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Biomass and soil carbon stocks of the main land use of the Allada Plateau (Southern Benin)

Issiakou Alladé Houssoukpèvi[a,b], Hervé Nonwègnon Sayimi Aholoukpè[b,c], Demayi Jorès Mauryo Fassinou[b], Murielle Nancy Rakotondrazafy[a], Guillaume Lucien Amadji[b], Lydie Chapuis-Lardy[a,d] and Tiphaine Chevallier[a]

[a]UMR Eco&Sols, Université de Montpellier, CIRAD, INRAe, IRD, Institut Agro Montpellier, Montpellier, France; [b]UR Ecopédologie, Laboratoire de Sciences du sol, Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, Cotonou, Benin; [c]Centre de Recherches Agricoles Plantes Pérennes (CRA-PP), Institut National des Recherches Agricoles du Bénin, Pobè, Benin; [d]LMI IESOL, Centre de recherche ISRA-IRD, Dakar, Sénégal

ABSTRACT
The inventory of the carbon (C) pools in Africa's ecosystems is not well documented, although it is crucial to support climate mitigation policies. We quantified the C stocks in plant biomass, woody necromass, litter and soil (0–30 and 30–100 cm) for the five main land uses – forest, tree plantation, young and adult palm groves, croplands – of Ferralsols on the Allada plateau in southeast Benin. Forests have the highest total C stocks (389 ± 54 Mg C ha^{-1}) compared with other land uses (222 ± 33, 154 ± 6, 105 ± 2, 77 ± 3 Mg C ha^{-1} in tree plantations, adult palm groves, young palm groves and croplands, respectively). The C stocks are higher in the biomass than in the soil (0–100 cm), e.g. in the forest, stocks were 279 ± 54 Mg C ha^{-1} in the biomass *versus* 83 ± 2 Mg C ha^{-1} in the soil. Differences of soil C stocks between land uses are low (≈ 28 Mg C ha^{-1}) and concentrated in topsoils. The structure and species diversity of the forest partly explained the variability and the high C biomass compared to tree plantations. Type of forest and plantations is important to consider in conserving C stocks in landscapes.

KEYWORDS
Organic stocks; carbon pools; climate change; allometric models

Introduction

Since the middle of the twentieth century, emissions of greenhouse gases (GHGs) including carbon dioxide (CO_2) into the environment have led to global warming and climate change. The agriculture, forestry and other land use (AFOLU) can contribute to 20–60% of the total mitigation potential of global GHG emissions by 2030 by reducing agricultural emissions, increasing carbon stock in soils and biomass products [1–3]. Moreover, carbon and changes in carbon stocks in terrestrial ecosystems is a major of issue in the efforts to control land degradation and preserve biodiversity. Thus C balance in natural ecosystems has been becoming a high priority issue on the global political agenda [1, 4–6].

National climate change adaptation and mitigation plans often involve actions in the AFOLU sector. This is mostly the case in African countries where activities in the agricultural and forestry sector are crucial for the economy [7]. These plans highlight the potential co-benefits of implemented actions for rural development, food security and ecosystem conservation. However, concrete initiatives regarding the quantification of carbon (C) sequestration, are scarce due to the lack of data on C stocks and storage potential under all land uses [8].

For these inventories, programmes such as the Clean Development Mechanism (CDM) initiated under the Kyoto Protocol and the Reduction of Emissions from Deforestation and Forest Degradation (REDD+) mechanism under the United Nations Framework Convention on Climate Change (UNFCCC) defined five carbon pools: aboveground biomass, belowground biomass, necromass, litter and soil organic carbon [9]. Several studies have reported great heterogeneity in the C stocks of these pools according to land cover, land use and soil type [10–18]. In most cases, natural

CONTACT Issiakou Alladé Houssoukpèvi alladeissiak@gmail.com UMR Eco&Sols, Université de Montpellier, CIRAD, INRA, IRD, 34060 Montpellier, France.

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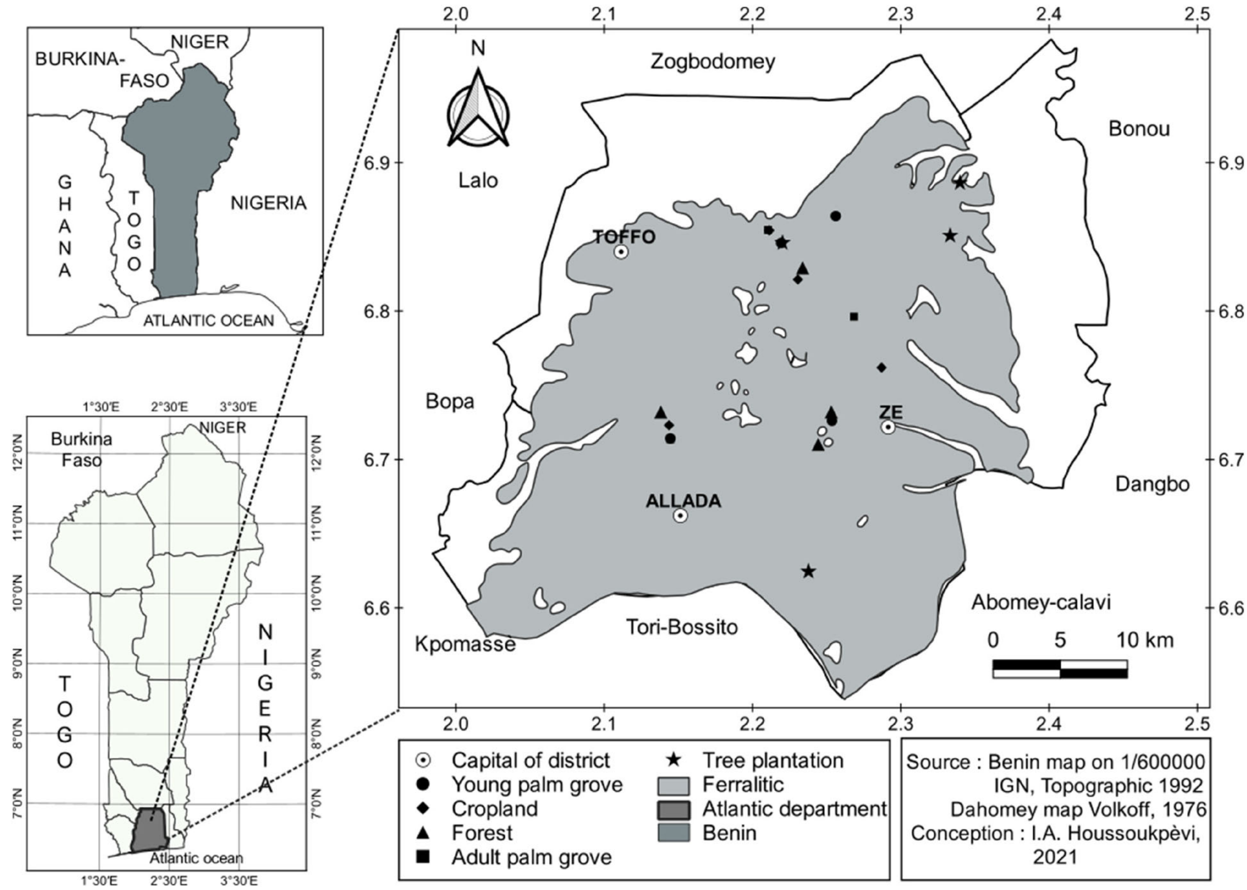

Figure 1. **Localisation of the study sites on the Allada plateau (southern Benin).**

formations or formations with the least human disturbance such as forests store more C in their aboveground biomass and soils per unit area than any other type of land use [15, 19–23]. Tree plantations also show high C stocks but often less than primary or secondary forest [24]. Tropical forests remain among the main focal points for initiatives to sequester large amounts of C, as well as to recover from biodiversity loss [25,26]. Face to wide spatial variation in forest C below ground and above ground biomass [15, 21], understanding the relationship between C storage potential and tree species composition of such ecosystem is compulsory for implementation of management strategies for tropical forest [27,28]. On the contrary, from a given region, soils of croplands have the lowest carbon stocks with variations caused by soil type and agricultural practices [29].

