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Partitioning main carbon pools in a semi-deciduous rainforest in eastern Cameroon

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A R T I C L E I N F O

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A B S T R A C T

Tropical forests contribute to climate change mitigation by absorbing carbon from the atmosphere and storing this in biomass and soil organic matter. However, there is still considerable uncertainty about the above- and belowground quantity and distribution of carbon stocks in African forests. Here, we evaluate how different carbon pools (aboveground live biomass, aboveground dead biomass, belowground biomass) contribute to total carbon stocks, and how different carbon components (e.g. large trees, understorey trees, coarse woody debris, roots, soil organic carbon etc.) contribute to carbon pools and total carbon stocks. We evaluated data of extensive inventories within 30 1-ha plots spanning the terra-firme semi-deciduous forest in eastern Cameroon. Hence, the plots were placed at a mean distance of 1 km from the nearest plot and we analyzed the data using variation partitioning, linear regressions and correlation tests. We found that the terra-firme semi-deciduous forests store 283.97 ± 51.42 Mg C ha^{-1}. The aboveground biomass pool, with a carbon stock of 180.99 ± 25.8 Mg C ha^{-1}, mostly explained variation in total carbon stocks (R^2 = 0.79). From all aboveground biomass components, carbon in large trees was most strongly correlated with total carbon stocks. The second most important carbon pool was belowground carbon (on average 85.06 ± 16.86 Mg C ha^{-1}; R^2 = 0.78), mainly explained by coarse root carbon. Carbon in dead biomass had only a small contribution to total carbon stocks (R^2 = 0.04). Hence, our results indicate that aboveground live biomass is a good predictor for variation in total carbon storage within this semi-deciduous terra-firme forest. However, aboveground live carbon and belowground carbon and their interactions explained most of the variation in total carbon stock, indicating that a whole-ecosystem approach is necessary for a full understanding of the carbon cycle.

1. Introduction

Terrestrial ecosystems are responsible for a net reduction of 2.6 ± 1.2 petagrams of carbon from the atmosphere per year, and therefore play a crucial role in the global carbon cycle by mitigating global warming (IPCC, 2013). A large proportion of this reduction is coming from tropical forests, where 55% of global forest carbon stocks are stored (Pan et al., 2011). Because of their dual roles in climate change mitigation and in the development of resilient and sustainable forestry systems, tropical forests are at the center of debates on climate change and sustainable forest management (Arasa-Gisbert et al., 2018; Bele et al., 2015; Bodegom et al., 2009; Poorter et al., 2016).

The Congo basin represents the second largest continuous area of tropical forest in the world, and stores up to 185 Mg C ha^{-1} in trees with a diameter > 10 cm (Lewis et al., 2013). The forests in Cameroon represent 42% of its national territory (FAO, 2011) and represent the second largest forest area in the Congo basin after forest of Democratic Republic of Congo. Most forest in Cameroon is tropical moist rainforest (75%), constituted by evergreen, semi-deciduous and transition forests (Mahonghol et al., 2016). The biomass maps produced for central Africa (Baccini et al., 2008; Mitchard et al., 2011) showed that a lot of uncertainties remains about the amount and spatial variation in biomass and carbon stocks, both above- and belowground, and that these uncertainties are mainly due to the scarcity of reliable estimates of carbon

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pools and their variation across landscapes and forest types (Pan et al., 2011). This limit the implementation of the measurement, reporting and verification (MRV) protocol at the national level. Successful implementation of the REDD + mechanisms depend on the monitoring of emission reductions, which also depends on mapping and monitoring the tropical forest carbon stocks over large geographic areas, and identifying the multiple drivers of land-use change and associated changes in the carbon budget (Maniatis and Mollicone, 2010). To improve the local and regional carbon estimates, it is urgent to provide essential data that enable the extrapolation of carbon stocks to ecosystems of biome-wide carbon cycle modelling (Houghton et al., 2009; Urquiza-Haas et al., 2007).

However, the few existing studies in Cameroon on the estimation of carbon stocks in semi-deciduous rainforest (e.g. Chimi et al., 2018; Fayolle et al., 2016) as well as in evergreen rainforests (e.g. Day et al., 2013; Djomo et al., 2011; Fayolle et al., 2016; Kabelong et al., 2018; Tabue et al., 2016) have focused only on aboveground carbon stocks. Differences in carbon storage may be determined by forest type, with higher aboveground carbon in semi-deciduous forests than evergreen forests (Fayolle et al., 2016). Besides forest type, also forest structure, such as the number of large trees and the stand basal area, can be drivers of biomass stocks (Poorter et al., 2015; van der Sande et al., 2017a). Several studies in tropical rainforests elsewhere have shown that large trees store more aboveground biomass than smaller trees (e.g. Chisholm et al., 2013; Lutz et al., 2018).

Deadwood is a major component of aboveground biomass (AGB) in tropical forests and is important for microorganisms and for nutrient cycling and carbon storage (Carlson et al., 2017). Few studies have assessed carbon stored in deadwood for African tropical forest (but see (Carlson et al., 2017; Djomo et al., 2011; Kabelong et al., 2018). It has been showed that coarse woody debris (CWD) is an important deadwood component of carbon storage in tropical forests (Gora et al., 2019). In undisturbed moist forests, it may account for approximately 10% of the total carbon storage (Pregitzer and Euskirchen, 2004) and can constitute up to 33% of the forests' AGB (Baker et al., 2007). A perturbation in forest usually causes big changes in deadwood stocks. The increased mortality due to disturbance favors the flow of carbon from the living mass to the deadwood pool (Rice et al., 2004), and the subsequent decomposition of dead trees increases the carbon emissions of the stand. Therefore, the quantification of deadwood stocks and flows helps us better understand the carbon balance of disturbed forests.

Furthermore, we have a poor understanding of the belowground carbon storage (Doetterl et al., 2015). Specifically, there is still a lack of knowledge on soil organic carbon (SOC) stocks in tropical forest, their controls and the relationship of biomass allocation and SOC stocks (Batjes, 2008; Malhi et al., 2009; Saiz et al., 2012). Available estimates suggest that soil carbon can contribute to as much as 32% of the carbon stock in the total ecosystem in tropical forests (Pan et al., 2011).

To our knowledge no studies have evaluated the major components of carbon stocks including multiple above- and belowground biomass pools (soil organic carbon and roots carbon) for semi-deciduous rainforests of Cameroon. Therefore, this study aims to assess the above- and belowground carbon stocks and the contribution of different carbon pools (aboveground, belowground and dead biomass) and their components (large trees (diameter at breast height (DBH) ≥ 10 cm), understorey trees (10 < DBH ≥ 5 cm), small stems (4.99 < DBH ≥ 1 cm), palms stems, standing dead trees, coarse (diameter ≥ 2.5 cm) and fine (diameter < 2.5 cm) woody debris, coarse and fine roots, and soil organic carbon (SOC) in 20 cm depth) in explaining the variation of total carbon stocks. Moreover, we wanted to link carbon stocks with forest structure (i.e. density of big size (> 70 cm DBH) trees), soil variables, topography and disturbance intensity. We assess the above- and below-ground carbon, using data from 30 1-ha plots in a terra-firme semi-deciduous forest in eastern Cameroon. We address two questions. Question 1: what is the contribution of each carbon pool, and the components of the different carbon pools, to total carbon stock? We hypothesize that the aboveground live carbon contributes most to the total carbon stock, because this has been found for evergreen forest in Cameroon (Djomo et al., 2011). We hypothesize that especially density of large trees and big size trees (DBH ≥ 70 cm) determine aboveground carbon stocks because their large and tall trunks have high carbon storage potential. Questions 2: what is the variability of each carbon pool and its components? We hypothesize that the variability of carbon pools and its component is high that is due to the heterogeneity of the forest. Question 3: how do longtime disturbance and abiotic factors (i.e. soil fertility/texture and topography) drive carbon pools and its components? We hypothesize that longtime disturbance will decrease carbon stocks of trees with DBH ≥ 5 cm while increasing carbon stocks of small stems. We hypothesize also that carbon pools and components will increase with resource availability.

