Global Ecology and Conservation 21 (2020) e00875

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

Agricultural land use reduces plant biodiversity and carbon storage in tropical West African savanna ecosystems: Implications for sustainability

Larba Hubert Balima [a, b, *], Blandine Marie Ivette Nacoulma [b], Philippe Bayen [b], François N'Guessan Kouamé [a], Adjima Thiombiano [b]

[a] WASCAL Graduate Research Program on Climate Change and Biodiversity, University Félix Houphoüet Boigny, B.P. 165, Abidjan 31, Republic of Côte d'Ivoire
[b] University Joseph Ki-Zerbo, Laboratory of Plant Biology and Ecology, 03 B.P. 7021, Ouagadougou 03, Burkina Faso

ARTICLE INFO

Article history:
Received 23 October 2019
Received in revised form 2 December 2019
Accepted 6 December 2019

Keywords:
Land disturbance
Woody flora diversity
Stand structure
Aboveground carbon stocks
Sudanian region

ABSTRACT

Savanna ecosystems in tropical West Africa undergo severe land use pressure, resulting in ecosystem degradation and biogenic carbon emissions. In such context, highlighting the key ecological attributes of land degradation and the underlying processes are essential within the national adaptation and mitigation plans. This study analyzed the impacts of land use on plant biodiversity, stand structure and carbon storage. Inventories of ligneous species were conducted on 240 plots laid out along four levels of land disturbance in Burkina Faso. Dendrometric data collected from 6035 shrubs and trees were converted to aboveground biomass and carbon density. The results revealed a $\gamma-$diversity of 107 woody species belonging to 73 genera and 35 families. Significant effect of land use was found on species diversity, stand structure and carbon density ($p < 0.001$). Agricultural lands had the lowest diversity, density and carbon stocks, whereas protected areas held the highest values. Carbon density ranged from 10.362 $\pm$ 1.209 Mg C.ha^{-1} in fallows to 42.663 $\pm$ 1.982 Mg C.ha^{-1} in protected areas. Principal Component Analysis showed tight links between carbon storage, species diversity and stand structure. The multiple linear regression revealed that tree density explained 21.25% of the variation in the plot-level total carbon stocks ($\alpha = 19.301$; $p < 3.38\text{e-}14$). Similarly, tree diameter and height together accounted for 45.43% of the variation in mean carbon stocks ($\alpha = 19.301$; $p < 2.2\text{e}-16$). This study demonstrated that the higher the land use pressure, the lower the species diversity and carbon storage in woody vegetation. The findings highlight the importance of accounting for improved or smart agricultural practices within the intended nationally determined contributions' framework.

* Corresponding author. WASCAL Graduate Research Program on Climate Change and Biodiversity, University Félix Houphoüet Boigny, B.P. 165, Abidjan 31, Republic of Côte d'Ivoire.

E-mail addresses: lhubertbalima@gmail.com (L.H. Balima), nblandine@gmail.com (B.M.I. Nacoulma), phbayen@yahoo.fr (P. Bayen), fnkouame3@gmail.com (F.N. Kouamé), adjima_thiombiano@yahoo.fr (A. Thiombiano).

https://doi.org/10.1016/j.gecco.2019.e00875

1. Introduction

The sustainability of tropical forest ecosystems is critical in international efforts to mitigate global climate change. Indeed, tropical forests represent about 45% of the World's forests (FAO, 2017) and store large amounts of carbon estimated at 55% of global carbon stocks (Pan et al., 2011). Therefore, these forests form the largest terrestrial carbon pools and sinks (Zomer et al., 2008; Pan et al., 2011; Baccini et al., 2012, 2017; Wood et al., 2012), playing a central role in the global carbon cycle (Canadell and Raupach, 2008; Lewis et al., 2009; Fonseca et al., 2011; Pan et al., 2011; Rahman et al., 2017). Tropical forests also constitute global epicentres of biodiversity (Cramer et al., 2004; Lewis et al., 2009; Wright, 2010), and thereby, contribute enormously to human livelihoods through the delivering of ecosystem goods (Cramer et al., 2004; Bonan, 2008; Wright, 2010). However, while their crucial role in offsetting global carbon inputs and climate change impacts are widely recognized, how tropical forest sustainability can be achieved lead to increasing debate (Rahman et al., 2017) among scientists and policy makers.

A growing body of literature reported tropical land use land cover changes (Cramer et al., 2004; Gibbs et al., 2010; Saatchi et al., 2011; Feldpausch et al., 2011; Harris et al., 2012; Wood et al., 2012; Vlam et al., 2014), and consequently, net carbon source from tropical forests (Pan et al., 2011; Baccini et al., 2012; Harris et al., 2012; Vieilledent et al., 2013; Houghton and Nassikas, 2017). Indeed, tropical land use emissions were approximatively equal to the total global land use emissions (Pan et al., 2011). Accordingly, tropical forests have turned to the largest terrestrial sources of biogenic atmospheric carbon emissions (Gibbs et al., 2010; Pan et al., 2011; Harris et al., 2012; Baccini et al., 2017; Houghton and Nassikas, 2017). Deforestation and land degradation represent the most important sources of tropical forest loss and carbon emissions (Gibbs et al., 2010; Pan et al., 2011; Baccini et al., 2017; Houghton and Nassikas, 2017). Tropical deforestation produces significant gross carbon emissions accounting for 40% of the global fossil fuel emissions (Pan et al., 2011). Agricultural expansion is the major driver of deforestation (Gibbs et al., 2010) and land use change across the tropics (Baccini et al., 2012, 2017; Vieilledent et al., 2013; Houghton and Nassikas, 2017).

Due to the significant impacts of tropical land use change on the global carbon budget (Gibbs et al., 2010; Pan et al., 2011; Saatchi et al., 2011; Feldpausch et al., 2011; Houghton and Nassikas, 2017), sustainable land management is central in forestry-based climate change mitigation policies (Houghton, 2014). Accordingly, land use practices enabling to achieve negative carbon emissions in the long-term are critical. In Africa where agricultural lands increase at the expense of forests (Gibbs et al., 2010; FAO, 2017), implementing smart agricultural systems reducing emissions from deforestation and forest degradation (REDD+) is essential within the national adaptation and mitigation frameworks. The operationalization of such systems requires accurate information on the geographic patterns of carbon stocks and carbon emissions (Feldpausch et al., 2011; Vieilledent et al., 2013). Yet, the lack of reliable estimates of tropical carbon stocks introduces large uncertainties into estimates of carbon emissions from land use change (Pan et al., 2011; Baccini et al., 2012; Feldpausch et al., 2011; Chave et al., 2014; Houghton and Nassikas, 2017). In such context, empirical indicators on the key ecological attributes of land degradation are fundamental for sustainable land management options and climate change mitigation.

The semi-arid areas of West Africa are dominated by savanna ecosystems that considerably contribute to human well-being (Bélem et al., 2007; Schumann et al., 2011; Sop et al., 2012; Ouédraogo et al., 2014; Zizka et al., 2015; Leßmeister et al., 2018). However, recent studies reported changes in land use and vegetation composition in savanna ecosystems (Landmann et al., 2010; Wegmann et al., 2010; Houessou et al., 2013; Dimobe et al., 2015, 2017; Leßmeister et al., 2018). In fact, human population growth and agricultural expansion in West Africa have reduced plant diversity (Nacoulma et al., 2011a; Houehanou et al., 2012) and induced land cover change (Landmann et al., 2010; Wegmann et al., 2010; Houessou et al., 2013; Dimobe et al., 2015, 2017). Such changes have potential impacts on the societal and ecological functions of savanna ecosystems.

Several empirical data supported positive relationships between biodiversity, ecosystem functioning and ecosystem services at the global scale (Balvanera et al., 2006; Egoh et al., 2009; Mace et al., 2012). Yet, such relationships are poorly documented in tropical African ecosystems. In fact, several studies in West Africa investigated the impacts of climate and land use on the vegetation diversity and woody species dynamics (Nacoulma et al., 2011a, 2011b; Schumann et al., 2011; Traoré et al., 2012a, 2012b; Ouédraogo et al., 2015). A recent studies in Burkina Faso reported land use as the major factor causing biodiversity loss (Nacoulma et al., 2011a; Ouédraogo et al., 2015; Dayamba et al., 2016) and ecosystem degradation (Dimobe et al., 2015, 2017). However, the process by which land use pressure affect species diversity, stand structure and carbon storage remain less documented. Additionally, the relationships between plant biodiversity, stand structure and carbon storage in woody vegetation are yet poorly understood. Such understanding is of great relevance for achieving the threefold goals of biodiversity conservation, climate protection and development. Highlighting the key ecological attributes of land degradation constitutes important insights towards sustainably managed ecosystems.

Hence, this study addressed the following research questions:

(i) How species diversity, stand structure and carbon density vary across land use types?
(ii) What are the relationships between stand diversity, stand structure and carbon density?
(iii) Which factors influence carbon storage in aboveground biomass of woody species?

2. Material and methods

2.1. Study area

The study was carried out across four land use types in four regions of Burkina Faso: East, West, Centre-south and Centre-west. The study sites included both protected areas and their surroundings. The protected areas were the W national park (WNP), the Nazinga game ranch (NGR), the wildlife reserve of Bontioli (WRB) and the classified forest of Comoé-Léraba (CFCL) (Fig. 1A). The WNP (11°54′–12°35′N, 1°46′–2°23′E) and the NGR (11°01′–11°18′N, 1°18′–1°43′W) are located in the Sudano-sahelian climatic zone. The WRB (10°70′–10°95′N, 3°02′–3°20′W) and the CFCL (9°25′–11°5′N, 5°35′–3°30′W) are located in the Sudanian climatic zone. All the study sites belong to the Sudanian regional centre of endemism. The study area is characterized by a unimodal rainfall regime lasting for about 4–6 humid months (May/June to September/October). The Walther-Lieth climate diagrams showed a long-term mean annual rainfall of 800 mm in WNP and 994 mm in WRB over the period 1970–2013, with mean annual temperature of 28.8 °C and 27.7 °C respectively (Fig. 1B). Long-term climate records were lacking for Nazinga and Comoé-Léraba sites. Topography in the study area varies from slopes to hills with elevation ranging between 199 and 371 m a.s.l. at WNP, 241–419 m a.s.l at Nazinga, 240–343 m a.s.l. at Bontioli, and 212–347 m a.s.l. at Comoé–Léraba. The vegetation in the four protected areas is characterized by various vegetation types including shrub savannas, tree savannas, woodlands, dry forests and gallery forests.