In African and sub-Saharan countries, where quantifications of soil carbon stocks at regional or country level are being produced [14, 30–33], systematic data are still lacking for some carbon pools of land uses. More importantly, rural areas, especially those close to large cities and densely populated, are generally a mosaic of land uses [34,35]. The likely very heterogeneous C stocks of these areas are not well characterized [14, 36]. It is essential to have carbon reference values in these regions where demography and land pressure are high and land uses are still in evolution. This is especially the case in the South-East of Benin on the Allada plateau close to the economic capital of the country. In this area, the dynamics of high value-added tree plantations and palm groves are important in combination with croplands [35, 37–39]. The urban development and cultivation pressure often leads to a decrease in C stocks, as woody biomass and necromass are negligible and annual soil C inputs are low in croplands. Moreover, significant mineralization of soil organic carbon (SOC) and erosion phenomena enhance the decline in C stocks in soils under the tropics [15]. On the Allada plateau, the decrease in SOC could be critical, as soils are mostly sandy [40]. However, the awareness of low SOC in tropical topsoils overlooked the potential of subsoil horizons storing high proportions of SOC stocks at depth [41]. To our knowledge, data in African soils are poorly quantified under a variety of land uses, e.g. in private smallholders tree plantations, and in soils deeper than 30 cm. There are also few studies that have examined the relationship between biodiversity and biomass C stock [11]. In Benin, most studies on C stocks have focused on the impact of

Table 1. **Sampling design and number or replicates per plots by land uses and practices for vegetative.**

Land use	Sites	Area (ha)	Municipality	Land use age (years)	Practices age (years)	Tree measures	Soil and litter replicates per plot
Forests							
Classified	Niaouli	75.5	Allada	>50	–	7 plots*	35
Sacred	Damè	11	Toffo	>50	–	5 plots*	25
Sacred	Domè sèko	5	Zè	>50	–	2 plots*	10
Sacred	Koundokpoé	2	Zè	>50	–	2 plots*	10
Tree plantations							
State	Teak	45	Zè	65	5	6 plots*	30
State	Teak	24	Zè	65	21	5 plots*	25
Private	Teak	0.5	Toffo	–	10	2 plots*	10
Private	Gmelina	1	Allada	–	5	2 plots*	10
Adult palm groves[§]	Maize	1	Allada	–	10	20 trees	16
	Pineapple	3	Zè	–	12	20 trees	25
	Cassava	2.5	Toffo	–	12	20 trees	22
Young palm groves[§§]	Maize	0.5	Toffo	–	<5	20 trees	10
	Pineapple	1	Zè	–	<5	20 trees	15
	Cassava	0.8	Toffo	–	<5	20 trees	10
	Tomato	0.5	Allada	–	<5	20 trees	10
Croplands	Maize	0.8	Zè	–	4		10
	Pineapple	1.5	Toffo	–	5		12
	Cassava	0.5	Toffo	–	2		10
	Tomato	1.5	Allada	–	3		12

*Square plots of 0.25 ha.
[§]Adult palm trees that were associated with Maize, Pineapple or Cassava at their young stage,.
[§§]Young palm trees that are currently associated with Maize, Pineapple, Cassava or Tomato.

cropland practices on soil C stocks [17, 20, 42] or on forest biomass C stocks [21]. It is then necessary to characterize the C stocks of all the land uses in these landscapes.

The main objective of the study was to quantify the different pools of C stocks and their variability according to the main land uses of the Allada plateau. We hypothesized that (i) C stocks would be higher in forest than in tree plantations or palm groves, and that biodiversity in tree species could be an explaining factor of the variation of the C stocks; (ii) the lower C stocks would be found in cropland and (iii) considering the predominance of Ferrasols with a sandy texture and the low capacity of these soils to store C [18, 38, 43–45], the variations in C stocks with land uses will be mainly derived from the biomass. The specific objectives of this study were (i) to fulfill the needs for sub-Saharan Africa data in vegetation and soil C stocks down to 1 m deep; (ii) to compare the C stocks in 5 land uses (forest, tree plantations, adult and young palms groves and croplands); and (iii) examine the relationship between forest biodiversity and biomass C stock. Finally, in the conclusion, we shortly considered how the results of the study could provide data and clues for local land use plans and policies.

Materials and methods

Study area

This study was conducted in the Lama's territory located on the Allada plateau (elevation from 3 to 175 m a.s.l., 6°20′–6°50′ N and 2°00′E) 30–50 km northwest of the economic capital. The region exposes a heterogeneous agricultural landscape, where relics of natural forests, state tree plantations and food crops were mixed with private tree plantations of smallholder farmers, oil palm plantations and pineapple cultivation [34,35]. The Lama's territory is composed of three municipalities, Allada, Toffo and Zè, located in the Atlantic Department in southern Benin (Figure 1). These three agricultural municipalities cover an area of 150,659 ha out of the 214,000 ha of the plateau. Among the 7 communes of the plateau, these three communes are the most extensive and diversified in terms of agricultural practices [46,47]. The study area is located in a tropical savannah zone with dry winter (Aw) according to the Köppen-Geiger climate classification scheme [48]. Average monthly temperatures range from 25 to 29 °C. Average annual rainfall is 1100 mm [49]. The dominant soil types in the region are Ferrallitic and Ferruginous soils, Vertisols and hydromorphic soils [50]. The Ferrallitic soils, or Ferralsols in the world reference base for soil resources [43], represent 70% of the soil cover (106,709 ha out of 150,659 ha) in these three municipalities [40, 51]. Ferralsols are formed on sandy-clay sediments from the continental terminal, and commonly called "terre de barre." The study focused on these Ferralsols only.

Land uses

The main land uses on the Allada plateau are (1) forests, (2) tree plantations, (3) adult palm groves,

(4) young palm groves, and (5) croplands including annual and biennial crops [34,35, 44,45]. To investigate the variability of C stocks under these land uses, the local diversity of plant cover and agricultural practices was explored for each land use.

The forest land use included two types of forest: (i) classified forests, i.e. relics of natural forests under the protection of a public structure, and (ii) sacred forests, often smaller forested areas under the protection of local communities. These sacred forests are found throughout the tropical zone and cover 0.16% of Benin's national territory [52]. They are used for cultural and traditional religious rituals. These community forests support biodiversity conservation [53], being refuges for endemic species, and provide many ecosystem goods and services to communities. However, they are sometimes degraded by insufficient management and illegal exploitation [54,55]. In this study, the C stocks were measured in 4 forests. The part of the classified forest of Niaouli which was located on the plateau in the municipality of Allada and managed by the Niaouli Agricultural Research Centre of the Institut National des Recherches Agricoles du Bénin (INRAB); Three sacred forests located in the villages of Domè-Seko and Koundokpoé (Municipality of Zè) and in the village Damè (Municipality of Toffo) (Table 1).

