Nitrogen availability determines the long-term impact of land-use change on soil carbon stocks in grasslands of southern Ghana

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Abstract. Enhancing the capacity of agricultural soils to resist soil degradation and to mitigate climate change requires long-term assessments of land-use systems. Such long-term evaluations, particularly regarding low-input livestock systems, are limited. In the absence of suitable long-term experiments, this study assessed the outcome of C inputs and outputs in across an array of plant functional groups in arable and permanent systems of a tropical Savannah after more than 50 years of consistent land use. Soil samples were taken (0–30 cm depth) from arable crop fields, grazed-seeded grassland, cut-use permanent crops and native grassland. Soil organic carbon (SOC) stocks ranged from 17 to 64 Mg SOC ha^{-1} (mean±sd = 32.9±10.2 Mg ha^{-1}). SOC stocks were lower for grazed-seeded grassland relative to cut-use grass, legume trees and shrubs. Accordingly, while converting the native grassland to grazed pastures was estimated to have lost 44 % SOC over the period, the conversion to woody legumes resulted in slight (5 %) increments. Within sown systems, nitrogen (N) availability seemed to be the most critical factor that determines the fate of the SOC stocks, with soil N concentration and the SOC being highly correlated ($r = 0.86$; $p<0.001$). In total N, P and K were significant predictors of SOC density in the soils. Moreover, secondary plant metabolites in legumes, namely tannins, were identified to have an impact on SOC. The results from this study provide the theoretical basis to test the hypothesis that improved soil fertility management, and the use of tannin-rich plants have the potential to promote SOC storage in the Savannah ecological region in the long-run. Our study also shows the potential of legume tree/shrub forage species as an environmentally sustainable land-use option to mitigate agricultural CO_2 emissions from low-input livestock systems in the grasslands of southern Ghana.

Keywords: grassland, land-use change, legumes, proanthocyanidins, soil carbon sequestration, soil properties, sub-Saharan Africa

1 Introduction

Increments in s carbon (C) sequestration rates in soils of 0.4 % per year were suggested to compensate for the global emissions of greenhouse gases by anthropogenic sources (Chabbi et al., 2017). Grasslands, on a global scale sequester around 0.14 Mg C ha^{-1} $year^{-1}$, thus storing 685 Gt C in the upper soil (to 1 m depth). This pool size is nearly 50 % more C than that of forests (346 Gt C), and 70 % more than wetlands (202 Gt C) (Grace et al., 2006; Gobin et al., 2011; Conant et al., 2017). About 60 % of all grasslands occur in the tropics, and these contain 10–30 % of the global soil C stocks (Caquet et al., 2012). Besides mitigating climate change, increased soil C sequestration could enhance ecological efficiency and delivery of other related ecosystem services, especially food, water and biodiversity (Stringer et al. 2012; Conant et al. 2017). However, large areas of native grasslands worldwide have undergone a substantial use-intensification or have been converted into pasture and croplands (Sterling and Ducharne, 2008; Taube et al., 2014). This action has led either to reduced C sequestration rates or net losses of soil organic C (SOC) (Johnston et al., 2009; Crews and Rumsey, 2017; Reinsch et al., 2018). This change is also visible in sub-Saharan Africa, where overgrazing and other land uses are factors that affect the C cycle (Grieco et al., 2012) and might constrain the attainment of the "4 per mille" agenda (Minasny et al., 2017) in the sub-region.

Generally, conversion of natural to managed ecosystems depletes soil C stocks, and the conversion of native grasslands to crop production results in approximately 50 % loss of SOC in global grassland ecosystems (Lal, 2018) as a consequence of destabilizing stored SOC. Adequate organic matter (OM) input into soils is necessary for increased C sequestration. However, sequestered C is sensitive to management and land-use changes, and particularly to grazing, changes in species composition as well as mineral nutrient availability (Conant et al., 2017). Nevertheless, management practices that increase the supply of quality OM could promote C storage in soils. Accordingly, soil nutrients have implications for plant primary productivity and ecosystem functioning (Post et al., 2012; Marques et al., 2016); however, their exact effects on C sequestration, particularly in grasslands dominated by C4 species, are not well understood (Milne et al., 2016). For example, the impact of N-fertilization on SOC dynamics remains controversial because of its dependence on other parameters such soil pH, available phosphorus (P) and potassium (K) as well as the frequency of tillage management (Khan et al., 2007; Lal, 2008, Reinsch et al., 2018).

Both the C input into soils derived from plant residues and organic manures, as well as the carbons stabilization in the soil are essential for an increased soil C sequestration. Some SOC stabilization mechanisms that have been proposed include physico-chemical protection of SOC by micro- and macro-aggregates, spatial separation of SOC from decomposers by encapsulation, occlusion and hydrophobicity and mineral-organic associations (Kleber et al., 2014; Song et al., 2018; Alberto Quesada et al., 2020). Moreover, plant secondary metabolites in both above- and below-ground biomass have recently been discussed to have an impact on both C and N cycles, with the potential to either increase or reduce C immobilization rates in soils (Kraus et al., 2003; Halvorson et al., 2011; Tamura and Tharayil, 2014; Chomel et al., 2016; Adamczyk et al., 2016, 2017; Kagiya et al., 2019). Condensed tannins (CT), for example, enter the soil as leachates and via decomposed litter from plant leaves and roots (Hättenschwiler and Vitousek, 2000). Although forages naturally contain lower levels of CTs to remain suitable for livestock feeding (Mueller-Harvey et al., 2018), the concentration of CTs may reach potent levels in the long-term, because CTs are recalcitrant and could remain in the soil for decades (Tamura and Tharayil, 2011). However, the role of CTs in mitigating CO_2 emissions, particularly from tropical soils, has received minimal attention.

In livestock systems, where a large part of the net primary production is exported from the soil as hay or silage, below-ground biomass is a significant source of C input. Mechanisms driving SOC sequestration in livestock systems, particularly low-input systems in the tropics, are not well understood, due to lack of research data, and sometimes with conflicting results even for such important factors as grazing (McSherry and Ritchie, 2013). Previous studies have shown mixed effects of grazing on soil C, including positive (Reeder and Schuman, 2002), neutral (Shrestha and Stahl, 2008) or adverse effects (Pei et al., 2008). Due to the complexity of the different above described controlling factors on SOC stocks, long-term experiments are ultimately necessary to validate the assumptions that have been made. In the absence of long-term experiments in Sub-Saharan Africa that were designed to answer this research question, we selected a research farm that has cultivated and managed plots of different plant species according to the same principles since 50 years. The research farm, located in the southern savannah belt of Ghana, used to be reserved government land, of which around 50 years ago, parts were simultaneously converted to farmland and research plots. The site offers the unique opportunity to test the long-term effects of converting native grassland to agricultural land, using the current SOC and nutrient stocks of the undisturbed grassland, which has not been converted within these 50 years, as reference baseline. The homogeneous environmental conditions across the entire sampling area would enable estimation of the divergence in SOC and nutrient stocks due to the different land-use changes when compared to the hypothetical SOC and nutrient stocks, represented by the undisturbed grassland. Thus, the main aim of this study was to assess the impact of long-term land-use practices on soil C storage as well as the potential role of tannin-rich forages and soil nutrient status.

In detail, the current case study was conducted to test the following hypotheses:

i. Soil C stocks in sub-Saharan Africa are profoundly affected by the type of land-use management
ii. Soil macro-nutrients and CT can predict long-term changes in SOC stocks of tropical grasslands
iii. Plant functional groups influence the relationship between SOC and soil N.