2.2. Sampling design and data collection

We selected four typical land use types describing different levels of human-driven land disturbances in West African ecosystems. The land use types included protected areas, zovics (local refuges and village zones of hunting interest), fallows

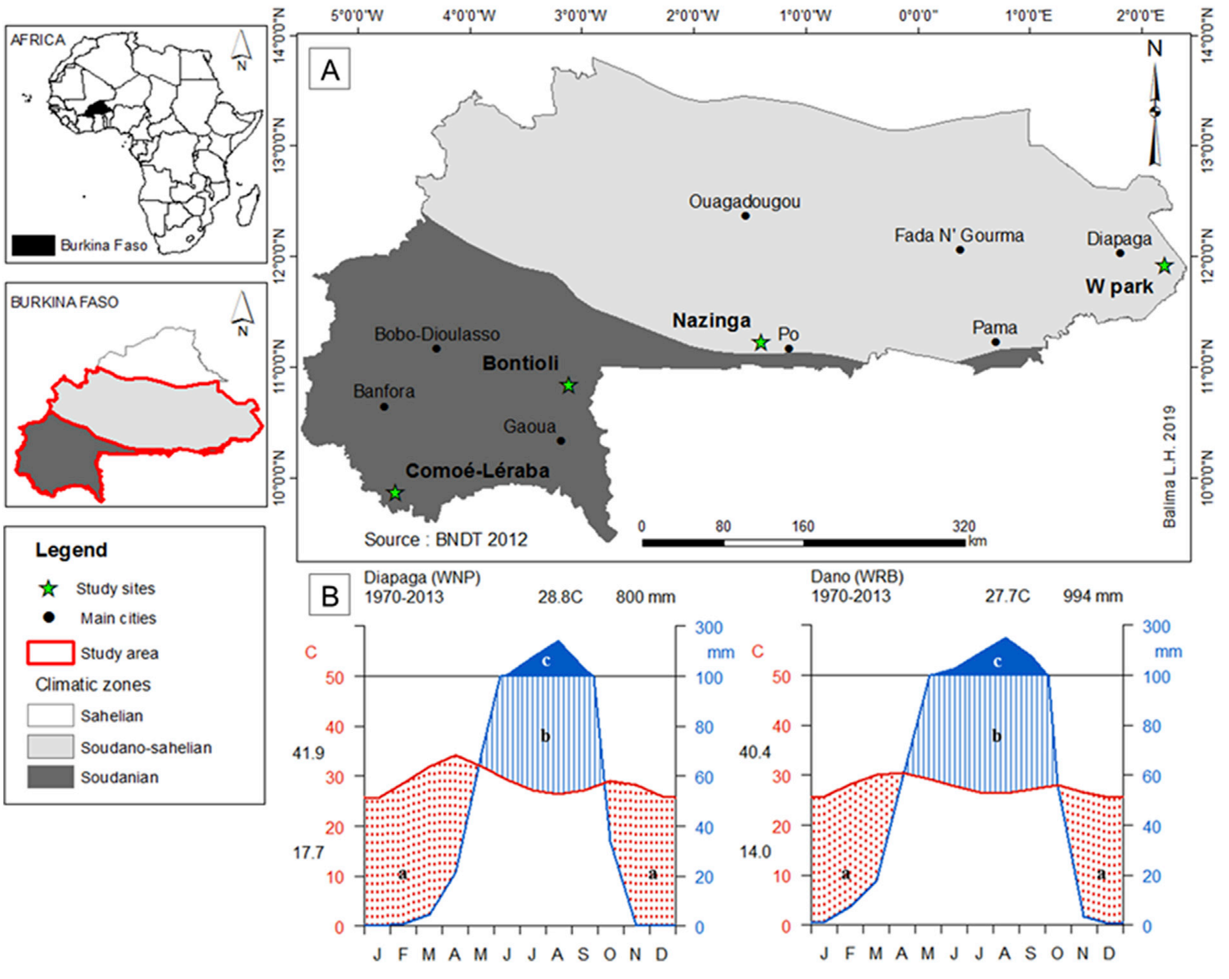

Fig. 1. (**A**) Location of the study sites in Burkina Faso and (**B**) Walther-Lieth (1960) climate diagram for WNP (W national park) and WRB (wildlife reserve of Bontioli). **Legend**: **a**–dry season, **b**–rainy season, **c**–major seasonal precipitation.

and farmlands. We considered protected areas as non-disturbed zones, zovics as moderate disturbed areas, and farmlands and fallows as highly disturbed areas. Zovics are buffer zones delineating protected areas from unprotected zones. These local hunting zones serve as barriers preserving protected areas from human disturbances. Farmlands and fallows known as agricultural lands or agroecosystems characterize traditional cropping systems in West Africa consisting in shifting cultivation. These agricultural systems are strongly affected by human activities such as fires, extensive grazing, clearing, selective logging and fuelwood cutting (Zida et al., 2009; Nacoulma et al., 2011a; Ouédraogo et al., 2015; Dayamba et al., 2016). Gibbs et al. (2010) reported that more than 55% of new agricultural lands across the tropics came at the expense of intact forests (Gibbs et al., 2010). In West Africa, agricultural lands arised from the conversion of unprotected natural stands (natural vegetation). These natural stands are unmanaged ecosystems contrary to protected areas. Nevertheless, in the absence of severe human pressure, natural stands may host high biodiversity comparable to that from protected areas.

Inventories of ligneous flora were carried out at each disturbance level during the rainy season (April to June 2017). Overall, 240 plots were laid out using an oriented stratified sampling based on the occurrence of different vegetation types. The number of plots was 112 in protected areas, 45 in zovics, 60 in farmlands and 23 in fallows. The low number of plots in fallows was due to the rarity of this land use type throughout the study area. The plot sizes followed the standard guidelines established for vegetation surveys in tropical West Africa (Thiombiano et al., 2016). In protected areas and zovics, plots measuring 1000 m^2 (50 m $\times$ 20 m) and 500 m^2 (50 m $\times$ 10 m) were installed in savannas/woodlands and gallery forests/dense forests respectively. The plot size was 2500 m^2 (50 m $\times$ 50 m) in agricultural systems. For all shrubs and trees with diameter at breast height (DBH) $\geq$ 5 cm, we recorded species names and measured stem DBH and tree height. Species names recorded *in situ* were further retrieved following the International Plant Names Index (http://www.ipni.org). A total of 6035 trees and shrubs with 4569 in protected area, 383 in zovics, 168 in fallow and 915 in farmland were measured.

2.3. Estimates of aboveground biomass and carbon density

Non-destructive method was used to convert ground-based measurements to tree biomass (AGB). Due to the lack of accurate site-specific allometric equations for biomass estimates in the Sudanian region of West Africa, we selected the widely accepted pantropical equation developed for biomass estimates in tropical dry forests (Chave et al., 2005). This equation predicts tree biomass as a function of tree diameter, height and wood density, as follow:

$$\mathrm{AGB} = 0.112 \times (\rho \mathrm{DBH}^2 \mathrm{H})^{0.916}$$

where AGB is aboveground biomass (in kg.tree^{-1}), ρ is wood specific density (in g.cm^{-3}), DBH is diameter at breast height (in cm) and H is tree total height (in m).

Values of wood density of individual species were obtained from the global wood density database (Zanne et al., 2009). The genus-level mean values were used when direct measurements were lacking for a given species in the database (Dayamba et al., 2016; Qasim et al., 2016; Dimobe et al., 2019). Aboveground biomass was first computed for each individual and summed up for each plot. The plot level AGB values (Mg.plot^{-1}) were then averaged for each land use type (Mg.ha^{-1}) based on the number of plots and finally converted to carbon density (Mg C.ha^{-1}) using the conversion factor of 0.50 (IPCC, 2003).

2.4. Statistical analysis

Several diversity indices are commonly used for comparing species diversity across stands or sites. However, using one diversity index will often not provide sufficient information to order sites from high to low diversity (Kindt and Coe, 2005). Therefore, we used the series of diversity numbers proposed by Hill (1973) to assess the effects of land use on woody species diversity. These diversity numbers were:

- N0 that represents the total number of species;
- $\mathrm{N1} = \exp\left(-\sum_{i=1}^{s} p_i \ln(p_i)\right) = \exp(\mathrm{H})$, where H represents Shannon's index;
- $\mathrm{N2} = 1/(p_1^2 + p_2^2 + \ldots + p_n^2) = 1/\mathrm{D}$, where D represents the Simpson's index

N0 represents the species richness ie-the total number of species or taxa present in a given area. N1 measures the number of abundant species in a plot, whereas N2 measures the number of very abundant species.

Diversity indices were computed at the plot-level using the R package 'BiodiversityR' (Kindt and Coe, 2005).

The mean values of tree density (ind.ha^{-1}), DBH (in cm), height (in m) and basal area (in m^2.ha^{-1}) were computed for each land use type. The basal area (G) was calculated for each individual tree and up scaled to stand level using the following formula:

$$G = \frac{\pi}{4S} \sum_{i=1}^{n} 10^{-4} * di^2$$

where S is the plot size (in ha) and d_i is the DBH of tree i.

