



Aboveground tree carbon stocks in West African semi-arid ecosystems: Dominance patterns, size class allocation and structural drivers



Sylvanus Mensah ^{a,*}, Florent Noulèkoun ^b, Expédit E. Ago ^{c,d}

^a Laboratoire de Biomathématiques et d'Estimations Forestières, Université d'Abomey Calavi, Cotonou, Benin

^b Department of Environmental Science and Ecological Engineering, Korea University, 145 Anamro, Seongbukgu, Seoul, 02841, South Korea

^c Laboratoire d'Ecologie Appliquée, Université d'Abomey Calavi, Cotonou, Benin

^d Biodiversité et Paysage, Université de Liège, Gembloux Agro Bio Tech, 27, avenue Maréchal Juin, 5030, Gembloux, Belgium

ARTICLE INFO

Article history:

Received 11 June 2020

Received in revised form 23 August 2020

Accepted 16 October 2020

Keywords:

Benin

Tree biomass

Dominant species

Large-size trees

Savannah

Stand structure

ABSTRACT

The importance of terrestrial ecosystems for carbon sequestration and climate regulation is acknowledged globally. However, the underlying structural drivers are still not well understood, particularly across distinct tropical forest ecosystems where trees species have different growth habits and potential to reach different maximal size. In particular, how important are different tree size classes in contributing to stand aboveground carbon (AGC) remains unclear across forest ecosystems. Here, we hypothesized that (i) tree size classes would contribute differently to stand AGC across forest ecosystems; and (ii) few species, possibly dominant, would determine most of stand AGC. We tested these hypotheses using a 17-ha sampled inventory data from gallery forests, woodlands and savannahs in the Republic of Benin. We examined (i) how AGC stocks vary among small- (<20 cm), medium- (20–40 cm) and large-size (>40 cm diameter at breast height - dbh) trees; (ii) how the large size class and its individual species contribute to AGC; and (iii) how size class-based taxonomic and structural variables influence AGC?

Stand AGC was 23 ± 5 , 30 ± 8 and 42 ± 12 MgC ha⁻¹ in savannah, woodland and gallery forest, respectively. There were significant main and interaction effects of vegetation types and size classes. As expected, medium and large-size classes contained more of the AGC, irrespective of the vegetation type. However, gallery forests had the lowest AGC in the <20 cm dbh class, but higher values in medium- and large-size classes as compared to woodlands and savannahs. The top 10 species contributed 82%, 89% and 91% of AGC in gallery forests, woodlands and savannahs, respectively. In addition, five of the top 10 dominant species were shared by the three vegetation types and alone contributed 70–76% of AGC. Tree basal area was the most constant structural attribute influencing AGC; however, its influence shifted with vegetation type and size class, with greater effects of large-size tree basal area in gallery forests, and of medium trees and small trees' basal area in woodlands and savannahs, respectively. The study shows that (i) AGC allocation to size class varied across vegetation types, and (ii) small and medium trees are also important in predicting AGC, especially in semi-arid environments dominated by high densities of small-size trees (e.g. woodlands and savannahs). It also highlights the importance of few dominant species in contributing a large proportion of AGC stocks. The conservation of these dominant species is essential to avoid substantial decline of AGC stock.

* Corresponding author.

E-mail address: sylvanus.m89@gmail.com (S. Mensah).

1. Introduction

Tropical forest ecosystems are habitats for a considerable number of plant and animal species that contribute to ecosystem functioning and sustainability of livelihoods around the globe. They are source of non-timber forest products (Belcher and Schreckenberg, 2007; Mensah et al., 2017a; Ticktin, 2004), provide floral resources to wild insect pollinators (Goulson, 1999; Mensah et al., 2017b), facilitate soil formation (Krishna and Mohan, 2017) and regulate local and global climate and its adverse effects by storing tons of atmospheric carbon (C) in their soil and living biomass (Malhi et al., 2002).

The importance of tropical forests for C sequestration and climate regulation cannot be overemphasized. They play a substantial role in the global carbon cycle by accounting for 55% of the current C stock of the world's forests (Pan et al., 2011). They sequester high quantity of C within the biomass of their living or non-living tree organs such as trunks, branches, leaves and roots (Malhi et al., 2002). Considering the increasing global CO₂ emissions, C storage is perceived as regulatory and vital function of tropical forest ecosystems for the benefits of humankind. Despite the widely acknowledged importance in reducing CO₂ emissions, there are still significant data gaps and uncertainties in forest C monitoring and accounting (Pan et al., 2011). This is particularly remarkable for most of West Africa, where C stock potential of many ecosystems has remained highly understudied, not only preventing their inclusion in global analyses, but also limiting our understanding of potential drivers of C stocks and dynamics. Whereas existing literature underlines the need for accurate and reliable information on biomass C stocks in less studied environment, e.g. West African ecosystems, it is crucial that we also advance our understanding of drivers controlling vegetation biomass C stocks, particularly across different types of ecosystems, as well as their implications for implementation of vegetation-based climate mitigation strategies (Goetz et al., 2015).

Previous research studies have largely explored biodiversity aspects (Cavanaugh et al., 2014; Liang et al., 2016; Lin et al., 2016; Mensah et al., 2016a, 2018a; Sadtighanh et al., 2019; Sullivan et al., 2017) or site/environnement influence (Gairola et al., 2011; Wu et al., 2015) on biomass C stocks. Other studies have further investigated the influence of stand structure on biomass and C over the last three decades (Fotis et al., 2018; Wang et al., 2011). Stand structures (tree density, basal area and height) have been shown to substantially influence stand productivity and biomass C (McNicol et al., 2018; Mensah et al., 2016b; Yoshida et al., 2017). Furthermore, few larger trees irrespective of their density and richness, have been reported to contain large portion of the stand basal area and aboveground biomass (Bastin et al., 2015; Mensah et al., 2017c), and strongly predict stand-level aboveground biomass and C (Lung and Espira, 2015; Mensah et al., 2016b; Slik et al., 2013). On the other hand, it has been reported that several small- and medium-size trees may not contribute equivalent biomass as a few large-diameter trees, despite their substantial contribution to carbon cycling (Lutz et al., 2018; Meakem et al., 2018). These insights suggest differential biomass allocation across small-, medium- and large-size trees, but it remains unclear whether the patterns of biomass C allocation hold or vary across different vegetation types. The change in patterns of species dominance and associated changes in C stock across vegetation types makes the quantification of biomass C critically important, especially in support to future climate mitigation actions. While it is expected that species richness, tree density and basal area or stand density are primary stand structural variables affecting biomass C stocks, the insights could be further advanced by incorporating size class related perspective.

In West Africa, forest habitats are differentiated by a variety of vegetation types from the Guinean littoral forests to the southern Sahel, with tropical rainforests occurring at 1500–3000 mm annual rainfall, forest-savannah mosaics (1200–1500 mm), woodland-savannahs (800–1200 mm), Sahel (200–500 mm), and desert (<200 mm) (Atsri et al., 2018; White, 1983). There are considerable contrasts among these vegetation types. Some (e.g., savannahs) exhibit lower diversity and low level structure and complexity owing to the sets of trophic groups and environmental gradients compared to others (Adomou, 2005), thereby reinforcing the need to improve our general understanding of biomass C allocation across vegetation types and size classes, and their underlying drivers.