The tree plantations modalities consist mostly of Teak (*Tectona grandis* L.f.) and Gmelina (*Gmelina arborea Roxb*) plantations. Two types of management were considered: (i) state plantations (that cover 13,000 ha nationally) under government management, in particular by the Office National des Bois (ONAB), and (ii) private smallholder plantations, which are generally small in the study area, about 0.44 ha on average [52, 56]. State teak plantations were established since 1949 mostly after a degraded forest. They are generally managed as even-aged stands for timber production with a revolution of 20 to 60 years [57]. Harvesting is regulated and regeneration is natural. The success of these state plantations has encouraged many landholders and farmers to establish plantations for the production and sale of service wood (posts and poles) with a diameter comprised between 5 and 15 cm [56, 58,59]. These private smallholder plantations are usually established after annual crops. The revolution is generally very short with an harvest each 5–10 years. In this study, the C stocks were measured in 4 tree plantations: (i) two state teak plantations, 5 and 21 years after the last harvest, located in the Djigbé sector (Zè municipality); (ii) two private plantations, one of teak and one of Gmelina, 10 and 5 years after last harvest respectively (Table 1).

The Atlantic department on the Allada plateau of Benin is recognized for its high number of oil palm trees, *Elaeis guineensis Jacq* [44]. During the first 6 years of the plantation, annual crops occupy the space between the young and non-exploited palms. This temporary agroforestry system is motivated by the lack of arable land for smallholder who usually farm less than 5 ha [47, 60–62]. In the study area, young palms are mostly associated to crops such as maize (83%), tomato (29%), pineapple (25%) and cassava (23%) [45]. In this study, C stocks were measured in four young palm groves under temporary agroforestry and in three adult palm groves. The four selected young palm plantations are at the end of their immature phase (*ca* 5 years) and associated with maize, pineapple, tomato or cassava. The three selected adult palm groves (10–12 years old) have supported maize, pineapple, or cassava crops at their young age (Table 1). As tomato cultivation is recent, we did not find any adult palm groves whose immature phase had been associated with tomato cultivation.

The local croplands are mainly cultivated with maize (*Zea mays*), pineapple (*Ananas comosus*), cassava (*Manihot esculentus*) and tomato (*Solanum lycopersicum*) [45, 63]. These crops are mainly rainfed. Before each cropping season, farmers clear the land, often by slash and burn. Fallow is rarely practiced in the study area due to the expanding population [34,35] and the limit access to land. The soil is manually tilled to a maximum depth of 20 cm using hoes. Mineral fertilizer application is low for food crops such as maize and cassava, but can be high in the form of urea and NPK fertilizer (14–23–14) for cash crops: about 159 kg N ha^{-1}, 49 kg P ha^{-1} and 34 kg K ha^{-1} split into two applications for tomato, and 480 kg N ha^{-1}, 70 kg P ha^{-1} and 93 kg K ha^{-1} split into three or four applications for pineapple [64]. Some producers return crop residues to the soil after harvest, especially for tomato and pineapple [65]. This study considers 4 fields under common practices with either maize, pineapple, tomato or cassava (Table 1).

Thus, 19 plots on Ferralsols and under the main land uses and management options founded in the three municipalities of Allada, Zè and Toffo were selected (Table 1). The age of the land use (plantation, forest, cultivation) and of the agricultural practices (harvesting, establishment of

Table 2. Equations used in the calculation of the biomass density of the different pools

Variables	Unit	Formulas	Sources
Forest and plantation			
Stem biomass in the plot (B_{stemp})	kg DM/0.25 ha	$\boldsymbol{B_{stemp}} = \Sigma_{ij}(\boldsymbol{B_{smi}} + \boldsymbol{B_{gmj}})$ with B_{smi} = biomass stock of p plot derived from specific model for i species (kg DM) and B_{gmj} = biomass stock of p plot derived from generic model for j species (kg DM)	[72]
Forest and plantation biomass (B)	Mg ha^{-1}	$\boldsymbol{B} = \boldsymbol{B_{stemp}} \times \boldsymbol{BEF} \times (1 + \boldsymbol{R})$ with B_{stemp} in Mg ha^{-1} ; BEF = biomass expansion factor at 3.4 and R = root-to-shoot ratio at 0.24 for broadleaf tropical forest (with D130 > 10 cm)	[73]
Oil palm groves			
Aboveground biomass of young oil palm groves (AGB)	kg	$\boldsymbol{AGB} = 0.0976 \times \boldsymbol{H} + 0.0706$ with H = tree height (m)	[74]
Mean biomass of an individual mature frond of an adult oil palm (MDW)	kg	$\boldsymbol{MDW} = 1.147 + 2.135 \times [1/3 \times (\boldsymbol{DW_{rachis17}} + \boldsymbol{DW_{rachis21}} + \boldsymbol{DW_{rachis25}})]$ with DW_{rachis} = dry weight of rachis of leaf 17, 21 and 25 respectively.	[75]
Dry weight of rachis (DW_{rachis})	kg	$\boldsymbol{DW_{rachis}} = 1.133 \times \left(\frac{DW_{frag}}{L_{frag}}\right) \times \boldsymbol{L_{rachis}}$ with DW_{frag} = dry weight of a fragment take on the rachis (kg); L_{frag} = fragment length (m) and L_{rachis} = rachis length (m).	[75]
Stem biomass of an adult palm (SAGB)	kg	$\boldsymbol{SAGB} = SLD_{150} \times H33 + (2 \times SLD_{150} + 570 \times S_{150} - 160) \times Ccurv$ with SLD_{150} = stem linear density at 1.5 m height, S_{150} = stem section at 1.5 m height and C_{curv} = coefficient linked to the variation of the SLD along the stem (H33 in m).	[76]
Stem section at 1.5 m height (S_{150})	m^2	$S_{150} = 3.14 \times (\frac{D150}{2})^2$ with D150 = Diameter at 1.5m height in m	[71]
Stem linear density at 1.5 m height (SLD_{150})	kg m^{-1}	$SLD_{150} = S_{150} \times \boldsymbol{Core\ density}\ (1.5\ \boldsymbol{m})$ with core density in kg m^{-3}	[71]
Coefficient linked to the variation of the SLD along the stem (C_{curv})		$C_{curv} = 0.84 \times [\ln(1 + H33/0.6) - H33/2.1]$ with H33 = Tree height measured at 33th leaf level (m)	[71]
Belowground biomass of oil palm groves (BGB)	Mg ha^{-1}	$\boldsymbol{BGB} = \boldsymbol{AGB} \times 0.235$ with AGB = aboveground biomass (Mg ha^{-1})	[77]
Necromass (NM)	Mg ha^{-1}	$\boldsymbol{NM} = \boldsymbol{B} \times 0.09$ with B = total biomass (Mg ha^{-1})	[78]
Litter biomass (LB)	Mg ha^{-1}	$\boldsymbol{LB} = (\boldsymbol{WT} \times \boldsymbol{SDW})/100$ with WT = total weight of litter and SDW = Dry matter obtained from the oven-dried litter sample	[79]

cassava, tomato or pineapple crops) were indicated in Table 1 when information are available.

Vegetation data and soil sample collection

The collection of soil samples and field data were carried out between August and September 2019. The vegetation and dendrometric data required for the estimation of biomass were collected on 20 trees in the adult and young palm plots and on 0.25 ha square plots in each forest and tree plantation sites [66,67]. The number of square plots (Table 1) depends on the size of the study site [68,69]. The dendrometric data collected were the tree stem height (H) and the tree diameter measured at 1.3 m above the floor (D130) in the studied tree plantations. For adult palms, in addition to H and diameter (measured for this species at 1.5 m height; D150), trunk cores and leaf samples were taken to assess trunk density at 1.5 m and rachis dry biomass of leaf in rows 17, 21 and 25 [70]. For young palms, only H was measured. All these data are necessary to run existing allometric models and estimate biomasses (Table 2).