Before statistical analyses, all data were statistically checked for meeting the assumptions of normality (Shapiro-Wilk test) and variance homogeneity (Levene test). Data were log-transformed when these assumptions were violated. Then, linear models were used to investigate the variations in diversity numbers, structural variables and carbon stocks. The differences between land use types regarding the diversity numbers (N0, N1, N2), tree structural variables (DBH, height, density, basal area) and carbon stocks were tested using a one-way analysis of variance (ANOVA). To assess the relationships between diversity, structure and carbon storage at the plot-level, a Principal Component Analysis (PCA) was performed using the R package 'FactoMineR' (Le et al., 2008). Multiple linear regression analysis was performed to determine factors affecting carbon storage in tree biomass. The plot-level carbon stocks (total and mean) were considered as response variables of stand diversity and structural variables. We first explored the relationships between the response variables and the predictors using scatter plots and Pearson correlation tests. Then, we used the independent variables that significantly correlated with carbon stocks in a backward multiple linear regression analysis to assess their contribution in the variations of carbon stocks. All the statistical analyses were performed using the R software *version 3.6.0* (R Core Team, 2019).

3. Results

3.1. Species richness and diversity

The overall species richness across the four land use types (γ−diversity) included 107 woody species from 73 genera and 35 families (Appendix 1). About 100 woody species were found in protected areas, 63 species in zovics, 51 species in fallows and 81 species in farmlands (Appendix 1). The mean species richness per plot (α−diversity) was significantly higher ($F = 16.813$, $p < 0.001$) in protected areas (13.601 ± 0.305) and zovics (13.529 ± 0.912) than in fallows (9.461 ± 1.254) and farmlands (8.970 ± 0.620). The number of abundant species increased with decreasing land use disturbance ($F = 16.246$, $p < 0.001$). Protected areas (10.677 ± 0.857) recorded the highest number of abundant species, whereas farmlands (6.882 ± 0.485) and fallows (6.433 ± 0.556) had the lowest values. The number of very abundant species also increased with decreasing land use pressures ($F = 16.312$; $p < 0.001$).

3.2. Stand structure and aboveground carbon density

Significant differences were found between land use types regarding all structural variables (Table 1). Stem DBH varied significantly between land use types ($F = 85.655$; $p < 2.2e{-}16$). In fallows and farmlands, trees had significantly higher mean DBH than in protected areas and zovics (Table 1). Similar variation was also found for mean height ($F = 13.453$; $p < 0.001$). Contrary to DBH and height, the mean density of trees increased significantly with decreasing land use pressure ($F = 123.78$; $p < 0.001$) ranging from an average of 321.12 ± 13.68 ind.ha^{-1} in protected areas to 51.69 ± 7.381 ind.ha^{-1} in fallows (Fig. 2). Similar trend was also observed for basal area (Fig. 2) that decreased significantly ($F = 6.575$; $p = 0.001$) from protected areas (12.434 ± 0.556 m^2 ha^{-1}) to fallows (7.667 ± 1.176 m^2 ha^{-1}). Significant effect of land use was also found on carbon density ($F = 71.048$; $p < 2.2e{-}16$). The highest carbon density (42.663 ± 1.982 Mg C.ha^{-1}) was held in protected areas (Tableau 1, Fig. 2).

Table 1
Variations in species diversity, stand structure and carbon stocks cross land use types.

Land use type	Protected areas	Zovics	Fallows	Farmlands
No. of ind.	4569	383	168	915
N0	$13.601^b \pm 0.305$	$13.529^b \pm 0.912$	$9.461^a \pm 1.254$	$8.970^a \pm 0.620$
N1	$9.719^b \pm 0.267$	$10.677^b \pm 0.857$	$6.433^a \pm 0.556$	$6.882^a \pm 0.485$
N2	$7.455^b \pm 0.253$	$8.745^b \pm 0.813$	$5.193^a \pm 0.273$	$5.496^a \pm 0.395$
DBH (cm)	16.821 ± 0.201^a	17.583 ± 0.826^a	25.669 ± 1.018^b	26.122 ± 0.629^b
Height (m)	8.098 ± 0.115^a	7.392 ± 0.386^a	10.038 ± 0.622^b	9.673 ± 0.280^b
Density (trees.ha^{-1})	319.51 ± 13.82^c	225.29 ± 23.36^b	51.69 ± 7.81^a	$55.88^a \pm 5.32^a$
G (m^2.ha^{-1})	12.434 ± 0.556^c	10.362 ± 1.185^b	7.667 ± 1.176^a	9.982 ± 1.143^b
AGB (Mg.ha^{-1})	85.327 ± 3.964^c	72.244 ± 7.856^b	20.725 ± 2.418^a	25.302 ± 2.679^a
AGC (Mg C ha^{-1})	42.663 ± 1.982^c	30.122 ± 3.927^b	10.362 ± 1.209^a	12.651 ± 1.339^a

Superscript alphabetic letters indicate significant differences ($p < 0.05$). *N0*, *N1* and *N2* represent Hill's diversity numbers; DBH: diameter at breast height; G: basal area; AGB: aboveground biomass; AGC: aboveground carbon stocks. All values (except the first two rows) represent mean and standard errors ($\mu \pm$ se).

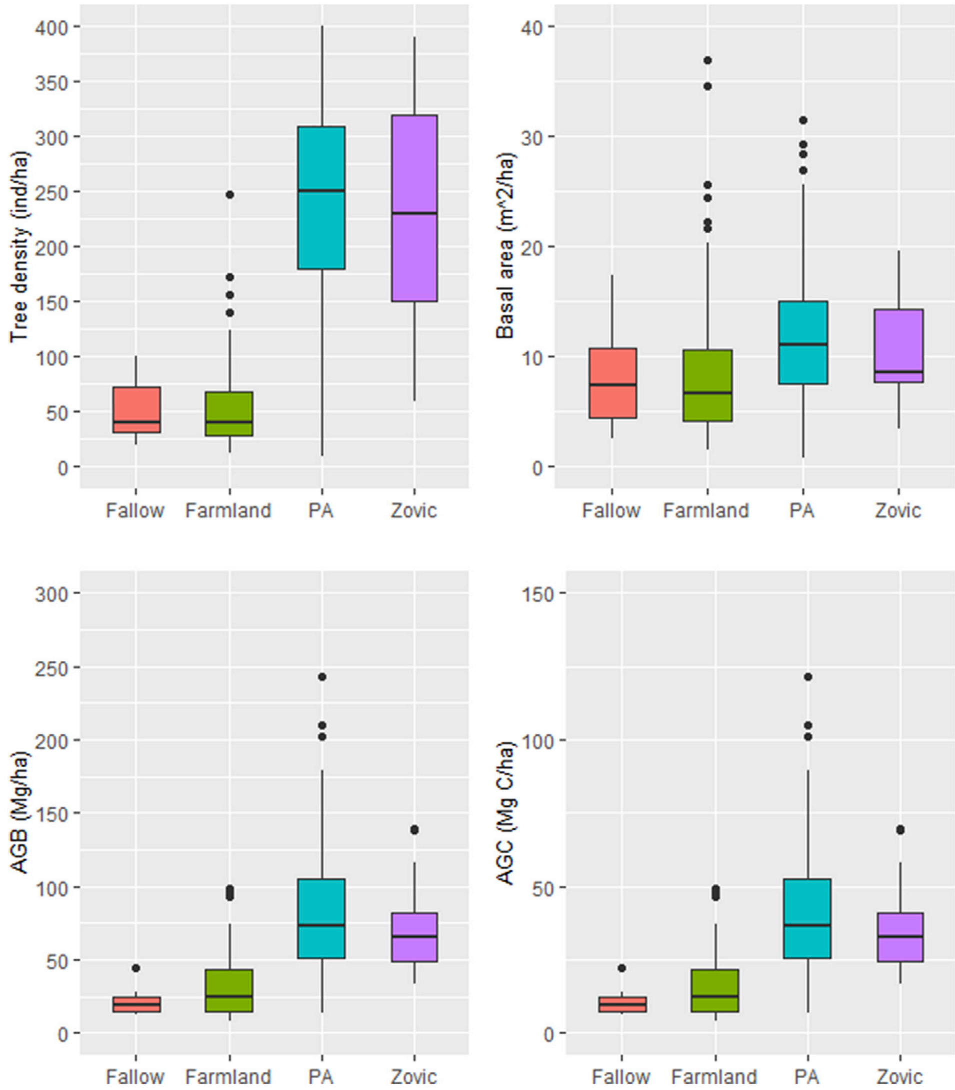

Fig. 2. Variations in tree density, basal area, aboveground biomass and carbon stocks across land use types. **Legend**: AGB: aboveground biomass; AGC: aboveground carbon; PA: protected areas.

3.3. Diversity, structure and carbon stocks relationships

The first two axis (PC#1 and PC#2) of the Principal Component Analysis explained together 61.15% of the total variance of the data set (Fig. 3). The results showed that species richness, the number of abundant species, the number of very abundant species and tree density were related to each other and positively correlated with the PC#1 (Fig. 3, Table 2). However, these variables were negatively associated with the plot-level mean DBH and height. The PC#2 explained 25.16% of the total variance and showed positive loading for plot-level carbon stocks (total and mean). Carbon stock was positively associated with basal area, the number of abundant species and the number of very abundant species.

3.4. Factors affecting carbon storage across land use types

Pearson correlation tests showed relationships between the plot-level carbon stocks and the diversity numbers (Fig. 4). The total carbon stocks positively correlated with the number of species per plot ($R = 0.274$; $p = 1.72e{-}5$) and the number of abundant species ($R = 0.184$; $p = 0.004$). However, no significant correlation was found between carbon stocks and the number of very abundant species ($R = 0.127$; $p = 0.05$). The plot-level mean carbon stocks did not show any correlation with species richness, the number of abundant species and the number of very abundant species (Fig. 4).