In this study, we used forest inventory data from a semi-arid zone of the Republic of Benin, to examine how aboveground C stocks vary across three natural vegetation types (i.e. gallery forests, tree/shrub savannahs and woodlands) and diameter classes (small-size, medium-size and large-size trees). In particular, we (1) investigated how small-size, medium-size and large-size tree species richness, density, basal area and AGC stock varied among gallery forests, tree/shrub savannahs, and woodlands; we tested for significant main and interaction effects of vegetation types and size classes. We (2) assessed the patterns of dominance in terms of large size class and species contribution to C stocks in each vegetation type. Finally, we (3) assessed size class-based structural variables that influence AGC.

2. Material and methods

2.1. Study area and data collection

This study was undertaken in the Bellefoungou Forest Reserve (BFR; Fig. S1), which is a complex of gallery forests, woodlands and tree/shrub savannahs, located in the commune of Djougou in the Republic of Benin. The BFR is situated

between 1°42'00" and 1°45'00" E longitude, and 9°46'40" and 9°49'00" N latitude, and occurs at low elevation of 405 m asl. The reserve experiences the Sudano-Guinean transition zone climate of northern Benin. The average daily temperature is 28 °C. The rainfall regime is unimodal with an annual rainfall of 1200 mm. The rain falls mostly between April and October, with one peak occurring between July and August (Adomou, 2005). More information about the BFR can be found in our previous studies (Mensah et al., 2020; Ago et al., 2016).

We collected data on tree species identity, individual species density, tree diameter at breast height (dbh) and total height (Ht) from 94 plots installed across three natural vegetation types: gallery forests, woodlands and tree/shrub savannahs (Fig. S2). We used a stratified random sampling scheme, taking into account the total area of each specific vegetation type to allocate sampling plots: 24 in the gallery forests, 40 in woodlands and 30 in tree/shrub savannahs. Plot size and shape were 60 m × 30 m in gallery forests and 42 m × 42 m (approximately 1800 m²) in the other vegetation types. In each plot, we measured dbh and Ht for all individual trees with dbh ≥ 5 cm, and identified trees at species and genus levels. Species nomenclature followed the flora of Benin (Akoègninou et al., 2006).

2.2. Aboveground carbon storage

Decades of research on forest biomass have helped document database across diversity of species and wide range of environmental conditions, and develop biomass equations at regional, continental and global level. These equations provide acceptable estimates of biomass for exploring several aspects. Here, the multispecies allometric biomass equation developed by (Chave et al., 2014) was used to calculate the aboveground biomass (AGB) for all individual trees present in the plots. The formula for the multispecies allometric biomass equation is: $AGB = 0.0673 \times (\rho \times dbh^2 \times Ht)^{0.976}$, where AGB is the aboveground tree biomass in kg, ρ the species-specific wood density (g·cm⁻³), dbh the diameter at breast height (cm), and Ht the total height (m). Data on species-specific wood density were obtained from local studies in West Africa (Amahowe et al., 2018; Chabi et al., 2016; Nygård and Elfving, 2000), and from the Global Wood Density Database (Zanne et al., 2009) when local species (or genus) data are not available. Aboveground tree carbon (AGC) was then determined by calculating the aboveground biomass for each individual tree measured and by applying a carbon fraction of 0.5. Tree carbon data were afterwards scaled up from tree to plot level.

2.3. Taxonomic and structural drivers of AGC

We computed plot-level species taxonomic and structural parameter metrics. In addition, we computed distributional variables to better depict the patterns of differences between vegetation types. We considered three diameter size classes: small-size (dbh < 20 cm), medium-size (20 ≤ dbh ≤ 40 cm) and large-size (dbh > 40 cm) classes. These classes were defined by taking into account the diameter range of trees in our study area (see Table S1; Mensah et al., 2016b, 2014).

To quantify taxonomic diversity metric, we used species richness, estimated as the number of species inside each plot within each vegetation type. In addition, we computed the plot-level species richness for each size class, i.e., for all trees belonging to <20 cm, 20–40 cm and >40 cm diameter classes. For structural variables, we calculated tree density and basal area values at plot level. Similar to species richness, we also computed for a given size class, the plot-level density and basal area values of all trees belonging to that diameter class. Thus, a total of nine (9) quantitative structural variables were considered for each vegetation type in subsequent analyses: species richness for small-size, medium-size and large-size classes; tree density for small-size, medium-size and large-size classes; and basal area for small-size, medium-size and large-size classes.

2.4. Data analyses

All statistical analyses were performed in the R statistical software package, version 4.0.1 (R Core Team, 2020). First, we used boxplots to explore the variation in plot-level species richness, tree density, basal area and AGC among the three vegetation types. We then tested for significant main and interaction effects of vegetation type and size class on species richness, tree density, basal area and AGC using separate Generalized Linear Mixed effects models (GLMM). In these GLMMs, vegetation type and size class were considered as fixed, and plot was treated as a random factor nested within vegetation, to account for unknown heterogeneity effects (Mensah et al., 2018b; Zuur et al., 2009). Species richness and density were analyzed as count data using Negative binomial GLMM. Basal area and AGC were modelled as continuous response variables, by applying GLMM with Gaussian distribution after log-transformation. Basal area and AGC were log-transformed to comply with the normality assumptions. The parameters for the mixed-effects models were estimated using the lme4 package with a restricted maximum likelihood (REML) estimator (Bates et al., 2015).

We used two approaches to assess the patterns of dominance in AGC stocks in each vegetation type. First, we assumed that large-size trees would contribute substantially to stand AGC stocks (Lutz et al., 2018). Thus we considered the large-size class (>40 cm; Fig. S3), determined for each vegetation type the individual species contributing to that class, and computed their overall relative density, basal area, and contribution to the stand AGC stock. Second, we computed the individual species contribution to the stand AGC stock in each vegetation, and retained the top ten species with the highest relative contribution.

Stand variables such as stem density and basal area are expected to influence positively AGC, as they are the stand level attributes that reflect the structures of the plant communities (McNicol et al., 2018; Mensah et al., 2016b). In a previous study,

we have shown that plot-level species richness influenced differently AGC across vegetation types (Mensah et al., 2020). To assess the structural variables influencing AGC in each vegetation type, we explored the bivariate relationships of AGC with size class-based taxonomic and structural variables as defined in section 2.3 (Figs. S4–S6). The slope values of the bivariate relationships between AGC and these variables were plotted. Further, multiple linear regression models were used to evaluate how AGC was influenced by taxonomic and structural variables in (i) small-size class (<20 cm), medium-size class (20–40 cm) and large-size class (>40 cm) separately and (ii) when pooled together. We ran a model averaging procedure to determine the optimal subset of predictor(s) for the joint effect of small-, medium- and large-size class effect (overall model). Environmental variables were not included given the small scale of the study. All possible subsets of the regression models were evaluated for each vegetation type using MuMin package (Barton, 2018). The most optimal and parsimonious model was selected based on the lowest AICc value (i.e. Akaike Information Criterion, adjusted for small sample sizes). The relative variable importance value was calculated for each variable in each model. In addition, the percent variation explained by each predictor was determined using the relaimpo package.