The litter and soil samples were collected in five quadrats of 1 m^2 along the diagonal of each 0.25 ha square plots in the forests and forest plantations. In the palm groves and cropping systems, 10 to 25 quadrats of 1 m^2 were collected depending on the size of the plots (Table 1). In each 1 m^2 quadrat, soil sampling was carried out at the following depths: 0–10 cm, 10–30 cm, 30–50 cm, 50–100 cm. To reduce the number of analyses while considering the heterogeneity of the plots, five composite of soil samples per depth per site were performed. In adult palm groves, to ensure that the high heterogeneity associated with pruning leaf swaths, representative of 10% of the plot [61], was taken into account, soils were also sampled from swaths (5 additional quadras per plot).

The soil bulk density (BD) was measured at 0–10 cm, 10–30 cm, 30–50 cm, 50–100 cm depth on each plot using the cylinder method (100 cm^3) [79]. The Ferralsols of the Allada plateau do not contain gravels and stones > 2 mm [40], so the soil BD was calculated as the dry weight (105 °C) of the soil divided by the volume of the sample (g cm^{-3}).

Soil analysis and soil carbon stock calculation

The collected soil samples were air-dried and sieved to 2 mm before analysis. Soil pH was determined in water:soil (2:1) suspension [80]. Available phosphorus (P) was determined by Bray-1 extraction followed by molybdenum blue colorimetry [81]. Total carbon and nitrogen contents were determined by total dry combustion of a finely crushed sample aliquot (< 200 µm) using an elementary analyzer (Thermo flash 2000 CN analyzer, Milan, Italy). As there is no carbonates in these soils, total C is SOC. Soil texture was determined by the Robinson pipette method [82].

The SOC stocks were calculated on each of the sampled soil layers based on IPCC procedures [13, 72], with equation 1:

$$C\ stocks\ \left(Mg\ C\ ha^{-1}\right) = 0.1\ \times C\ \times BD\ \times T \quad (1)$$

Where, C is the SOC content (g C kg^{-1} soil); BD is the soil bulk density (g cm^{-3}) and T is the thickness of the soil layer (cm). Calculations of stocks at greater depths were done by adding up the corresponding soil layers. The comparisons of SOC stocks between land uses were done on equivalent soil thickness basis or on equivalent soil mass basis (ESM). Bulk density was used to calculate the soil mass, i.e. 4000, 11000 and 15000 Mg ha^{-1} for approximatively 0–30, 30–100 and 0–100 cm depth (Equation 2).

$$ESM\ \left(Mg\ ha^{-1}\right) = 100 \times \mathrm{BD}\ \times \mathrm{T} \quad (2)$$

Where, BD is the soil bulk density (g cm^{-3}) and T is the thickness of the soil layer (cm).

For soils under adult palm groves, stocks per hectare were calculated from the carbon content under the swaths for 10% of the plot surface and outside the swaths for the remaining 90%.

Biomass and litter estimation and biomass carbon stock calculation

Woody biomass, necromass and litter (grasses and plant debris) estimations were carried out for forest, tree plantations, adult and young palm groves. Above- and below-ground biomasses of trees were estimated using equations detailed in Table 2, and expressed as dry matter (DM).

In forests, an inventory of the tree species in each plot was carried out. In the Niaouli forest managed by INRAB, the species of most of the trees were labelled. For unlabeled trees and in sacred forests, species were determined using the Benin analytical flora [46]. In forest and tree plantations, stem or trunk biomasses were estimated using species-specific biomass models when available or generic models if not [83–85]. These models were fed with measured H and D130 values (Supplementary Material 1). The above and belowground biomass (B) were calculated using the stem biomass of the trees (Table 2). The biomass expansion factor (BEF) used to estimate forest and plantation biomass was the BEF values for tropical broadleaf forests established by the IPCC, [86,87] in the good practice guidance for land use, land use change and forestry. The value of 3.4 adapted to growing stock biomass in the forest or plantation stands was used. We considered that forests and plantation are dynamic due to regular logging or natural tree falls. Indeed, in the forests illegal logging activities are frequent, especially in the sacred forests. In state-managed plantations, logging is regulated and regular, whereas in private plantations logging is not controlled.

For young palm groves (< 6 years), the aboveground biomass (AGB) of each palm was calculated from H (Table 2). In adult palm groves, AGB of each palm was calculated by adding the biomass of the mature fronds (MDW) and the stem biomass (SAGB) (Table 2) The belowground biomass (BGB) of young or adult palms (Table 2) was estimated from the AGB [76]. The biomass (B) is the sum of AGB and BGB and then scaling up using the density of palms of 143 ha^{-1} reported for the area [64].

For logistic reasons, the dead biomass or necromass (NM) of forests and tree plantations were not measured but calculated from the biomass (B) by an equation established in tropical forest (Table 2). In palm groves, there were hardly no dead trees, so NM was considered negligible.

The method used for biomass in litter was the full collection of litter [88–90] according to the guidelines of the UNFCCC [78]. In each 1 m^2 quadrat, weeds and plant debris were collected and weighed after drying at 65 °C. In the rows of adult palm groves, the biomass of pruning leaves in swath was also estimated. The litter biomass (LB) was calculated using the equation mentioned in Table 2.

The carbon stocks of the vegetation compartments (above- and belowground biomass (B); necromass (NM); litter biomass (LB) were estimated from equation 3 [72, 91]:

$$\left[Biomass\ carbon\ stock\ \left(Mg\ C\ ha^{-1}\right)\right] = \left[Biomass\ \left(Mg\ ha^{-1}\right)\right] \times 0.47 \quad (3)$$

Carbon stock variability analysis

Standard deviation and the coefficient of variation (CV) were used to assess the variation in the C stock of each C pool within each land use. The variability of biomass (B) and the associated C stock within forests and tree plantations were analyzed with the structure of the stands, i.e. tree density, basal area, D130, and biodiversity indices,

Table 3. Physico-chemical properties of soils (mean ± standard deviation).