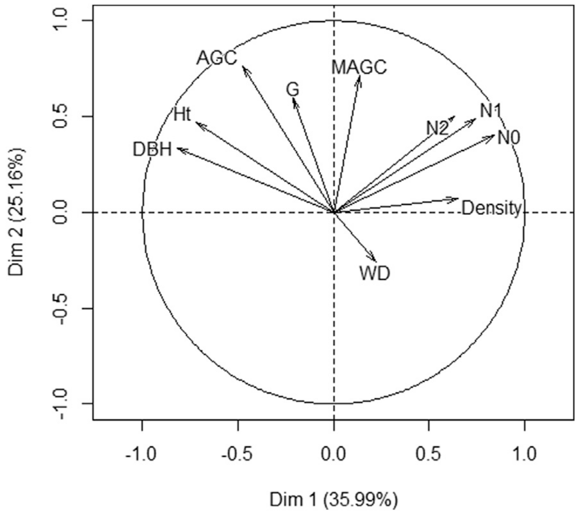

Fig. 3. Principal component analysis showing the plot-level relationships between diversity, structure and aboveground carbon (AGC) stocks. **Legend**: AGC: aboveground carbon; DBH: diameter at breast height; MAGC: mean aboveground carbon stocks; N0, N1 and N2 represent Hill's diversity numbers; Ht: mean height; G: basal area; WD: wood density.

Bivariate relationships were also found between the plot-level aboveground carbon stocks and the structural variables (Fig. 5). The plot-level total carbon stock positively correlated with tree density (R = 0.465; $p = 3.38e{-16}$) but not with mean DBH and height. Inversely, the plot-level mean carbon stock was positively correlated with mean DBH (R = 0.587; $p < 2.2e{-16}$) and height (R = 0.664; $p < 2.2e{-16}$) but negatively correlated with tree density (R = −0.256; $p = 5.85e{-5}$).

Linear regression analysis (Table 3) revealed that tree density contributed the most to the variation in the plot-level total carbon stock (21.25%). The mean DBH and height together explained only 5.52% of the variance of the total carbon stocks, whereas species richness and the number of abundant species together explained 8.79%. However, about 45.43% of the variation in the plot-level mean carbon stock was explained by mean DBH and height.

4. Discussion

4.1. Plant biodiversity across land use types

The overall woody species richness (γ−diversity) reported in this study (107 species) accounted for 20.15% of the woody flora of Burkina Faso (Nacoulma et al., 2018). The recorded species richness was lower than that reported by Traoré et al. (2012a) in the Sudanian zone (208 species) of the country. Hill's diversity numbers revealed that species diversity increased significantly with decreasing gradient of land use pressure. The highest species diversity was recorded in protected areas, corroborating previous studies in West Africa (Nacoulma et al., 2011a; Traoré et al., 2012a; Ouédraogo et al., 2015). Inversely, highly disturbed areas such as fallows and farmlands had the lowest species diversity. This suggests a loss in species diversity and highlights the negative effects of agricultural land use-related disturbances. In fact, agricultural lands undergo severe disturbances such as fires, browsing, tree logging and fuelwood extraction (Zida et al., 2009; Nacoulma et al., 2011a). Such land use pressures increase tree mortality and reduce stand diversity (Zida et al., 2009; Nacoulma et al., 2011a; Dayamba et al., 2016). The higher diversity found in protected areas highlight the great potential of these non-disturbed ecosystems in biodiversity conservation (Nacoulma et al., 2011a).

4.2. Stand structure and carbon density across land use types

As species diversity, significant effect of land use was also found on the structural variables. The mean DBH and height were significantly higher in highly disturbed areas than in undisturbed areas. The increase in stem diameter with increasing land disturbance corroborates Traoré et al. (2012b) who found trees of large DBH in unprotected areas. This suggests that agricultural ecosystems are characterized by the dominance of ageing individuals (Traoré et al., 2012b) that could be attributed to practices such as fires, wood cutting and annually shrubs clearing (Zida et al., 2009; Nacoulma et al., 2011b; Leßmeister et al., 2018). Such practices reduce competition effects and tree density, and thereby, increase tree growth. This finding was consistent with the variation in mean density that was five times lower in highly disturbed areas than in protected areas. The increase of tree density with decreasing gradient of land disturbance was consistent with Nacoulma et al. (2011b) who found that tree density was two to three times higher in protected areas than in parklands. A decline in tree density in unprotected areas was also reported by Traoré et al. (2012b) and Ouédraogo et al. (2015) in Burkina Faso. The

Table 2
Correlation of the variables to the principal components.

Variables	Axis 1	Axis 2
N0	0.838	0.400
N1	0.744	0.491
N2	0.628	0.501
mean DBH	−0.819	0.338
mean height	−0.718	0.468
Density	0.647	0.071
Basal area	−0.213	0.599
Wood density	0.219	−0.258
Carbon stocks	−0.475	0.766
Mean carbon stocks	0.138	0.714

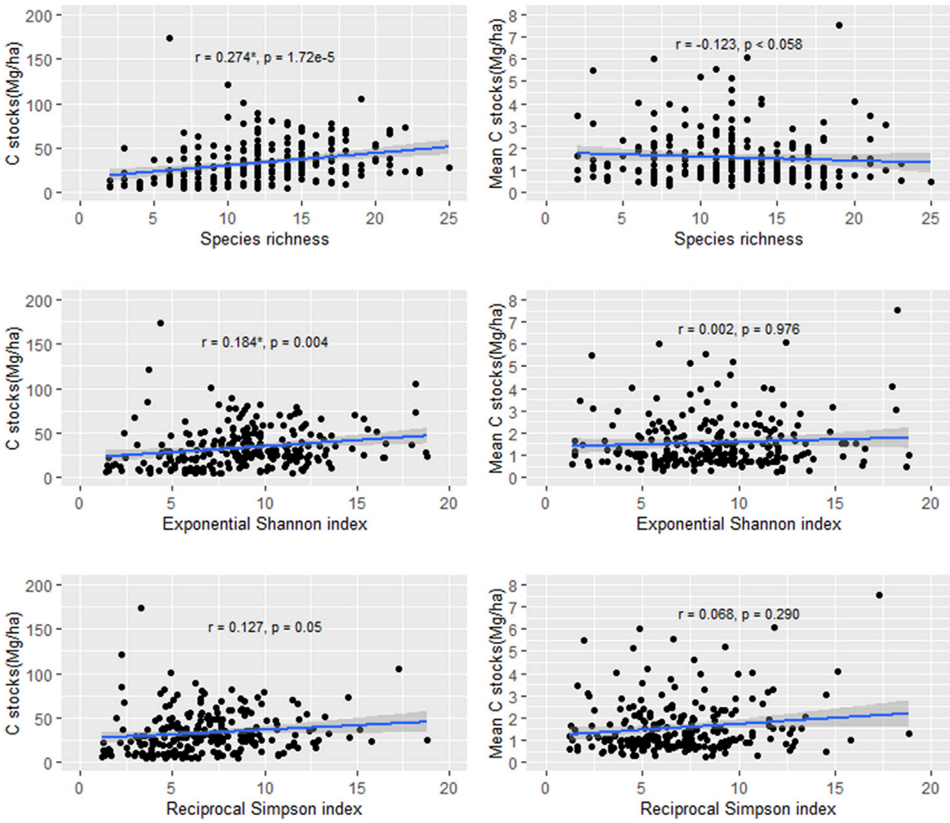

Fig. 4. Relationships between plot-level carbon stocks and diversity numbers. **Legend**: AGC: aboveground carbon.

dominance of old trees in the agricultural lands provides evidence on the lack of young individuals and altered stand structure. These findings corroborate several authors (Sinsin et al., 2004; Nacoulma et al., 2011b; Schumann et al., 2011; Traoré et al., 2012b; Ouédraogo et al., 2015) who reported negative impacts of land use pressures on woody species structure and stand dynamics.

The findings showed that carbon density also increased with decreasing gradient of land disturbance. Across all land use types, protected areas had the greatest carbon density, whereas agricultural lands had the lowest value. Carbon density was four times greater in non-disturbed areas (protected areas) than in highly disturbed areas. Such impacts of land use pressure on carbon storage were also reported elsewhere across the tropics. Dayamba et al. (2016) reported variations in mean carbon density between fallow lands, tree plantations and natural vegetation in Burkina Faso. Similarly, Islam et al. (2017) found that carbon storage in tree biomass was significantly higher in contiguous forests (31.21 ± 2.75 Mg C.ha^{-1}) than in fragmented forests (16.3 ± 1.37 Mg C.ha^{-1}) of Bangladesh. The increase in carbon density with decreasing level of land use pressures confirms that the conversion of forested stands to agricultural lands reduces tree density and biomass, resulting in land degradation and carbon emissions (Gibbs et al., 2010; Houghton, 2014; Baccini et al., 2017; Houghton and Nassikas, 2017; Islam et al., 2017; Pellikka et al., 2018). This finding also suggests that non-disturbed stands such as protected areas remain the

