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

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Abstract

Despite the potential of secondary tropical forests to store and sequester substantial amounts of carbon, little is known about their above-ground carbon (AGC) stocks and the factors affecting them, especially in West Africa. This information is of key importance if the countries in this region want to achieve their forest restoration and climate mitigation commitments. To fill in this gap, we investigated how environmental and local management (e.g. remnant trees) factors influenced AGC and tree species richness in secondary forests at seven sites across Guinea, Sierra Leone and Liberia. We established 140 plots (20 x 50m) in fallows <15 years (20 plots per site) and sampled all trees ≥10 cm diameter following standardised protocols. We found that AGC stocks and tree species richness increased with fallow age, but were highly variable across sites driven by both climatic and local management practices. While drought stress negatively affected AGC, remnant trees had a positive effect. AGC recovery rates ranged between 0.72 Mg C ha⁻¹ y⁻¹ (second driest site) and 13.76 Mg C ha⁻¹ 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 $\text{ha}^{-1} \text{ y}^{-1}$) 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 $4.9 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ 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

environmental gradients and broad geographic scales, therefore it is necessary to conduct the study across environmental gradients and broad geographic scales in the West Africa forest region.

This study, focused on seven sites in three countries (Guinea, Sierra Leone and Liberia), aims to provide better understanding of forest recovery trajectories across the West Africa forest region. We addressed the following research questions: (a) What are the relative rates of above-ground carbon and tree diversity recovery in abandoned agricultural fields in West Africa? (b) What is the relative influence of regional climatic and local variables (e.g. number of remnant trees) on these recovery rates? (c) What lessons can be drawn for the management of secondary forests in West Africa? We expect faster recovery rates in wetter sites compared to drier sites, and also faster for patches with remnant trees compared to those without.

2. Materials and Methods

2.1 Study sites

The study was conducted in the secondary forests surrounding seven protected areas in Guinea (Pinselli-Soyah-Sabouyah National Park and Massif du Ziama Biosphere Reserve), Sierra Leone (Outamba-Kilimi National Park, Gola Rainforest National Park) and Liberia (Gola Forest National Park, Wologizi-Wonegizi Nature Reserve, Sapo and Grebo Krahn National Park) (Fig. 1). These sites were selected to represent an environmental gradient from drier (Pinselli and Outamba) to wetter (Sapo and Grebo Krahn) sites, while also representing different farming practices at the local level (Table 1). In the drier sites of Pinselli and Outamba, the natural vegetation comprises dry forests and savannas, while in the other sites the forests are evergreen lowland *terra firme*. Outside the protected areas secondary forests of different ages and old-growth forests are distributed in patches within the landscape due to the rotation between slash-and-burn agriculture and the following for forest regrowth.

2.2 Vegetation sampling

In each study area we sampled 20 plots of 20 m x 50 m (total number of plots =140). To capture spatial variation, we sampled two young (5-7 years) and two old (10-15 years) fallows in five different villages per study site. Fallow age was determined by local farmers from each village. We chose these two fallow categories as younger still had open canopy while the older had closed canopies. Within each plot, we recorded tree diameter at 1.3 m along the stem from the ground (or above buttresses if present) of each tree ≥ 10 cm diameter, following RAINFOR protocols (<http://www.rainfor.org/>). We choose a 10-diameter threshold as smaller stems contribute little to plot-level above-ground biomass, as shown for different forest types in nearby Togo (Atsri et al., 2020). Stems were identified to species where possible by a professional botanist (co-author M.N.S.), and samples of unidentified trees were collected for identification at either Institut de Recherche Agronomique de Guinea in Sereidou (Guinea), the Herbaria of Njala University (Sierra Leone) or Forestry Training institute (Liberia). Families and species names follow the African Plant Database (<http://africanplantdatabase.ch>). The final dataset consists of 5,247 stems, of which 95.8 % were identified to species, 99.73 % to genus and 99.86 % to family. Data collection took place between October 2022 and April 2023.

2.3 Aboveground carbon stocks and species composition

For each tree we used Chave et al. (2014) equation to estimate above-ground biomass (AGB), which includes tree diameter (D), wood mass density (ρ) and tree height (H), and is as follows: $AGB = 0.0559(\rho D^2 H)$. The best taxonomic match wood density of each stem was extracted from a global database (Chave et al., 2009, Zanne et al. 2009) following (Lewis et al., 2009). For tree height, we built site-level allometric models to predict height (H) from tree diameter (D) using measurements of tree height in adjacent old-growth forests at each site (Sullivan et al., 2018). We compared Weibull, Michalis-Menten and log-log model forms, and selected the Weibull model form $[H = a (1 - \exp(-bD^c))]$, where a, b and c are estimated parameters and D is diameter at breast height] as it was consistently the best or occasionally second best (lowest root mean square error between predicted and observed height) at each site, and we wanted to use a consistent model form across sites for