Soil properties	Soil depth (cm)	Forests $n = 20$	Plantations $n = 20$	Adult palm $n = 15$	Young palm $n = 20$	Croplands $n = 20$
Sand (g kg^{-1})	0–10	757 ± 38 a	767 ± 29 a	838 ± 46 a	833 ± 27 a	773 ± 66 a
	10–30	753 ± 53 a	778 ± 30 a	826 ± 56 a	809 ± 31 a	747 ± 68 a
	30–50	657 ± 61 a	681 ± 81 a	6506 ± 37 a	697 ± 34 a	659 ± 64 a
	50–100	542 ± 60 a	602 ± 94 a	584 ± 50 a	568 ± 40 a	615 ± 39 a
Silt (g kg^{-1})	0–10	125 ± 27 a	166 ± 26 a	68 ± 36 a	75 ± 29 a	135 ± 61 a
	10–30	114 ± 27 a	134 ± 27 a	65 ± 39 a	61 ± 18 a	122 ± 61 a
	30–50	151 ± 35 a	171 ± 46 a	167 ± 14 a	124 ± 34 a	172 ± 45 a
	50–100	215 ± 41 a	225 ± 53 a	179 ± 34 a	203 ± 29 a	180 ± 23 a
Clay (g kg^{-1})	0–10	103 ± 27 a	63 ± 18 a	79 ± 17 a	72 ± 8 a	78 ± 10 a
	10–30	128 ± 33 a	85 ± 25 a	88 ± 22 a	111 ± 16 a	115 ± 13 a
	30–50	181 ± 28 a	138 ± 39 a	160 ± 30 a	170 ± 24 a	151 ± 27 a
	50–100	234 ± 28 a	158 ± 47 a	213 ± 27 a	214 ± 30 a	189 ± 22 a
Bulk density (g cm^{-3})	0–10	1.3 ± 0.02 ab	1.3 ± 0.02 ab	1.3 ± 0.01 b	1.3 ± 0.02 b	1.4 ± 0.01 a
	10–30	1.4 ± 0.02 ab	1.4 ± 0.02 a	1.4 ± 0.01 b	1.4 ± 0.02 ab	1.4 ± 0.02 a
	30–50	1.5 ± 0.02 b	1.5 ± 0.01 b	1.6 ± 0.01 a	1.5 ± 0.02 b	1.5 ± 0.02 b
	50–100	1.6 ± 0.01 b	1.6 ± 0.01 b	1.7 ± 0.03 a	1.6 ± 0.02 b	1.6 ± 0.01 b
pH	0–10	5.8 ± 0.1 b	6.2 ± 0.2 a	5.6 ± 0.1 b	5.6 ± 0.1 b	5.5 ± 0.1 b
	10–30	5.4 ± 0.2 a	5.6 ± 0.2 a	5.6 ± 0.1 a	5.3 ± 0.1 a	5.3 ± 0.2 a
	30–50	5.1 ± 0.2 a	5.1 ± 0.2 a	5.5 ± 0.1 a	5.2 ± 0.1 a	5.2 ± 0.1 a
	50–100	4.9 ± 0.2 a	4.7 ± 0.2 a	5.2 ± 0.1 a	4.9 ± 0.1 a	4.9 ± 0.1 a
Extractable Phosphorus (mg kg^{-1} soil)	0–10	4.5 ± 0.2 c	4.3 ± 0.4 c	3.7 ± 0.1 c	5.5 ± 0.3 b	7.4 ± 0.3 a
	10–30	3.1 ± 0.2 b	3.7 ± 0.5 ab	3.1 ± 0.2 b	4 ± 0.1 a	4.1 ± 0.4 ab
	30–50	2.6 ± 0.3 a	3.1 ± 0.5 a	3.2 ± 0.1 a	3.1 ± 0.1 a	2.6 ± 0.2 a
	50–100	2.5 ± 0.2 b	3.3 ± 0.4 ab	3.5 ± 0.1 a	2.3 ± 0.2 b	2.6 ± 0.2 b
Total Carbon (g C kg^{-1} soil)	0–10	19 ± 1.1 a	12.5 ± 0.6 b	9.1 ± 0.6 c	8.8 ± 0.4 c	9.1 ± 0.8 c
	10–30	6.4 ± 0.3 a	5.2 ± 0.3 b	4.2 ± 0.2 c	4.3 ± 0.3 c	6.1 ± 0.7 ab
	30–50	3.9 ± 0.2 a	3.5 ± 0.3 ab	3.6 ± 0.3 a	2.9 ± 0.1 b	4.2 ± 0.3 a
	50–100	3.5 ± 0.2 bc	3.1 ± 0.2 cd	3.7 ± 0.2 ab	3.0 ± 0.1 d	3.9 ± 0.2 a
Total Nitrogen (g N kg^{-1} soil)	0–10	1.84 ± 0.15 a	1.08 ± 0.05 b	0.73 ± 0.04 c	0.69 ± 0.03 c	0.7 ± 0.06 c
	10–30	0.79 ± 0.09 a	0.52 ± 0.02 b	0.41 ± 0.01 c	0.42 ± 0.02 c	0.51 ± 0.04 b
	30–50	0.49 ± 0.02 a	0.44 ± 0.02 ab	0.4 ± 0.01 bc	0.37 ± 0.01 c	0.43 ± 0.02 b
	50–100	0.48 ± 0.02 a	0.43 ± 0.01 bc	0.45 ± 0.01 ab	0.41 ± 0.01 c	0.43 ± 0.01 bc
C-to-N ratio	0–10	12.7 ± 0.1 a	13 ± 0.3 a	11.2 ± 1.1 b	12.6 ± 0.4 a	11.6 ± 0.1 b
	10–30	10.2 ± 0.4 b	11.8 ± 0.4 a	8.8 ± 0.5 c	10.2 ± 0.4 b	9.9 ± 0.3 b
	30–50	7.9 ± 0.3 b	9.7 ± 0.3 a	7.9 ± 0.2 b	8.9 ± 0.5 b	7.8 ± 0.4 b
	50–100	7.5 ± 0.2 bc	9.2 ± 0.2 a	7.2 ± 0.2 c	8.2 ± 0.4 b	7.2 ± 0.4 bc

Means that do not share a letter are significantly different between land uses for the same soil depth ($p < 0.05$).

i.e. species richness (S), Shannon diversity index (H) and Pielou evenness (Eq). [11, 21].

The trees in each 0.25 ha square plot were classified into five D130 classes: ≤15, 15–30, 30–45, 45–50, ≥50 cm. The densities of each D130 class (trees ha^{-1}) were calculated in forest and tree plantations. Basal area (m^2 ha^{-1}) is the sum of the cross-sectional areas at 1.3 m above ground level of each trees [92].

The species richness (S) of a stand is the number of species counted in that stand (**Supplementary Material 2**). The Shannon index (H) was calculated using equation 4 [93]. This specific diversity index takes into account the number of species present and the distribution of the population within these species.

$$H = -\sum \left(\frac{ni}{N}\right) Log_2 \left(\frac{ni}{N}\right) \quad (4)$$

where n_i is the number of individuals for the i species; N the total number of individuals of all species.

The Pielou evenness (Eq), calculated with equation 5, expresses the distribution of species within a stand [93]. This index varies from 0 to 1. Equal to 1, each species has identical abundances in the stand. Equal to 0, a single species dominates the entire stand. Both indices were measured on a 0.25 ha plot.

$$Eq = \frac{H}{log_2 S} \quad (5)$$

where S is the total number of species, and H the Shannon index.

Data analysis

For each studied variable, a statistical analysis was carried out with the R software version 3.6.3 [94] to assess the effect of land use on these variables. The general linear mixed effect model was used to test the difference between land uses depending on soil depths. Post-hoc comparisons of means tests were performed for the independent factor (land use) using the Tukey-HSD test at the 5% probability level. Pearson correlations of forest and plantation biomass C stocks with basal area, tree density of D130 > 30 cm and Shannon biodiversity index were performed using the "chart.correlation" function of the PerfomanceAnalytics package [95].

Table 4. Soil organic carbon stock (SOC, mean ± standard deviation) and equivalent soil mass.

	Land Use				
	Forest	Tree plantations	Adult palm	Young palm	Croplands
Equivalent soil thickness basis					
0–30 cm	43 ± 1.9a	31.4 ± 1.2b	22.8 ± 1.1c	23.1 ± 1.3c	30.5 ± 2.8b
30–100 cm	40 ± 1.8ab	35.4 ± 2.4b	41.9 ± 2.0ab	32.4 ± 1.0c	43.2 ± 1.7a
0–100 cm	82.5 ± 2.4a	68.4 ± 2.7bc	64.7 ± 2.7c	54.2 ± 2.0d	75.9 ± 4.5b
Equivalent soil mass basis					
4000 Mg ha^{-1}	41.9 ± 1.8a	30.3 ± 1.2b	23 ± 1.1c	22.9 ± 1.3c	28.8 ± 2.6b
11000 Mg ha^{-1}	40.3 ± 1.8ab	35.8 ± 2.4b	40.1 ± 1.9ab	32.8 ± 1.0c	44.4 ± 1.7a
15000 Mg ha^{-1}	82.4 ± 2.4a	68.3 ± 2.7bc	62.8 ± 2.6c	54.2 ± 2.0d	75.9 ± 4.5b

Means that do not share the same letters in a row are significantly different ($p < 0.05$).