2. Material and methods

2.1. Study site

The study was conducted within the Doume Communal Forest (DCF) in eastern Cameroon located between 4°31′0″S and 13°47′5″W. DCF is managed by the Doume municipality with an area of 40,402 ha divided into two blocks of different size (22,987.6 ha for block 1 and 17,412.4 ha for block 2). The first block is located between 4°16′N and 4°32′S latitude, 13°16′E and 13°32′W longitude and shares boundaries with the Doumaintang Communal and Bayong community forests. The second block is located between 4°8′N and 4°16′S latitude, 13°12′E and 13°32′W longitude and shares boundaries with the Angossas Communal forest (Fig. 1). Topographically, the forest is slightly uneven with a succession of low hills interspersed with small well-marked streams, or swampy, sometimes vast depressions (several hundred meters) without a distinct watercourse (Management Plan of the Doume Communal forest, 2015). Doume Communal Forest is a moist semi-deciduous forest belonging to the guineo-Congolese domain also called Sterculiaceae and Ulmaceae forest, after the most dominant families (Letouzey, 1985). The soils are ferralitic with high sand content and hence a high capacity for water retention, and with a high content of humus resulting from the decomposition of plants and organic matter. The altitude varies from 605 to 760 m, with some particularly marked summits, culminating at < 700 m. Climatically, the Doume locality belongs to the tropics with a mean annual temperature of 25 °C and annual rainfall between 1300 and 1800 mm.

2.2. Plot selection, sample design and forest inventory

The fieldwork was conducted from June to August 2018 using 30 1-ha sampling plots. We focused only on terra-firme forest and avoided rivers and swampy vegetation types, because terra-firme forests represent the majority (86%) of the forest in the locality. Previous studies using remote sensing and geographical information systems defined the land use and land cover in the study area (Zekeng et al., 2019). We combined "Satellite pour l'Observation de la Terre" (SPOT) 7 and the topography map (elevation, curvature and aspect) obtained after Aster images of the DCF analysis to select the representative and homogeneous area for sampling. Aspect is the direction of a slope faces, and cos (aspect) and sin (aspect) were calculated to make aspect data usable in linear models (Baldeck et al., 2013; Wang et al., 2017).

The DCF was subject to normal and legal exploitation under the licensing regime between 1971 and 1980. It was also illegaly exploited between 2009 and 2014 in the form of wild sawing (Management Plan of the Doume Communal forest, 2015). Therefore, some plots have experienced logging of varying intensity, mirroring the status of a large fraction of forests in the Congo basin (Doetinchem et al., 2013). During the field inventory, we found trees stumps in some plots, which is evidence for logging disturbance. To take disturbance variation among

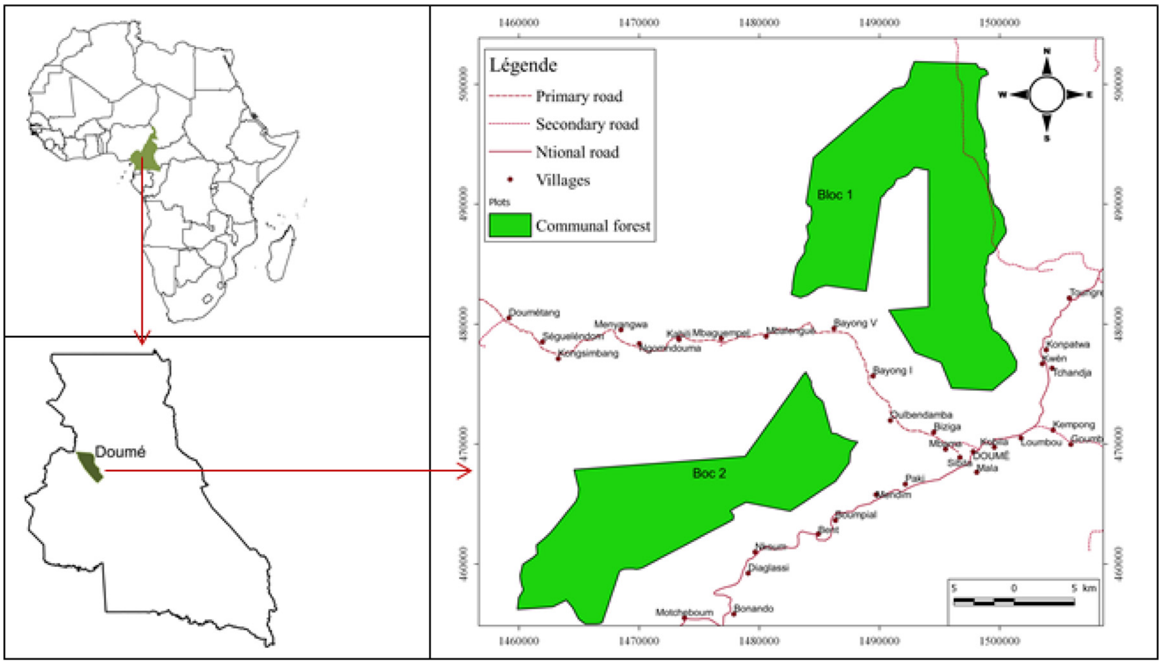

Fig. 1. Map and localization of the Doume Communal forest, showing the two blocks (FC DOUME block 1 and 2) of the Doume Communal forest.

plots into account, we quantified the basal area of trees damaged using the equation: $\alpha_B = 0.01439 * exp^{(0.1829 * N_{log})}$ (Durrieu de Madron et al., 1998), where α_B is the proportion of damaged basal area and $N_{log,}$ the number of trees logged (in our case the tree stumps). Logging disturbance was computed as a continuous disturbance variable because logging disturbance depends on the distribution and density of commercial species and is therefore not evenly distributed in space (Appendix 1). The relative logging disturbance (in %) was computed per ha, based on the basal area of all trees that were logged + damaged basal area divided by the total pre-logging basal area of the plot.

This study aimed to evaluate total aboveground and belowground carbon stocks based on all vascular plants of diameter ≥ 1 cm and all herbaceous plants. We focus on 3 carbon pools (aboveground, belowground, and dead biomass), together composed by 12 components: palms, herbaceous vegetation, fine woody debris (2.5–9.9 cm DBH), coarse woody debris (≥10 cm), standing dead trees, litter, fine and coarse roots, soil organic carbon in 20 cm depth, vascular plants with DBH ≥ 10 cm (referred to as 'Large trees'), trees between 5 and 9.9 cm DBH (refer to as 'Understorey trees'), and stems between 1 and 4.9 cm diameter (i.e. 'Small stems').

The 1-ha (100 × 100 m) plots were subdivided into 25 subplots of 20 m × 20 m following the field protocols of RAINFOR (Phillips et al., 2010). In the whole plot, large trees and palms ≥ 1 cm DBH were identified and measured, and in thirteen subplots, understorey trees and palms were identified and measured. In the subplots situated in the four corners and center of each 1-ha plot, a quadrat of 5 m × 5 m was installed to inventory small stems. Furthermore, in each of these five subplots, we established two subplots of 50 cm × 50 cm at the midpoint of the southern and western margins to evaluate the biomass of litter, and one subplot of 1 m × 1 m at the eastern margin to collect biomass data of herbaceous vegetation. Hence, in total per 1-ha plot, we sampled all trees and palms ≥ 10 cm DBH, trees and palms between 5 and 9.9 cm DBH in 5200 m^2, small trees and palms between 1 and 4.9 cm diameter at 30 cm (D_{30} cm) in 125 m^2, litter in 2.50 m^2, and herbaceous species in 5 m^2.