3. Results

3.1. Species richness, stand structure and AGC in gallery forests, woodlands and tree-shrub savannahs

Species richness was 46, 43 and 35 in gallery forests, woodlands and tree-shrub savannahs, respectively. The plot-level values of species richness varied from 8 to 24 in gallery forests, 8 to 18 in woodlands and 8 to 14 in tree-shrub savannahs. Minimum and maximum tree density, basal area and AGC are summarized in Table S1. Overall, species richness, structure and AGC differed significantly ($p < 0.001$) among gallery forests, woodlands and tree-shrub savannahs, but also between the size classes (Table 1). In addition, we found significant interaction effects of vegetation type and size class ($p < 0.001$; Table 2), which suggests that variation of species richness, tree density, basal area and AGC among the size classes depends on the vegetation types. As expected for the three vegetation types, species richness and tree density were significantly higher in the small- and medium-size classes than in the large-size class (Fig. 1). Gallery forests showed the lowest density and similar richness (as compared to savannahs and woodlands) in the small-size class, but exhibited significantly higher values for both parameters in medium- and large-size classes (Fig. 1). As also expected, for the three vegetation types, the medium- and large-size classes had the highest values of basal area and AGC. The patterns of interaction between vegetation types and size classes observed for basal area and AGC were similar to that of tree density: gallery forests showed significantly lowest basal area and AGC in the small-size class compared to savannahs and woodlands, but significantly higher values in medium- and large-size classes (Fig. 1).

3.2. AGC stocks and species dominance patterns

Average carbon stocks of $42 \pm 12 \text{ MgC ha}^{-1}$, $30 \pm 8 \text{ MgC ha}^{-1}$ and $23 \pm 5 \text{ MgC ha}^{-1}$ were estimated for the aboveground compartment in gallery forests, woodlands and savannahs, respectively. Large-size trees (dbh > 40 cm) contributed 41%, 35% and 29% of AGC stock with 14, 4 and 4 species in gallery forests, woodlands and savannahs, respectively (Table S2). Similar patterns were observed for the contribution to basal area. *Anogeissus leiocarpa* (DC.) Guill. & Perr., *Isoberlinia doka* Craib & Stapf, *Daniellia oliveri* (Rolfe) Hutch. & Dalziel, and *Isoberlinia tomentosa* (Harms) Craib & Stapf are the four species making up the large-size class diameter in both savannahs and woodlands (Table S2). In addition, these species remain the top four in the ranking of species with dbh > 40 cm that contributed to AGC in gallery forests.

When we assessed the patterns of dominance in terms of individual species contribution to AGC stocks in each vegetation type, we found that the top 10 species contributed at least 80% of the AGC stock (Fig. 2). In gallery forests, the top 10 species stored 82% of the AGC stocks and the 36 remaining species contributed 18%. In woodlands, the top 10 species contributed 89% of the AGC stocks and the 33 remaining species accounted for 11%. In savannahs, the top 10 species represented 91% of the AGC stocks while the 25 remaining species contributed 9%. A common pattern for all the three vegetation types was that five of the 10 species consistently contributed substantially (70–76%) to AGC: *I. doka*, *I. tomentosa*, *A. leiocarpa*, *D. oliveri* and *Vitellaria paradoxa* C.F.Gaertn. (Fig. 2).

Table 1

Results of GLMMs testing the main and interaction effects of vegetation and size class on species richness, tree density, basal area, and aboveground carbon (AGC) across 94 inventory plots in the Bellefougou Forest Reserve.

	Species richness		Tree density		Basal area		AGC	
	F value	Pr (>F)	F value	Pr (>F)	F value	Pr (>F)	F value	Pr (>F)
Vegetation type	21.57	<0.001	19.49	<0.001	71.23	<0.001	32.55	<0.001
Size class	183.42	<0.001	678.80	<0.001	171.55	<0.001	124.05	<0.001
Vegetation type: Size class	6.12	<0.001	28.73	<0.001	31.23	<0.001	16.08	<0.001

Table 2

Results of the integrated size class-based regression analyses and selected optimal models of the effects of taxonomic and structural attributes on aboveground carbon (AGC) in the three vegetation types in the Bellefoungou Forest Reserve. Size of inventory: 94 plots. RC: Relative contribution (%), Est: coefficient estimate. P values < 0.05 are in bold. The blank cells indicate that variables were not retained in the selected models.

	Gallery forests				Woodlands				Tree-shrub savannahs			
	RC	Est	t	P	RC	Est	t	P	RC	Est	t	P
(Intercept)	—	2.61	0.64	0.527	—	3.55	1.05	0.296	—	6.79	1.82	0.081
Species richness in small size class (<20 cm)	0.09				0.00				0.02			
Tree density in small size class (<20 cm)	0.12				0.08	-0.06	2.41	0.016	0.20	-0.06	-2.43	0.022
Basal area in small size class (<20 cm)	0.01				0.27	5.85	4.11	<0.001	0.34	3.72	2.95	0.007
Species richness in medium size class (20–40 cm)	0.13				0.04				0.10			
Tree density in medium size class (20–40 cm)	0.07				0.06				0.03			
Basal area in medium size class (20–40 cm)	0.14	1.93	5.76	<0.001	0.40	4.50	4.82	<0.001	0.11	2.46	7.16	<0.001
Species richness in large size class (>40 cm)	0.06				0.09				0.02			
Tree density in large size class (>40 cm)	0.03				0.02				0.00			
Basal area in large size class (>40 cm)	0.34	4.10	11.41	<0.001	0.04				0.17	3.13	12.93	<0.001
Model fit statistics												
F (p value)		72.5 (<0.001)				105.1 (<0.001)				79.77 (<0.001)		
R Square		0.86				0.96				0.92		
AICc		145.05				175.35				119.43		

3.3. AGC and size class-related taxonomic and structural drivers

The analyses of the bivariate relationships showed that the size class-related taxonomic and structural drivers of AGC shifted with vegetation type, although some common patterns were observed for the three vegetation types. Particularly, species richness, tree density and basal area of the largest trees (dbh > 40 cm) were individually and strongly correlated with AGC in the three vegetation types (Figs. S4–S6; Fig. 3). AGC was also positively and significantly correlated with species richness, tree density and basal area of medium-size trees in savannahs and woodlands only, but not with those of small-size trees in the three vegetation types (Figs. S4–S6). These initial results also suggest that taxonomic and structural effects increased with size class.

The results of the regression analyses for the joint effects of the size classes showed that stand basal area was the most constant structural attribute influencing AGC. However, its effects shifted with the vegetation type. Accordingly, we found that while basal area of large-size trees had stronger effect (highest relative contribution; $\beta = 4.10$; Table 2) in gallery forests, basal area of medium-size and small-size trees had the strongest influence in woodlands and savannahs, respectively (Table 2). Apart from basal area, tree density of small-size trees was also retained, with negative effects in the final models for woodlands and savannahs (Table 2).