Results

Basic soil properties

Soil textures were not significantly different between the land uses ($p > 0.05$, Table 3). Soils were sandy with more than 750 g sand kg^{-1} soil at the surface and slightly less sand in depth. The soils studied were acidic, with low pH values (5.5 to 5.8). Only the soils under tree plantations are slightly less acidic (pH = 6.2) at the surface (0–10 cm).

Bulk density (BD), available phosphorus (P), total nitrogen (N), soil organic carbon (SOC) and soil C:N ratio were significantly ($p < 0.001$) affected by land use regardless of sampling depth (Table 3).

Soil BD values were slightly higher under crops than under palm trees at the surface (0–10 cm), but at the depth 50–100 cm, BD of soils under adult palm plantations were higher than under crops. The BD of soils under forest and plantations were more variable and globally not significantly different from values of other land uses.

The SOC and N contents were higher under forest than under other land uses at all depths except 50–100 cm for the SOC. Unexpected slightly higher SOC contents in croplands and adult palm plots were observed. Soil texture did not explain SOC contents differences observed between land uses. Fine particles (0–20 μm) contents were not correlated to SOC contents in topsoils (0–30 cm) but did at depth (30–100 cm) (Supplementary materials 3 and 4). Soil C:N ratios was sometimes statistically different between land use, slightly higher under forest and tree plantations but the differences were generally less than 1.5 units. Available P levels was higher in croplands soils than in young palm groves, from +1 to nearly +3 mg P kg^{-1} soil, but only at the surface and probably due to the mineral fertilization applied to the crops.

Soil organic carbon stock

For the 0–30 cm soil layer, the SOC stocks were significantly ($p < 0.001$) higher in forests than in tree plantations, croplands, or young and adult palm groves (Table 4). Within this layer, the SOC stocks were not significantly different ($p > 0.05$) between tree plantations and croplands. Considering the 30–100 cm layer, the SOC stocks in the young palm groves were significantly lower ($p < 0.001$) than in the other land uses. The highest SOC stock values at this depth were observed in croplands and the lowest in young palm groves and tree plantations, with significant differences ($p < 0.01$) between these sites. On the other hand, no clear difference (at $p > 0.05$) between SOC stocks in forests, adult palm groves, tree plantations and cropland were found at this soil depth. Looking at the soil profile from 0 to 100 cm depth, the SOC stock was significantly ($p < 0.001$) higher in forests compared to other land uses. The lowest value was observed in young palm groves. The largest difference in carbon stocks was thus measured between forest and young palm groves and was only 28.3 Mg C ha^{-1} over 0–100 cm or 27.8 Mg C ha^{-1} for an equivalent soil mass in both land uses of *ca.* 15000 Mg ha^{-1}.

Biomass carbon stocks

Woody biomass (i.e. aboveground and belowground), necromass and litter biomass varied significantly ($p < 0.001$) with land use (Table 5). Forests had the highest biomass and necromass stocks, while adult palm groves had the highest litter stock. Forests stored about 2 times more carbon in biomass than tree plantations (+ 139 Mg C ha^{-1}), 3.5 times more than adult palm groves and 5.8 times more than young palm groves (Table 5). Noticeably, the litter in adult palm groves constituted a significant C stock of 11.2 Mg C ha^{-1} much higher than that in the forest, tree plantations or croplands.

Total carbon stock distribution in the carbon pools of each land use

The total C stock, i.e. the C stock contained in all vegetation compartments and the first meter

Table 5. **Biomasses and derived carbon stocks (mean values ± standard deviation) of plant compartments (woody biomass, necromass, and litter)**

	Land use				
Pools	Forests	Plantations	Adult palm	Young palm	Croplands
Biomass					
in Mg ha⁻¹	592.8 ± 114.8 a	296.8 ± 70.5 b	166.1 ± 11.7 c	102.6 ± 2.3 d	–
in Mg C ha⁻¹	278.6 ± 54.0 a	139.5 ± 33.1 b	78.1 ± 5.5 c	48.2 ± 1.1 d	–
Necromass					
in Mg ha⁻¹	53.4 ± 10.3 a	26.7 ± 6.3 b	–	–	–
in Mg C ha⁻¹	25.1 ± 4.9 a	12.6 ± 3 b	–	–	–
Litter					
in Mg ha⁻¹	6.1 ± 0.4 b	7.6 ± 0.7 b	23.9 ± 1.7 a	3.1 ± 0.4 c	2.7 ± 0.4 c
in Mg C ha⁻¹	2.9 ± 0.2 b	3.6 ± 0.3 b	11.2 ± 0.8 a	1.5 ± 0.2 c	1.3 ± 0.2 c

Means that do not share the same letters in a row are significantly different ($p < 0.05$)

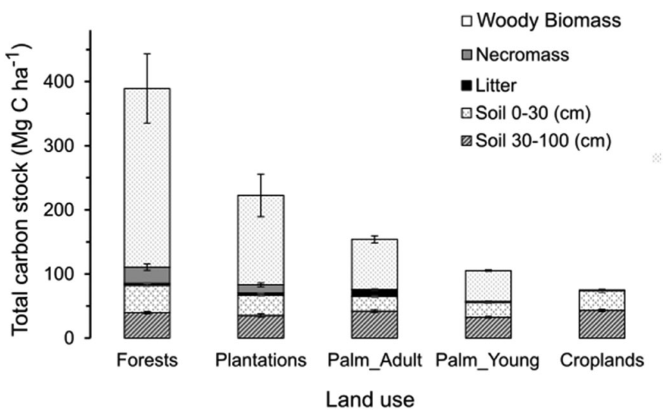

Figure 2. **Total carbon stocks and their distribution across the different carbon pools in the different land uses (error bars are standard deviation).**

of soil, decreased in the following order: Forests > Tree plantations > Adult palm groves > Young palm groves > Croplands, with values of 389 ± 54, 222 ± 33, 154 ± 6, 105 ± 2, 77 ± 3 Mg C ha^{-1} respectively (Figure 2). Forests stored approximately 1.75 times more than tree plantations, 2.5 times more than adult palm plantations, and 5 times more than croplands. Adult palm groves stored 2 times more carbon than croplands (Figure 2). Except for soils under croplands and to some extent young palm groves, a large majority of the C stock was contained in the living plant biomass. In forest, plantation and adult palm groves, the biomass C stock represented 72%, 63% and 51% of the total C stock respectively (Figure 2). In the young palm groves and croplands, C stocks were mainly in the soil (0–100 cm depth) which contained 54% and 98% of total C stocks respectively. Differences in C stocks between land uses were mainly explained by differences in C stocks in the woody biomass.

Carbon stock variability in each land use

The C stocks were more variable in biomass and necromass in the forests and in the tree plantations than in the litter and soil (Table 6, and see standard deviation of C stocks in Tables 4 and 5). The C stock variations were greater in tree plantations and forests than in both palm groves and croplands. This is due to the variations in biomass C stocks, for example as assessed by the standard deviations that varied in the order: Forests > Plantations > Adult palm groves > Young palm groves with respectively the values of 54.0 > 33.1 > 5.5 > 1.1 Mg C ha^{-1} (Table 5). By contrast, the variation in C stocks in soils and litter in the young palm groves and in the croplands presented higher coefficient of variation than in the other land uses (Table 6).