2.3. Carbon stock estimation

The biomass of all components (see next sections) was converted to carbon using conversion factors according to the recommendation of IPCC (2006): a conversion factor of 0.47 (Chimi, 2018) was used for aboveground live biomass (large trees, understorey trees, small trees, palms, herbaceous vegetation) and of 0.50 for the rest of the biomass components (IPCC, 2006).

2.3.1. Aboveground biomass assessment

2.3.1.1. Large trees. Within each 1-ha plot, all vascular plants with a DBH ≥ 10 cm were measured at 1.3 m breast height or, if applicable, 50 cm above the top of the buttresses or 2 cm above the deformity (Condit, 1998). The aboveground biomass (AGB) for large trees was obtained by converting the DBH into AGB using Eq. (1) of Chave et al. (2014) but see Réjou-Méchain et al. (2017). This equation is a refinement of a Chave et al. (2005) earlier model developed for humid forest using data from multiple sites but that did not include data of African sites. Nevertheless, this allometric equation was used to facilitate the comparisons of our results with those of other studies.

$$AGB = \exp[-2.024 - 0.896E + 0.920\ln(WD) + 2.795\ln(DBH) - 0.0461[\ln(DBH)^2]] \quad (1)$$

Where E is a measure of environmental stress of the site, which depends on temperature seasonality and water deficit and is extracted from http://chave.ups-tlse.fr/pantropical_allometry/readlayers.r with the retrieve_raster function in R. DBH is the diameter at breast height (cm), and WD is the wood density (g cm^{-3}). WD was based on local wood density if available, and otherwise on wood density obtained from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). For 61.5% of the species in the plots we used average species-level WD, and for 31.9% of the species we used genus- or family-average WD. For the few cases (forty-six species) without genus- or family-level WD (5.6%), we used WD averaged per plot. Note that this wood density assignation also included small trees, of which AGB estimation is explained in the next section. The AGB for the large trees of the 25 (20 m × 20 m) subplots were summed to give the AGB in Mg ha^{-1}.

2.3.1.2. Understorey and small trees. Understorey trees were identified and measured in each second plot of 20 m × 20 m subplot per 1-ha plot, covering in total 13 subplots. Small stems (5 < D_{30} cm ≥ 1 cm) were identified and measured in 5 m × 5 m quadrats in five subplots (the four corners and center) per 1-ha plot. The DBH of understorey trees with DBH between 5.0 and 9.9 cm was converted to AGB using Eq. (1), while $D_{30\ cm}$ of small stems was converted to AGB using Eq. (2) developed by Ntonmen Yonkeu (unpublished data). This equation was developed using a sample of 793 small stems, and the good fit of the model were the relative mean square error (0.200), residual standard error of the estimate (0.433), adjusted coefficient of determination (0.852), Akaike Information Criterion (9 2 8) and correction factor (CF; 0.09). The average AGB of understorey trees and small stems was scaled to Mg ha^{-1}.

$$AGB_{\text{small\_stems}} = \exp[-2.145 + 2.451 * \ln(D) + 1.120 * \ln(WD)] \quad (2)$$

2.3.1.3. Palms. Within each plot, all palms with diameter ≥ 1 cm were measured and recorded. During the inventory, only the height was carefully measured using a clinometer, as Eq. (3) developed by Frangi and Lugo (1985) requires only total height (m) as an independent variable for predicting biomass for palm. As there are no available allometric equations developed destructively for palms in the Congo basin, Eq. (3) developed by Frangi and Lugo (1985) for Amazonian (Neotropical) forest was used. Aboveground biomass of palms was expressed in Mg ha^{-1}

$$AGB_{Palms} = (-10.0 + (6.4 * H))/10^3 \quad (3)$$

2.3.1.4. Herbaceous vegetation. Aboveground biomass of herbaceous vegetation was estimated within quadrats of 1 m × 1 m of five subplots per 1-ha plot, using the destructive method. In each quadrat, all the herbaceous vegetation was cut, weighed and packaged. Then, the sample obtained was oven-dried at a temperature of 80 °C until a constant dry mass was obtained (Segura and Kanninen, 2005). The average biomass per plot was expressed in Mg ha^{-1}.

2.3.1.5. Woody debris. Woody debris was estimated non-destructively using the planar-intersect method (Brown, 1974; Van Wagner, 1968). Fine (2.5–9.9 cm diameter) and coarse (≥10 cm diameter) woody debris fractions were estimated separately within five 20 m × 20 m subplots using two 15 m long perpendicular transects per subplot. For each transect, fine debris was sampled along the first 5 m while coarse debris was sampled along the entire transect. Deadwood density (Appendix 2) was categorized, on the basis of the resistance of wood to penetration of a metal (in our study a cutlass) into the body of the woody debris (Clark et al., 1998; Lambert et al., 1980) using the three following decomposition stages (Delaney et al., 1998; Pearson and Brown, 2005): Class 1 (sound): the sound state included logs that had little or no surface breakdown, intact branches and bark, strong wood structure, and the ability to support its weight. Class 2 (intermediaire): the intermediate state included logs that had some surface breakdown, the bark was not always present, and wood structure was weaker, but the bole could support its weight. Class 3 (rotten): the rotten state included logs that had an extensive surface breakdown, no bark, poor wood structure, and often could not support their weight.

For each class, woody debris mass was estimated using Eq. (4) from Pearson and Brown (2005) decomposition state as follows:

$$Necromass\,(Mg.\ ha^{-1}) = \frac{\pi^2 WD \sum_{i=1}^{n} (d_1^2 + d_2^2 + \ldots + d_n^2)}{8L} \quad (4)$$

where WD is wood density (g cm^{-3}), d_1, d_2,…, dn represent the diameters of the intersected pieces of dead wood given in m, and L is the total length of the transect in m. In this study we used the wood density of 0.43 Mg m^{-3} for sound debris, 0.34 Mg m^{-3} for intermediate debris and 0.19 Mg m^{-3} for rotten debris taken obtained by Pearson and Brown (2005). The necromass of each state was summed to obtain necromass woody debris.

2.3.1.6. Standing dead trees. During the botanical inventory of the 1-ha plots, the DBH and height of standing but dead trees were systematically recorded. Each standing dead tree was assigned to one of the following three states and the biomass assess as follow (Pearson and Brown, 2005; Pearson et al., 2007):

state 1: snags with branches and twigs resembling a living tree (except for foliage); his dry necromass was estimated using Eq. (1) reduced by 2.5% to compensate for the loss of leaves and small branches;

state 2: standing dead trees with large branches and those without twigs but still with large; as the state 1, his dry necromass was estimated using also Eq. (1) but reduced by 17.5% to compensate for the loss of leaves, twigs and small branches;

state 3: trunk only without branches; as there are no available allometric equations developed destructively in the Congo basin for standing dead trees, Eq. (5) (Graça et al., 1999) was used to estimate the necromass of trees with damaged crowns (or without crowns, i.e. decomposition state 3). This equation which includes a form factor, or the ratio of the volume of the commercial trunk or bole to the volume of a cylinder with diameter equal to the DBH and height equal to the commercial height (the distance from the ground to the first branch) has been used. In this study, the value of 0.78, derived by Fearnside (1992) using to form factors by diameter class calculated based on 309 trees measured near Manaus, Amazonas and the distribution of bole volume into different DBH classes at the same Manaus site. The value used is applicable only to estimates based on commercial (as opposed to total) height. The mass of the standing dead tree at the scale of hectare was obtained by summing the value obtained in all 20 m × 20 m plots.

$$Necromass_{tree} = BA * h * WD * F \quad (5)$$

where BA is the basal area (m^2), h the commercial height (m), F the form factor and WD the wood density (Mg m^{-3}). Here, we used the same wood density of 0.43 Mg m^{-3} for the state 1–3.