4. Discussion

4.1. Patterns of tree dominance and AGC

The analysis of the structure and composition of the size classes using various forest structural attributes (Fig. 1) revealed that the landscape of the BFR is characterized by a large number of tree species and individuals of small- (53% of the total number of trees) and medium size (38% of the total number of trees) and a few species and individuals of large size (8% of the total number of trees) (see also Fig. S3). This finding is consistent with the common pattern of size class distribution in most forest and in West African Sudanian ecosystems (Dimobe et al., 2018, 2019). The dominance of small-size trees is interesting for the long-term survival of vegetation in the BFR. However, the larger (i.e. medium and large) size classes held the greatest proportion of basal area and AGC stock. More importantly, the few large trees (dbh > 40 cm) contributed up to 41% of the overall AGC stock while only five of the top 10 species in terms of relative contribution to AGC stock accounted for more than two-thirds of the total AGC stock. These findings accord with the prediction of the scaling theory (Enquist and Niklas, 2001; West et al., 2009). The current trend of higher contribution of particularly large-size trees to aboveground biomass and AGC thereof despite their low density and species richness has been previously reported in various vegetation types at both regional and global scales (Bastin et al., 2015; Dimobe et al., 2019; Lutz et al., 2018; McNicol et al., 2018; Slik et al., 2013). For instance, Lutz et al. (2018) found that the largest 1% of trees accounted for 50% of the overall forest biomass and hence AGC stock but comprised few species and relatively abundant individuals of these species globally. Dimobe et al. (2019) reported that large trees (dbh ≥ 25 cm) represented 8% of the total number of inventoried trees but accounted for over two-thirds of the total biomass across four vegetation types (i.e. gallery forest, shrub savannah, tree savannah and woodland) in the semi-arid zone of Burkina Faso. The higher proportion of AGC stock represented by the medium- and large-diameter individuals is likely the result of their greater height and heavier crowns, which enable them to occupy growing space not reachable by smaller-diameter individuals and various light niches within the canopy. While our findings support the general observation

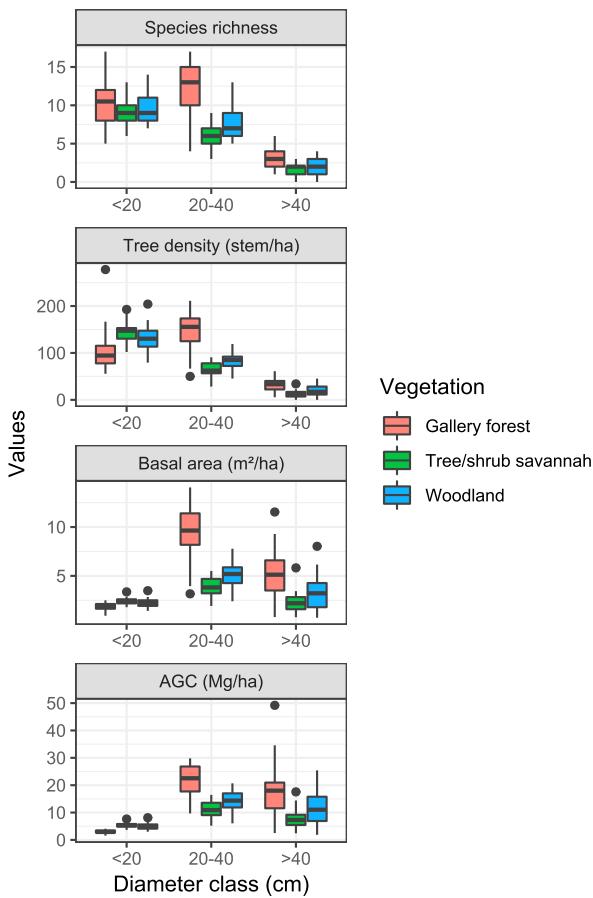


Fig. 1. Variation of species richness, tree density, basal area and AGC among diameter size classes (<20 cm; 20–40 cm and >40 cm) and across vegetation types in the Bellefoungou Forest Reserve.

that large trees are the greatest contributors to AGC stock, they also demonstrate the important contribution of medium-size trees to the overall C pool in semi-arid natural ecosystems.

Interestingly, the overall AGC stock was strongly skewed towards five locally dominant species (*I. doka*, *I. tomentosa*, *A. leiocarpa*, *D. oliveri* and *V. paradoxa*), which held over 70% of the measured AGC stock across the vegetation types. These species are known to mature into large trees, with diameters ranging between 60 cm (*I. doka*) and 200 cm (*D. oliveri*) at maturity (Fern, 2014). These findings suggest that most biomass and C productivity in these West African semi-arid ecosystems is channelled through a relatively few number of large-size tree species as previously reported for seasonally dry ecosystems in Tanzania (McNicol et al., 2018) and forests at a global scale (Lutz et al., 2018). The additional finding that the five species were consistently dominant in the three vegetation types supports the opinion that species attaining large diameters are members of the common species groups (Lutz et al., 2018). Together with previous findings, our results reinforce the importance of a few larger-size tree species for C sequestration and productivity in West African semi-arid ecosystems.

4.2. AGC allocation to size class varied across ecosystem types

Among the natural vegetation types, gallery forests were species richer and denser in trees of medium and large sizes than the woodlands and savannahs, which translated into higher basal area and AGC stock. Similar findings were reported by previous studies, which compared species diversity and C density between gallery forests, woodlands and tree/shrub savannahs in semi-arid West Africa (Dimobe et al., 2019; Mensah et al., 2020). Conversely, woodlands and savannahs had greater AGC stocks in the small size class than the gallery forests. These results suggest that AGC allocation to size class varied across ecosystem types. Two main reasons could explain the observed differential effects of size class on AGC stock among the vegetation types: resource availability and the growth habit of tree species. On the one hand, the higher AGC stock and associated higher tree diversity and density in the larger-size classes in gallery forests may be attributed to (i) the better plant growing conditions (e.g. higher water and nutrient availability) induced by the presence of river and (ii) the availability of a larger pool of species able to attain large diameters in these ecosystems. On the other hand, the higher AGC stock in the small-

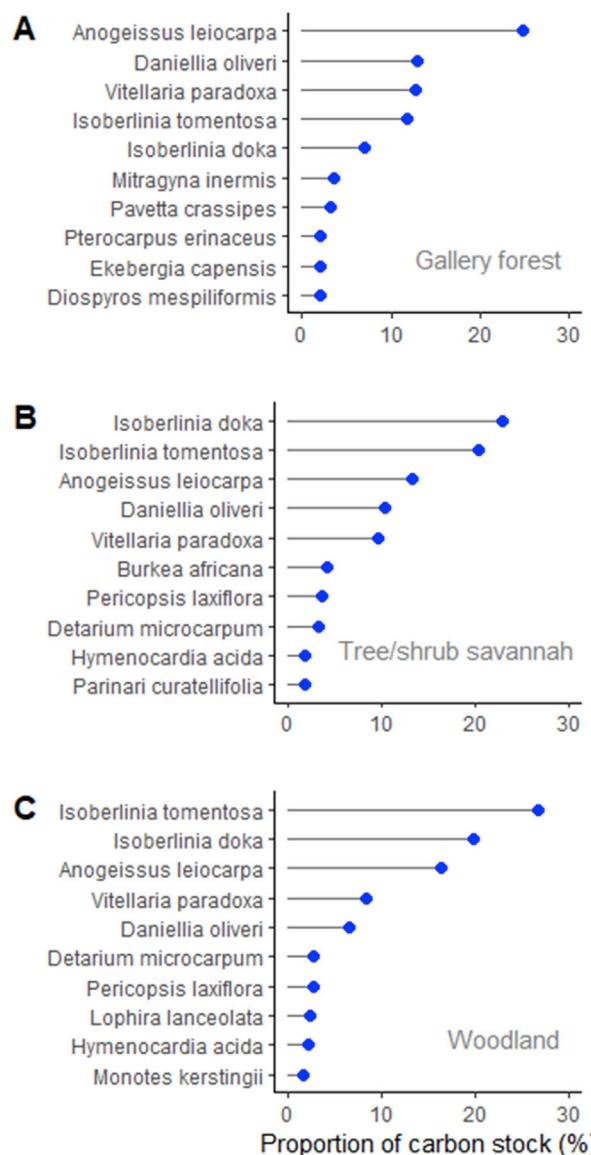


Fig. 2. Relative contribution of the top ten species to aboveground carbon (AGC) stock in each vegetation type in the Bellefoungou Forest Reserve.