Biodiversity and structure of forests and tree plantations

The species richness was two times higher in the classified Niaouli forest than in the sacred forests (Table 7). In addition, the Niaouli forest showed more diverse species communities than the sacred forests (high Shannon index, Table 7). In contrast to the Shannon index, the Pielou's evenness index revealed no clear difference between the classified Niaouli forest and the sacred forests (Table 7). The species were quite uniformly distributed among all the forests studied. Tree densities were higher in the tree plantations (166–469 trees ha^{-1}) than in the forests (69–146 trees ha^{-1}). However, forests, especially classified Niaouli forest and the sacred forest of Koundokpoe, had higher tree densities in DBH classes > 50 cm (Table 8). Basal areas were highly variable and generally higher under forest (6–48 m^2 ha^{-1}) than under tree plantation (5–18 m^2 ha^{-1}). However, the 21-year-old teak plantation had notably a high basal area (18 m^2 ha^{-1}; Table 7). The biomass C stocks of forests and tree plantations were correlated with basal area and with the density of trees with DBH >30 cm (Figure 3). The biomass C stocks in the forests were also correlated with the Shannon biodiversity index (Figure 3).

Discussion

Soil carbon stock down to 1 m deep

The highest SOC stocks (0–30 cm) in forests compared to other land uses are consistent with other studies on similar soil types. This is attributed on one hand to the high biomass production resulting from the large amount of vegetation under the forest canopy [96] and on the other hand to the contribution of decaying tree leaves, shoots and roots to the soil [76, 97]. The difference in soil C stock between forests and tree plantations could be due to the large layers of litter and organic inputs from plant biomass and dead roots available in forests [13]. However, in our study only the woody necromass and not the litter biomass were higher in forests compared to tree plantations. It can be explained by the forest aged more than 50 years while tree plantations ranged from 5 to 21-years-old during which organic matter decomposed and accumulated. Besides, the higher plant diversity in forest could enrich the soil with a diversity of organic carbon inputs that contribute to favor the SOC stock [98,99]. At a depth of 0–30 cm, the SOC stocks were similar in tree plantations and croplands, while palm groves had lower stocks. These differences remain moderate and less than 10 Mg C ha^{-1} (Table 4). These differences could be partly explained by a slightly higher equivalent soil mass at 0–30 cm in the croplands, i.e. for an equivalent soil mass basis of 4230 Mg soil ha^{-1}, compared to the palm groves, i.e. for an equivalent soil mass basis of 3960 Mg soil ha^{-1}, and by the crop rotation or the organic management of the fields. Although the soils of cropland store few amount of C per hectare, the promotion of organic input management practices and nutrient recycling such as the return of crop residues or pruning leaves should be promoted to sustain soil fertility, agricultural production and carbon sequestration [3].

Table 6. Coefficient of variation (%) of the C stocks by pools and land uses.

Land cover	Woody Biomass	Necromass	Litter	Soil
Forests	19	19	7	3
Tree plantations	24	24	9	4
Adult palm	7	–	7	4
Young palm	2	–	12	4
Croplands	–	–	15	6

Table 8. Distribution of tree density (number ha^{-1}) according to diameter at 1.3 m, i.e. D130 classes (cm) for the forest and tree plantations.

Land use	D130 classes (cm)				
	<15	15–30	30–45	45–50	>50
Classified forest of Niaouli	0	17	11	2	116
Sacred forest of Dome seko	18	26	44	0	14
Sacred forest of Dame	6	32	19	4	8
Sacred forest of Koundokpoe	4	22	20	0	46
21 years_old state teak plantation	166	201	90	0	2
5 years-old state teak plantation	319	54	2	0	0
10 years-old private teak plantation	8	158	6	0	0
5 years-old private Gmelina plantation	38	124	2	0	2

Table 7. Biodiversity and structure of the forests (all > 50 years-old) and the tree plantation (of different ages) (mean values ± standard deviation)

Parameters	Forests				Tree plantations			
	Niaouli (classified)	Domè Seko (sacred)	Damè (sacred)	Koundokpoé (sacred)	21 years-old State teak	5 years-old State teak	10 years-old Private teak	5 years-old Private gmelina
Tree density tree ha^{-1}	146 ± 13	102 ± 20	69 ± 10	92 ± 23	459 ± 87	375 ± 22	172 ± 51	166 ± 93
Species richness	14	6	7	8	1	1	1	1
Shannon diversity	2.92 ± 0.3	1.74 ± 0.53	2.17 ± 0.13	2.75 ± 0.04	–	–	–	–
Pielou evenness	0.88 ± 0.06	0.75 ± 0.1	0.88 ± 0.01	0.92 ± 0.01	–	–	–	–
Basal area m^2 ha^{-1}	47.5 ± 6.2	9.9 ± 0.2	6.3 ± 1.5	25.1 ± 7.1	18.5 ± 2.6	4.9 ± 0.5	6.7 ± 1.5	5.1 ± 2.4
Biomass Mg ha^{-1}	1052.2 ± 62.8	154.2 ± 16	120.2 ± 9.0	604.4 ± 92.9	627.6 ± 92.3	117.2 ± 17.6	249.8 ± 0.9	55.2 ± 26.0
C biomass Mg C ha^{-1}	494.6 ± 29.5	72.5 ± 7.5	56.5 ± 42.3	284.1 ± 43.7	295.0 ± 43.4	55.1 ± 8.3	117.4 ± 0.4	26.0 ± 12.2

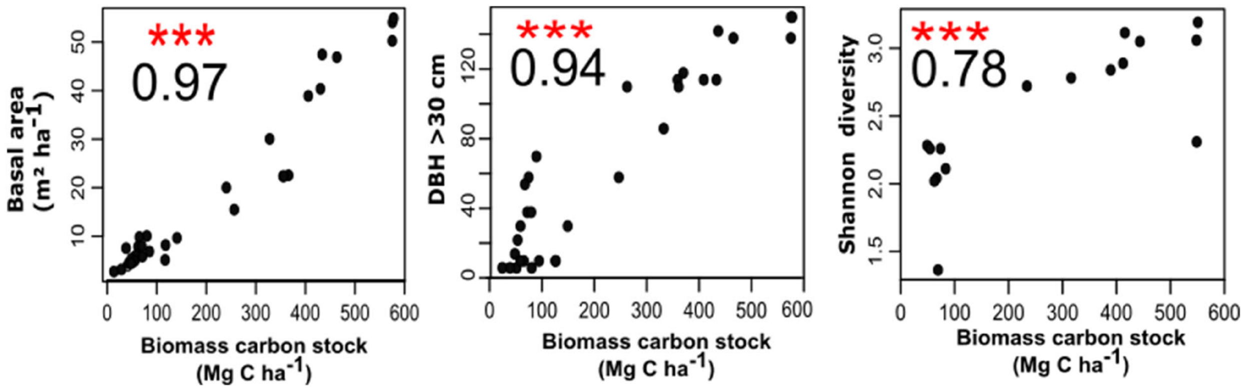

Figure 3. Correlation between biomass C stocks with basal area, density of trees with diameter at 1.3 m (D130) >30 cm and Shannon index.
On top the coefficient of determination (R^2) and stars indicates that the *p*-value (Pearson's test) is less than 0.001 for the correlation between the biomass carbon stock and the others factors.

With differences of less than 10 Mg C ha^{-1}, SOC stocks appear to be little affected by the land use at higher depths (30–100 cm) (Table 4). The slightly higher stocks observed in cropland and adult palm groves at 30–100 cm could be explained by higher soil bulk density in cropland and palm groves [13,14, 100]. Soil texture did not explain SOC contents differences observed between land uses. There was no significant difference of clay contents between land use and the range of soil texture (25–300 g clay kg^{-1} soil) was covered for all land uses at each depth (Supplementary materials 3 & 4). In cropland the unexpected slightly higher SOC contents at 30–100 cm could be derived from previous land uses or accumulated charcoal from regular slash and burn practices [4].