consistency of cross-site comparisons. Above-ground biomass was then summed across stems in each plot, and converted to above-ground carbon (AGC) stocks using a carbon fraction of 0.456 (Martin et al., 2018). For each plot we computed AGC including and excluding remnant trees. Following Cuni-Sanchez & Lindsell. (2016), stems from non-pioneer species with annual growth >3 cm year⁻¹ (minimum annual growth rates calculated by dividing tree diameter by fallow age) were considered remnant trees. For each plot we also calculated AGC recovery rate (slope of the regression relationship between carbon stocks and fallow age, in Mg C ha⁻¹ y⁻¹), tree species richness (number of tree species per plot), proportion of N-fixing stems (all stems) and proportion of N-fixing remnant trees. We assigned species as N-fixing or not according to (Sprent, 2009) and (Diabate et al., 2005). Overall, 19 species in the dataset were found to be N-fixers (see Table S1). To have an indication of differences in tree community composition across sites studied, we also quantified the three most abundant species (in terms of number of stems) in young and old fallows with and without remnant trees at each study site.

2.4 Climatic and landscape data

We extracted monthly precipitation at each plot location from the Worldclim V2 database (Fick & Hijmans, 2017), and used this to calculate maximum cumulative water deficit (MCWD). Starting from the wettest month at each location, we calculated the difference between monthly precipitation and evapotranspiration, taking a figure of 100mm for the latter following (Malhi et al., 2013). If precipitation exceeded evapotranspiration, the excess was assumed to have run off so there was a net balance of zero, while if evapotranspiration exceeded precipitation there would be a negative water balance. This water balance was used as the starting point for the next month, to which the monthly precipitation was added, and the monthly evapotranspiration subtracted. This process was repeated iteratively across the year, and the lowest value was taken as a measure of maximum water deficit. For ease of interpretation, we then switched the sign, so higher MCWD values indicate greater water deficits. We also extracted the average maximum annual temperature and average

annual shortwave radiation from Worldclim V2 (see Table 1), but these were not further included in analysis because they were strongly correlated with MCWD (i.e. all sites were on a gradient from hot, sunny and dry to cooler, wetter and cloudier).

To have an indicator of potential forest connectivity in the study areas, we estimated forest cover in a 4-km buffer around the villages sampled, using the Hansen Global Forest Change (v1.11) dataset (Hansen et al., 2013). We expect that the extent of forest in the local area will provide some indication of propagule pressure and habitat for forest-associated seed dispersers (Selwyn et al., 2023), but note that these could also be influenced by the spatial configuration of forest. We subtracted forest loss (up to 2022) from the tree cover map for the year 2000 (considering canopy closure greater than 30%). While we cannot determine the age of forests, this method ensures that only forest that has remained for at least 22 years is included. Only patches greater than 0.5 hectares (FAO definition of forest) were considered. Google Earth Engine and QGIS 3.34.6 were used to extract spatial data on forest cover.

2.5 Data analysis

We assessed variation in i) AGC stocks (all stems) and ii) AGC stocks (excluding remnant trees) between sites and with fallow age using linear mixed effects models, with site identity as a random effect. Age was included as a random intercept, permitting variation in stand age effects between sites. AGC stocks were log-transformed to meet model assumptions of normality of residuals and homogeneity of variances across fitted values. P values were obtained using Satterthwaite's approximation. This analysis was repeated for tree species richness (all stems). For tree species richness (excluding remnant trees), we used generalised linear mixed effects models with a Poisson error distribution as the response variable was an integer count.

We assessed how site-level variation in AGC stocks and tree species richness related to MCWD using linear and Poisson generalised linear (respectively) models with fallow age, MCWD and their interaction as explanatory variables. To further investigate within-site variation in our response variables, we used the mixed-effects modelling framework described above with age now treated as

a continuous variable rather than grouped into age classes, and RT density, % N-fixers (all stems), and their two-way interactions with fallow age also included as explanatory variables. Alternative models with remnant trees density replaced with N-fixer remnant tree density were considered but were less well supported ($\Delta AIC > 20$). The potential for the effect of remnant trees to be non-linear (e.g. facilitation at low densities switching to inhibition at high densities) was assessed by adding a polynomial term for remnant trees, but this model was less well supported than the linear-term only model ($\Delta AIC = 5.6$). Finally, we assessed whether MCWD influenced the effect of remnant trees by adding a two-way interaction between MCWD and remnant trees' density into the above mixed effects models. As forest cover was quite similar across the sites studied (see Table 1), we did not include this as an explanatory variable in the analyses. In highly forested landscapes of DRC, surrounding forest cover did not influence AGC recovery rates in young secondary forests (Moonen et al., 2019).

All data analysis was conducted in R version 4.2.2 (R Core Team 2022), with the raster package (Hijmans, 2023) used to process spatial environmental variables, the BIOMASS package (Rejou-Mechain et al., 2017) used to estimate above-ground carbon stocks, the lme4 package (Bates et al., 2015) used to fit mixed effects models, and the lmerTest package (Kuznetsova et al., 2017) used to obtain P values from mixed effects models.