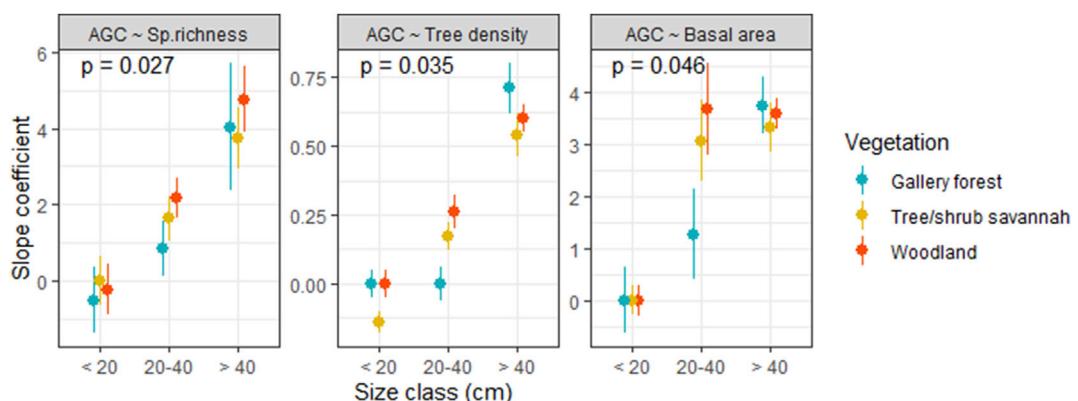


Fig. 3. Slope coefficients of the bivariate relationships of stand aboveground carbon (AGC) with size class-based species structural variables. These coefficients were compared among tree size classes.

size class in woodlands and tree/shrub savannahs, as compared to the same class in gallery forests, likely reflects the higher abundance of small-diameter individuals such as shrubs. Moreover, the unfavourable conditions of drought and low soil humidity in woodlands and savannahs, induced by the prevailing semi-arid climatic conditions may limit the prevalence of large-size trees and favour small-size trees since larger-size trees are reportedly more susceptible to drought mortality than smaller-size trees (Allen et al., 2015; Bennett et al., 2015). The finding that the high number of small-size trees and corresponding AGC stock in woodlands and savannahs did not translate into similar patterns of dominance in the medium- and large-size classes further suggests that the recruitment of species able to reach large diameters from juvenile to adult stage could be altered by other factors including natural and anthropogenic disturbances (Dimobe et al., 2018; Birhane et al., 2020). For instance, wood harvesting for fuelwood and charcoal production from native woodlands and savannahs have been reported as major causes of loss of trees and rarity of large-size trees in West African semi-arid areas (Dimobe et al., 2018). It is thus likely that the lower levels of disturbances in the gallery forests compared to woodlands and savannahs may have allowed the recruitment of trees to larger size and AGC to accrue over time. Hence, in addition to resource availability and species growth habit, natural and human disturbances could mediate the variation of the effects of size class on AGC among the three vegetation types as previously reported (McNicol et al., 2018).

4.3. Tree size as a driver of AGC

The relationships between AGC stock and the taxonomic and structural attributes revealed important patterns and contrasts among size classes and vegetation types. Across the vegetation types, we found that species richness, tree density and basal area of large-size trees positively and significantly influenced AGC stock (Figs. S4–S6). Similar trends were observed in the medium-size class but in woodlands and savannahs only (Figs. S5–S6), whereas the attributes of small-size trees did not influence AGC stock across the vegetation types. These results reflect the stronger effects of larger (i.e. large and medium)-size trees on AGC stock, which may arise from the dominance effects (i.e. competitive constraints) of larger-size trees, thus suggesting that the selection effect is a mechanism operating in these forests (Mensah et al., 2018a; Van Pelt et al., 2016; Yachi and Loreau, 2007). However, our finding that medium-size tree species richness, density and basal area further promotes AGC stock in woodlands and savannahs indicates efficient use of available resources by medium-size trees, suggesting that niche complementarity might be operating in woodlands and savannahs, in addition to the effects of selection. This is also in line with a previous study that reported effects of selection from emergent species and niche complementarity effects for sub-canopy and canopy species (Mensah et al., 2018a).

Overall our findings corroborate with previous studies that showed increased AGC with increasing diversity and tree density in Mistbelt forests in South Africa (Mensah et al., 2016b), in savannahs, woodlands and forests in South-East Tanzania (McNicol et al., 2018) and in Burkina Faso semi-arid vegetation (Dimobe et al., 2019). Interestingly, our findings in woodland and savannah support the increasing evidence that both niche complementarity and selection effects are non-mutually exclusive mechanisms interacting to regulate biomass C storage. The sole significant effects of large-size trees attributes (i.e. species richness, density and basal area) on AGC in gallery forests further suggests a greater mediation of selection effects compared to the complementarity effects. Therefore, the importance of the selection and complementarity may vary with forest ecosystems. As these forest ecosystems contain species of different growth habits, further studies on functional traits, especially functional diversity and identity, may shed more light on the relative importance of the mechanisms of selection and complementarity.

4.4. Tree size as a driver of AGC

Conclusions and implications for large-size tree species conservation and long-term forest survival

In this study, we investigated dominance patterns, size class allocation and structural drivers of aboveground tree C stocks across forests, woodlands and savannahs in West African semi-arid ecosystems. The results showed that AGC allocation to size class varied across vegetation types. For instance, gallery forests showed significantly lowest AGC in the <20 cm dbh class, but higher values in medium- and large-size classes as compared to woodlands and savannahs. Few dominant species shared by the three vegetation types contributed 70–76% of AGC. We also found that large-size trees had greater effects on AGC in forest while medium and smaller trees' basal area had a comparatively greater contribution to plot AGC in woodlands and savannahs. These results indicate that small- and medium-size trees are also important in predicting AGC, especially in semi-arid environments dominated by high densities of small-size trees (e.g. woodlands and savannahs).