2.3.1.7. Litter. Biomass of the litter was estimated using two quadrats of 50 cm × 50 cm within each of the five 20 m × 20 m subplots used for herbaceous inventory. The litter was collected, weighed using 1 kg spring scales in the field, packaged and oven-dried at 80 °C until the constant dry weight was obtained (Pearson and Brown, 2005; Pearson et al., 2007). The average biomass of litter was scaled to Mg ha^{-1}.

2.3.2. Belowground biomass

2.3.2.1. Root biomass. Coarse root biomass was estimated based on published root: shoot biomass ratios. Biomass of coarse root trees with DBH ≥ 5 cm corresponds to 0.235 AGB of the corresponding tree (Mokany et al., 2006; Nasi et al., 2009) while for trees with diameter < 5 cm it corresponds to 0.32 AGB (Djomo et al., 2011). Fine root biomass was estimated using destructive methods. During the botanical inventory, fine roots were collected from one sample with a radius of 2.5 cm and depth of 20 cm in the five 20 m × 20 m subplots per 1-ha plot. The fine roots collected were washed to remove all the soil, oven-dried for 48 h at 80 °C, and weighted. The fine root mass of the five sampling points per ha was averaged and scaled to Mg ha^{-1} of 20 cm depth (i.e. 2000 m^3), to compare values with aboveground biomass stocks that were also expressed in Mg ha^{-1}.

2.3.2.2. Soil organic carbon and soil parameters. At the same sampling points as fine root sampling described above, two soil samples were taken between 0 and 20 cm depth a cylinder of 392.6991 cm^3 (r = 2.5 cm and h = 20 cm). Soil samples were collected at the same time as the field inventory in June-August 2018. The five sample per plot were mixed in equal volume to form a unique sample per 1-ha plot. The soil parameters texture (proportion of sand, silt, clay), pH, electric conductivity (EC), moisture content (MC), cation exchange capacity (CEC), bulk density (g cm^{-3}), weatherable elements (Ca, Mg, K, Na, etc.), P, N, ratio C:N, ratio N:P, and carbon content were analyzed at the soil laboratory of the Environmental Science

Table 1
Descriptive statistics for all abiotic variables (soil fertility, disturbance and topography) across the 1-ha plots. Mean, standard error (SE), minimum (Min) and maximum (Max) are given.

Variables	Unit	Indicator of	Mean	SE	Min	Max
Electric conductivity	µSiemens	Soil fertility	134.64	33.53	89.30	224.00
pH		Soil fertility	6.42	0.63	4.87	7.00
Clay content	%	Soil physic fertility	8.38	4.46	1.46	18.36
Sand content	%	Soil physic fertility	77.65	17.24	0.00	94.97
Silt content	%	Soil physic fertility	13.97	16.44	3.57	97.28
Moisture content	%		26.87	5.95	14.26	38.25
Cation exchange capaty (CEC)	cmol/kg	Soil fertility	6.73	0.32	6.26	7.49
Phosphorus (P)	%	Soil fertility	0.01	0.007	0.00	0.03
Nitrogen (N)	%	Soil fertility	0.23	0.09	0.06	0.37
N:Psoil ratio		Soil fertility and nutrient limitations	25.66	22.75	3.64	88.47
C:Nsoil ratio		Soil fertility and nutrient limitations	25.93	19.42	7.51	84.09
Disturbance	%	Light availability	3.12	3.02	0.00	8.31
Elevation	m	Topography	702.43	26.14	640.00	754.76
Slope	%	Topography	3.08	2.48	0.00	14.91
Curvature	°	Topography	2.08	24.26	−60.50	56.50
Sine aspect		Topography	0.13	0.65	−0.99	1.00
Cosine aspect		Topography	−0.09	0.76	−0.99	0.99

Department at the University of Botswana (Table 1). The soil samples collected for bulk density were oven-dried for 48 h at 104 °C, after which dry mass was measured and divided by 392.6991 cm^3 to obtain bulk density in g cm^{-3}. SOC was measured by the $K_2Cr_2O_7$-H_2SO_4 oxidation method of Walkey and Black (Nelson and Sommers, 1982). The volume of 2000 m^3 was multiplied by the percentage of carbon in soil, and the dry bulk density of the soil to obtain Mg C ha^{-1} in the upper 20 cm depth. As this method suffers of some limitation to extract stable and recalcitrant carbon forms (Allison, 1960; De Vos et al., 2007; Lettens et al., 2007), and hence may result in an underestimation of the carbon concentration, we used a correction factor of 1.32 to compensate the incomplete oxidation (Walkley and Black, 1934).

2.4. Uncertainty estimates of carbon pools and components

For each carbon pool and its components, we estimated the total uncertainty in two ways: the uncertainty of each pool within plots due to measurement errors (S_{within}) and the spatial variation among plots ($S_{between}$). For all components, the spatial variation ($S_{between}$) was calculated as the mean standard deviation of the mean among plots. For all trees with DBH ≥ 5 cm, we used the AGBmontecarlo function available in the BIOMASS library (Réjou-Méchain et al., 2017) to assess the S_{within} uncertainty due to error propogation of the measurements of DBH, WD and allometric model (see Réjou-Méchain et al., 2017). As we used different equations to AGB for all trees with diameter between 1 and 4.9 cm, we calculated their S_{within} uncertainty as $\sigma_A = B\sqrt{\exp(MSE) - 1}$ (Sierra et al., 2007), with B as the estimate of the average carbon for $S_{d:1\text{-}4.9}$, and MSE the mean square error from the biomass Eq. (2). To estimate the S_{within} uncertainty of all dead carbon components, fine roots and soil carbon components, we used the average variation between the subplots within the plot. The spatial variation ($S_{between}$) was estimated as the standard deviation of the mean carbon among plots. Using the estimated uncertainty of each component and assuming normal distributions of the mean carbon values per plot, we used a Monte Carlo procedure to estimate the uncertainty of the final estimates of AGC, ADC, BGC, TAGC and Total carbon (Sierra et al., 2007). Total uncertainty (S_{total}), was estimated as the square of the sum of the S_{within} and $S_{between}$ uncertainty for every pool and component ($S^2_{total} = S^2_{within} + S^2_{between}$; Sierra et al., 2007).

2.5. Statistical analysis

To assess the relative contribution of each of the three carbon pools to total carbon stock, a variation partitioning analysis was used. Variation partitioning analysis attempts to partition or resolve the explanatory power of different explanatory variables (i.e. the main pools, aboveground live carbon (AGC), aboveground dead carbon (ADC) and belowground carbon (BGC) in this study) in relation to the response variable (i.e. total carbon stock). A first variation partitioning analysis was run using all carbon pools including all its components as explanatory variables in relation to the same response variable (total carbon stock) and then a second variation partitioning analyses was run using only the significant components of each carbon pool (i.e. AGC, ADC and BGC) in relation to the total carbon stock. We tested how components within each carbon pool were correlated, and how all components correlated with total carbon stock. A trees size distribution of aboveground carbon stock was calculated and drawn using a bar chart with a distribution range of 10 cm. A linear regression was used to evaluate the effect of the density of big size trees (> 70 cm DBH) on aboveground and total carbon stocks.