In line with results obtained in the 0–30 and 30–100 cm soil layers, the SOC stocks in the first meter of soil appeared slightly impacted by land use. Oil palm groves and especially at young age had the lowest SOC stocks (54 Mg C ha^{-1}) compared to forest (83 Mg C ha^{-1}) or even croplands (76 Mg C ha^{-1}). Young oil palm groves could have especially low SOC stocks due to a specific management of the field, e.g. regular weeding and no fallow, to favor the set-up of the palm trees [64]. In these sandy soils, measuring SOC stocks at deeper depth than 0–30 cm did not change our conclusions on the impact of land use on SOC stocks but slightly modify the quantitative difference between SOC stocks (ΔC between forests and croplands = 12 ± 4 Mg C ha^{-1} at 0–30 cm and 7 ± 5 Mg C ha^{-1} at 0–100 cm).

Biomass and litter carbon stocks

Croplands supported only few litter biomass because crop residues are burnt or exported for domestic animal feed. The biomass of forests, tree plantations and palm groves was in the range (50–749 Mg DM ha^{-1}) reported in other studies conducted in tropical forests [21, 101–103]. The forests, tree plantations and palm groves of the Allada plateau had a relatively high biomass and store a significant amount of carbon. Biomass was especially high in forests and was much higher than in tree plantations, adult palm groves and young palm groves. This could be due to the stand structure in link with the age of stand and characteristics of the forest trees, reflecting their high biomass production [11, 21, 99, 104]. Palm *et al.* [105] measured C stocks in African rainforests (255 Mg C ha^{-1}) of the same order as in our study (279 ± 54 Mg C ha^{-1}). However, our results are superior to those obtained by Mitchard *et al.* [106] using remote sensing data. This difference can be explained on the one hand by the quality of the biomass mapping which strongly depends on the different sensors used (optical, RADAR or LiDAR) and on the other hand by the allometric equation used to convert forest inventory data into biomass [107].

The C stocks in litter was particularly high in adult palm groves (11 Mg C ha^{-1}), in contrast to tree plantations and forests (3 to 4 Mg C ha^{-1}). This difference can be explained by the restitution of palm pruned leaves in the form of swaths during the maintenance of these palm groves, a practice that is beneficial for improving the physico-chemical properties and carbon stock of the soil [42].

Total carbon stocks

The total C stock and its distribution in the four C pools: biomass, necromass, litter and soil varied with the land use. Total C stocks decreased from forests (389 ± 54 Mg C ha^{-1}) to total plantations

(222 ± 33 Mg C ha^{-1}), adult palm groves (154 ± 6 Mg C ha^{-1}), young palm groves (105 ± 2 Mg C ha^{-1}) and croplands (77 ± 3 Mg C ha^{-1}). The different pools also contributed differently to total C stocks across land uses. The dominant pool in forests, tree plantations and adult palm groves was the biomass C stock, which is in line with the general trend reported in the literature [15, 17, 108–111]. This result confirmed that in forests, but also in tree plantations and adult palm groves, the tree living biomass are the main C reservoir of tropical forest ecosystems [112,113]. This is especially true for ecosystems on sandy soils which contain little SOC [18] such as the studied Ferralsols. On the contrary, the SOC stock is the predominant C pool in croplands and in young palm groves frequently cultivated in temporary agroforestry (palm + maize, cassava, tomato or pineapple) in Benin [14, 45, 114].

Consequently, the differences in C stocks between land use were mainly located in the C biomass pool (e.g. between forests and croplands ΔSOC = 5–12 Mg C ha^{-1} *vs* ΔC biomass 270 Mg C ha^{-1}). These results confirm that on sandy soils, the differences in C stocks between the land uses are mainly due to the C biomass pool [99, 115].

Our study fulfilled the lack of C data in biomass, necromass, litter and soil for various land use from a sub-Saharan region. It confirms the expected low capacity of sandy Ferralsols to store C. The variations in SOC stocks with land uses are moderate even if the measurements have been performed down to 1 m deep. The variations in C stocks with land uses are mainly located in the C biomass pool.

Carbon stock variability and biodiversity

The variations in measured C stock were most obvious in the biomass measurements than in soils or in litter (26 to 495 Mg C ha^{-1} *vs* 4 and 1 Mg C ha^{-1} respectively). These variations in C biomass were partly explained by forests and tree plantations characteristics, such as tree species diversity and richness, tree density, basal area and tree density distribution in DBH classes [11, 84,85]. All forest aged more than 50 years. The age of the tree plantations (21 years *vs* 10 years) explained the presence of larger trees with a larger basal area than in the younger plantations and thus the higher C stock in the biomass of the 21-year-old state teak plantation compared to the younger state or private teak plantations. Despite the fact that tree density was higher in teak plantations than in forests, the high C stocks in the classified Niaouli forest could be explained by the predominance of species with large DBH > 30 cm and even > 50 cm (Table 7). This is consistent with previous studies, which have shown that the C content of tree species is positively correlated with their diameter at breast height [116,117]. Our result revealed that the C biomass stock in the forest were positively correlated with biodiversity (Shannon diversity index) which confirms previous studies [118–120]. Indeed, our study in four forests showed that tree species diversity, and especially the presence of large and dense trees with a high C storage potential, could also explain their high biomass C stocks. Large and dense trees include *Antiaris toxicaria*, *Ceiba pentandra, Dialium guineense, Senna siamea* et *Triplochiton scleroxylon* [83,84, 115, 121]. The correlation between tree density of DBH >30 cm and biomass C stock confirmed that large trees contribute significantly to carbon storage [108]. The presence of large trees in the Koundokpoé sacred forest explained its high C biomass stock compared to other sacred forests. However, the C biomass stock in these forests look a little bit overestimated despite using specific models. It could be explained by the application of generic models for biomass stock estimation of tree species for which there is no specific model [107]. Protecting the trees in the sacred forests would increase their long-term carbon storage potential.

Conclusion

The C stocks data measured and calculated in this study confirmed that forest store much more C than tree plantations (teak, gmelina or palm groves). Cropland store small amount of C, mainly because (i) C biomass in the studied cropland is minor and (ii) SOC in Ferralsols, whatever the land use, is poor. The high variability in the biomass C stocks measured between forests was partly explained by the tree species of the forests. Our study gives evidence to support the hypothesis that biodiversity in tree species, and especially the presence of large trees with dense wood, could be an explaining factor of the variation of the C stocks. These data provide evidence to focus C local land use plans and policies on C biomass stocks and on the biodiversity of the forest preserved or reforested. As there is small difference in SOC stocks between land use types, our results seem to show that, on the Allada plateau, purely

C-centered policies must above all encourage biomass amount and diversity increasing. This involves preserving forests and forest resources, encouraging afforestation with a diversity of tree species, and supporting local communities in managing and securing sacred forests. In an effort to reduce the concentration of GHGs in the atmosphere and at the same time improve the economic conditions of the smallholders, it is necessary to undertake studies on the C storage potential of the planted trees and associated farming systems. These studies must include the optimization of the growth rate, but also studies on the fate of the products of the plantations (poles, planks, etc.) in order to establish the long-term carbon balance of these tree plantations. In agriculture, agroforestry can also be promoted to enhance the C stock in biomass of agricultural fields. Finally, further studies are needed to assess the surface dedicated to each land use and the global C budget of the Allada plateau, and then help to design C policies.

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Disclosure statement

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Data availability statement

The data that support the findings of this study are available from the corresponding author, upon reasonable request.

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