2 Materials and Methods

2.1 Site characteristics

The study was conducted at a research farm of the Council for Scientific and Industrial Research (CSIR), Ghana, located at 5° 70'N, 0° 29'W and 49 m a.s.l, located some few km from Accra (Fig. 1). The mean monthly temperature ranged from 21 to 31 °C and a monthly rainfall of 13–205 mm (annual rainfall is approximately 800 mm). The major rainy season is from April to mid-July with the minor rainy season in October (Fig. 2). Thus, the climate is moist semi-arid with a growing period lasting between 120–180 days (Ghana Meteorological Services Department, 2018). The surface lithology is of non-carbonate sedimentary with coarse sandy loam soils belonging to the Haplic acrisol group (IUSS, 2014). The soil at the site had the following features at the 0-10 cm soil depth: sand 80.34 %, silt, 12.64 %, clay, 7.02 %, pH (water) 5.86; N, 0.133 %, available P, 2.10 ppm; available K, 55 ppm and O.M., 2.61 % (Barnes, 1999). The native land cover of the study location is a tropical grassland Savannah.

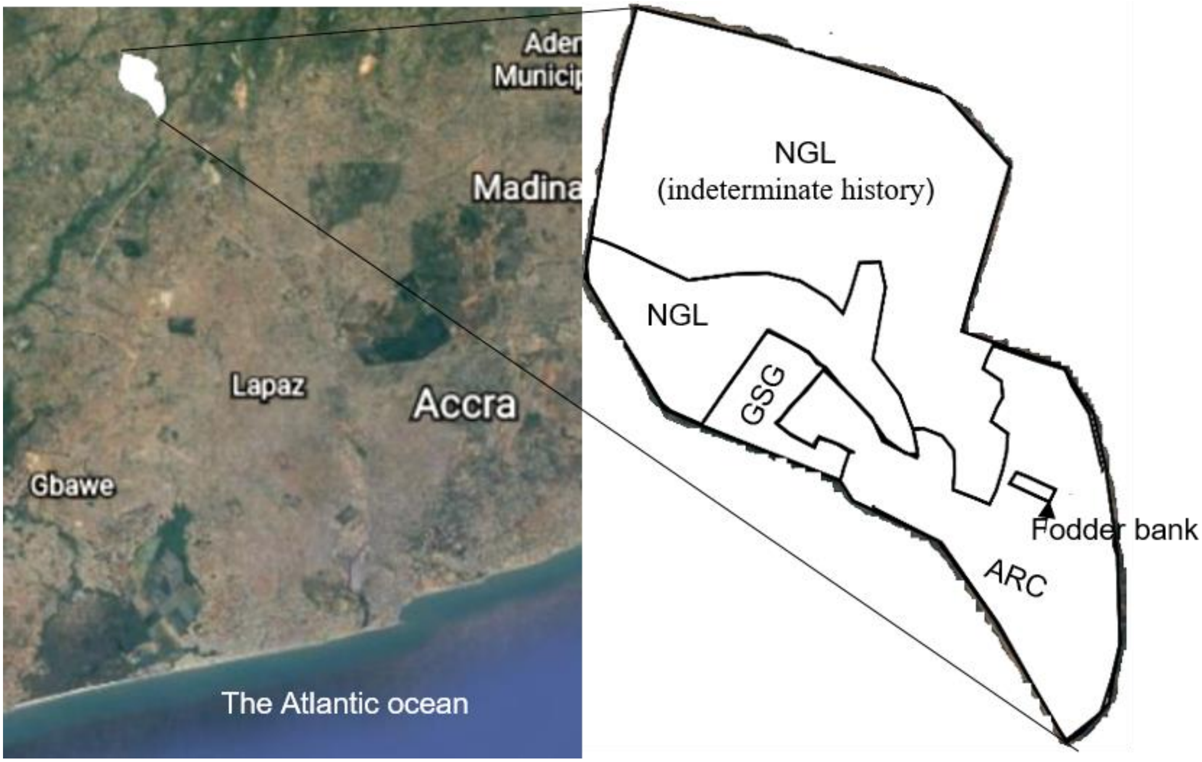

Figure 1: Location and plan of the study site. The native grassland (NGL) remains uncultivated since the farm was established in 1966. The portion of NGL labelled "indeterminate history" was excluded from the study due to high uncertainty associated with its history. The fodder bank consisted of cut-use grasses (CG), legume herbs (CLH), legume tree/shrubs (CLTS) and non-legume tree/shrubs (CNLTS); Map from Google Earth (2020).

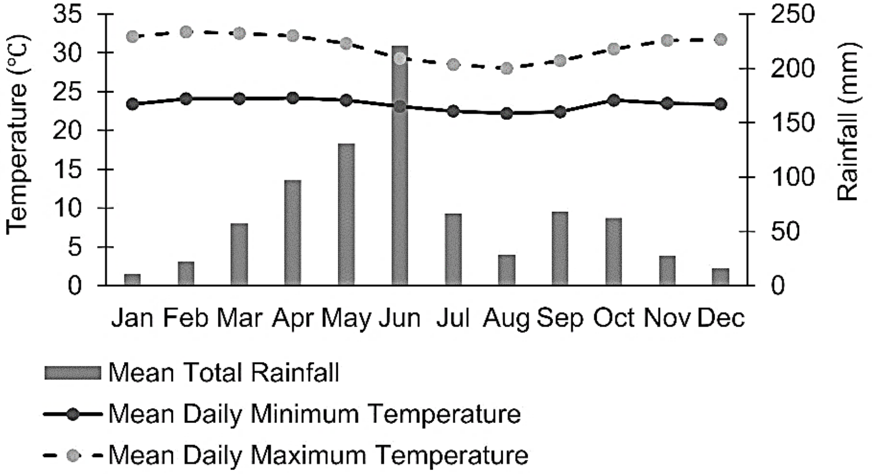

Figure 2: Climate (30-year average) of the study area (Data source: Ghana Meteorological Services Department, 2019)

The research farm, located on the grazed-seeded grasslands (GSG) keeps Sanga cattle, a cross between the humped Zebu type cattle and the local West African Shorthorn, known for their resistance against trypanosomiasis (adult weight ranging 300-330 kg), and Djallonké sheep (adult weight ranging 25-37 kg), managed semi-intensively. These animals are grazed rotationally on seeded-pastures during the raining season (April – October) and fed on conserved fodder harvested from arable fields and a fodder bank. While the exact stocking density is not recorded, typical stocking capacity around that region has been reported to be in the range of 3.5-5 LU ha^{-1} (Timpong-Jones et al., 2013). Compared to that, the Native grasslands (NGL) is infrequently grazed in a nomadic fashion. Also here, no records about stocking densities are recorded, yet grazing is limited to the dry season when feed is scarce at the GSG-plots.

The site was selected due to its suitability for agriculture, its proximity to the capital city and its vegetation and climate which are representative for the largest grassland type of Ghana (Guinea Savannah). Ostensibly, the site had a uniform land usage until parts were converted to different uses in 1966 and beyond (Fig. 1). Briefly, the land uses we encountered comprised arable field crops and grazed-seeded grasslands (both at field scales with at least 1 ha), as well as a fodder bank that also served as a forage museum, housing live plant species brought from all over the world. Our study considered 59 species with relevance for forage production (Table S1), representing four plant functional groups: cut-use grasses (38 species), cut-use legume herbs (11 species), cut-use legume trees and shrubs (7 species), and cut-use non-legume trees and shrubs (3 species) at plot scales (25–30 m^2). As for a subset of species, several accessions of the same species were present, and we sampled 72 plots from the 59 species. The management practices associated with the land-use types are summarized in Table 1.