We determined the contribution of environmental drivers (i.e. topographic and edaphic factors) and disturbance on the variability of carbon stocks. Therefore, linear models were developed to test the relationship between disturbance (% basal area removed), topography, and soil variables on each carbon pool and component, using data from the 30 1-ha plots. To avoid collinearity of the soil and topographic variables, all subsets regression analyses were performed to select the variables with the highest relative importance value on carbon pools and components. Then per carbon pool and component, linear regression models were run, from which we selected the models with the highest explained adjusted variation (adj.R^2) of the carbon pool or component, and the lowest values of Aikake information Criteria (AIC) and the residual standard error (RSE).

All analyses were performed in R.3.5.1 (R Development Core Team, 2018). Variation partitioning analyses were computed using the *varpart* function in the vegan package (Oksanen et al., 2018). The significance of fractions of interest was obtained after variation partitioning using the *ANOVA* function from the car package. The Tukey posthoc test (on the tree diameter class effect on total carbon) was performed using the *glht* function of the *multcomp* package. Pearson correlations were evaluated using the *rcorr* function of the *Hmisc* package. For all subsets regression analyses and model averaging, the *lm* function for the linear regression models, the *dredge* function and the model.avg function of the *MuMIn* package (Barton, 2015) were used respectively.

3. Results

3.1. Total carbon stock variation

The total carbon in the main carbon components across the 30 1-ha

Table 2
Carbon stored and uncertainty in different carbon pools (aboveground live carbon, aboveground dead carbon, belowground carbon) and their carbon components in the 30 1-ha plots in Doume communal forest (Total variation (S_{total}) partitioned between within (**S_{within}**) and between (**$S_{between}$**) variation, n: number of sampling plots; SE: standard error of the mean and the mean per pool and component are given. AGC = adult trees + juvenile trees + sapling trees + palms + HV; ADC = Litter + FWD + CWD + STD; BGC = root (fine + coarse) + SOC; Total aboveground carbon = AGC + ADC; Total carbon stock = AGC + ADC + BGC).

Carbon pool	Carbon component	S_{within}	$S_{between}$	Stotal	n	S.E.	Mean (Mg C ha^{-1})
Aboveground live carbon (AGC)		18.55	33.59	38.39	30	6.14	182.62
	Large trees (> 10 cm DBH)	16.18	33.47	37.18	30	6.09	177.61
	Understorey trees (5–10 cm DBH)	0.06	0.45	0.80	30	0.14	2.80
	Small stems (< 5 cm DBH)	0.75	0.20	0.12	30	0.22	1.60
	Palms stems	NA	NA	NA	05	0.09	0.21
	Herbaceous vegetation (HV)	0.03	0.31	0.31	30	0.11	0.40
Aboveground dead carbon (ADC)		85.67	15.35	87.03	30	2.80	17.92
	Litter	0.09	1.09	1.10	30	0.09	2.93
	Fine woody debris (FWD)	0.06	0.16	0.17	30	0.15	1.50
	Coarse woody debris (CWD)	68.80	15.81	70.59	30	1.38	10.90
	Standing dead trees (SDT)	0.04	2.74	2.74	30	0.50	2.59
Belowground carbon (BGC)		15.86	18.65	24.48	30	2.90	85.06
	Fine Root trees (FRT)	0.002	0.02	0.02	30	0.007	0.02
	Coarse Root trees (CRT)	8.47	18.54	20.48	30	1.55	45.65
	Soil organic carbon (SOC)	12.50	31.7	34.07	30	2.28	39.39
TOTALS							
Total aboveground carbon (TAGC)		20.54	40.90	45.80	30	7.49	200.54
Total carbon		18.03	51.19	54.28	30	9.40	285.6

plots of semi-deciduous sample plot forest in eastern Cameroon varied from 173.17 to 349.23 Mg C ha^{-1}, with an average and standard deviation of 285.60 ± 54.28 Mg C ha^{-1} (Table 2). This carbon estimate includes carbon in aboveground live biomass, aboveground dead biomass, belowground biomass, and soil organic carbon.

Variation partitioning used to determine the contribution of different carbon pools and as their components in explaining the variation of total carbon stocks showed that all pools well explained total carbon stock. Fig. 2a shows that the most important pools explaining the variation were AGC and BGC, while large trees and coarse roots, were the most important components of AGC and BGC(Fig. 2b).

Average AGC was 182.62 ± 33.59 Mg C ha^{-1} (Table 2). Among all AGC components, carbon in large trees was most strongly correlated with AGC ($r > 0.99$, $p < 0.001$). Carbon in large trees also explained most variation in total carbon stocks (13.1%, $p < 0.01$, Fig. 2b, Table 3), and represented on average 63% of total carbon stocks (Fig. 4). The relative contribution of AGC in explaining the variation of total carbon stock increased when only carbon of large trees was used (Fig. 2a vs. b).

Average belowground carbon (BGC) was 85.06 ± 18.65 Mg C ha^{-1}. Among all BGC components, carbon in coarse roots was most strongly correlated with BGC ($r = 0.94$, $p = 0.001$, Fig. 3), and it represented on average 16% of total carbon stocks (Fig. 4) and significantly explained variation in total carbon stock (4.3%, $p < 0.01$, Fig. 2b, Table 3). As found for AGC, the relative contribution of BGC in explaining total carbon stock also increased when only coarse root carbon was included (Fig. 2a vs. b).

Aboveground dead carbon (ADC) was 17.92 ± 15.35 Mg C ha^{-1}. Of all dead carbon components, coarse woody debris (10.90 ± 15.81 Mg ha^{-1}) contributed most strongly to total carbon stock variation (0.10%, $p < 0.001$, Table 3; Fig. 2). Coarse woody debris was also the most important ADC component for total carbon stocks (4%, $r = 0.51$, $p < 0.001$, Figs. 3 and 4). Contrary to AGC, the relative contribution of ADC in explaining the variation of total carbon stock decreased when only carbon of coarse woody debris was used (Fig. 2a vs. b).

3.2. Drivers of carbon pools and components

The subsets regression analyses showed that disturbance has higher importance relative and significant positive effects only on carbon stocks of small stems and litter ($\beta \leq 0.03$; $p < 0.05$; Appendix 5 while it has significant negative effect on carbon stock of understorey trees ($\beta = -0.08$, $p < 0.05$). Therefore, it was included as predictor variable only for understorey trees, small stems and litter carbon stocks. Disturbance intensity reduced carbon stocks for understorey trees and litter ($\beta = -0.04$, $p > 0.05$), but increased carbon stocks for small stems ($\beta = 10.01$, $p < 0.05$; Appendix 6). Slope of the terrain and soil variables have signifcants negative and positive effects on carbon pools and its components (Appendix 5). Slope and clay proportion were found

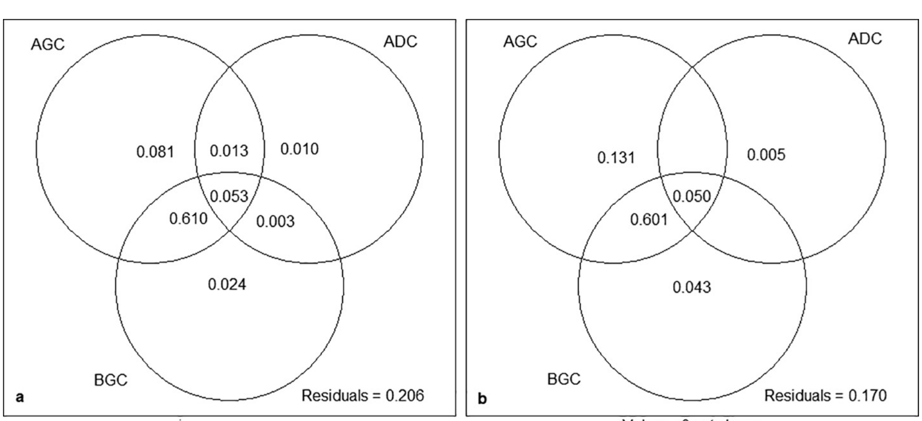

Fig. 2. Venn diagram of variation partitioning results of total carbon stock: (a) with all components (see Table 2) of aboveground carbon (AGC), aboveground dead carbon (ADC) and belowground carbon (BGC); (b) with the best components of each carbon pool: large trees (AGC), coarse woody debris (ADC) and coarse root (BGC) (see Table 3). Values provided in circles represent the semi-partial correlation coefficient of a shared and pure fraction of carbon pools (for details on shared and pure fractions of carbon pools, see Appendix 4).

