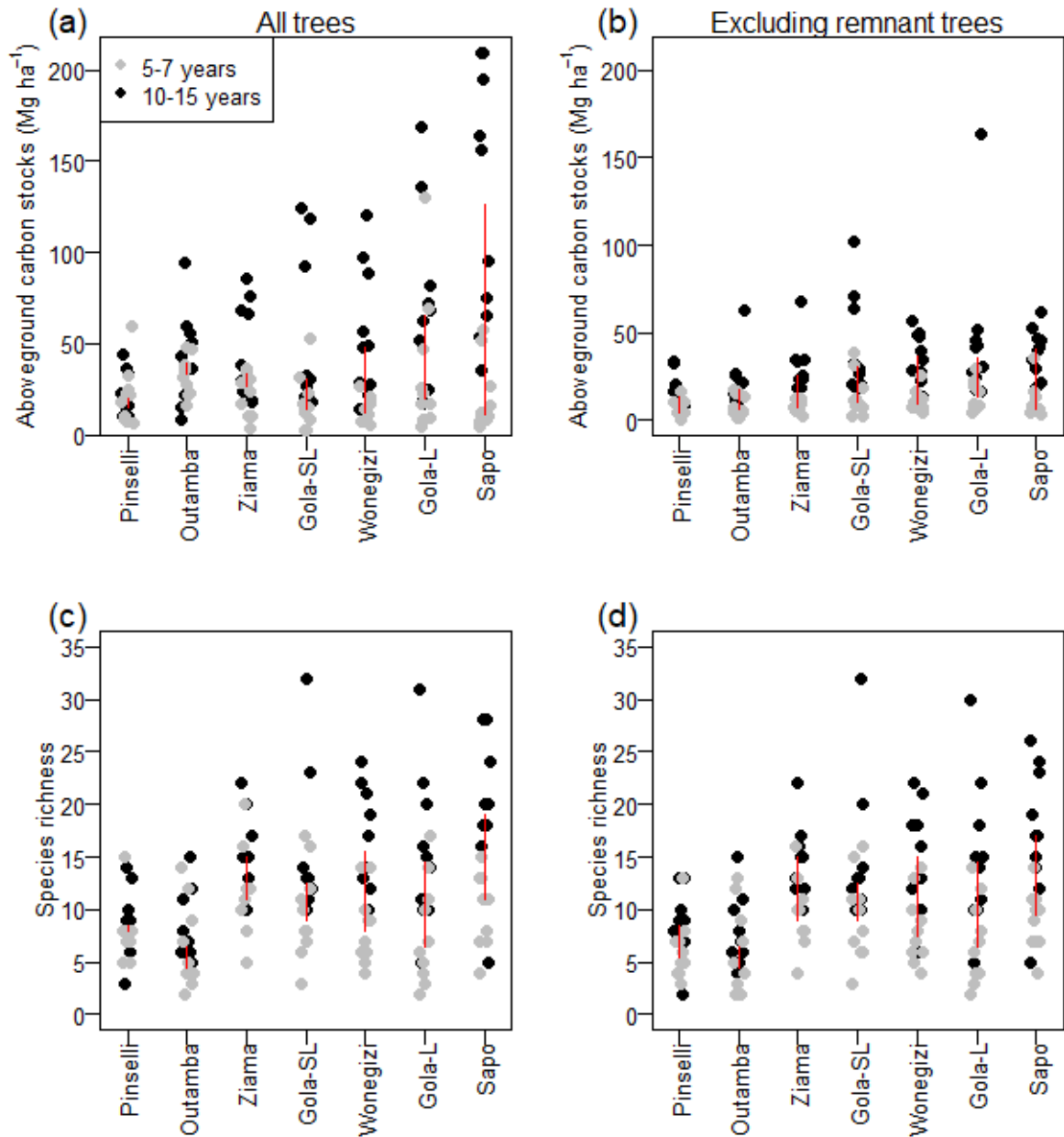
363

Figures and Tables