2.2 Soil sampling

Field/plot selection was based on two main criteria- (i) that the field was established in 1966 and (ii) the management remained relatively stable over the 50-year time-frame. Information regarding management of fields and biomass productivity of the species were obtained from documentations available at the farm. Plots/fields that underwent some changes in management or re-established for any reason were omitted from the study. Consequently, there were no replicated plots, as in a traditional agricultural experiment, in the case of the cut-use forage species, to control for variation. Hence, we categorized the forage species into functional groups, with the individual species of each functional group constituting a pseudo-replicate.

Table 1. Brief description of land-use types at the study site

Land-use type	Description
Native grassland (field) (NGL)	Dominant plant species included *Panicum maximum, Cyperus spp, Talinum triangulare* and *Panicum decumbens* and intermittent occurrence of shrubs, including *Acacia sp.* and *Azadirachta indica*, lightly grazed by sheep and cattle; aboveground biomass yield is 5.7 – 7.2 t ha^{-1} (Timpong-Jones et al., 2013); uncultivated since the last 50 years
Arable crop production (ARC) (field)	*Three fields; sown crops: Manihot esculenta*, *Arachis hypogea*, *Zea mays* and *Vigna unguiculata*, as well as fodder grasses and legume herbs; two fields utilized zero tillage, while one was fully tilled; only one of the fields received fertilizer
Grazed-seeded grasslands (GSG) (field)	Single-species pastures -*Brachiaria brizantha*, *B. ruziziensis* and *Digitaria decumbens*; grazed rotationally by Djallonke sheep (25-37 kg adult weight) and Sanga cattle (300-330 kg adult weight).
Cut–use forage plots	Monoculture (25-30 m^2); 38 species of grasses (CG), 11 species of legume herbs (CLH), 7 species of legume trees/shrubs (CLTS) and 3 species of non-legume trees/shrubs (CNLTS), respectively, no soil amendments. Plots were weeded to maintain plot purity and harvested twice in the wet season and once in the dry season. Prostate and erect grasses and herbaceous legumes were harvested at 6-10 cm and 10-20 cm high, respectively while shrubs were defoliated at 30 cm high. Annual dry matter yields (mean±sd) from the forages were 8.63±3.57, 4.08±1.41 and 6.53±2.17 Mg ha^{-1} for shrub/trees, legume herbs and grasses, respectively.

Soil samples were taken from the native grasslands and arable crop fields by zone-based composite sampling, where we divided the fields into three zones (northern, central, and southern). For the seeded-grazed paddocks, we randomly selected three paddocks out of the nine for soil sampling. We collected 10 – 20 subsamples (depending on the size of the zone) spread evenly across each zone in a zig-zag pattern, to constitute a composite sample, each composite soil constituting a replicate. In the case of the plot-scale samples, the sampling procedure followed recommendations by Saiz and Albrechts (2016). Sampling locations were determined by roughly locating the first at the centre of the field, with three replicates laid out according to a pattern of three axes separated 120° to a primary axis pointing north. Replicates were selected along these axes at approximately mid-distance between the centre of the field and its boundaries.

Before any sampling, surface litter was removed by hand. For each sampling plot or field, soil samples were taken (0–30 cm soil depth) using a soil probe of 1-inch diameter. Replicate samples obtained were bulked, thoroughly mixed, and a representative sample taken into a zipped polythene bag for analyses. Due to the higher number of accessions, the total number of soil samples obtained from the cut-use forages was 72, derived from 59 species. For the estimation of soil bulk density, 3-8 sets of soil samples were taken from each experimental unit (replicate plots/fields), depending on size, using a stainless-steel core sampler at depths of 0–5, 5–10, 10–15, 15–20 and 20–25 cm. Soil bulk density and C stock were estimated according to methods by Guo and Gifford (2002).

2.3 Soil analyses

Soil samples meant for C and nutrient analysis were initially oven-dried at 30ºC for 48 hours. Dried samples were sieved with a 2 mm sieve to remove coarse particles and plant roots. Sieved samples were milled and stored in a desiccator before analyses. Soil samples were analyzed for C and total soil N (*t*N) using the C-/N analyser (Vario Max CN, Germany), using aspirin (50 mg; N = 9.7 %; C = 34.0 %) and a standard soil sample (1 g; N = 1.2 %; C = 1.4 %) after every 10 test soil samples to aid calibration of the equipment. Bulk density was estimated after oven drying at 105ºC. It was assumed that soil samples did not contain inorganic C because pH values were less than seven and because no liming or any other amendment was carried out during the past 50 years; therefore, total C was considered as SOC. Additional randomly performed HCl tests confirmed this assumption.

Soil pH was determined according to methods by Wiesmeier et al. (2012). Soil pH was measured directly with a pH meter (Microprocessor pH/ION Meter, PMX 3000, WTW) after adding 0.0125 M $CaCl_2$ solution to each sample in the ratio of 1:2.5 (soil: $CaCl_2$ solution). Plant available P and exchangeable K were extracted from 1 g air-dried fine soil (<2 mm) using Bray 2 solution, the reagents being 0.1 M HCl and 0.03 M NH_4F (Bray and Kurtz, 1945). K was determined using flame-photometry, and P measured calorimetrically at 882 nm (Miller and Arai, 2016) after reaction with ammonium molybdate and development of the 'Molybdenum (Mo) Blue' colour (within 30 min.).

2.4 Plant sampling and proanthocyanidin analyses

Plant samples for CT determination harvested from forage species at the time of soil sampling, which was during the late annual growth stage. Sampling included leaves and leaf stalks from dicots, which consisted of legume herbs, legume and non-legume tree and shrub species (Supplementary table S-1). After cutting, samples were immediately cooled on ice before being freeze-dried, milled with a ball mill and stored in a freezer at -28 °C until further analyses. Condensed tannins (CT, syn. proanthocyanidins), which consisted of extractable CTs (ECT), protein-bound tannins (PCT) and fibre-bound tannins (FCT), were determined according to methods prescribed by Terrill et al. (1992). Despite newer analytical techniques being available, Terrill et al. (1992) provide the benefit of separating again between protein- and fibre-bound tannins and hence was considered to be most suitable. Extractable condensed tannins (ECT) were extracted from 20 mg plant samples using an acetone/water mixture (80/20 v/v), vortexed for 5 minutes and shaken on a plenary shaker (280 min^{-1}) at 4 °C overnight. The samples were then centrifuged for 10 minutes (14,000 rpm) and decanted into 2 mL Eppendorf tubes. Residues were extracted again using the same setup with the plenary shaker now shaking for 3 hours, centrifuged and the supernatant decanted on top of the first extract. Acetone was evaporated in each case in an Eppendorf concentrator plus (Eppendorf, Hamburg, Germany) at room temperature for 90 min. Extracts were frozen overnight and after that freeze-dried for 24 hrs. 1 mL of UPLC-grade water was added to the freeze-dried extracts, vortexed and filtered with a PTFE filter (0.2 µm).