3.Results

3.1 AGC stocks

Across sites older fallows contained significantly more AGC (mixed effects model: $t = 3.5$, $df = 6.0$, $P = 0.013$ for all stems, $t = 19.8$, $df=50.2$, $P<0.001$ excluding RT), but this difference was less pronounced in drier sites (Fig. 2, a-b). Mean AGC estimates (all stems) for old fallows ranged between 21.1 Mg C ha⁻¹ (Pinselli, driest) and 125.9 Mg C ha⁻¹ (Sapo, wettest) while AGC recovery rates were 0.72 Mg C ha⁻¹ y⁻¹ (Outamba, second driest) and 13.76 Mg C ha⁻¹ y⁻¹ (Sapo, wettest). Mean AGC estimates (all stems) for young fallows ranged from 13.6 Mg C ha⁻¹ (Wonegizi, third wettest) to 35.1 Mg C ha⁻¹ (Gola-L, second wettest).

AGC stocks (all stems) showed a significantly negative relationship with MCWD ($t = 3.3$, $df = 10$, $P = 0.009$), which was more pronounced in older fallows than younger fallows (Fig. 3a). The MCWD-age interaction was not statistically significant for AGC stocks excluding remnant trees ($t = 1.0$, $df=10$, $P = 0.323$), but absolute differences were modelled to be greater in wetter sites because of back transforming long-scale predictions (Fig. 3b). Within-site variation in AGC stocks increased with fallow age and with number of remnant trees (Fig. 4, Table S2). When remnant trees were excluded from AGC calculations, there was a significant interaction between age and number of remnant trees, meaning that older fallows with more remnant trees had higher AGC stocks in non-remnant trees than fallows with fewer remnant trees (Fig. 4b, Table S2).

3.2 Tree diversity and composition

Across sites older fallows contained significantly more tree species (Poisson mixed effects models, $z = 5.2$ and 6.8 for all stems or excluding remnant trees respectively, $df= 135$, $P<0.001$), but this difference was again less pronounced in drier sites (Fig. 2, c-d). Tree species richness (all stems) showed a significantly negative relationship with MCWD ($t=2.6$, $df = 10$, $P = 0.026$), which was more pronounced in older fallows than younger fallows (Fig. 3c). Tree species richness (excluding remnant trees) also showed a significantly negative relationship with MCWD ($t = 2.3$, $df = 10$, $P = 0.048$) (Fig. 3d). As for AGC, within-site variation in tree species richness increased with fallow age and with number of remnant trees (Fig. 4c-d, Table S2). In terms of tree composition, most abundant species varied across sites, especially between the two driest sites (Pinselli and Outamba) and the others (Table 2). Except in these two driest sites, rapidly-growing pioneer species (such as *Musanga cecropioides* and *Macaranga* spp.) were more abundant in plots without remnant trees while long-lived pioneer species (*Funtumia* and *Albizia* spp.) were more abundant in plots with remnant trees (see Table 2).

At site level there was positive relationship between tree diversity (mean tree species richness) and AGC change (slope = 1.43 , $SE = 0.43$, $t = 3.37$, $df = 5$, $P = 0.020$), but this is probably because both were related to a moisture gradient. AGC stocks also increased with tree diversity (slope with log

carbon = 0.106, SE = 0.010, $t = 11.0$, $df = 138$, $P < 0.001$). When all stems were considered, there was a marginally non-significant interaction between fallow age and the proportion of N-fixers ($P = 0.056$, Table S2), with an initially negative effect of N-fixer dominance in young fallows reversing to be positive in old fallows. N-fixer dominance (with regard to % of stems) varied considerably across sites, from 2.4% to 35% (Pinselli and Ziama respectively, see Table 2).

4. Discussion

4.1 AGC stocks

We found that AGC stocks of 10-15-year fallows ranged from 21 to 126 Mg C ha⁻¹ across the landscapes studied (including remnant trees, see Fig. 2), with rates of recovery influenced by both regional climatic factors and by local scale factors. Our results add to the evidence that water availability is a key constraint on AGC recovery of tropical forests (Fig. 3). This pattern has been well documented in tropical American forests (Chazdon et al., 2016; Heinrich et al., 2021), but was found to be weaker in Central African forests, potentially due to the inherent drought resistance of African tropical forest tree communities (Heinrich et al., 2023). By sampling of the hotter and drier Upper Guinean forests, our results show that West African tropical forests do show a pronounced biomass recovery response to water availability. Our results also showed that the effect of water availability was not limited to AGC recovery, as tree species richness of secondary forests was also lower when water availability was most limited. The support our study provides for the role of water availability limiting forest recovery in West Africa has implications for biome-wide predictions of forest recovery, as water availability, together with other climate variables, could be used to predict secondary forest recovery. The sensitivity of secondary forests to water availability also has implications for the temporal sustainability of forest restoration in climates that have the potential to become drier in the future.

Our results also provide support for the role of remnant trees in determining AGC recovery and species richness of non-remnant trees (see Fig. 4). This is consistent with previous research in West Africa (e.g. Amani et al., 2022; Cuni-Sanchez & Lindsell, 2016), but extends this research by showing

that effects persist over a broad climate gradient, and provides further support for their effect on tree species richness (Sandor & Chazdon, 2014). The positive relationship between the number of remnant trees and the AGC and tree species richness of newly established trees is consistent with remnant trees facilitating the establishment of other trees (i.e. facilitated succession sensu Connell & Slatyer, 1977, e.g. by modifying the local microclimate through shading), or could also arise through remnant trees attracting seed dispersers (Guevara et al., 1986).