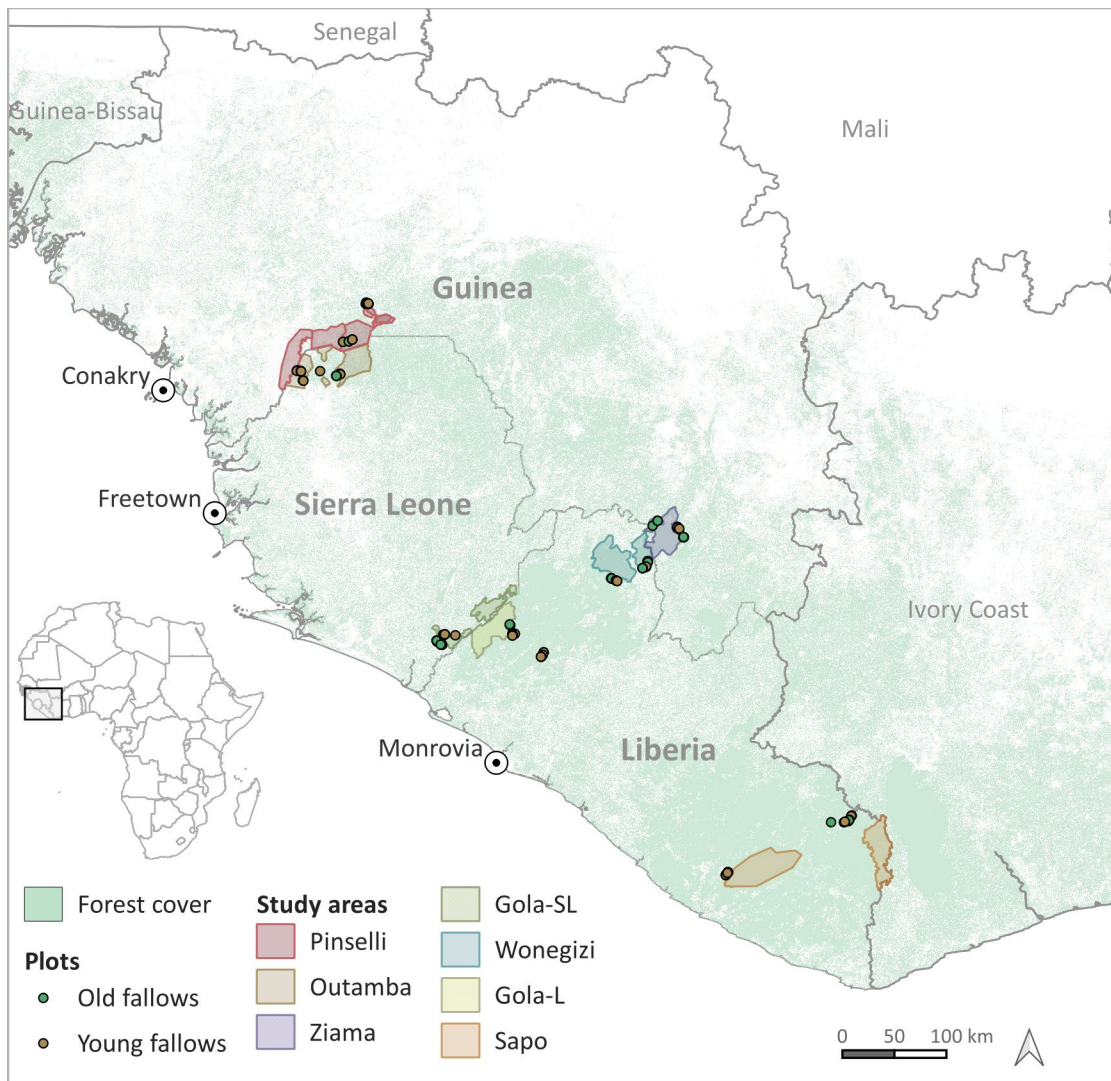
Fig. 1. Selected study sites. For details see Table 1.