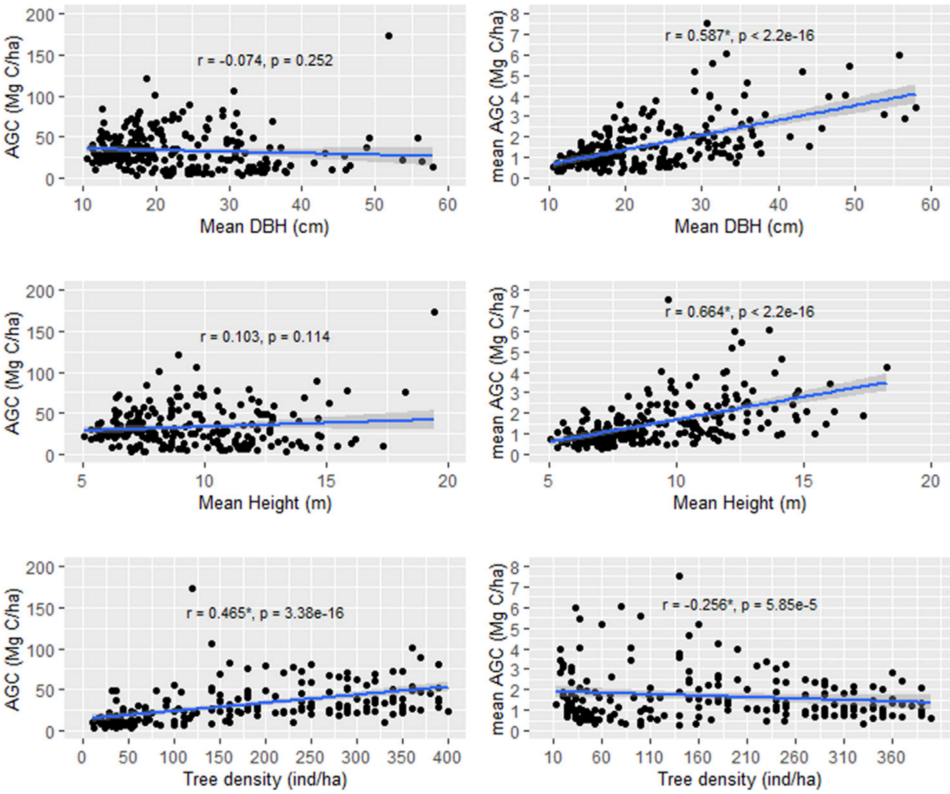

Fig. 5. Relationships between plot-level carbon stocks and structural variables. **Legend**: AGC: aboveground carbon; DBH: diameter at breast height.

Table 3
Effects of stand diversity and structure on aboveground carbon density.

Models	Coefficient	α	SE	t value	Pr (>t)	Adj.R^2 (%)	p-value
Plot level total AGC							
Density	Intercept	19.301	2.167	8.906	<2.2e-16	21.25	3.38e-14
	Density	0.061	0.007	8.076	3.38e-14		
mean DBH	Intercept	37.105	3.898	9.517	2e-16	0.06	0.2519
	mean DBH	−0.181	0.157	−1.149	0.252		
mean H	Intercept	26.323	4.468	5.891	1.31e-8	0.631	0.1144
	mean H	0.702	0.443	1.585	0.114		
mean DBH + mean H	Intercept	28.593	4.0401	6.497	4.82e-10	5.522	0.0004
	mean DBH	−0.846	0.232	−3.643	0.0003		
	mean H	2.497	0.655	3.810	0.0002		
N0+N1	Intercept	16.771	4.065	4.125	5.13e-15	8.794	7.085e-6
	N0	2.871	0.714	4.019	7.87e-5		
	N1	−2.094	0.906	2.311	0.0217		
Plot level mean AGC							
Density	Intercept	2.142	0.154	13.874	2.2e-16	6.21	5.86e-5
	Density	−0.002	0.001	−4.092	5.86e-5		
mean DBH	Intercept	−0.475	0.206	−2.30	0.022	34.19	<2.2e-16
	mean DBH	0.093	0.008	11.16	<2e-16		
mean H	Intercept	−1.171	0.219	−5.345	2.12e-7	43.88	<2.2e-16
	mean H	0.297	0.022	13.679	2e-16		
mean DBH + mean H	Intercept	−1.257	0.218	−5.760	2.61e-8	45.43	<2.2e-16
	mean DBH	0.032	0.011	2.780	0.006		
	mean H	0.229	0.032	7.059	1.85e-11		
N0 + N1	Intercept	2.072	0.267	7.746	2.8e-13	7.27	9.489e-5
	N0	−0.214	0.047	−4.546	8.74e-6		
	N1	0.244	0.059	4.099	5.71e-5		

AGC: aboveground carbon; DBH: diameter at breast height; N0: species richness; N1: number of abundant species; α: estimates of regression coefficient; SE: standard error of means; Adj.R^2: percentage of explained variance.

major carbon pools and sinks (Dayamba et al., 2016; Qasim et al., 2016; Islam et al., 2017; Dimobe et al., 2019). Our results concur with the global agreement that agricultural expansion constitutes the major diver of tropical deforestation and carbon loss (Zomer et al., 2008; Gibbs et al., 2010; Pan et al., 2011; Feldpausch et al., 2011; Baccini et al., 2017; Houghton and Nassikas, 2017). Therefore, reducing rates of deforestation in the short-term, and stopping deforestation in the long-term (Canadell and Raupach, 2008; Houghton, 2014) are critical to reduce carbon emissions from land use. Similarly, the sustainable conservation of non-disturbed forests such as protected areas provides high potential for cost-effective contribution to carbon mitigation (Canadell and Raupach, 2008; Gibbs et al., 2010; Houghton and Nassikas, 2017).

The mean carbon stock in fallows (10.362 ± 1.209 Mg C ha^{-1}) was similar to the estimates of Dayamba et al. (2016) on *Vitellaria paradoxa* parklands (10.71 ± 1.4 Mg C.ha^{-1} to 11.95 ± 2.97 Mg C ha^{-1}). Similarly, carbon density in farmlands (12.651 ± 1.339 Mg C.ha^{-1}) was comparable to that of *Eucalyptus camaldulensis* stand (12.38 ± 5.04 Mg C.ha^{-1}) in the Sudanian zone of Burkina Faso (Dayamba et al., 2016). The mean carbon densities in agricultural lands were within the range of carbon stocks in West African agroforestry systems estimated to range between 0.29 and 15.21 Mg C.ha^{-1} (Nair et al., 2009). Carbon density in protected areas was higher than previous reports in similar managed areas of Burkina Faso. In fact, carbon stocks were reported to range between 3.27 ± 4.22 Mg C.ha^{-1} at Nazinga game ranch to 3.56 ± 3.41 Mg C.ha^{-1} at Bontioli faunal reserve (Qasim et al., 2016). Moreover, a recent study in W national park reported mean carbon stocks of 12.3 ± 1.8 Mg C.ha^{-1} (Dimobe et al., 2019). These differences in carbon estimates highlight the high uncertainties of tropical carbon stocks (Pan et al., 2011; Baccini et al., 2012, 2017; Feldpausch et al., 2011; Chave et al., 2014). Such differences can be attributed to variations in stand characteristics (Zhang et al., 2016), differences in climatic conditions (Schippers et al., 2015; Zhao et al., 2017) and field sampling efforts. The observed differences also highlight the fact that carbon estimates for mixed protected areas considered as a single land use type may not accurately reflect carbon stocks of a given ecosystem from that land use type. The mean carbon stocks reported in this study (10.362–42.663 Mg C.ha^{-1}) were lower than the regional scale carbon density (82 Mg C.ha^{-1}) reported for tropical Africa (Baccini et al., 2012).

4.3. Diversity-structure-carbon relationships and drivers of carbon storage

The study showed significant effect of land use on species diversity, stand structure and carbon storage in tree biomass. The highest diversity and carbon stocks were held in non-disturbed areas namely protected areas. Similar findings were also reported in previous studies across the tropics (Dayamba et al., 2016; Islam et al., 2017). The Principal Component Analysis revealed strong links between carbon storage potential, stand structure and species diversity. The PC#1 indicated that stand density increases with species diversity. Yet, high stand diversity and density increase competition among species. Through the PC#2, we found that plot-level carbon stocks were related to tree basal area, the number of abundant species and the number of very abundant species. The multiple linear regression revealed that tree density explained 21.25% of the variation in the total carbon stocks, whereas mean DBH and height accounted for 45.43% of the variation in mean carbon stocks. These results corroborate previous studies supporting that carbon storage in tree aboveground biomass was influenced by both stand composition and structure (Dayamba et al., 2016; Islam et al., 2017). Furthermore, findings from Dimobe et al. (2019) showed that carbon storage was largely controlled by stand composition than local ecological conditions in Burkina Faso. Pellikka et al. (2018) reported land-use change as the main driver of carbon storage in Kenya. Stem DBH and tree height that accounted for the highest variation of mean carbon stocks were reported as the best biomass predictors across many tropical (Basuki et al., 2009; Feldpausch et al., 2011; Kuyah et al., 2012; Chave et al., 2014) and subtropical ecosystems (Paul et al., 2013; Xu et al., 2015; Xiang et al., 2016). Our findings stress the fact that changes in vegetation composition and stand structure consecutively to forest conversion and land degradation decrease stand diversity, tree biomass and carbon stocks (Islam et al., 2017; Pellikka et al., 2018; Dimobe et al., 2019).