Table 3
Variation partition results of carbon pools and their components on total carbon stock. F-values and P-values are given only for carbon pools and its significant components.

Carbon pool	Carbon component	Adjusted R^2	F-value	P-value
Aboveground live biomass (AGC)		0.79	22.23	0.001
	Large trees (> 10 cm DBH)	0.75	87.54	0.002
	Understorey trees (5–10 cm DBH)	0.04		
	Small stems (< 5 cm DBH)	0.07		
	Palms stems	0.01		
	Herbaceous vegetation (HV)	−0.03		
Aboveground dead Carbon (ADC)		0.04	1.23	0.324
	Litter	0.001		
	Fine woody debris (FWD)	−0.02		
	Coarse woody debris (CWD)	0.04	2.18	0.143
	Standing dead trees (SDT)	−0.02		
Belowground biomass (BGC)		0.78	67.89	0.001
	Fine Root trees (FRT)	0.01		
	Coarse Root trees (CRT)	0.77	97.60	0.002
	Soil organic carbon (SOC)	0.005		
All	All	0.10	1467	0.001

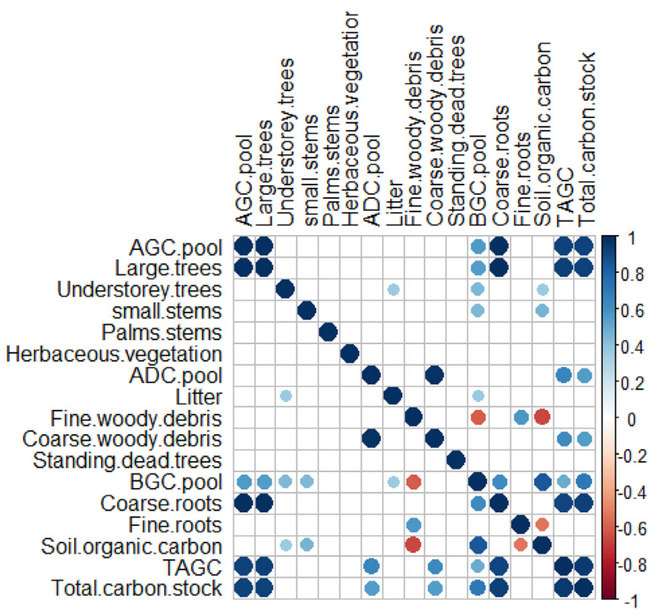

Fig. 3. Significant Pearson correlations ($p < 0.05$) between all carbon pools and components. Positive correlations are displayed in blue and negative correlations in red see (Appendix 4 for all correlation values and their significance). The color intensity and the size of the circles are proportional to the correlation coefficients. To the right side of the correlogram, the legend color shows the correlation coefficients and the corresponding colors. Each carbon pool is followed by its components. AGC = aboveground live carbon, ADC = aboveground dead carbon, BGC = belowground carbon, TAGC = total aboveground carbon. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to be the main driver explaining variation in total carbon stock, AGC, large trees and coarse root carbon stocks (Appendix 6). The explanatory variables explained between 17% and 91% of the total variance among the carbon pools and components (Appendix 6, Adjust R^2).

3.3. Linking aboveground live carbon with forest structure

One objective of this study was to link carbon stocks with forest structure (i.e. tree size and density of big-size trees (> 70 cm DBH) trees), soil variables, topography and disturbance intensity. Distribution of carbon stock per tree size class showed that most carbon was found in trees between 20 and 80 cm DBH (Fig. 5). When density of big size trees

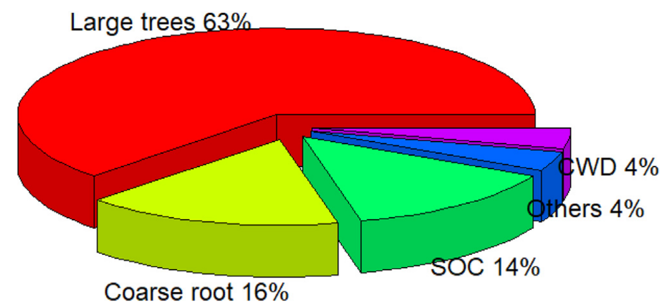

Fig. 4. The proportion of carbon components in total carbon. Note that this figure is different from Fig. 2 because it is not based on variation partitioning. SOC = soil organic carbon; CWD = coarse woody debris; others represent the rest of the eight components (see Table 2).

increased, both total carbon stock (Fig. 6a, adj.R^2 = 0.41, β = 5.57, $p < 0.001$) and aboveground carbon (Fig. 6b, adj.R^2 = 0.38, β = 3.47, $p < 0.001$) increased. Although trees from 1 to 10 cm DBH accounted for 92.1% of the stems, they accounted for only 2.8% of total aboveground carbon. Big-size trees (DBH ≥ 70 cm), on the other hand, accounted for only 0.3% of all stems, but 39% of aboveground live carbon and 25% of total carbon stocks

3.4. Uncertainty estimations

Aboveground live carbon was the largest carbon pool and had the highest $S_{between}$ (33.60 Mg Mg C ha^{-1}) which is higher than S_{within}. These uncertainties were mainly explained by large trees carbon stocks between plots (Table 2). For all carbon pools and components, except for aboveground dead carbon and its main contributor coarse woody carbon stock, we found that $S_{within} < S_{between}$, suggesting that the uncertainty in measuring each carbon pools and components within each plot is lower than the spatial variation of carbon among plots (Table 2). Belowground carbon pool has the least S_{within} and the second $S_{between}$ among the main carbon pools and that these uncertainties were mainly explained by SOC carbon stock.

4. Discussion

4.1. Total carbon stock partitioning

This study is one of the few providing a comprehensive estimate of the main carbon pools in moist tropical semi-deciduous rainforest of the Congo Basin. We found that total carbon stock of our semi-deciduous

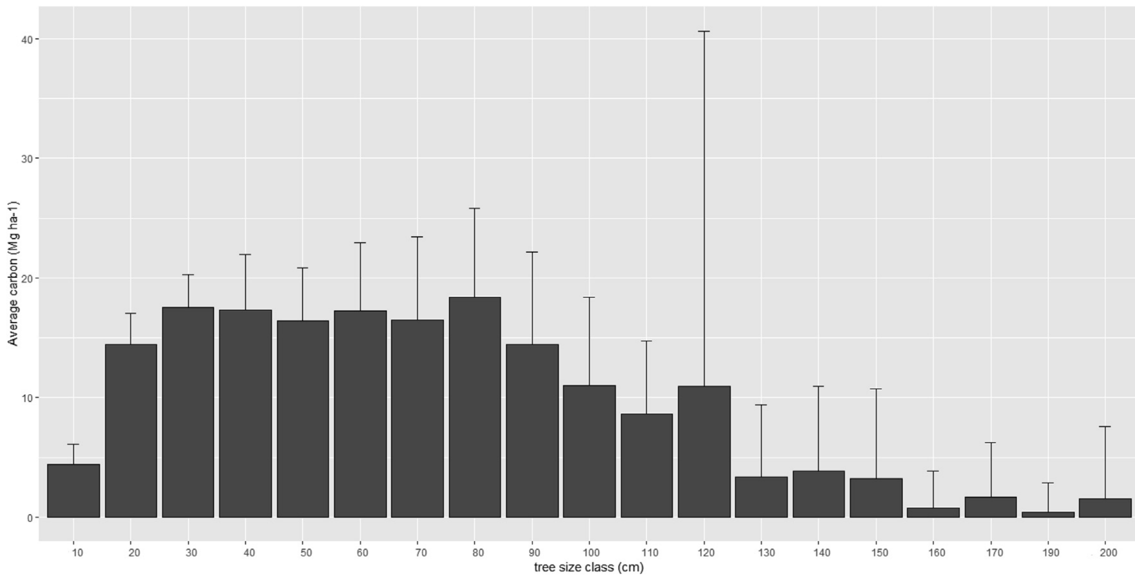

Fig. 5. Average carbon storage with standard error per tree diameter class. Each diameter class contains a 10-cm diameter range, with the value underneath each bar representing the upper limit of that class.