Protein-bound condensed tannins (PCT) were extracted twice from the residues by adding 10 g L^{-1} sodium dodecyl sulphate (SDS) and 50 g L^{-1} 2-mercaptoethanol in 10 mM Tris/chloride adjusted to pH of 8, vortexed for 5 min and then placed in a continually boiling water bath for 60 min and cooled on ice to room temperature. The mixture was then centrifuged for 10 min and the supernatant decanted into 2 mL Eppendorf tubes in triplicates. For analysis, 960 µL of n-Butanol/HCl (95:5 v/v) solution was added to 240 µL of the extract of either ECT or PCT, vortexed for 5 min and heated in an oven at 90 °C for 90 mins, cooled on ice and transferred to a spectrophotometer (Libra S22, Biochrom) and analyzed at 550 nm to determine the CT concentrations. For the fibre-bound condensed tannin (FBCT) concentration in the samples, 1200 µL of BuOH/HCl (95/5, v/v) and 120 µL SDS was added to the residues from the extracts, vortexed for 5 mins, centrifuged for 10 mins and heated in an oven for 90 mins at 90 °C, before being cooled on ice to room temperature, centrifuged for 1 min and then measured in the spectrophotometer at 550 nm. Total CT (*t*CT) was calculated as the sum of ECT, PCT and FCT for each candidate species. Annual *t*CT was estimated by multiplying *t*CT with the mean biomass yield of each functional group. The dataset, as well as a brief description of the site, materials and methods adopted to generate data, is available in Nyameasem et al. (2020).

2.5 Calculations and statistics

Due to lack of data regarding the initial SOC stocks of the farmland or the experimental plot, we estimated per cent changes in soil C stock using a pseudo baseline. This pseudo baseline is the natural grassland, which represents the SOC and nutrient stocks that all other sampled areas would have, had they not been converted to farmland and the agricultural research plots, respectively. We believe this assumption to be valid, as all sampled areas were part of the same natural grassland until being converted around the same time to their current land-use. With environmental conditions and atmospheric deposition being identical for all sites due to their proximity, the variation between plots is assumed to be a result of the land-use change only. Thus, the natural grassland represents the trajectory for soil conditions as they would occur across the entire grassland region, without land-use change and thus represents the baseline against which all sites were tested. To analyze the effect of the different land-use types on SOC and soil properties, we performed a one-way ANOVA using generalized linear models. Also, we tested the effects of plant functional group (legume trees/shrubs, legume herbs, non-legume trees/shrubs) and plant part (leaves, leaf stalks) on the polyphenol content of the forages in a two-way ANOVA using linear mixed-effect modelling, with species as a "random factor". *P*-values were estimated based on type II sum of squares (SS) in the case of the one-way ANOVA and type III SS in the case of the two-way ANOVA due to the dissimilarity of the sample sizes (Fox and Weisberg, 2019). In cases where *P*-values were significant, Tukey's post hoc tests, using the 'lsmeans' function of the 'multcomp' package (Bretz et al., 2011) was performed to permit pairwise comparisons of means.

Before the ANOVA, data were checked for normality and homogeneity of variance. In cases of abnormality or heteroscedasticity, data were log-transformed or corrected using 'White-adjusted heteroscedasticity corrected standard errors' from 'car package of R. Where data normality or the equality of variances were not confirmed even after log-transformation, a non-parametric test (Kruskal-Wallis) was used, followed by Dunnett's test post hoc tests to permit pairwise comparisons of means of the unequal sample sizes (Zar, 2010). Full correlations, bivariate (linear and exponential) and a full hierarchical model were fitted to the datasets to establish relationships between the measured variables and SOC as well as to identify main effects and interaction terms as predictors of SOC. Akaike's Information Criterion with small-sample bias adjustment (AIC_C, Akaike, 1985; Burnham et al., 2011) was estimated and used to identify the best-fit model. All the statistics were performed using in R (R Core Team, 2019).

3 Result

3.1 Land-use change, soil C stocks and soil chemical properties

The land-use types impacted soil C stocks in the upper soil layer (0–30 cm), with group means ranging from 19.9 to 36.8 Mg C ha^{-1} and with a mean and standard deviation of 32.9±10.2 Mg ha^{-1}. Whereas SOC stocks did not differ between the agricultural soils and native grassland soils ($P>0.05$), grazed-seeded grassland soils had 86 % and 77 % less ($P<0.01$) SOC density relative to cut-use trees/shrubs and grasses, respectively (Fig. 3A). Among the cut-use forage systems, SOC was 36 % higher for cut-use grasses relative to legume herbs ($P<0.05$). Using the native grassland as a pseudo baseline, we observed SOC stock changes ranging from -44–5 %, with a mean loss of -15 % and the most considerable negative change occurring in grazed-seeded grassland soils (Fig. 3B). However, there appeared to be near zero to positive changes in cut-use grass and legume trees/shrub soils. Among the cut-use fodder groups, SOC losses in soils of cut-use legume herbs were 26 % greater relative to cut-use grass soils.

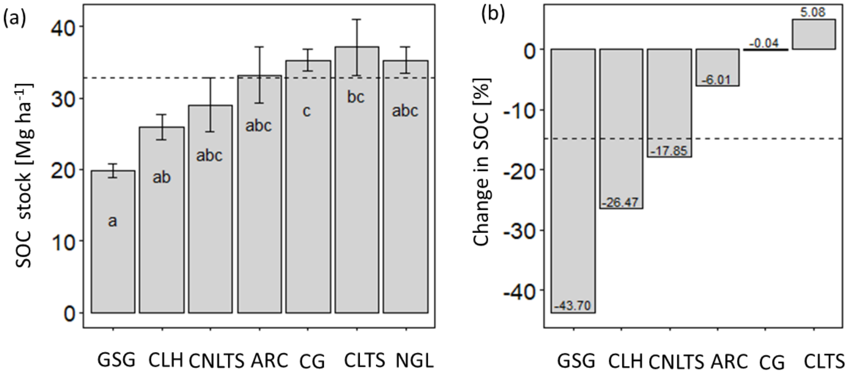

Figure 3. Barplots (with error bars) of SOC stocks (A) and per cent changes in SOC stocks (B) due to native grassland conversion under different land-use scenarios. [Different lowercase letters indicate significant

differences between the land-use types (p<0.05; se = 1.13); CLTS= cut-use legume trees/shrubs; NGL= native grassland; CG= cut-use grasses; ARC= arable crops; CNLTS=Cut-use non-legume trees/shrubs; CLH= cut-use legume herbs; GSG = grazed-seeded grasslands; broken horizontal line indicate the means].

Table 2. Soil organic carbon, soil macro-nutrients and other chemical properties of soils under different long-term management

Soil chemical trait	Native grassland	Arable crops	Grazed-seeded grassland	Cut-use forage production				*P*-value	SEM
				Grass	Legume herb	Legume trees/shrub	Non-legume tree/shrubs		
tN, Mg ha^{-1}	2.52^{ab}	2.48^{ab}	1.75^{ab}	2.66^{b}	1.94^{a}	2.55^{ab}	1.93^{ab}	0.0196	0.09
AvP, kg ha^{-1}	89.6^{ab}	185^{b}	15.0^{a}	37.8^{a}	28.1^{a}	112^{b}	73.6^{ab}	< 0.0001	8.23
K, Mg ha^{-1}	6.96^{ab}	16.6^{b}	3.34^{a}	7.42^{ab}	4.45^{a}	7.43^{ab}	4.80^{ab}	0.0028	0.52
C: N ratio	14.4^{b}	13.6^{ab}	11.3^{a}	13.5^{ab}	13.6^{ab}	14.6^{ab}	15.2^{b}	0.0489	0.22
Soil pH	5.69^{bc}	5.80^{c}	4.71^{ab}	5.35^{bc}	4.79^{a}	5.27^{abc}	5.42^{abc}	0.0037	0.05

tN= soil total nitrogen; Av. P= plant-available phosphorus; K= soil potassium. ^{abc}Mean values in the same horizontal row with different letters are significantly different (*p*< 0.05); SEM, standard error of the mean