5. Conclusion and implications

This study provided empirical evidences on the impacts of human-driven land disturbances on plant biodiversity and carbon sequestration. The lower diversity, density and carbon stocks in agricultural lands as opposed to that in protected areas suggest that stand conversion to agricultural lands decreases woody flora diversity, and their potential to remove atmospheric CO_2. The findings highlight the importance to account for sustainable agriculture and forest conservation in climate and development policies. The alteration of stand structure and the loss of species diversity and carbon due to agricultural land use have significant implications for climate mitigation that represent the target 13 of the sustainable development goals. Indeed, the dominance of ageing individuals in agricultural areas implies that agricultural systems may be net sources of carbon. In such context, improved agricultural practices reducing forest clearing and tree logging will greatly contribute to carbon removal through forest regrowth, enhancing thereby land cover, carbon sinks and climate change mitigation. Similarly, the enhancement of carbon sinks within the agricultural lands through afforestation will enrich development and climate policies for multiple environmental and economic benefits such as agrobiodiversity conservation and REDD + credit. This will also enhance the resilience of farmers to climate change through the delivering of ecosystems goods. Forest fragmentation and conversion to agricultural lands will increasingly occur in West Africa due to the growing demand for croplands. These changes will reduce carbon pools and sinks, and jeopardize climate mitigation efforts in the longer term. Optimizing the contribution of forestry to climate mitigation requires strengthening the conservation of protected areas and preserving unprotected natural stands from deforestation and degradation. Sustainable land managment and improved agricultural practices are also required for achieving negative carbon emissions as well as enhanced crop production and food security. In this perspective, the restoration of degraded agricultural lands is highly fundamental especially in the semi-arid areas of Sub-Saharan Africa. Sustainable agriculture and smart agroforestry practices should be considered in land use policies for achieving the threefold goals of sustainable land management, biodiversity conservation and climate mitigation.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Data availability

The data sets analyzed in this study are available from the corresponding author upon reasonable request.

Funding sources

This study was fully supported by the German Federal Ministry of Education and Research (BMBF) through the West African Science Service Centre on Climate Change and Adapted Land Use (WASCAL) program. The funding contributed in the study design and data collection and analysis.

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.

Acknowledgements

The authors are grateful to the German Federal Ministry of Education and Research (BMBF), for their financial supports through the graduate research program Climate Change and Biodiversity of WASCAL program. The authors are also grateful to Doctor Issouf Zerbo for his significant help in the computing of diversity indices.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00875.

List of woody species across land use types

Species	Family	Land use type
Acacia erythrocalyx Brenan	Fabaceae-Mimosoideae	I
Acacia gourmaensis A.Chev.	Fabaceae-Mimosoideae	I, II, III, IV
Acacia macrostachya Rchb. ex DC.	Fabaceae-Mimosoideae	I, II, III, IV
Acacia nilotica (L.) Willd. ex Delile	Fabaceae-Mimosoideae	I, II
Acacia polyacantha Willd.	Fabaceae-Mimosoideae	I
Acacia senegal (L.) Willd.	Fabaceae-Mimosoideae	I, II, III, IV
Acacia seyal Delile	Fabaceae-Mimosoideae	I
Acacia sieberiana DC.	Fabaceae-Mimosoideae	I, III, IV
Adansonia digitata L.	Malvaceae	I, II, IV
Afzelia africana Sm.ex Pers.	Fabaceae-Caesalpinioideae	I, II, III, IV
Anacardium occidentale L. [cult.]	Anacardiaceae	IV
Andira inermis (W.Wright) DC.	Fabaceae-Faboideae	I
Annona senegalensis Pers.	Annonaceae	I, II, III, IV
Anogeissus leiocarpa (DC.) Guill. & Perr.	Combretaceae	I, II, III, IV
Azadirachta indica A.Juss. [cult.]	Meliaceae	I, IV
Balanites aegyptiaca (L.) Delile	Zygophyllaceae	I, II, III, IV
Bombax costatum Pellegr. & Vuill.	Malvaceae	I, II, IV
Bridelia scleroneura Müll.Arg.	Phyllanthaceae	I, III, IV
Burkea africana Hook.	Fabaceae-Caesalpinioideae	I, II, III, IV
Capparis sepiaria L.	Capparaceae	I, IV
Cassia sieberiana DC.	Fabaceae-Caesalpinioideae	I, II, IV
Ceiba pentandra (L.) Gaertn.	Malvaceae	I, IV

(continued on next page)

(*continued*)

Species	Family	Land use type
Combretum aculeatum Vent.	Combretaceae	II
Combretum adenogonium Steud. ex. A.Rich.	Combretaceae	I, II, III, IV
Combretum collinum Fresen.	Combretaceae	I, II, III, IV
Combretum glutinosum Perr. ex DC.	Combretaceae	I, II, III, IV
Combretum molle R.Br. ex G.Don	Combretaceae	I, II, III, IV
Combretum nigricans Lepr. ex Guill. & Perr.	Combretaceae	I, II, III, IV
Cordia myxa L.	Boraginaceae	IV
Crossopteryx febrifuga (Afzel. ex G.Don) Benth.	Rubiaceae	I, II, III, IV
Cussonia arborea Hochst. ex A.Rich.	Araliaceae	I, III
Daniellia oliveri (Rolfe) Hutch. & Dalziel	Fabaceae-Caesalpinioideae	I, II, III, IV
Detarium microcarpum Guill. & Perr.	Fabaceae-Caesalpinioideae	I, II, III, IV
Dichrostachys cinerea (L) Wight & Arn.	Fabaceae-Mimosoideae	I, II, III, IV
Diospyros mespiliformis Hochst. ex A.DC.	Ebenaceae	I, II, III, IV
Dombeya quinqueseta (Delile) Excell	Malvaceae	I, II,
Entada africana Guill. & Perr.	Fabaceae-Mimosoideae	I, II, IV
Erythrina senegalensis A.DC.	Fabaceae-Faboideae	I
Faidherbia albida (Delile) A.Chev.	Fabaceae-Mimosoideae	IV
Feretia apodanthera Delile	Rubiaceae	I, II, IV
Ficus abutilifolia (Miq.) Miq.	Moraceae	I, IV
Ficus glumosa Delile	Moraceae	I
Ficus ingens (Miq.) Miq.	Moraceae	IV
Ficus platyphylla Delile	Moraceae	I, II, IV
Ficus sur Forssk.	Moraceae	IV
Ficus sycomorus L.	Moraceae	III, IV
Ficus thonningii Blume	Moraceae	I, III
Ficus vallis-choudae Delile	Moraceae	I, II
Flueggea virosa (Roxb. ex Willd.) Voigt	Phyllanthaceae	II, IV
Gardenia aqualla Stapf & Hutch.	Rubiaceae	I
Gardenia erubescens Stapf & Hutch.	Rubiaceae	I, II, III, IV
Gardenia sokotensis Hutch.	Rubiaceae	I, II
Gardenia ternifolia Schumach. & Thonn.	Rubiaceae	I, III, IV
Grewia barteri Burret	Malvaceae	I, II
Grewia bicolor Juss.	Malvaceae	I, II
Grewia lasiodiscus K.Schum.	Malvaceae	
Guiera senegalensis J.F.Gmel.	Combretaceae	I, IV
Gymnosporia senegalensis (Lam.) Loes.	Celastraceae	I, II, III, IV
Hexalobus monopetalus (A.Rich.) Engl. & Diels	Annonaceae	I, II, III
Hymenocardia acida Tul.	Phyllanthaceae	I
Isoberlinia doka Craib & Stapf	Fabaceae-Caesalpinioideae	I, III, IV
Khaya senegalensis (Desr.) A.Juss.	Meliaceae	I, II, III
Lannea acida A.Rich.	Anacardiaceae	I, II, III, IV
Lannea microcarpa Engl. & K.Krause	Anacardiaceae	I, II, III, IV
Lannea velutina A.Rich.	Anacardiaceae	I, III, IV
Lophira lanceolata Tiegh. ex Keay	Ochnaceae	I, IV
Manilkara multinervis (Baker) Dubard	Sapotaceae	I, III, IV
Maranthes polyandra (Benth.) Prance	Chrysobalanaceae	I, II, III, IV
Monotes kerstingii Gilg	Dipterocarpaceae	I, II, IV
Opilia amentacea Roxb.	Opiliaceae	I, III, IV
Ozoroa obovata (Oliv.) R.Fern. & A.Fern.	Anacardiaceae	I, IV
Parinari curatellifolia Planch. ex Benth.	Chrysobalanaceae	I, II, IV
Parkia biglobosa (Jacq.) R.Br. ex G.Don	Fabaceae-Mimosoideae	I, II, III, IV
Paullinia pinnata L.	Sapindaceae	I
Pavetta crassipes K.Schum.	Rubiaceae	I
Pericopsis laxiflora (Benth.) Meeuwen	Fabaceae-Faboideae	I, II, III, IV
Philenoptera laxiflora (Guill. & Perr.) Roberty	Fabaceae-Faboideae	I, II, IV
Piliostigma reticulatum (DC.) Hochst.	Fabaceae-Caesalpinioideae	II, IV
Piliostigma thonningii (Schumach.) Milne-Redh.	Fabaceae-Caesalpinioideae	I, II, III, IV
Prosopis africana (Guill. & Perr.) Taub.	Fabaceae-Mimosoideae	I, IV
Pseudocedrela kotschyi (Schweinf.) Harms	Meliaceae	I, II, IV
Pteleopsis suberosa Engl. & Diels	Combretaceae	I, II, III, IV
Pterocarpus erinaceus Poir.	Fabaceae-Faboideae	I, II, III, IV
Quassia undulata (Guill. & Perr.) F.Dietr.	Simaroubaceae	I, IV
Saba comorensis (Bojer ex A.DC.) Pichon	Apocynaceae	I
Saba senegalensis (A.DC.) Pichon	Apocynaceae	I, II, III, IV
Sarcocephalus latifolius (Sm.) E.A.Bruce	Rubiaceae	I, II, IV
Securidaca longipedunculata Fresen.	Polygalaceae	I, II, IV
Sterculia setigera Delile	Malvaceae	I, II, III, IV
Stereospermum kunthianum Cham.	Bignoniaceae	I, II, III, IV
Strychnos innocua Delile	Loganiaceae	I, II, III, IV

(*continued*)

Species	Family	Land use type
Strychnos spinosa Lam.	Loganiaceae	I, II, III, IV
Synsepalum pobeguinianum (Pier. ex Lec.) Aké Assi & L.Gaut.	Sapotaceae	I
Syzygium guineense (Willd.) DC.	Myrtaceae	I
Tamarindus indica L.	Fabaceae-Caesalpinioideae	I, III, IV
Terminalia avicennioides Guill. & Perr.	Combretaceae	I, II, IV
Terminalia laxiflora Engl. & Diels	Combretaceae	I, II, III, IV
Terminalia macroptera Guill. & Perr.	Combretaceae	I, II, III, IV
Terminalia mollis M.A.Lawson	Combretaceae	I, II, III, IV
Trichilia emetica Vahl	Meliaceae	I, IV
Vitellaria paradoxa C.F.Gaertn	Sapotaceae	I, II, III, IV
Vitex chrysocarpa Planch. ex Benth.	Lamiaceae	I
Vitex doniana Sweet	Lamiaceae	I, IV
Xeroderris stuhlmannii (Taub.) Mendonça & E.C.Sousa	Fabaceae-Faboideae	I, II, IV
Ximenia americana L.	Ximeniaceae	I, II, III, IV
Zanthoxylum zanthoxyloides (Lam.) Zepern. & Timler	Rutaceae	I, IV
Ziziphus mucronata Willd.	Rhamnaceae	I, IV

I: Protected area; II: Zovics, III: Fallow; IV: Farmland.