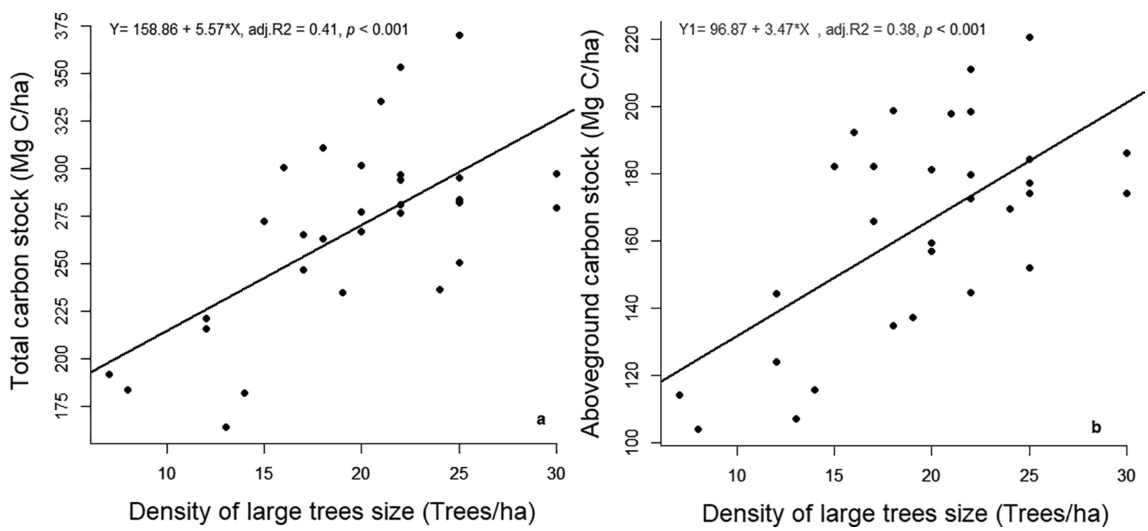

Fig. 6. Relationships of the density of big-size trees (70 cm DBH; X) with (a) total carbon stock (Y) and (b) aboveground carbon stock (Y1).

rainforest in east Cameroon was on average 285.6 ± 51.19 Mg C ha^{-1}, and mainly explained by aboveground carbon (AGC), which was on average 182.62 Mg C ha^{-1}. As found in other studies (e.g. Djomo et al., 2011; Kabelong et al., 2018; Nascimento and Laurance, 2002), our results (Tables 2 and 3) showed that variation in AGC was mainly determined by large trees, suggesting that carbon in large trees gives the best prediction of total carbon stored in these forest ecosystems. This provides important implications, as carbon in large trees is relatively easy to measure for large areas. Aboveground carbon stock in our forest (182.66 Mg C ha^{-1}) was higher than the 154.9 Mg C ha^{-1} found in tropical evergreen rainforest of southern Cameroon (Djomo et al., 2011) and the value of 162.15 Mg C ha^{-1} found in tropical semi-deciduous forest in eastern Cameroon (Chimi et al., 2018). These differences maybe caused by the poorer soil fertility and lower rainfall in our forest, which results in a higher abundance of dense-wooded species (van der Sande et al., 2018) that accumulate high amounts of carbon. Furthermore, the floristic composition and the structural variables (basal area, height-diameter allometry, etc.) explain a large part of the spatial variation of biomass in tropical African forests (Marshall et al., 2012; Shirima et al., 2015): forest with high stand basal area (Day et al., 2013) have generally high aboveground biomass.

Across 260 African forests, Lewis et al. (2013) found an average AGC (DBH ≥ 10 cm) of 185 Mg C ha^{-1}, slightly higher than the values found in our forest (177.61 Mg C ha^{-1}). Lewis et al. (2013) showed, however, that AGC decreases in areas with strong seasonality, such as our forest (which has also been found for Neotropical forests; Poorter et al., 2015). Other studies support that carbon stock is higher in humid compared to dry African forests (Day et al., 2013), and in semi-deciduous compared to evergreen forests (Fayolle et al., 2016). This would indicate that climate seasonality leads to lower carbon storage, whereas low soil fertility may lead to higher carbon storage.

African forests have been found to store more aboveground carbon than Amazonian forests (Lewis et al., 2013; Malhi et al., 2006). These differences may be associated with taller trees, higher stem density, higher wood density, and history of lower-frequency disturbances in African forests compared to Amazonian forests (Lewis et al., 2013). Further studies need to disentangle the role of biogeography, disturbance, soil and climate in determining above and belowground carbon storage in the semi-deciduous forest of Cameroon.

We found that belowground carbon (BGC) was the second most important pool contributing to total carbon stock, and that its both components (root biomass and soil organic carbon; SOC) were important (Table 2), with a slightly more important contribution of coarse roots (Fig. 4). We used a root:shoot ratio to estimate coarse root carbon, causing a strong correlation between coarse root carbon and AGC (Fig. 3). Since our forest had higher AGC than evergreen tropical rainforest (Djomo et al., 2011) and the semi-deciduous forest in Cameroon (Chimi et al., 2018), this may explain the higher coarse root carbon in our forest compared to these forests.

SOC contributed slightly more weakly to BGC than root biomass, probably because it varied more strongly among plots ($S_{between}$ = 32 Mg C ha^{-1}, compared to 19 Mg C ha^{-1} for coarse root carbon). The variation in SOC among our plots may be explained by a variety of factors. The fact that our study site is poor in nutrients suggests that turnover and, hence, carbon input from litter is low. This may explain the lower SOC carbon in our forest (40 Mg ha^{-1}) compared to the evergreen rainforest in southern Cameroon (Djomo et al., 2011) and multiple tropical African forests (Dixon et al., 1994).

We found that aboveground dead carbon (ADC) was the least important contributor to total carbon stocks (5%, Fig. 2 and Table 3), and was mainly determined by coarse woody debris. These results agree with deadwood mass in moist tropical Amazonian forests, which has been estimated to be < 10% (Delaney et al., 1998) of total aboveground carbon stocks. We found that ADC and its components varied widely (Table 2) among our plots, and that this variation was due mostly to environmental factors (Appendix 5). We found that ADC increased when aspect decreased ($\beta = -8.40$, $p < 0.01$) while it increased when terrain slope increased ($\beta = 3.43$, $p < 0.001$). Interestingly, disturbance had no effect on ADC, in contrast to earlier studies (Pfeifer et al., 2015; Rozak et al., 2018), probably because disturbance was relatively low and occurred 20 years ago (Garbarino et al., 2015; Osone et al., 2016; Weedon et al., 2009). Differences in decomposition rates among species (Barbosa et al., 2017; Harmon et al., 1995) and structural forest traits (Pfeifer et al., 2015) may also explain the large heterogeneity in ADC among our plots.