Table 3. Condensed tannin (CT) profile and CT yield from three plant functional groups growing at the experimental

Functional group	Condensed tannins (g kg^{-1} DM)				*t*CT yield* (kg ha^{-1} yr-1)
	ECT	PCT	FCT	*t*CT	
Legume herbs	2.63^{a}	2.60^{a}	2.78^{a}	8.01^{a}	32.7^{a}
Legume trees/shrubs	10.6^{b}	8.52^{b}	6.07^{b}	25.1^{b}	217^{b}
Non-legume trees/ shrubs	5.83^{ab}	3.24^{ab}	4.79^{ab}	13.9^{b}	120^{b}
P-value	<0.001	<0.0001	<0.0001	<0.0001	<0.0001
SEM	1.06	0.72	0.65	1.99	16.9

ECT= extractable condensed tannins; PCT= protein-bound condensed tannins; FCT= fibre-bound condensed tannins; *t*CT= total condensed tannins (ECT+PCT+FCT); By plant functional groups, values in a same column with different letters are significantly different. *Annual *t*CT yield was estimated using the mean annual dry matter yields

The mean (±sd) OM, *t*N, *av*P and exchangeable K concentrations observed for the site were 1.32±0.41 %, 0.057±0.02 %, 10.4±11.9 mg kg^{-1} soil and 68.1±36.7 mg kg^{-1} soil, respectively. Whereas *t*N, *av*P and K concentrations among the native grassland and agricultural soils (*P*>0.05), cut-use grasses soils contained 37 % more N compared with legume herb soils (Table 2). Arable crop soils contained 5, 7 and 12 times more *Av*P density compared with cut-use grass, herbs and seeded-grazed soils (*P*<0.001), respectively (Table 2), while exchangeable K density in arable crop soils was five and four times higher (*P*<0.05) compared with seeded-grazed and legume herb soils, respectively (Table 2). CN ratio was 27 % higher in native grassland soils (*P*<0.05) compared with seeded-grazed and was lower (*P*<0.05) for grazed-seeded grasslands compared with non-legume trees/shrubs. It appears CN-ratio was not different among the forage species (*P*>0.05). Soil pH ranged from moderately acidic to neutral and was affected by the land-use types, and was more acidic in the cut-use herb soils relative to the grasses, arable crop and native grassland soils and was more acid for seeded-grazed fields relative to arable crop soils (*P*<0.05).

3.2 Plant secondary metabolites in cut-use forages

The CT distribution in the forages was affected by plant functional groupings (*P*<0.001) but not by the part of plant analyzed or by plant group - plant-part interaction terms (*P*>0.05). Accordingly, the functional group effect on CT distribution in the forages is presented in Table 3. ECT, PBCT and FCT in the legume herbs were 4, 3 and 2 times, respectively, lower (*P*<0.001) compared with legume trees/shrubs but not with non-legume trees/shrubs ($P>0.05$). However, *t*CT per DM and total annual *t*CT yield were 2-3 times and 4–6 times, respectively, higher ($P<0.001$) in both tree/shrubs compared with the herbs (Table 3).

3.3 Relationships between soil organic carbon and soil/plant chemical parameters

Pairwise correlation between the measured variables suggested significant ($P<0.01$) positive associations between SOC and all the soil chemical properties (Table 4), with the strongest association between SOC and *t*N (r = 0.86). Although the CT variables correlated positively with SOC and *t*N, the associations were weak and insignificant except for annual *t*CT yield (Table 4). Whereas *t*N, *ExK* and CN ratio related exponentially with SOC, *AvP* and soil pH related linearly with SOC (Figure 4a–e). Generally, higher *tN*, avP and soil pH appeared to be associated with higher SOC stocks; however, there appears to be a weaker association between SOC and *t*N at higher soil N concentrations. Whereas the response of SOC to *t*N was similar for non-legume trees/shrubs, grasses and legume-herbs (mean slope=10.5), it was about 36% higher compared with legume tree/shrubs (slope = 14); Figure 5). Higher soil K density was associated with higher SOC stocks, but amounts beyond 16 Mg ha^{-1} appeared to depress SOC accumulation whilst the relationship between SOC and CN ratio appeared positive only beyond a ratio of 15 (Figure 4c-d). SOC related exponentially with *t*CT yield with generally higher biomass CT associating positively with SOC at increased rates beyond 200 kg ha^{-1} (Figure 6). A full regression model predicting SOC density using the measured soil and plant chemical variables as predictors showed significant effects of *t*N, *Av*P, K and *t*CT as well as *Av*P x pH and *t*N x avP x K interaction terms ($P<0.05$) in the model, with *t*N having the greatest effect (Table 5).

Table 4. Pearson correlation coefficients showing the relationships between soil and plant chemical parameter

	Soil pH	*ECT*	*PBCT*	*FBCT*	*tCT*	*Ann. tCT*	*AvP*	*ExK*	*SOC*	*tN*
CN ratio	0.01	0.24*	0.15	0.21*	0.24*	0.33*	0.18	0.14	0.29**	-0.22*
Soil pH		0.02	-0.05	-0.11	-0.04	0.28*	0.24*	0.30**	0.53***	0.55***
ECT			0.59***	0.66***	0.90***	0.84***	0.22*	-0.04	0.14	-0.01
PBCT				0.66***	0.84***	0.78***	0.22*	-0.04	0.12	0.02
FBCT					0.87***	0.63***	0.05	-0.08	0.01	-0.13
tCT						0.93***	0.20*	-0.06	0.11	-0.04
Ann. tCT							0.31*	0.39**	0.47***	0.29*
AvP								0.27**	0.29**	0.19*
ExK									0.62***	0.55***
SOC										0.86***

ECT= extractable condensed tannins; PCT= protein-bound condensed tannins; FCT= fibre-bound condensed tannins; *t*CT= total condensed tannins (ECT+PCT+FCT); Ann. *t*CT = annual *t*CT yield; Significance levels *<0.05, **<0.01, ***<0.001.