370

371 **Fig. 2.** Variation in above-ground carbon (AGC) stocks (a-b) and tree species richness (c-d) within and

372 between sites. Sites have been ordered from driest (left) to wettest (right) based on the maximum

373 cumulative water deficit. Grey points: young fallows (5-7 years old); black points: old fallows (10-15

374 years old). The red lines show the difference between the mean AGC stocks (or tree species richness)

375 in young/old fallows in each site.

376

377
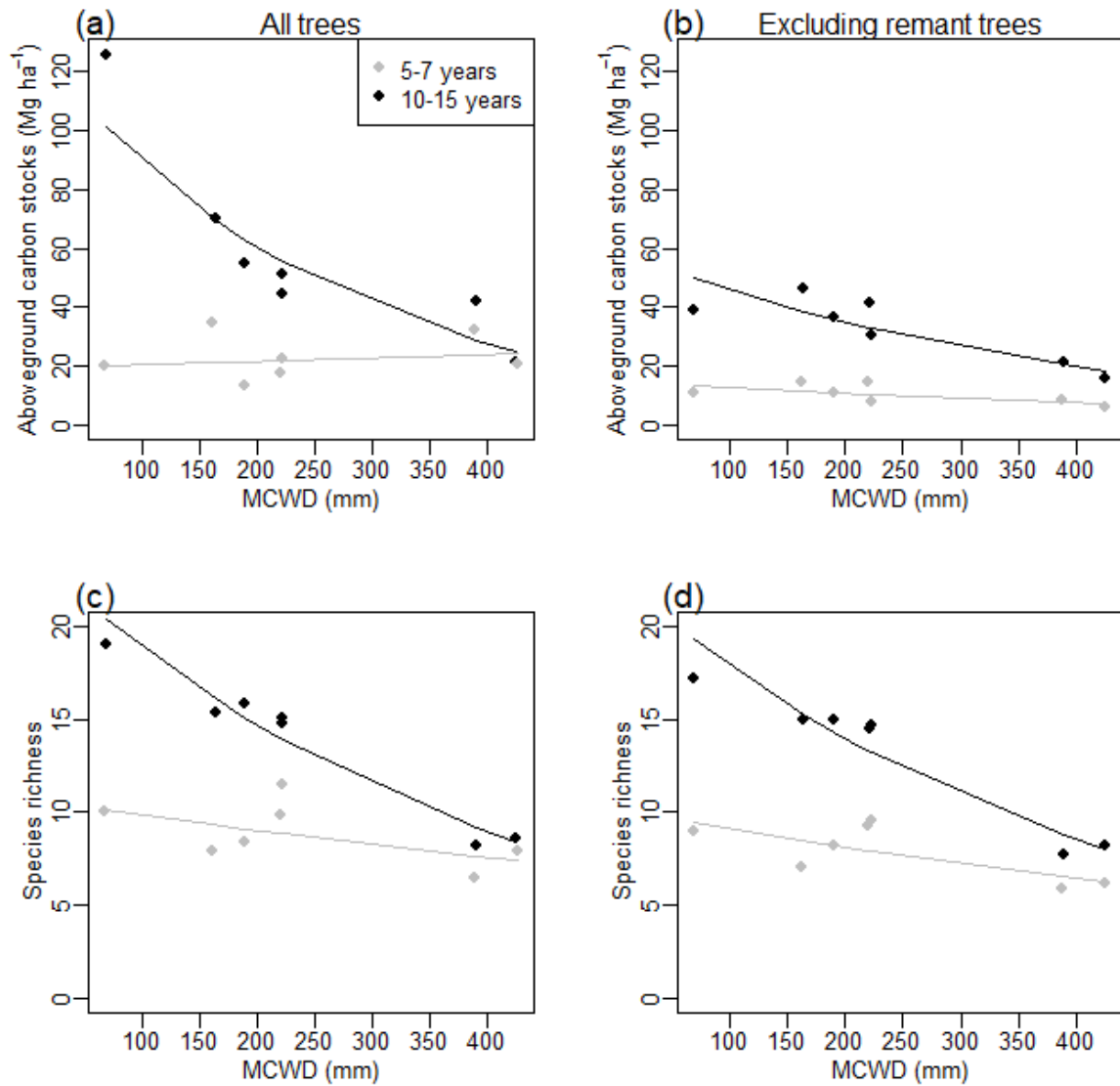
Fig. 3. Relationship between the maximum cumulative water deficit (MCWD) and above-ground