4.2. Carbon partitioning among forest carbon components

We found that carbon in large trees was the main component of total carbon stock, followed by root carbon, soil organic carbon and coarse woody debris (Fig. 4). Furthermore, most of the carbon in large trees came from the big size trees in the forest (> 70 cm DBH; Fig. 5). Therefore, in this semi-deciduous forest, the carbon stored by big-size trees could be used as a useful proxy for total carbon stock. The role of big size trees in driving forest carbon stocks is well recognized (Bastin et al., 2018; Lutz et al., 2018; Slik et al., 2013) and the amount of biomass in big-size trees has been quantified recently across the tropics (Bastin et al., 2018; Bastin et al., 2015; Lutz et al., 2018; Poorter et al., 2015; Slik et al., 2013; Stegen et al., 2011). A Pantropical analysis for 120 lowland tropical forests showed that 70% of the site variation in aboveground biomass was determined by the density of big size trees (DBH > 70 cm) (Lewis et al., 2013). Furthermore, the authors showed that African forests are dominated by relatively low-frequency disturbance regimes, allowing trees time to grow large and stands to self-thin, and therefore reaching higher carbon stocks than forests in South America and Asia. Because of their importance for aboveground biomass, big size trees play an important role in ecosystem functioning, such as primary productivity (Stephenson et al., 2014).

Even though small and medium-sized trees (10–40 and 40–70 cm DBH) occur in higher density, they cannot provide carbon storage equivalent to the few large canopy and emergent trees. In order to maintain high carbon stocks in the long term, trees should be allowed to reach these large sizes. Therefore, the diversity and abundances of trees with DBH < 10 cm should be safeguarded, so that forests will maintain high carbon storage also in the future (Memiaghe et al., 2016).

We found very low carbon storage by understorey vegetation. Although the forest understorey trees was often quite dense with many small stems, the herb layer was much smaller than in many other forests (e.g. Djomo et al., 2011; Kabelong et al., 2018; Nascimento and Laurance, 2002). This difference is probably due to the poor soils and the disturbance history of the forest. In our study, the carbon stored by small trees (DBH < 10 cm; 4.40 Mg C ha^{-1}) was similar to that in old secondary evergreen forest in Deng Deng (region of east Cameroon; Kabelong et al., 2018) and higher than in evergreen managed forest in southern Cameroon (Djomo et al., 2011).

As hypothesized, longtime disturbance did not have a significant influence on most carbon pools and components. It only signicantly increased aboveground carbon stocks of small stems, possibly because disturbance increases the availability of light and the reduces competition in the understorey vegetation. This finding has been shown in the Amazonian forest where disturbance increased growth of small trees but did not or negatively affect mature trees (Holm et al., 2014; van der Sande et al., 2017b). It has been also shown in Neotropical forest that disturbance increase biomass growth and recruitment (Poorter et al., 2017).

Carbon stored in coarse woody debris (10.90 Mg C ha^{-1}) in our forest was lower compared to values of 16.1 Mg C ha^{-1} found in a moist lowland tropical forest in Central Panama (Gora et al., 2019). Coarse woody debris is determined by the input of dead wood and output through decomposition. In old-growth, lowland tropical forests growing on very nutrient-poor soils, or in very dry sites, coarse woody debris is often low due to low rates of CWD input (Baker et al., 2007). In our forest on poor soils, the input of woody debris may also be low, causing slow accumulation and low carbon stocks in coarse woody debris.

Standing dead wood contributed 16% to aboveground dead carbon, and 1% to total carbon. Carbon in dead biomass from our site was higher than in old secondary forest in eastern Cameroon (Kabelong et al., 2018), possibly because our forest has higher tree density and total biomass, which could lead to a higher input of dead biomass. Even though standing dead wood is only a small part of total carbon, its carbon storage across large areas can be substantial. Estimates of standing dead wood are therefore important for validating carbon cycling models (Chambers et al., 2000). However, these data, as well as carbon estimates of woody debris, trees with dbh ≤ 5 cm and litter, are available only for few tropical forest sites.

4.3. Correlations among carbon components

We expected that total carbon stock would be positively correlated with its underlying carbon pools and components. Furthermore, all carbon components would be positively correlated, as a forest with higher total biomass and tree density would have more biomass and carbon in all components. We indeed found strong positive correlations between total carbon stock and aboveground carbon pool, and aboveground dead carbon pool and belowground carbon pool (Fig. 3).

As we are in a managed forest, we expected that carbon stored in large trees would be negatively correlated with woody debris and standing dead trees, because plots with higher disturbance would have fewer large trees and more debris. Furthermore, forests with high carbon stocks in large trees would be denser with less light reaching the understory and, hence, have a more open forest understorey. Interestingly, we found that carbon in large trees was strongly positively correlated with root carbon, but not with any of the other carbon components (Fig. 3). Abovegroung carbon stocks depend on the long-term buildup of carbon, and are balanced by mortality and decomposition. For that reason, the amount of carbon present in different components, of which the buildup and removal are driven by different factors, may be unrelated.

We found a positive correlation between litter and carbon in understorey trees, probably because the high density of understorey trees can increase the amount of litter produced. Moreover, we found only a weak correlation between carbon in live components and carbon in dead trees, probably because most dead carbon is derived from large trees that die, but mortality of these large trees is largely a stochastic process (van der Sande et al., 2017b).

Variation partitioning results showed that ADC and coarse woody debris were positively correlated with total carbon stock (Fig. 2; Table 3), though more weakly than the two other carbon pools. We found a negative correlation between soil organic carbon and fine woody debris (Fig. 3). This is striking, as a higher input of fine woody debris would automatically lead to a higher input of carbon to the soil, which would suggest a positive correlation between the two. Perhaps the input of fine woody debris is limited, and decomposition would reduce carbon in fine woody debris while increase soil organic carbon.

4.4. Implications for sustainable forest management

Our results highlight that large canopy and emergent trees play an important role in forest community structure and ecosystem carbon storage. Preserving large trees, as well as leaving dead biomass in the forest, could therefore enhance and maintain forest carbon stocks. Furthermore, management techniques that enhance carbon storage (e.g. protecting young so that they can reach the canopy, not removing canopy trees, etc.) would be very important in enhancing the forest's capacity to store carbon. These measures would contribute to the effectiveness and efficiency of the REDD + mechanism, as well as the sustainable management of the Cameroon forests. Moreover, controlling disturbance intensity and combining it with silvicultural guidelines (Sist et al., 2003) are still relevant to minimize the impact of disturbance to AGB and stand damage. Strengthening and monitoring the adoption of reduced-impact logging (RIL) would help prevent logging damages and carbon emissions (Rozak et al., 2018).

5. Conclusion

Here, we aimed to obtain a better understanding of the carbon cycle and contribute to reducing the uncertainties in the distribution of carbon stocks. We found that aboveground carbon was the main pool explaining the variation in total carbon stock, followed by belowground carbon. Large trees were the main contributor to aboveground carbon stocks, while carbon in roots was the main contributor to belowground carbon stocks. Belowground and aboveground carbon stocks were significantly correlated with total carbon stock. However, smaller carbon components (e.g. understorey trees and small stems, herbaceous vegetation, fine woody debris, standing dead trees) contribute little and were only weakly correlated with total carbon stock. This indicates the importance of large trees for carbon storage, and of the protection of smaller trees to secure long-term carbon storage. Management techniques/plans can enhance the forest's potential to sequester and store carbon, and hence maximize the forest' contribution to climate change mitigation.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117686.

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