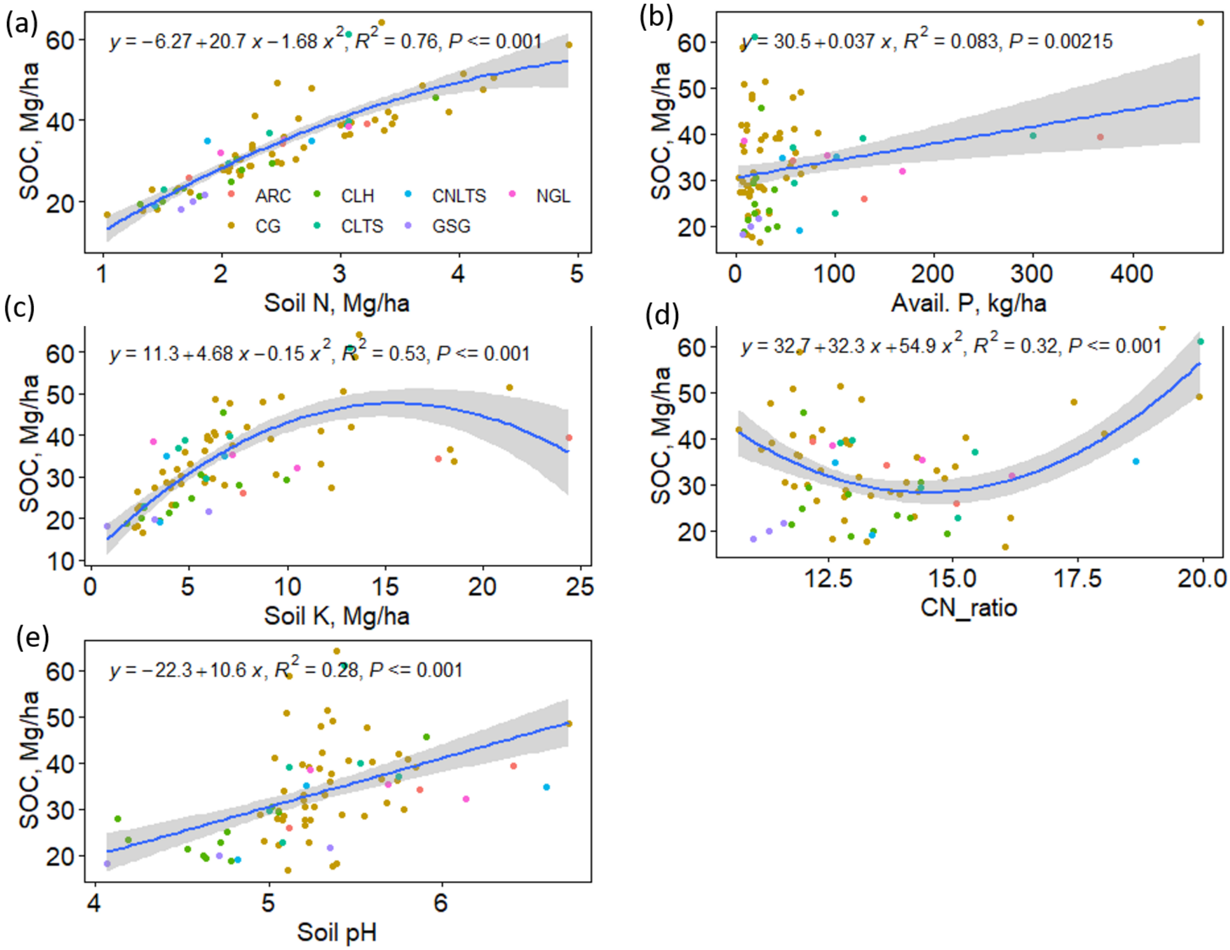

Figure 4: Bivariate regression curves showing the relationship between SOC and the measured soil variables. [The grey band shows the 95 % confidence interval; CLTS= cut-use legume trees/shrubs; NGL= native grassland; CG= cut-use grasses; ARC= arable crops; CNLTS=Cut-use non-legume trees/shrubs; CLH= cut-use legume herbs; GSG = grazed-seeded grasslands]

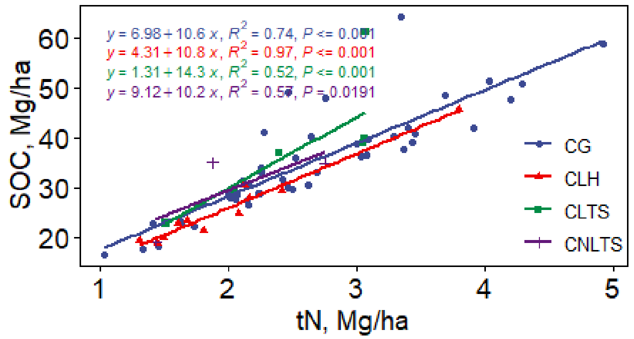

Figure 5: **Relationships between SOC and soil total N as influenced by plant functional groups.** [CLTS= cut-use legume trees/shrubs; CG= cut-use grasses; CNLTS=Cut-use non-legume trees/shrubs; CLH= cut-use legume herbs]

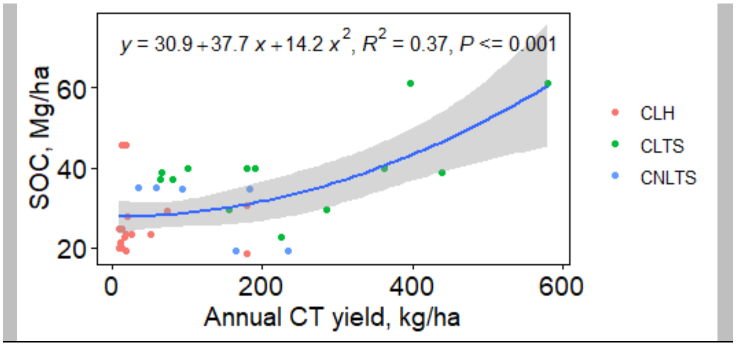

Figure 6: **A graph showing the stoichiometric relationship between SOC and leaf biomass CT** [The grey band shows the 95 % confidence interval; CLTS= cut-use legume trees/shrubs; CNLTS=Cut-use non-legume trees/shrubs; CLH= cut-use legume herbs]

4.0 Discussion

4.1 Land use change and carbon stocks

We observed a wide range of SOC stocks (17–64 Mg SOC ha^{-1}) across the land-use types at the study site, which largely agrees with previously reported ranges of 10–50 Mg SOC ha^{-1} for vegetation gradients varying from Sudanese-Sahelian Savannah to a sub-tropical forest (Saiz et al., 2012; Bessah et al., 2016). Similar to previous reports (Olson, 2013; Bessah et al., 2016), the use of grassland for agriculture resulted in both positive and negative responses by soil C dynamics. Tan et al. (2009) projected changes of -4 to -23 % in soil C stocks of cultivated savannahs of Ghana on a hundred-year scale, depending on the climate change scenarios. Hence the 15 % loss of SOC in 50 years appears to be on the higher side. Nevertheless, there was an indication of C sequestration in the case of cut-use legume trees/shrub production. Similarly, a previous study (Shanmugam et al., 2018) reported a mean annual change of 0.67±0.95 Mg C ha^{-1} for tropical mineral soils of secondary woodland or Savannah converted to cultivated pasture or cropland. Therefore our observations are not surprising as the type of land management adopted after converting native vegetation affects soil C cycling and determines the ultimate C storage potential of soils (Amézquita et al., 2008; Stahl et al., 2016). From our study, SOC stocks of arable crop farming did not differ from the native grassland. Arable crop production is known to deplete SOC due to tillage effect, which tends to facilitate SOC cycling. Among the three arable crop fields considered in this study, only one of them occasionally adopted conventional tillage. On that particular field, however, crop production was on a rotational basis and occurred only occasionally, i.e. tillage occurred only infrequently. On the other crop fields, soils were manually minimum-tilled using simple farm implements such as hoes and sometimes weedicides. Thus, this is, of course, a much less invasive technique compared to regular ploughing (but a representative for many farms in that area) and hence it appears that the net effect of the mixed management practices on the arable crop farms did not impact SOC stocks significantly.