References

Baccini, A., Goetz, S.J., Walker, W.S., Laporte, N.T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P.S.A., Dubayah, R., Friedl, M.A., Samanta, S., Houghton, R.A., 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nat. Clim. Chang. 2 (3), 182–185. https://doi.org/10.1038/nclimate1354.

Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., Houghton, R.A., 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and losses. Science 358 (6360), 230–234. https://doi.org/10.1126/science.aam5962.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol. Lett. 9 (10), 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x.

Basuki, T.M., van Laake, P.E., Skidmore, A.K., Hussin, Y.A., 2009. Allometric equations for estimating the aboveground biomass in tropical lowland Dipterocarp forests. For. Ecol. Manag. 257, 1684–1694. https://doi.org/10.1016/j.foreco.2009.01.027.

Bélem, B., Nacoulma, B.M.I., Gbangou, R., Kambou, S., Hansen, H.H., Gausset, Q., Lund, S., Raebild, A., Lompo, D., Ouédraogo, M., Theilade, I., Boussim, I.J., 2007. Use of non-wood forest products buy local people bordering the parc national kaboré tambi, Burkina Faso. J. Transdiscipl. Environ. Stud. 6 (1), 21.

Bonan, G.B., 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320 (5882), 1444–1449. https://doi.org/10.1126/science.1155121.

Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. Science 320 (5882), 1456–1457. https://doi.org/10.1126/science.1155458.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 78–99. https://doi.org/10.1007/s00442-005-0100-x.

Chave, J., Rejou Mechain, M., Burquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martinez-Yrizar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the above ground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.

Cramer, W., Bondeau, A., Schaphoff, S., Lucht, W., Smith, B., Stephen Sitch, S., 2004. Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. Philos. Trans. R. Soc. B 359 (1443), 331–343. https://doi.org/10.1098/rstb.2003.1428.

Dayamba, S.D., Djoudi, H., Zida, M., Sawadogo, L., Verchot, L., 2016. Biodiversity and carbon stocks in different land use types in the Sudanian Zone of Burkina Faso, West Africa. Agric. Ecosyst. Environ. 216, 61–72. https://doi.org/10.1016/j.agee.2015.09.023.

Dimobe, K., Ouédraogo, A., Soma, S., Goetze, D., Porembski, S., Thiombiano, A., 2015. Identification of driving factors of land degradation and deforestation in the wildlife reserve of Bontioli (Burkina Faso, West Africa). Glob. Ecol. Conserv. 4, 559–571. https://doi.org/10.1016/j.gecco.2015.10.006.

Dimobe, K., Goetze, D., Ouédraogo, A., Forkuor, G., Wala, K., Porembski, S., Thiombiano, A., 2017. Spatio-temporal dynamics in land use and habitat fragmentation within a protected area dedicated to tourism in a Sudanian savanna of West Africa. J. Landsc. Ecol. 10 (1), 75–95. https://doi.org/10.1515/jlecol-2017-0011.

Dimobe, K., Kuyah, S., Dabré, Z., Amadé Ouédraogo, A., Thiombiano, A., 2019. Diversity-carbon stock relationship across vegetation types in W National park in Burkina Faso. For. Ecol. Manag. 438, 243–254. https://doi.org/10.1016/j.foreco.2019.02.027.

Egoh, B., Reyers, B., Rouget, M., Bode, M., Richardson, D.M., 2009. Spatial congruence between biodiversity and ecosystem services in South Africa. Biol. Conserv. 142 (3), 553–562. https://doi.org/10.1016/j.biocon.2008.11.009.

FAO, 2017. Global Forest Land-Use Change from 1990 to 2010: an Update to a Global Remote Sensing Survey of Forests. Forest Resources Assessment Working Paper 187. Rome: FAO, United Nations.

Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., França, M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patiño, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodt, F., Sonké, B., Taedoumg, H.E., Tan, S., White, L., Wöll, H., Lloyd, J., 2011. Height-diameter allometry of tropical forest trees. Biogeosciences 8, 1081–1106. https://doi.org/10.5194/bg-8-1081-2011.

Fonseca, W., Alice, F.E., Rey-Benayas, J.M., 2011. Carbon accumulation in aboveground and belowground biomass and soil of different age native forest plantations in the humid tropical lowlands of Costa Rica. N. For. 43 (2), 197–211. https://doi.org/10.1007/s11056-011-9273-9.

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc. Natl. Acad. Sci. U. S. A. 107 (38), 16732–16737. https://doi.org/10.1073/pnas.0910275107.

Harris, N.L., Brown, S., Hagen, S.C., Saatchi, S.S., Petrova, S., Salas, W., Hansen, M.C., Potapov, P.V., Lotsch, A., 2012. Baseline map of carbon emissions from deforestation in tropical regions. Science 80 (336), 1573–1576. https://doi.org/10.1126/science.1217962.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54 (2), 427–432. https://doi.org/10.2307/1934352.

Houehanou, T.D., Glèlè Kakaï, R.L., Assogbadjo, A.E., Kindomihou, V., Houinato, M., Wittig, R., Sinsin, B.A., 2012. Change in the woody floristic composition, diversity and structure from protected to unprotected savannahs in Pendjari Biosphere Reserve (Benin, West Africa). Afr. J. Ecol. 51, 358–365. https://doi.org/10.1111/aje.12046.

Houessou, L.G., Teka, O., Toko, I.I., Lykke, A.M., Sinsin, B., 2013. Land-use and land cover change at “W” biosphere reserve and it surrounding area in Benin republique (West Africa). Environ. Nat. Resour. Res. 3 (2), 87–101. https://doi.org/10.5539/enrr.v3n2p87.

Houghton, R.A., 2014. Land management options for mitigation and adaptation to climate change. In: Freedman, B. (Ed.), Global Environmental Change. Handbook of Global Environmental Pollution, 1, pp. 389–398. https://doi.org/10.1007/978-94-007-5784-4_9.

Houghton, R.A., Nassikas, A.A., 2017. Global and regional fluxes of carbon from land use and land cover change 1850–2015. Glob. Biogeochem. Cycles 31 (3), 456–472. https://doi.org/10.1002/2016GB005546.

IPCC, 2003. Good Practice Guidance for Land Use, Land-Use Change and Forestry. IPCC National Greenhouse Gas Inventories Programme Technical Support Unit. Japan, p. 590.

Islam, M., Deb, G.P., Rahman, M., 2017. Forest fragmentation reduced carbon storage in a moist tropical forest in Bangladesh: implications for policy development. Land Use Policy 65, 15–25. https://doi.org/10.1016/j.landusepol.2017.03.025.

Kindt, R., Coe, R., 2005. Tree Diversity Analysis. A Manual and Software for Common Statistical Methods for Ecological and Biodiversity Studies. World Agroforestry Centre (ICRAF), Nairobi, ISBN 92-9059-179-X.

Kuyah, S., Dietz, J., Muthuri, C., Jamnadass, R., Mwangi, P., Coe, R., Neufeldt, H., 2012. Allometric equations for estimating biomass in agricultural landscapes: I. Aboveground biomass. Agric. Ecosyst. Environ. 158, 216–224. https://doi.org/10.1016/j.agee.2012.05.011.

Landmann, T., Machwitz, M., Schmidt, M., Dech, S., Vlek, P., 2010. Land cover change in West Africa as observed by satellite remote sensing/Current state of Biodiversity in West Africa. In: Thiombiano, A., Kampmann, D. (Eds.), Biodiversity Atlas of West Africa, II. Ouagadougou & Frankfurt/Main, pp. 92–97.

Leßmeister, A., Bernhardt-Römermann, M., Schumann, K., Thiombiano, A., Wittig, R., Hahn, K., 2018. Vegetation changes over the past two decades in a West African savanna ecosystem. Appl. Veg. Sci. 22 (2), 230–242. https://doi.org/10.1111/avsc.12428.

Le, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. J. Stat. Softw. 25 (1), 1–18. https://doi.org/10.18637/jss.v025.i01.

Lewis, S.L., Lopez-Gonzalez, G., Sonke, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo, K.M.N., Ewango, C.E., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J., Taylor, D., Thomas, S.C., Votere, R., Wöll, H., 2009. Increasing carbon storage in intact African tropical forests. Nature 457, 1003–1006. https://doi.org/10.1038/nature07771.

Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends Ecol. Evol. 27 (1), 19–26. https://doi.org/10.1016/j.tree.2011.08.006.