Within a West African context, we found some differences between our results and patterns of forest recovery from previous work. Our AGC estimates are greater than those reported for Ivory Coast: e.g. below 20 Mg C ha⁻¹ were recorded for 10-year fallows in several sites across that country (Amani et al., 2022) while 22.1 Mg C ha⁻¹ were recorded for 20-year fallows in the south-east (N'Guessan et al., 2019). This would be consistent with the higher forest degradation and lack of dispersing agents in Ivory Coast limiting forest recovery there relative to our study areas. Our AGC estimates are within those reported for similar-aged fallows elsewhere in the Congo Basin (see Table 3), although our estimates from our wettest site are slightly greater, probably because of larger number of trees left when land clearing in Sapo.

In terms of recovery rates, estimated rates ranged between 0.7 and 13.7 Mg C ha⁻¹ y⁻¹ across the landscapes studied, also being greater in wetter sites. Our findings differ from those from Ivory Coast, where AGC recovered faster in the drier northern region (compared to central or southern regions) and authors linked it lower competition between understory annual herbaceous plants and tree seedlings in that region (compared to central/southern regions with perennial herbaceous plants) (Amani et al., 2022). In all our study sites, given high canopy cover, perennial herbaceous plants were rare in the understory (M.S. Pers. Obs. 2024), which is very different from the situation reported in Ivory Coast. Another possible explanation of differences in AGC recovery rates between Ivory Coast and our study is crop(s) cultivated and farming practices. N'Guessan et al. (2019) showed lower AGC recovery rates for abandoned rice fields compared to yam, cassava or maize abandoned

fields, which were all grown in mostly monocropping systems. In our study sites, though, polycropping is the norm (as shown in Table 1). AGC recovery estimates in our wetter sites are much greater than estimates from elsewhere in tropical Africa, probably because of larger number of trees left when land clearing. For instance, 1.98 Mg C ha⁻¹ year⁻¹ have been reported for the Congo Basin (Heinrich et al., 2023), while 3.2 Mg C ha⁻¹ year⁻¹ has been reported for Kenya (Ojoatre et al., 2024). Previous work from Cameroon also reported relatively high rates which range from 3.9 Mg C/ha⁻¹year⁻¹ (see Njomgang et al., 2011) to 9.4 Mg C ha⁻¹ year⁻¹ (see Kotto-Same et al., 1997) . Most likely greater number and sizes of remnant trees left when land clearing in our wetter sites explain these differences, although local soil properties – which we did not investigate in this study- might also be of importance.

4.2 Tree diversity and composition

Tree diversity and composition were also highly variable across the landscapes studied, modulated by climate (MWCD) and remnant trees (Fig. 3-4), with higher diversity in wetter sites and in plots with remnant trees. Our results support previous work from southern Sierra Leone (Cuni-Sanchez & Lindsell, 2016) showing that rapidly growing pioneer species such as *Musanga cecropioides*, or *Macaranga* spp. are more abundant in plots without remnant trees while long-lived pioneer species are more abundant in plots with remnant trees, indicating that remnant tree presence shortened fallow tree species' composition recovery. In a certain way, remnant trees facilitated the establishment of the 'second stage' of the succession with abundant longer-lived pioneers like *Albizia* or *Funtumia* spp., skipping the 'first stage' of the short-lived *Musanga cecropioides* . Results from secondary forests in Ivory Coast have highlighted that tree diversity recovers faster than composition or AGC (Amani et al., 2022), with no details on species recorded, so we were unable to compare our results with theirs. In Yangambi in DRC, *Musanga cecropioides* and *Albizia adianthifolia* were also amongst the three most abundant tree species in 5–10-year fallows (Mangaza et al., 2022), indicating what would be a mix of the first and second stage of the succession as we describe here in West Africa.

When considering tree diversity effects on AGC, we found a weak positive relationship between tree diversity and AGC recovery, but this is likely to be driven by moisture effects rather than niche complementarity as both AGC and tree species richness increased along the gradient of moisture availability. Other studies on secondary forests have found that tree species diversity alone was not a good predictor of AGC change over time. For example, in secondary forests in Mexico, forest age-mediated effects on stand structural changes and species composition were better predictors of AGC than the changes in tree diversity during succession (Aryal et al., 2024). In South Africa, niche complementarity between canopy, sub-canopy, and emergent tree species explained the relationships between stand diversity and biomass storage (Mensah et al., 2018).