The strong relationships between the large-size class attributes and AGC stock suggests that the potential of the studied vegetation types to sequester C depends largely on the abundance and richness of trees with dbh >40 cm. However, largest individuals were few with a relatively low diversity, meaning that the loss of large-size trees could alter forest function and C cycling through reduced structural stratification (or heterogeneity) and biomass and C storage (Lutz et al., 2018; Mensah et al., 2020; Needham et al., 2016). Moreover, the commonly dominant species are endemic to tropical Africa woodlands, where their survival is threatened by anthropogenic disturbances due to their harvest for timber and charcoal production (Assogbadjo et al., 2009; Fern, 2014; Glèlè Kakaï et al., 2011; Glèlè Kakaï and Sims, 2009). Therefore, the conservation of the large-size trees is crucial to sustain forest ecosystem functions and services because the long time required for trees to develop into large sizes implies that the restoration of ecosystem functions following the loss of large-size individuals may take decades (Lindenmayer et al., 2012).

Existing evidence suggests that global climate change will affect large-diameter trees. Larger-size trees will be more vulnerable to increasing drought than smaller-size trees because larger trees are exposed to high radiation loads and susceptible to sapwood cavity (Allen et al., 2015; Bennett et al., 2015). Therefore, the projected increase in aridity over the drylands of West Africa entails an increase in the future mortality rates of large-size trees. The long-term persistence of large-size trees and tree-based ecosystems will however depend on whether the regrowth and recruitment of individuals of functionally similar species will eventually buffer the increasing mortality rates of large-size trees (Lutz et al., 2018). The higher overall species richness and subsequent higher diversity of large-size trees in gallery forests suggest more resilience to climate change because different species adaptions would allow the survival and persistence of at least some species (Musavi et al., 2017). In contrast, a decline in large-size tree density due to climate warming in woodlands and savannahs would be exacerbated by the low diversity and abundance of large-size trees. These results highlight the need for novel management strategies to protect the population of large-size trees and ensure the recruitment of smaller-size trees with potential of reaching large sizes to do so.

From a conservation point of view, the finding that more C dense areas harbour greater large-size tree species diversity across the vegetation types indicate that C and biodiversity conservation can be achieved simultaneously. Therefore, policies and conservation schemes that target the preservation of large-size trees would yield double benefits of biodiversity conservation and maintenance of AGC.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

We are grateful to the colleagues at the Laboratoire de Biomathématiques et d'Estimations Forestières, Université d'Abomey Calavi, for assisting with data collection. Sylvanus Mensah acknowledges the support from the African Forest Forum (AFF) through the Research Grant on Land Use, Land Use Change and Forestry Linked to Climate Change. Florent Noulèkoun acknowledges the support provided by the BK21 PLUS Program (Brain Korea 21 Program for Leading Universities and Students), the National Research Foundation (NRF) of Korea and the OJEong Resilience Institute (OJERI), which allowed fruitful international collaboration. Expedit Ago acknowledges the support from the Académie de Recherche et d'Enseignement Supérieur (ARES) for the postdoctoral grant Elan 2017. The authors are grateful to the anonymous reviewers for the comments on the earlier version of this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01331>.

References

- Adomou, A., 2005. *Vegetation Patterns and Environmental Gradient in Benin: Implications for Biogeography and Conservation*. Wageningen University.
- Ago, E.E., Agbossou, E.K., Cohard, J.-M., Galle, S., Aubinet, M., 2016. Response of CO₂ fluxes and productivity to water availability in two contrasting ecosystems in northern Benin (West Africa). *Ann. For. Sci.* 73, 483–500. <https://doi.org/10.1007/s13595-016-0542-9>.
- Akoegninao, A., Burg, W.J., van der Maesen, L.J.G., 2006. *Flore analytique du Bénin*. Backhuys Publishers, Leiden.
- Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6, 1–55. <https://doi.org/10.1890/ES15-00203.1>.
- Amahowe, I.O., Gaoue, O.G., Natta, A.K., Piponiot, C., Zobi, I.C., Hérault, B., 2018. Functional traits partially mediate the effects of chronic anthropogenic disturbance on the growth of a tropical tree. *AoB Plants* 10, 1–13. <https://doi.org/10.1093/aobpla/ply036>.
- Assogbadjo, A.E., Glèlè Kakai, R.L., Sinsin, B., Pelz, D., 2009. Structure of *Anogeissus leiocarpa* Guill. & Perr. natural stands in relation to anthropogenic pressure within wari-maro forest reserve in Benin. *Afr. J. Ecol.* 46, 644–653.
- Atsri, H.K., Konko, Y., Cuni-Sánchez, A., Abotsi, K.E., Kokou, K., 2018. Changes in the West African forest-savanna mosaic, insights from central Togo. *PloS One* 13, 1–19. <https://doi.org/10.1371/journal.pone.0203999>.
- Barton, K., 2018. *MuMin: Multi-Model Inference. R Package version 1.42.1*.
- Bastin, J.F., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatidis, D., De Haulleville, T., Baya, F., Beeckman, H., Beina, D., Couteron, P., Chuyong, G., Dauby, G., Doucet, J.L., Droissart, V., Dufréne, M., Ewango, C., Gillet, J.F., Gonmadje, C.H., Hart, T., Kavali, T., Kenfack, D., Libalah, M., Malhi, Y., Makana, J.R., Pélassier, R., Ploton, P., Serckx, A., Sonké, B., Stewart, T., Thomas, D.W., De Cannière, C., Bogaert, J., 2015. Seeing Central African forests through their largest trees. *Sci. Rep.* 5 <https://doi.org/10.1038/srep13156>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using **lme4**. *J. Stat. Software* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Belcher, B., Schreckenberg, K., 2007. Commercialisation of non-timber forest products: a reality check. *Dev. Pol. Rev.* 25, 355–377. <https://doi.org/10.1111/j.1467-7679.2007.00374.x>.
- Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. *Native Plants* 1. <https://doi.org/10.1038/nplants.2015.139>.
- Birhane, E., Asgedom, K.T., Tadesse, T., Hishe, H., Abrha, H., Noulèkoun, F., 2020. Vulnerability of baobab (*Adansonia digitata* L.) to human disturbances and climate change in western Tigray, Ethiopia: conservation concerns and priorities. *Global Ecol. Conserv.* 22, e00943.
- Cavanaugh, K.C., Gosnell, J.S., Davis, S.L., Ahumada, J., Boundja, P., Clark, D.B., Mugerwa, B., Jansen, P.A., O'Brien, T.G., Rovero, F., Sheil, D., Vasquez, R., Andelman, S., 2014. Carbon storage in tropical forests correlates with taxonomic diversity and functional dominance on a global scale. *Global Ecol. Biogeogr.* 23, 563–573. <https://doi.org/10.1111/geb.12143>.