The low SOC stock in grazed-seeded grasslands was half (20 vs 35 t SOC ha^{-1}) that of cut-use grasses and legume trees/shrubs, suggesting a utilization effect. The effect size of grazing on SOC stocks might be dependent on the interactions of several factors, including grazing intensity (McSherry and Ritchie, 2013). Overgrazing has been widely reported as responsible for the loss of SOC and a decrease in soil fertility in West Africa (Schönbach et al., 2011; Saiz et al., 2012). Generally, higher grazing intensities decrease soil C and N by direct removal of above-ground herbaceous biomass, thus reducing the potential of CO_2 fixation in photosynthetic tissue and reduction in below-ground C inputs through lower root production and higher root litter turnover (Semmartin et al., 2010). On the other hand, moderate grazing may increase tiller density and aboveground productivity, particularly in C4 dominated grasslands (McSherry and Ritchie, 2013), compared to cut-use systems, thus leading to higher C inputs because of additions from crop residues, when abiotic factors such as irrigation and nutrient supply are appropriate. Thus, reducing grazing intensity can not only protect the aboveground biomass of grasslands but also improve soil texture to enhance the accumulation of organic C (Xu et al., 2018).

Table 5. Results of full univariate ANCOVA model to explain the status of soil organic carbon density at the study site (R^2 = 0.848, Adjusted R^2 = 0.853, Adj. R^2= 0.830, AIC_C = 698.60*)

Source	df	Type III sum of squares	F value	Pr(>F)
*t*N	1	2694	144.9	0.000
*av*P	1	73.53	3.955	0.049
K	1	414.1	22.27	0.000
pH	1	34.99	1.882	0.173
*t*CT	1	230.6	12.40	0.001
*t*N x *av*P	1	28.62	1.539	0.218
*t*N x K	1	3.316	0.178	0.674
*av*P x K	1	202.1	10.87	0.001
*t*N x pH	1	56.44	3.036	0.085
*av*P x pH	1	116.7	6.277	0.014
K x pH	1	9.120	0.491	0.485
*t*N x *av*P x K	1	73.85	3.972	0.049
*t*N x *av*P x pH	1	13.26	0.713	0.400
N x K x pH	1	11.33	0.609	0.437
*av*P x K x pH	1	11.76	0.632	0.428
*t*N x *av*P x K x pH	1	33.69	1.812	0.181
Residuals	100	1859		

Akaike's Information Criterion (AIC) (Akaike, 1985; Burnham & Anderson, 1992) with the small-sample bias adjustment (AICC = n[ln (SSE/n)] + 2K + [(2K*(K + 1))/(n-K-1)]) (Hurvich & Tsai, 1995; Burnham & Anderson, 2002); *t*N = total N, *t*CT= total condensed tannins, *av*P = available P.

The effect of plant functional differences on SOC stock was evident in this study. Under similar growing conditions, we observed higher C stocks in fodder grass fields (36 % higher; $p<0.01$) compared to legume herb fields. Earlier reports (Alonso et al., 2012; Shanmugam et al., 2018) suggested that species composition of grasslands influences the quantity and quality of OM input, and for that matter, C sequestration in the soil. Dry matter productivity is an essential factor that influences the accumulation of soil C. Above-ground biomass productivity is relatively higher for fodder trees/shrubs, followed by grasses and lowest in herbaceous legumes (Table 1). SOC stocks under the cut-use forages appear to follow a similar trend (Table 2, Figure 3). Thus, the higher SOC stocks observed under legume trees/shrubs relative to legume herbs could be partly attributed to the higher ability of legume trees/shrubs to produce relatively high biomass (Barnes and Addo-Kwarfo, 1999; Adjolohoun et al., 2008), maintain soil fertility (as shown in Table 2), control runoff soil erosion (Franzel et al., 2014) and to maintain SOM.

Grasslands containing more C4 grass species were reported to store more SOC compared with grasslands with more C3 and legume species (Yang et al., 2019). The grass species considered in this study consisted mainly of C4 grasses, whereas the legume herbs were mainly C3 shallow-rooted plants. C4 plants possess morphogenic and architectural traits that enhance their ability to out-perform C3 plants, particularly under harsh environmental conditions (Lanttanzi, 2010). They tend to develop high leaf area index, which enhances their ability to capture light, N and water compared to their C3 counterparts. Besides, C4 plants have higher photosynthetic efficiency in the use of water and N and yield higher quantum productivity (Taylor et al., 2010) compared to C3 plants. The inherently lower Rubisco concentration and the more lignified tissue in C4 plants limit organic matter decomposition, thus producing more recalcitrant organic C (Yang et al., 2019).

Moreover, C4 plants are reported to partition C towards roots in N limited situations; thus, they have a higher ability to fix soil C under N-stress situations (Sage and Pearcy, 1987; Long, 1999). Another reason could be that C4 plants have a higher concentration of amino acids and organic acids in their root exudates compared to C3 plants (Nabais et al., 2011) which could protect SOC and N from microbial decomposition. Therefore, the relative differences in aboveground biomass characteristics could be responsible for the observed differences in SOC stocks under fodder grass and legume herbs fields.

4.2 Impact of differential land uses/plant types on soil quality

We observed higher N concentration in cut-use grass fields compared to legume herb fields although legumes are known to fix atmospheric N in soils. Indeed, in semi-arid and Savannah ecosystems of sub-Saharan Africa, legume herbs and legume browse species could fix about 8–217 and 61–643 kg ha-1 yr-1 atmospheric N, respectively (Hassen et al., 2017). Accordingly, legume-based systems can produce high biomass yield even in the absence of fertilizer application, showing a high N-cycling efficiency (Schmeer et al., 2014), generally increasing soil N concentration. However, several factors might affect the ability of the legumes to synthesize N, including environmental conditions, N uptake by plants and soil pH (Nutman, 1977; Sage and Pearcy, 1987). Pure grass stands may show a high fraction of C and N allocation below-ground (Loges et al., 2018), particularly when the root-functional-traits equilibrium theory is considered (Brouwer, 1983), and have amino acid-rich roots (Nabais et al., 2011), leading potentially to a more excessive N and C accumulation in the soil. These attributes of grasses might explain why soils in grass plots had higher tN compared to the legume herbs. The fairly tight C: N ratio (14:1) observed for the agricultural systems reflects the stoichiometry of stable soil OM at the study site.

The site has seen a general decline in soil fertility (tN and SOM) although there were marginal increases in available P and K when compared to values reported for the site by Barnes (1999). While P and K densities were moderate in arable crop soils, they were low in the other land-use types (Bationo et al., 2018; Apal Agricultural Laboratory, 2019). The relatively high P and K levels observed in the food crop fields may probably be as a result of annual supply through fertilizer application (Table 1). Cut-use grasses and legume herbs appeared to deplete soil P, but not legume of non-legume trees and shrubs (numerically if not statistically). This trend might be partly related to differences in the root architecture. The grasses and herbs are shallow-rooted and therefore exploit nutrients from within the upper soil depth, while the trees/shrubs have roots below the 30 cm soil depth considered in this study, and therefore might not be able to exploit nutrients extensively from the upper depth of the soil. The relatively low nutrient concentration observed in the grazed-seeded grasslands matches the low C stocks (Table 2). It is, particularly, striking that P and K are much lower in grazed grassland despite the high excreta deposition associated with grazing. Although we could not ascertain the stocking rate on the grazed-seeded pastures, it appears there was frequent overgrazing of the pastures, which is a regular feature in this region, exposing the soils to nutrient loss via erosion (Bationo et al., 2018).