With regard to N-fixer effects on AGC recovery, we found limited effects. N-fixation tends to be common in early stages of the forest recovery succession – as there is abundant light and trees can easily provide carbohydrates to their nitrogen-fixing symbionts (Batterman et al., 2013). But it declines over time as light availability in the stand drops (Matsuo et al., 2021), and nitrogen fixation becomes too costly (Battmerman et al., 2013). In DRC, a decrease in abundance of pioneer species and an increase in N-fixing species early in succession of secondary was observed after repeated clearing (Bauters et al., 2021). It is possible differences in clearing cycles or local soil properties, such as Phosphorous or other Cations being more limiting than N in some sites, explain some of the differences observed across the seven sites we studied, factors which should be considered in future research. Future research focusing on tree diversity or composition should also consider using a smaller tree diameter threshold, as trees <10cm diameter might not be major contributors to plot-level AGC, but can be important components of forest composition and diversity (e.g. (Atsri et al., 2020)).

4.3 Implications of the findings

What specific lessons can be drawn for the management of secondary forests in West Africa? First, our findings show that previous work on trajectories of secondary forest recovery in Ivory Coast (a country characterised by high forest degradation, see Traoré et al. 2024) is not applicable to

secondary forests found in Guinea, Sierra Leone or Liberia. Second, our findings also show that AGC recovery is highly variable in these countries, driven by both regional climate (e.g. MWCD) and local farming practices (e.g. remnant trees). Therefore, insights into local contexts should be gathered before making any decision on their management. We recommend the consideration of MCWD instead of other climatic variables such as annual rainfall or precipitation seasonality (used by e.g. Amani et al. 2022; Traoré et al. 2024), as this variable has been shown to be more meaningful in tropical forest contexts (Sullivan et al., 2020), including in the study of secondary forests (Heinrich et al., 2021, 2023).

Overall, our findings also highlight the potential role of passive restoration of secondary forests for carbon sequestration in most of the West African landscapes we studied, except in driest sites, where active restoration might be needed. Apart from helping contribute to these countries' restoration commitments in the Bonn Challenge (see Bonn Challenge 2020), secondary forests are likely to gain importance to local communities, as old-growth forests continue to disappear. In fact, a complete loss of old-growth forest before 2100 has been predicted for Guinea and Sierra Leone under a business-as-usual scenario, including inside protected areas (see, Vieilledent et al., 2022). Notably, for secondary forests to be left to continue recovering and sequestering carbon, local farmers would need to change their farming practices from slash-and-burn to permanent farming, in which case both external support and training would be needed. As secondary forests remain a source of important ecosystem services to local communities, such as wild edible fruits and medicinal plants(Cuni-Sanchez et al. in press), continued access to these important ecosystem services should be ensured, even if carbon sequestration is a management priority at regional or national level.