carbon stocks (a-b) and tree species richness (c-d). High MCWD values indicate greater moisture

limitation. Black and grey points indicate mean values per site considering old (10-15 years) and

young (5-7 years) fallows, respectively. Lines indicate modelled relationships from linear models with

MCWD, age category and their interaction as explanatory variables.
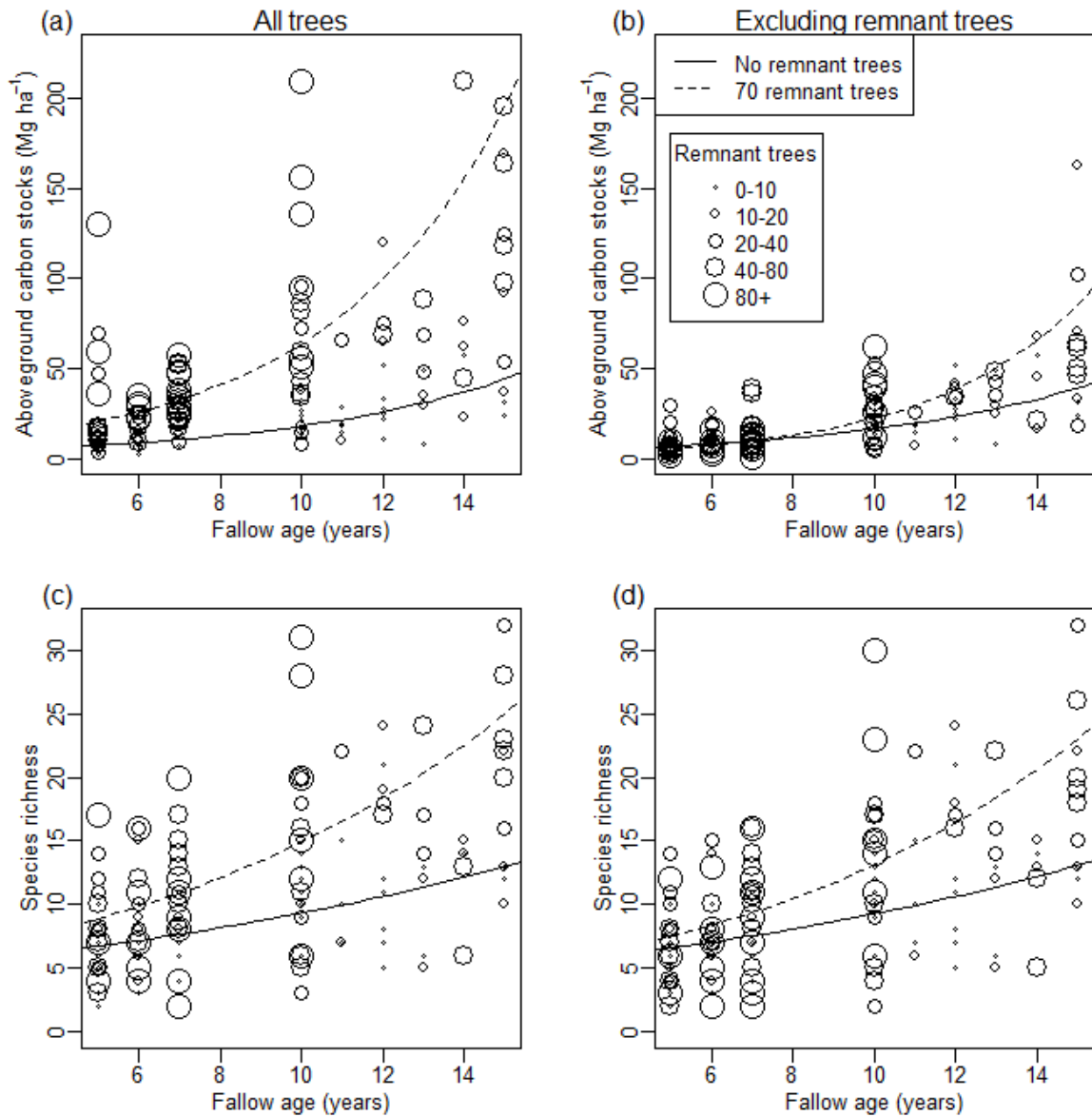
383