Nacoulma, B.M.I., Schumann, K., Traoré, S., Bernhardt-Römermann, M., Hahn, K., Wittig, R., Thiombiano, A., 2011a. Impacts of land-use on West African Savanna vegetation: a comparison between protected and communal area in Burkina Faso. Biodivers. Conserv. 20 (14), 3341–3362. https://doi.org/10.1007/s10531-011-0114-0.

Nacoulma, B.M.I., Traoré, S., Hahn, K., Thiombian, A., 2011b. Impact of land use types on population structure and extent of bark and foliage harvest of *Afzelia africana* and *Pterocarpus erinaceus* in Eastern Burkina Faso. Int. J. Biodivers. Conserv. 3 (3), 62–72.

Nacoulma, B.M.I., Ouédraogo, I., Kangbéni, D., Thiombiano, A., 2018. Phytodiversity of Burkina Faso: selected countries in Africa. Glob. Biodivers. 33 (Chapter 1), Volume 3, In book.

Nair, P.K.R., Kumar, B.M., Nair, V.D., 2009. Agroforestry as a strategy for carbon sequestration. J. Plant Nutr. Soil Sci. 172 (1), 10–23. https://doi.org/10.1002/jpln.200800030.

Ouédraogo, I., Nacoulma, B.M.I., Hahn, K., Thiombiano, A., 2014. Assessing ecosystem services based on indigenous knowledge in south-eastern Burkina Faso (West Africa). Int. J. Biodivers. Ecosystem. Serv. Manag. 10 (4), 313–321. https://doi.org/10.1080/21513732.2014.950980.

Ouédraogo, O., Bondé, L., Boussim, I.J., Linstädter, A., 2015. Caught in a human disturbance trap: responses of tropical savanna trees to increasing land-use pressure. For. Ecol. Manag. 354, 68–76. https://doi.org/10.1016/j.foreco.2015.06.036.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Philips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world’s forests. Science 333 (6045), 988–993. https://doi.org/10.1126/science.1201609.

Paul, K.I., Roxburgh, S.H., Ritson, P., Brooksbank, K., England, J.R., Larmour, J.S., Raison, R.J., Peck, A., Wildy, D.T., Sudmeyer, R.A., Giles, R., Carter, J., Bennett, R., Mendham, D.S., Huxtable, D., Bartle, J.R., 2013. Testing allometric equations for prediction of above-ground biomass of mallee eucalypts in southern Australia. For. Ecol. Manag. 310, 1005–1015. https://doi.org/10.1016/j.foreco.2013.09.040.

Pellikka, P.K.E., Heikinheimo, V., Hietanen, J., Schäfer, E., Siljander, M., Heiskanen, J., 2018. Impact of land cover change on aboveground carbon stocks in Afromontane landscape in Kenya. Appl. Geogr. 94, 178–189. https://doi.org/10.1016/j.apgeog.2018.03.017.

Qasim, M., Porembski, S., Sattler, D., Stein, K., Thiombiano, A., Lindner, A., 2016. Vegetation structure and carbon stocks of two protected areas within the South-sudanian savannas of Burkina Faso. Environments 3 (4), 25. https://doi.org/10.3390/environments3040025.

Rahman, M., Islam, M., Islam, R., Sobuj, N.A., 2017. Towards sustainability of tropical forests: implications for enhanced carbon stock and climate change mitigation. J. Forest. Environ. Sci. 33 (4), 281–294. https://doi.org/10.7747/JFES.2017.33.4.281.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W., Zutta, B.R., Buermann, W., Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M., Morel, A., 2011. Benchmark map of forest carbon stock in tropical regions across three continents. Proc. Natl. Acad. Sci. U. S. A. 108 (24), 9899–9904. https://doi.org/10.1073/pnas.1019576108.

Schippers, P., Sterck, F., Vlam, M., Zuidema, P.A., 2015. Tree growth variation in the tropical forest: understanding effects of temperature, rainfall and CO_2. Glob. Chang. Biol. 21, 2749–2761. https://doi.org/10.1111/gcb.12877.

Schumann, K., Wittig, R., Thiombiano, A., Becker, U., Hahn, K., 2011. Impact of land use type and harvesting on population structure of a non-timber forest product providing tree in a semi-arid savanna, West Africa. Biol. Conserv. 144 (9), 2369–2376. https://doi.org/10.1016/j.biocon.2011.06.018.

Sinsin, B., Eyog-Matig, O., Assogbadjo, A.E., Gaoué, O.G., Sinadouwirou, T., 2004. Dendrometric characteristics as indicators of human pressure on *Afzelia africana* Sm dynamic changes in trees found in different climatic zones of Benin. Biodivers. Conserv. 13, 1555–1570.

Sop, T.K., Oldeland, J.S., Bognounou, F., Schmiedel, U., Thiombiano, A., 2012. Ethnobotanical knowledge and valuation of woody plants species: a comparative analysis of three ethnic groups from the sub-Sahel of Burkina Faso. Environ. Dev. Sustain. 14 (5), 627–649. https://doi.org/10.1007/s10668-012-9345-9.

Thiombiano, A., Glèlè Kakaï, R., Bayen, P., Boussim, I.J., Mahamane, A., 2016. Méthodes et dispositifs d’inventaires forestiers en Afrique de l’Ouest: état des lieux et propositions pour une harmonisation. In: Methodes de collecte et d’analyse des données de terrain pour l’évaluation et le suivi de la végétation en Afrique. Annales des Sciences Agronomiques, 20, pp. 15–31.

Traoré, L., Ouédraogo, A., Thiombiano, A., 2012a. To what extent do protected areas determine the conservation of native flora? A case study in the Sudanian zone of Burkina Faso. Int. Scholar. Res. Netw. Bot. 2012 (10) https://doi.org/10.5402/2012/168196.

Traoré, L., Sop, T.K., Dayamba, S.D., Salifou Traoré, S., Hahn, K., Thiombiano, A., 2012b. Do protected areas really work to conserve species? A case study of three vulnerable woody species in the Sudanian zone of Burkina Faso. Environ. Dev. Sustain. 15 (3), 663–686. https://doi.org/10.1007/s10668-012-9399-8.

Vieilledent, G., Grinand, C., Vaudry, R., 2013. Forecasting deforestation and carbon emissions in tropical developing countries facing demographic expansion: a case study in Madagascar. Ecol. Evol. 3 (6), 1702–1716. https://doi.org/10.1002/ece3.550.

Vlam, M., Baker, P.J., Bunyavejchewin, S., Zuidema, P.A., 2014. Temperature and rainfall strongly drive temporal growth variation in Asian tropical forest trees. Oecologia 174, 1449–1461. https://doi.org/10.1007/s00442-013-2846-x.

Wegmann, M., Machwitz, M., Schmidt, M., Dech, S., 2010. Fragmentation of rain forest-endanging biodiversity/current state of biodiversity in West Africa. In: Thiombiano, A., Kampmann, D. (Eds.), Biodiversity Atlas of West Africa. Ouagadougou & Frankfurt/Main Vol II, pp. 86−91.

Wood, T.E., Cavaleri, M.A., Reed, S.C., 2012. Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes. Biol. Rev. 87 (4), 912−927. https://doi.org/10.1111/j.1469-185X.2012.00232.x.

Wright, S.J., 2010. The future of tropical forests. Ann. N. Y. Acad. Sci. 1195, 27. https://doi.org/10.1111/j.1749-6632.2010.05455.x.

Xiang, W., Zhou, J., Ouyang, S., Zhang, S., Lei, P., Li, J., Deng, X., Fang, X., Forrester, D.I., 2016. Species-specific and general allometric equations for estimating tree biomass components of subtropical forests in southern China. Eur. J. For. Res. 135 (5), 963−979. https://doi.org/10.1007/s10342-016-0987-2.

Xu, Y., Zhang, J., Franklin, S.B., Liang, J., Ding, P., Luo, Y., Lu, Z., Bao, D., Jiang, M., 2015. Improving allometry models to estimate the above- and belowground biomass of subtropical forest, China. Ecosphere 6 (12), 15. https://doi.org/10.1890/es15-00198.1.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Global Wood Density Database.

Zhang, H., Song, T., Wang, K., Yang, H., Yue, Y., Zeng, Z., Peng, W., Zeng, F., 2016. Influences of stand characteristics and environmental factors on forest biomass and root−shoot allocation in southwest China. Ecol. Eng. 91, 7−15. https://doi.org/10.1016/j.ecoleng.2016.01.040.

Zhao, Y., Ding, Y., Hou, X., Li, F.Y., Han, W., Yun, X., 2017. Effects of temperature and grazing on soil organic carbon storage in grasslands along the Eurasian steppe eastern transect. PLoS One 12 (10), e0186980. https://doi.org/10.1371/journal.pone.0186980.

Zida, D., Tigabu, M., Sawadogo, L., Tiveau, D., Odén, P.C., 2009. Long-term effects of prescribed early fire, grazing and selective tree cutting on seedling populations in the Sudanian savanna of Burkina Faso. Afr. J. Ecol. 47 (1), 97−108. https://doi.org/10.1111/j.1365-2028.2008.01011.x.

Zizka, A., Thiombiano, A., Dressler, S., Nacoulma, B.M.I., Ouédraogo, A., Ouédraogo, I., Ouédraogo, O., Zizka, G., Hahn, K., Schmidt, M., 2015. Traditional plant use in Burkina Faso (West Africa): a national-scale analysis with focus on traditional medicine. J. Ethnobiol. Ethnomed. 11 (9) https://doi.org/10.1186/1746-4269-11-9.

Zomer, R.J., Trabucco, A., Bossio, D.A., Verchot, L.V., 2008. Climate change mitigation: a spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. Agric. Ecosyst. Environ. 126, 67−80. https://doi.org/10.1016/j.agee.2008.01.014.