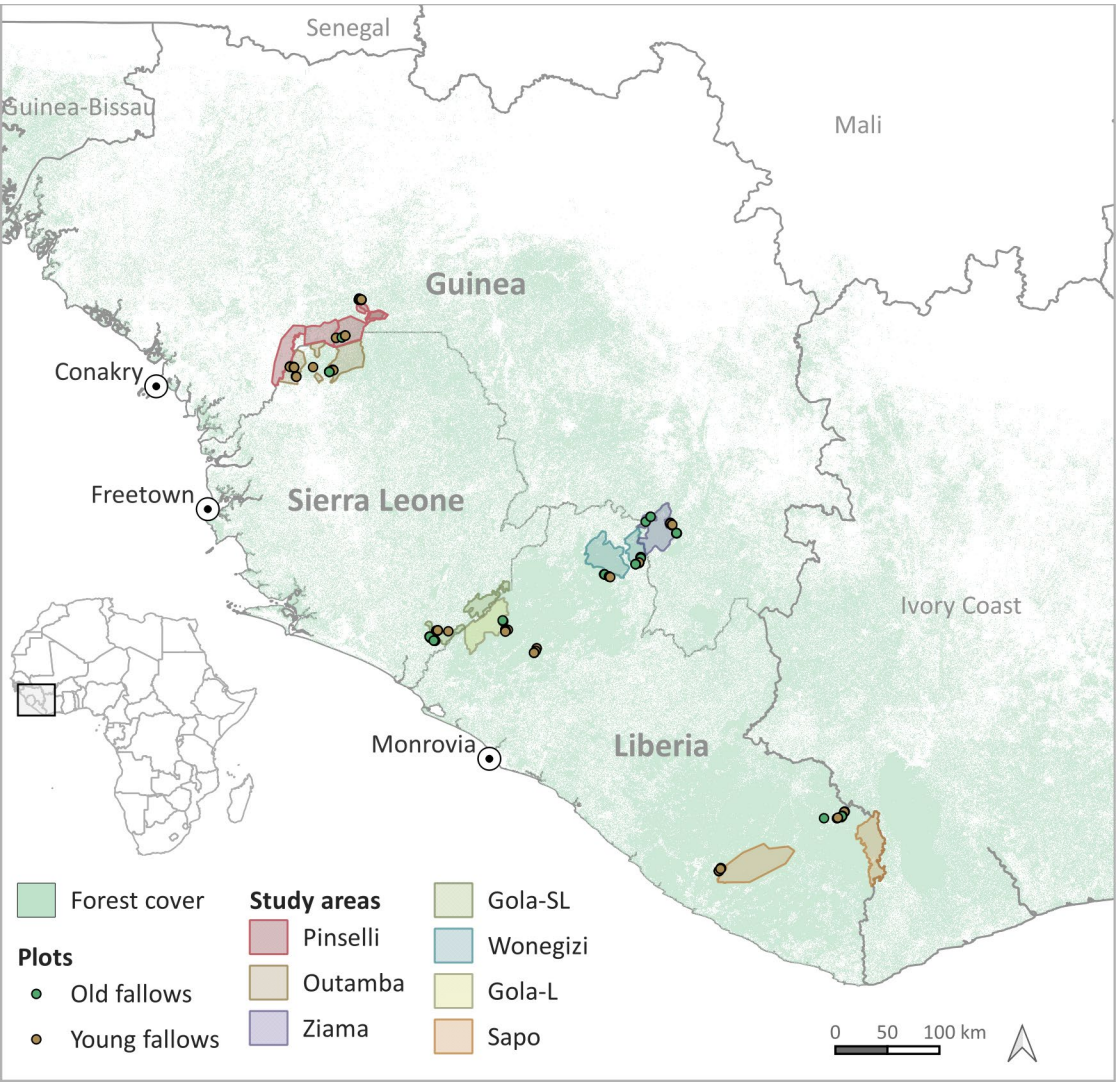


Fig. 1. Selected study sites. For details see Table 1.

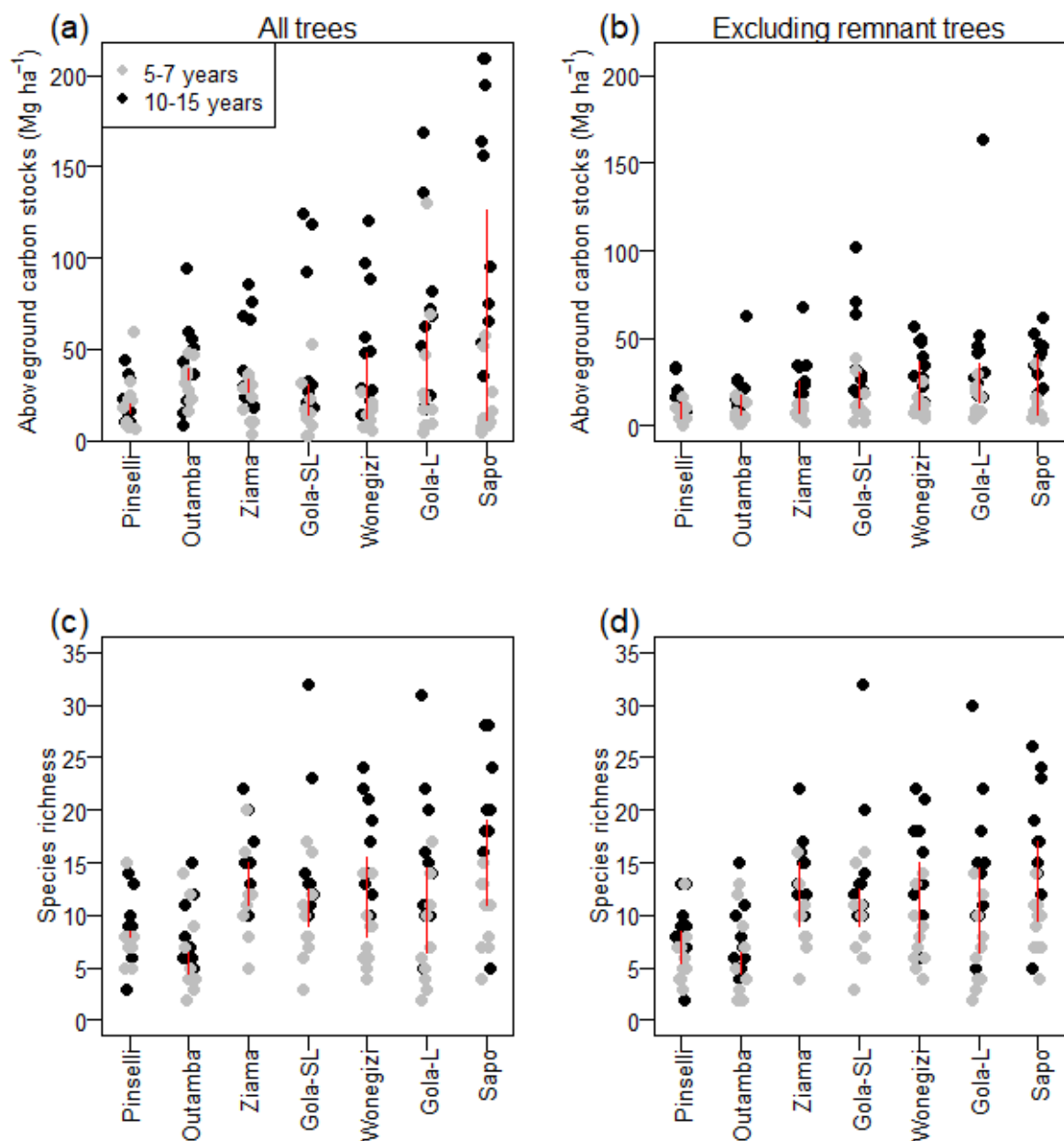


Fig. 2. Variation in above-ground carbon (AGC) stocks (a-b) and tree species richness (c-d) within and between sites. Sites have been ordered from driest (left) to wettest (right) based on the maximum cumulative water deficit. Grey points: young fallows (5-7 years old); black points: old fallows (10-15 years old). The red lines show the difference between the mean AGC stocks (or tree species richness) in young/old fallows in each site.