384 **Fig. 4.** Effect of fallow age and number of remnant trees on above-ground carbon stocks (a-b) and

385 tree species richness (c-d). Symbol sizes indicate the number of remnant trees. Lines show model

386 predictions with no remnant trees (solid line) and 70 remnant trees (dashed line, representing one

387 standard deviation above the mean). Model coefficients are presented in Table S1.

388

Table 1. Overview of selected study sites, ordered by maximum cumulative water deficit (MCWD).

Code	Full name	Annual rainfall (mm)	Maximum temperature-warmest month (℃)	Mean annual temperature (℃)	MWCD (mm)	Dry season length (months)*	Shortwave radiation (kJ m^{-2} day^{-1})	Main crops**	Forest cover (%)
Pinselli	Pinselli-Soyah-Sabouyah National Park (Guinea)	1959	34.1	26.1	426	6	18350	peanuts, rice, millet	65
Outamba	Outamba-Kilimi National Park (Sierra leone)	2445	35.4	27.6	389	5	18055	peanuts, rice, millet, sesame	56
Ziama	Massif du Ziama Biosphere Reserve (Guinea)	2270	32.7	24	222	4	16635	rice, cassava, banana	76
Gola-SL	Gola Rainforest National Park, Sierra Leone	2933	32.5	26.2	221	4	16216	rice, cassava, sweet potatoes	66
Wonegizi	Wonegizi Nature Reserve (Wologizi is proposed only) (Liberia)	2331	33.4	24.6	190	3	16289	rice, cassava, banana	55
Gola-L	Gola Forest National Park, Liberia	2684	32.5	25.5	163	3	16006	rice, cassava, sweet potatoes	91
Sapo	Sapo and Grebo Krahn National Parks (Liberia)	2542	31.8	25.5	69	2	16174	rice, cassava	82

*Dry season length defined as months with <100mm precipitation, **order of main crops does not reflect importance.

Table 2. Comparison between the top three most abundant tree species in old fallows at each study site, considering plots with or without remnant trees. (n) refers to number of plots. * indicates N-fixing species

	No remnant tree	With remnant tree
	Pinselli (n=6)	Pinselli (n=4)
1	*Piliostigma thonningii 37*	*Spondias mombin 28*
2	*Terminalia schimperiana 22*	*Ficus sur 15*
3	*Margaritaria discoidea 21*	*Anthonotha crassifolia 14*
% stems	47.4	44.2
% N fixers	2.4	6.5
No. of Spp. recorded	26	20
	Outamba (n=5)	Outamba (n=5)
1	*Pterocarpus erinaceus* 36*	*Gmelina arborea 30*
2	*Combretum glutinosum 30*	*Spondias mombin 20*
3	*Crossopteryx febrifuga 27*	*Sterculia setigera 11*
% stems	51.7	37.4
% N fixers	25.9	14.4
No. of Spp. recorded	19	35
	Ziama (n=6)	Ziama (n=4)
1	*Albizia zygia* 36*	*Albizia zygia* 18*
2	*Cathormion altissimum 21*	*Funtumia africana 18*
3	*Margaritaria discoidea 21*	*Funtumia elastica 10*
% stems	34.8	26.9
% N fixers	35.3	27.6
No. of Spp. recorded	47	48
	Gola-SL (n=7)	Gola-SL (n=3)
1	*Macaranga barteri (95)*	*Smeathmannia pubescens(16)*
2	*Margaritaria discoidea(44)*	*Funtumia africana (15)*