- Chabi, A., Lautenbach, S., Orekan, V.O.A., Kyei-Baffour, N., 2016. Allometric models and aboveground biomass stocks of a West African Sudan Savannah watershed in Benin. *Carbon Bal. Manag.* 11 <https://doi.org/10.1186/s13021-016-0058-5>.
- Chave, J., Réjou-Méchain, M., Bürquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Müller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélassier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biol.* 20, 3177–3190. <https://doi.org/10.1111/gcb.12629>.
- Dimobe, K., Kouakou, J.L.N., Tondoh, J.E., Zoungnara, B.J.B., Forkor, G., Ouédraogo, K., 2018. Predicting the potential impact of climate change on carbon stock in semi-arid west African savannas. *Land* 7. <https://doi.org/10.3390/land7040124>.
- Dimobe, K., Kuyah, S., Dabré, Z., Ouédraogo, A., Thiombiano, A., 2019. Diversity–carbon stock relationship across vegetation types in W National park in Burkina Faso. *For. Ecol. Manage.* 438, 243–254. <https://doi.org/10.1016/j.foreco.2019.02.027>.
- Enquist, B.J., Niklas, K.J., 2001. Invariant scaling relations across tree-dominated communities. *Nature* 410, 655–660. <https://doi.org/10.1038/35070500>.
- Fern, K., 2014. Useful tropical plants database [WWW document]. accessed 6.8.20. <https://www.feedipedia.org/node/21211>.
- Fotis, A.T., Murphy, S.J., Ricart, R.D., Krishnadas, M., Whitacre, J., Wenzel, J.W., Queenborough, S.A., Comita, L.S., 2018. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. *J. Ecol.* 106, 561–570. <https://doi.org/10.1111/1365-2745.12847>.
- Gairola, S., Sharma, C.M., Ghildiyal, S.K., Suyal, S., 2011. Live tree biomass and carbon variation along an altitudinal gradient in moist temperate valley slopes of the Garhwal Himalaya (India). *Curr. Sci.* 100, 1862–1870. <https://doi.org/10.3732/ajb.0800405>.
- Glélé Kakaï, R., Akpona, T.J.D., Assogbadjo, A.E., Gaoué, O.G., Chakeredza, S., Nganglé, P.C., Mensah, G.A., Sinsin, B., 2011. Ecological adaptation of the shea butter tree (*Vitellaria paradoxa* C.F. Gaertn.) along climatic gradient in Bénin, West Africa. *Afr. J. Ecol.* 49, 440–449. <https://doi.org/10.1111/j.1365-2028.2011.01279.x>.
- Glélé Kakaï, R., Sinsin, B., 2009. Structural description of two Isoberlinia dominated vegetation types in the Wari-Marö Forest Reserve (Benin). *South Afr. J. Bot.* 75, 43–51. <https://doi.org/10.1016/j.sajb.2008.07.003>.
- Goetz, S.J., Hansen, M., Houghton, R.A., Walker, W., Laporte, N., Busch, J., 2015. Measurement and monitoring needs, capabilities and potential for addressing reduced emissions from deforestation and forest degradation under REDD+. *Environ. Res. Lett.* 10 <https://doi.org/10.1088/1748-9326/10/12/123001>.
- Goulson, D., 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspect. Plant Ecol. Evol. Systemat.* 2, 185–209. <https://doi.org/10.1078/1433-8319-00070>.
- Krishna, M.P., Mohan, M., 2017. Litter decomposition in forest ecosystems: a review. *Energy Ecol. Environ.* 2, 236–249. <https://doi.org/10.1007/s40974-017-0064-9>.
- Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.D., McGuire, A.D., Bozzato, F., Pretzsch, H., De-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchekabakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H., Lei, X., Schelhaas, M.J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruehlheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleurie, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Batazy, R., Oleksyn, J., Zawita-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitarioho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity–productivity relationship predominant in global forests. *Science* 80, 354. <https://doi.org/10.1126/science.aaf8957>.
- Lin, D., Anderson-teixeira, K.J., Lai, J., Mi, X., Ren, H., Ma, K., 2016. Traits of dominant tree species predict local scale variation in forest aboveground and topsoil carbon stocks. *Plant Soil* 409, 435–446. <https://doi.org/10.1007/s11104-016-2976-0>.
- Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. *Science* 338, 1305–1306. <https://doi.org/10.1126/science.1231070>.
- Lung, M., Espira, A., 2015. The influence of stand variables and human use on biomass and carbon stocks of a transitional African forest: implications for forest carbon projects. *For. Ecol. Manage.* 351, 36–46. <https://doi.org/10.1016/j.foreco.2015.04.032>.
- Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-teixeira, K.J., Becker, K.M.L., Andrade, A., Baltzer, J., Blomdahl, E.M., Bourg, N.A., Bunyavejchewin, S., Burslem, D.F.R.P., Cansler, C.A., Fischer, G.A., Fletcher, C., Freund, J.A., Giardina, C., Germain, S.J., 2018. Global importance of large-diameter trees. *Global Ecol. Biogeogr.* 27, 849–864. <https://doi.org/10.1111/geb.12747>.
- Malhi, Y., Meir, P., Brown, S., 2002. Forests, carbon and global climate. *Philos. Trans. R. Soc. A Math. Phys. Eng. Sci.* 360 (1797), 1567–1591. <https://doi.org/10.1098/rsta.2002.1020>.
- McNicol, I.M., Ryan, C.M., Dexter, K.G., Ball, S.M.J., Williams, M., 2018. Aboveground carbon storage and its links to stand structure, tree diversity and floristic composition in South-eastern Tanzania. *Ecosystems* 21, 740–754. <https://doi.org/10.1007/s10021-017-0180-6>.
- Meakem, V., Topley, A.J., Gonzalez-Akre, E.B., Herrmann, V., Muller-Landau, H.C., Wright, S.J., Hubbell, S.P., Condit, R., Anderson-Teixeira, K.J., 2018. Role of tree size in moist tropical forest carbon cycling and water deficit responses. *New Phytol.* 219, 947–958. <https://doi.org/10.1111/nph.14633>.
- Mensah, S., du Toit, B., Seifert, T., 2018a. Diversity–biomass relationship across forest layers: implications for niche complementarity and selection effects. *Oecologia* 187, 783–795. <https://doi.org/10.1007/s00442-018-4144-0>.
- Mensah, S., Houehanou, T.D., Sogbohossou, E.A., Assogbadjo, A.E., Glélé Kakaï, R., 2014. Effect of human disturbance and climatic variability on the population structure of Afzelia africana Sm. ex pers. (Fabaceae–Caesalpinoideae) at country broad-scale (Bénin, West Africa). *South Afr. J. Bot.* 95, 165–173. <https://doi.org/10.1016/j.sajb.2014.09.008>.
- Mensah, S., Pierna, O.L., Kunneke, A., du Toit, B., Seydack, A., Uhl, E., Pretzsch, H., Seifert, T., 2018b. Height – diameter allometry in South Africa's indigenous high forests: assessing generic models performance and function forms. *For. Ecol. Manage.* 410, 1–11. <https://doi.org/10.1016/j.foreco.2017.12.030>.
- Mensah, S., Salako, V.K., Seifert, T., 2020. Structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation types. *Funct. Ecol.* 34 (8), 1731–1745. <https://doi.org/10.1111/1365-2435.13585>.
- Mensah, S., Veldtman, R., Assogbadjo, A.E., Glélé Kakaï, R., Seifert, T., 2016a. Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance. *Ecol. Evol.* 6, 7546–7557. <https://doi.org/10.1002/ece3.2525>.
- Mensah, S., Veldtman, R., Assogbadjo, A.E., Ham, C., Glélé Kakaï, R.L., Seifert, T., 2017a. Ecosystem service importance and use vary with socio-environmental factors: a study from household-surveys in local communities of South Africa. *Ecosyst. Serv.* 23, 1–8. <https://doi.org/10.1016/j.ecoser.2016.10.018>.
- Mensah, S., Veldtman, R., du Toit, B., Glélé Kakaï, R., Seifert, T., 2016b. Aboveground biomass and carbon in a South African Mistbelt forest and the relationships with tree species diversity and forest structures. *Forests* 7. <https://doi.org/10.3390/f7040079>.
- Mensah, S., Veldtman, R., Seifert, T., 2017b. Potential supply of floral resources to managed honey bees in natural mistbelt forests. *J. Environ. Manag.* 189, 160–167. <https://doi.org/10.1016/j.jenvman.2016.12.033>.
- Mensah, S., Veldtman, R., Seifert, T., 2017c. Allometric models for height and aboveground biomass of dominant tree species in South African Mistbelt forests. *South Afr. Folklore* 79, 19–30. <https://doi.org/10.2989/20702620.2016.1225187>.
- Musavi, T., Migliavacca, M., Reichstein, M., Kattge, J., Wirth, C., Black, T.A., Janssens, I., Knolh, A., Loustau, D., Rouspard, O., Varlagin, A., Rambal, S., Cescatti, A., Gianelle, D., Kondo, H., Tamrakar, R., Mahecha, M.D., 2017. Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity. *Nat. Ecol. Evol.* 1, 1–6. <https://doi.org/10.1038/s41559-016-0048>.
- Needham, J., Merow, C., Butt, N., Malhi, Y., Marthews, T.R., Morecroft, M., McMahon, S.M., 2016. Forest community response to invasive pathogens: the case of ash dieback in a British woodland. *J. Ecol.* 104, 315–330. <https://doi.org/10.1111/1365-2745.12545>.
- Nygård, R., Elfving, B., 2000. Stem basic density and bark proportion of 45 woody species in young savanna coppice forests in Burkina Faso. *Ann. For. Sci.* 57, 143–153.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. *Science* 333, 988–993. <https://doi.org/10.1126/science.1201609>.