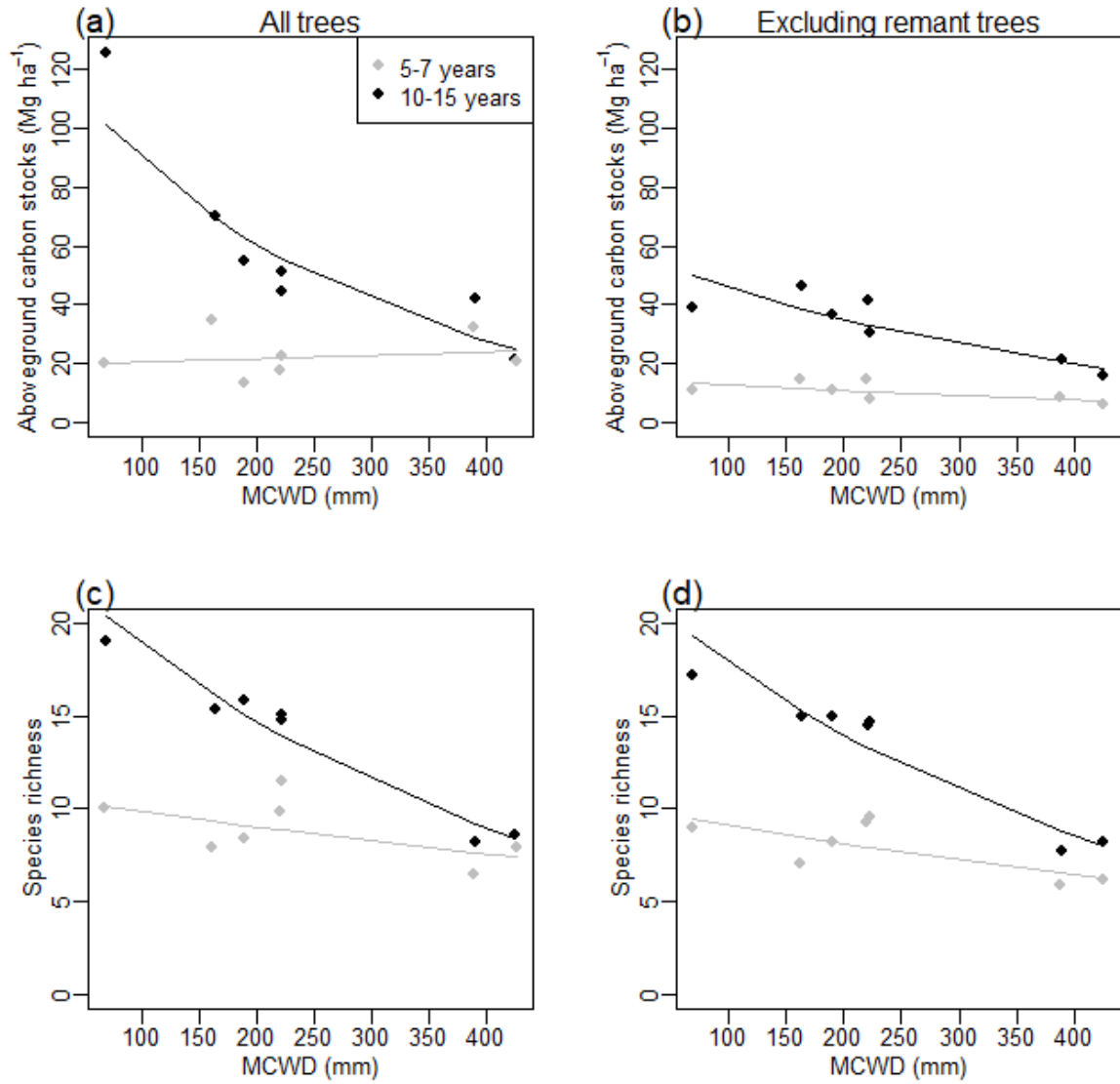


Fig. 3. Relationship between the maximum cumulative water deficit (MCWD) and above-ground carbon stocks (a-b) and tree species richness (c-d). High MCWD values indicate greater moisture limitation. Black and grey points indicate mean values per site considering old (10-15 years) and young (5-7 years) fallows, respectively. Lines indicate modelled relationships from linear models with MCWD, age category and their interaction as explanatory variables.