3	*Musanga cecropioides (27)*	*Baphia nitida* (15)*
% stems	47.03	25.7
% N fixers	13.2	16.3
No. of Spp. recorded	37	45
	Wonegizi (n=7)	Wonegizi (n=3)
1	*Albizia zygia* 47*	*Funtumia africana 19*
2	*Albizia adianthifolia* 39*	*Albizia zygia* 12*
3	*Macaranga barteri 39*	*Myrianthus libericus 12*
% stems	39.6	26.7
% N fixers	33.8	20.6
No. of Spp. recorded	64	46
	Gola-L (n=4)	Gola-L (n=6)
1	*Musanga cecropioides (66)*	*Macaranga barteri 66*
2	*Harungana madagascariensis 33*	*Ficus mucuso 31*
3	*Margaritaria discoidea 20*	*Funtumia africana 26*
% stems	63.6	30.9
% N fixers	7.3	13.0
No. of Spp. recorded	21	66
	Sapo (n=1)	Sapo (n=9)
1	*Albizia zygia* 9*	*Funtumia africana 105*
2	*Macaranga barteri 8*	*Macaranga barteri 50*
3	*Funtumia africana 7*	*Macaranga hurifolia 28*
% stems	88.9	37.6
% N fixers	37.0	9.7
No. of Spp. recorded	5	85

Table 3. Literature-derived estimates of above-ground carbon (AGC Mg C ha^{-1}), AGC change (in Mg C ha^{-1} y^{-1}), number of plots sampled, minimum tree diameter sampled (Diam, in cm), equation used to estimate AGC and references.

Location	AGC	AGC change	No plots	Plot age	Diam	AGB equation	Publication
Seven sites across Guinea, Sierra Leone and Liberia	21-125	0.7 -13.7	70	10-15 yrs	10	Chave et al., 2014	this study
Gola-SL, Sierra Leone	80	4.9	33	7-10 yrs	5	Chave et al., 2014	Cuni-Sanchez & Lindsell, 2016
Agbo I State Forest, south-east Ivory Coast	22.16*	2.1	26	<11 yrs	2.5	Chave et al., 2014	N'guesssan et al., 2019
Eight sites across Ivory Coast	<10.94*		32	<11 yrs	2.5	Chave et al., 2014	Amani et al., 2022
Maringa- Lopori- Wamba landscape, Tshopo Province, DRC	65.7		3	<25 yrs	10	Chave et al., 2014	Bauters et al., 2019
3 villages, Tshopo Province, DRC	34.66*		6	10 yrs	5	Chave et al., 2014	Moonen et al., 2019
Yangambi Forest, Tshopo Province, DRC	13.68*		4	5-10yrs	10	Chave et al., 2014	Mangaza et al., 2022
Yoko Forest, Tshopo Province, DRC	25		3	5yrs	10	Chave et al., 2014	Makelele et al., 2021
Mean Congo Basin (remote sensing analysis)	50	1.98	na	20 yrs	na	na	Heinrich et al., 2023
Five permanent forest estates, Ghana	47.25*		17	48 yrs	10	Chave et al., 2014	Brown et al., 2020

*values reported in publication refer to AGB, converted to AGC using 0.456 ratio.

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Author contributions

M.N.S. and A.C.-S. conceived the study. P.N.T and M.N.S. led the field campaigns, assisted by U.K., R.A.S.K, A.M, T.M.K, and B.K.B, with help from E.A., A.L. P.N.T, M.J.P.S. and A.C.-S. analysed the plot data and wrote the manuscript. All co-authors read and approved the manuscript.

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