- R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Satdichanh, M., Ma, H., Yan, K., Dossa, G.G.O., Winowiecki, L., Vägen, T.G., Gassner, A., Xu, J., Harrison, R.D., 2019. Phylogenetic diversity correlated with above-ground biomass production during forest succession: evidence from tropical forests in Southeast Asia. *J. Ecol.* 107, 1419–1432. <https://doi.org/10.1111/1365-2745.13112>.
- Slik, J.W.F., Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Araujo-Murakami, A., Nagamasu, H., Nilus, R., Nurtjahya, E., Oliveira, Á., Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen, J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira, M., Spironello, W., ter Steege, H., Stevert, T., Navarro-Aguilar, G.E., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., van der Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda, T., Zang, R., Zhang, M.G., Zweifel, N., 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. *Global Ecol. Biogeogr.* 22, 1261–1271. <https://doi.org/10.1111/geb.12092>.
- Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sánchez, A., Hubau, W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A., Sonké, B., Sunderland, T., Ter Steege, H., White, L.J.T., Affum-Baffoe, K., Aiba, S.I., De Almeida, E.C., De Oliveira, E.A., Alvarez-Loayza, P., Dávila, E.Á., Andrade, A., Aragão, L.E.O.C., Ashton, P., Aymard, G.A., Baker, T.R., Balinga, M., Banin, L.F., Baraloto, C., Bastin, J.F., Berry, N., Bogaert, J., Bonal, D., Bongers, F., Brienen, R., Camargo, J.L.C., Cerón, C., Moscoso, V.C., Chezeaux, E., Clark, C.J., Pacheco, Á.C., Comiskey, J.A., Valverde, F.C., Coronado, E.N.H., Dargie, G., Davies, S.J., De Canniere, C., Djuiukouo, M.N., Doucet, J.L., Erwin, T.L., Espejo, J.S., Ewango, C.E.N., Fauset, S., Feldpausch, T.R., Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J., Hart, T.B., Kartawinata, K., Kho, L.K., Kitayama, K., Laurance, S.G.W., Laurance, W.F., Leal, M.E., Lovejoy, T., Lovett, J.C., Lukas, F.M., Makana, J.R., Malhi, Y., Maracahipes, L., Marimon, B.S., Junior, B.H.M., Marshall, A.R., Morandi, P.S., Mukendi, J.T., Mukinzi, J., Nilus, R., Vargas, P.N., Carnacho, N.C.P., Pardo, G., Peña-Claros, M., Pétronelli, P., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Primack, R.B., Priyadi, H., Quesada, C.A., Reitsma, J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E., Salim, K.A., Salomão, R.P., Samsøedin, I., Sheil, D., Sierra, R., Silveira, M., Slik, J.W.F., Steel, L., Taedoumg, H., Tan, S., Terborgh, J.W., Thomas, S.C., Toledo, M., Umunay, P.M., Gamarría, L.V., Vieira, I.C.G., Vos, V.A., Wang, O., Willcock, S., Zemagho, L., 2017. Diversity and carbon storage across the tropical forest biome. *Sci. Rep.* 7, 1–12. <https://doi.org/10.1038/srep39102>.
- Ticktin, T., 2004. The ecological implications of harvesting non-timber forest products. *J. Appl. Ecol.* 41, 11–21. <https://doi.org/10.1111/j.1365-2664.2004.00859.x>.
- Van Pelt, R., Sillett, S.C., Kruse, W.A., Freund, J.A., Kramer, R.D., 2016. Emergent crowns and light-use complementarity lead to global maximum biomass and leaf area in *Sequoia sempervirens* forests. *For. Ecol. Manage.* 375, 279–308. <https://doi.org/10.1016/j.foreco.2016.05.018>.
- Wang, W., Lei, X., Ma, Z., Kneeshaw, D.D., Peng, C., 2011. Positive relationship between aboveground carbon stocks and structural diversity in spruce-dominated forest stands in New Brunswick, Canada. *For. Sci.* 57, 506–515. <https://doi.org/10.1111/oik.01525>.
- West, G.B., Enquist, B.J., Brown, J.H., 2009. A general quantitative theory of forest structure and dynamics. *Proc. Natl. Acad. Sci. U. S. A* 106, 7040–7045. <https://doi.org/10.1073/pnas.0812294106>.
- White, F., 1983. The Vegetation Map of Africa. Unesco, Paris.
- Wu, X., Wang, X., Tang, Z., Shen, Z., Zheng, C., Xia, X., Fang, J., 2015. The relationship between species richness and biomass changes from boreal to subtropical forests in China. *Ecography* 38, 602–613. <https://doi.org/10.1111/ecog.00940>.
- Yachi, S., Loreau, M., 2007. Does complementary resource use enhance ecosystem functioning? A model of light competition in plant communities. *Ecol. Lett.* 10, 54–62. <https://doi.org/10.1111/j.1461-0248.2006.00994.x>.
- Yoshida, T., Naito, S., Nagumo, M., Hyodo, N., Inoue, T., Umegane, H., Yamazaki, H., Miya, H., Nakamura, F., 2017. Structural complexity and ecosystem functions in a natural mixed forest under a single-tree selection silviculture. *Sustain. Times* 9, 9–11. <https://doi.org/10.3390/su9112093>.
- Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: towards a worldwide wood economics spectrum. Dryad. <https://doi.org/10.5061/dryad.234>. Digit. Repos.
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health. Springer New York, New York, NY. <https://doi.org/10.1007/978-0-387-87458-6>.