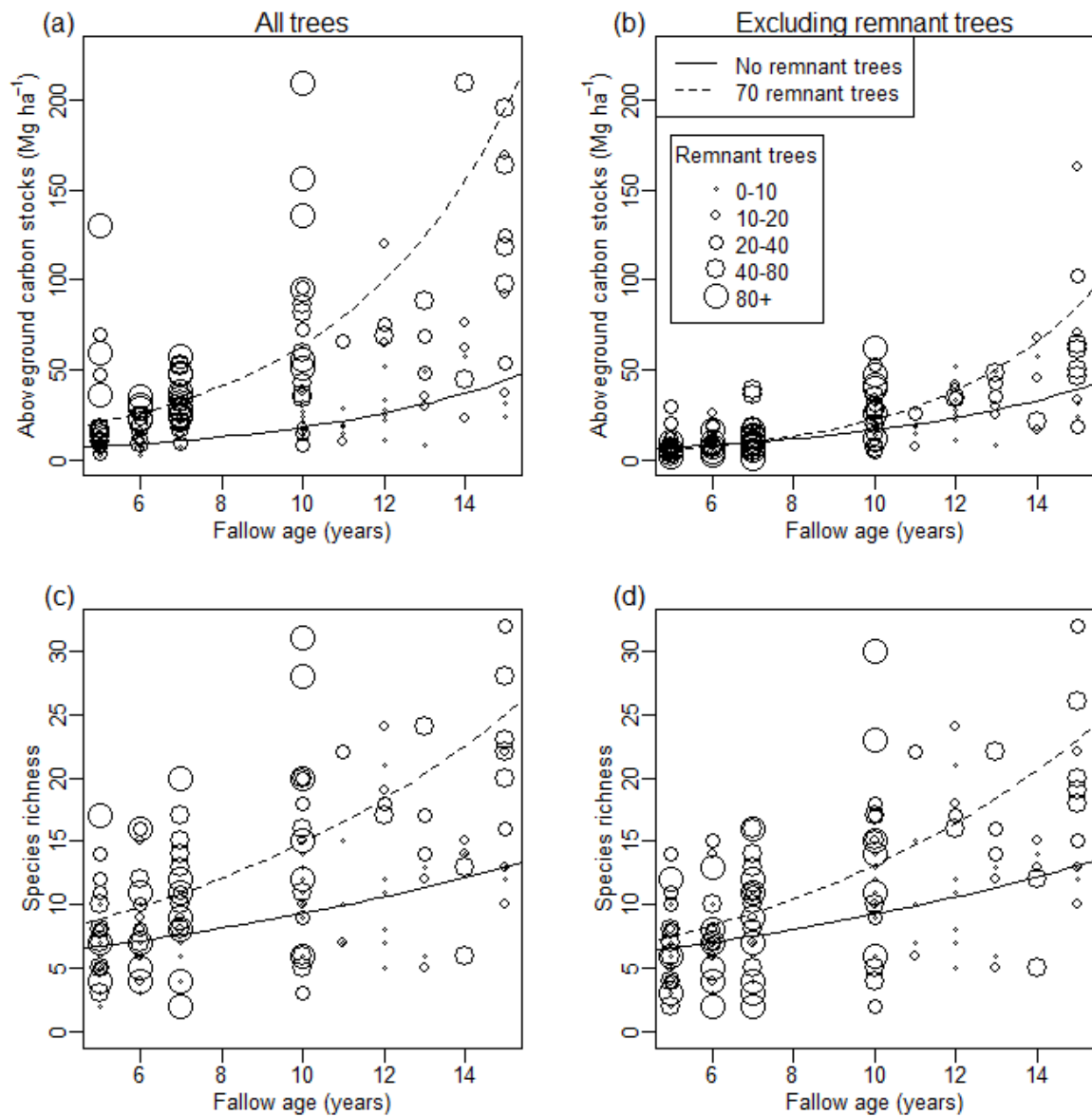


Fig. 4. Effect of fallow age and number of remnant trees on above-ground carbon stocks (a-b) and tree species richness (c-d). Symbol sizes indicate the number of remnant trees. Lines show model predictions with no remnant trees (solid line) and 70 remnant trees (dashed line, representing one standard deviation above the mean). Model coefficients are presented in Table S1.

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

Code	Full name	Annual rainfall (mm)	Maximum temperature-warmest month (°C)	Mean annual temperature (°C)	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	<i>Piliostigma thonningii</i> 37	<i>Spondias mombin</i> 28
2	<i>Terminalia schimperiana</i> 22	<i>Ficus sur</i> 15
3	<i>Margaritaria discoidea</i> 21	<i>Anthonotha crassifolia</i> 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	<i>Pterocarpus erinaceus</i> * 36	<i>Gmelina arborea</i> 30
2	<i>Combretum glutinosum</i> 30	<i>Spondias mombin</i> 20
3	<i>Crossopteryx febrifuga</i> 27	<i>Sterculia setigera</i> 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	<i>Albizia zygia</i> * 36	<i>Albizia zygia</i> * 18
2	<i>Cathormion altissimum</i> 21	<i>Funtumia africana</i> 18
3	<i>Margaritaria discoidea</i> 21	<i>Funtumia elastica</i> 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	<i>Macaranga barteri</i> (95)	<i>Smeathmannia pubescens</i> (16)
2	<i>Margaritaria discoidea</i> (44)	<i>Funtumia africana</i> (15)

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