The soils were generally acidic, a common characteristic of tropical soils (Jayne et al., 2015), however, the < 5.5 pH observed in grazed-seeded grasslands, cut-use legume herbs and non-legume trees/shrubs soils might cause aluminium and manganese toxicities. Low pH could also cause molybdenum, calcium, magnesium or potassium deficiencies and perhaps reduced microbial activity (Apal Agricultural Laboratory, 2019). Among the land use systems, cut-use legume herbs and seeded-grazed soils appeared more acidic relative to the others. Legume plants commonly form symbiotic associations with rhizobia and accumulate most of their N through symbiotic N fixation. During this process, legume plants take up more cations than anions and release more H^+ ions from roots to the soil, leading to low pH values in both the rhizosphere and bulk soil (Zhao et al. 2009; Yang et al. 2016). This effect might differ between legume herbs and legume trees/shrubs due to differences in their root architecture. Grazing fields are associated with high N and C returns from animal excreta, but C and N cycles might cause acidification in grazed fields, for example, nitrate leaching might increase the concentration of H ions, which might lead to decreased soil pH (Ridley et al., 1990).

4.3 Condensed tannin concentration in cut-use forages as affected by functional group differences

The total CT of below 67 g kg^{-1} DM observed in this study is similar to values reported for tropical forages, with lower concentrations in legume herbs compared to browses (Mupangwa et al., 2000; Sottie et al., 2016). CTs may have both positive and negative effects on livestock, depending on the concentration of CT in the plants. The nutritional implication of CTs is particularly vital with tropical shrubs and tree species where high CTs are known to impair protein availability (Jayanegara et al., 2018). Previous authors have reported higher values of more than 70 g CT kg^{-1} DM for some tropical shrubs and trees (Jackson et al., 1996; Rosales, 1999; Pereira et al., 2018), which invariably limits their use as fodder for ruminant livestock.

The proportion of total CT allocated to ECT was similar to the range of 12–44 % reported by Mupangwa et al. (2000) but lower than 70–95 % reported for some tropical browse species (Jackson et al., 1996). Compared with other tropical forage species, the *t*CT shares of below 7 % indicate comparably low tannin concentrations, which indicates their suitability for livestock feeding (Mupangwa et al., 2000; Jackson et al., 1996). However, further analyses on forage quality parameters and tannin composition, as well as on other plant secondary metabolites might be required to give reliable estimates of digestibility.

4.4 Relationships between SOC and soil and plant chemical properties

Our correlation and regression analyses (Figure 4, Tables 4 and 5) indicated significant relationships between the soil chemical properties and SOC. Similar to reports of Stahl et al. (2016), we found a close association between C and N. Nevertheless, the relationship between N and SOC is ambiguous in the literature, with evidence of different responses of soil CO_2 fluxes to N levels in soils (Yan et al., 2016), including increases (Wang et al., 2015), decreases (Jiang et al., 2010), and no significant differences (Li et al., 2012). N cycle is strongly interconnected with the C cycle, as N is required to build up biomass (and hence C). Whereas Six et al. (2002) attributed the positive relationship between soil C and N to protection by both macro- and micro-aggregates against mineralization, Waldrop et al. (2004) explained that greater N availability reduces decomposition rate of SOC by regulating production and activity of microbial extracellular enzymes. Indeed, when N becomes available in N-limited soils, photosynthetic reaction increases, thus enhancing SOC storage, but small N may limit CO_2 fertilization (Lal, 2018). Accordingly, Tan et al. (2009) observed that increasing N application to about 30–60 kg ha^{-1} $year^{-1}$ could result in positive changes in soil C stocks of cultivated grasslands of Ghana. Indeed, the multiple linear regression model (Table 5) showed that *t*N had the most significant effect on SOC density, and with a greater effect size in legume tree/shrub species compared with the legume hers, non-legume trees/shrubs and grasses (Figure 5).

Interaction effects involving N, P and K as well as pH and K were significantly associated with SOC stocks ($p<0.05$), suggesting that the effect of N on SOC sequestration might be dependent on the availability of P, K and soil pH. The associative effect of N and P on SOC density was also reported by an earlier study (Bradford et al., 2008) where P and N additions led to a more significant C sequestration in soils. In a simulated study (Li et al., 2014), a combination of N and P fertilizers increased SOC storage but reduced microbial activity, as well as C mineralization, compared to adding N or P fertilizer alone or no fertilization. In contrast, Graham et al. (2014) reported a significant release of CO_2 when soil N increased. In the current study, it the relative proportions of soil nutrients impact SOC storage, and soils deficient in P might not be able to use N efficiently, which might increase N losses by gaseous emissions and leaching and deplete SOC pools.

The theoretical basis, according to linear mixed-effects regression models (Table 5), suggested *t*CT concentration in aboveground biomass as one of the potential factors that might affect SOC storage at the site (Table 5). This observation partly confirms our hypothesis that aboveground CT concentration might be influential in C storage. Although CT concentrations in the soils were not considered in this study, we speculate that the higher CT content in legume trees/shrubs (Table 3) might have slowed the decomposition rate of soil OM (Dong et al., 2016) to promote SOC accumulation (Kraus et al., 2003; Halvorson et al., 2011; Tamura and Tharayil, 2014; Chomel et al., 2016; Adamczyk et al., 2016, 2017; Kagiya et al., 2019). By extension, the higher potential of the tree/shrubs to produce more mass and more CTs per unit area might explain the higher

SOC stocks under trees/shrubs relative to the herbs. However, the bivariate regression analysis showed that positive associations between *t*CT and SOC only occurred at concentrations above 200 kg ha^{-1} yr^{-1} (45 mg kg^{-1} DM). Although tropical herbs contained relatively higher CTs than their grass counterparts, the CT concentration might not be potent enough to impact SOC storage as shown in this study (*t*CT = 10±8; < 45 mg kg^{-1} DM). Although tropical herbs contained higher CTs than their grass counterparts, SOC density was lower in soils under the herbs compared with grasses. Even when the CT concentration in the biomass is low, it might be that in the rhizosphere it is higher due to accumulation. Below-ground biotic and abiotic conditions, including the presence of some fungi (e.g., *Basidiomycetes* and *Ascomycetes*) and bacteria species (e.g., *Pseudomonas*), temperature, pH, oxygen and substrate availability are factors that affect the degradation of phenolic compounds in soils (Min et al., 2015). Although the effect of pH on polyphenol degradation is not consistent, under laboratory conditions low soil pH (< 5) was shown to be optimal for extracellular enzymes involved in degrading phenolic compounds in soils (Min et al., 2015). In our study, soil pH was lower in soils under the legume herbs compared with the grasses (Table 2). This low soil pH might have facilitated a faster degradation of potential accumulated CTs and mitigated the assumed effect of CTs on SOC.

We observed significant positive associations between annual CT yield and all the measured soil parameters. A previous study (Mudau et al., 2007) demonstrated that regardless of season, application of N, P and K fertilizers increased the total polyphenols in bush tea, suggesting that N, P and K limitation might affect the synthesis of CTs by plants and for that matter SOC storage. The low nutrient density in the soils might partly explain the lower concentration of CTs in the forages compared to earlier reports on similar species (Jackson et al., 1996; Rosales, 1999; Pereira et al., 2018). Thus, the proportion of extractable CTs and bound CTs, even within species, might change with plant maturity and environmental conditions (Jackson et al., 1996) and might influence the feeding value of the forage. In consequence, increased soil fertility might have some implications for CT concentration in forages for that matter, livestock feeding and SOC storage.

We speculate that at the farm level, where climatic and soil properties are relatively uniform, differences in land use might influence the quantity and quality of organic matter added to the soil. These variables might have induced plant-soil feedbacks to regulate soil C cycling at the micro level to cause local variations in C stocks (Post et al., 1982; Saiz et al., 2012; Chen et al., 2018).

4.5 Implications of the study

This study shows that soil nutrients have implications for SOC input and removal, and by extension, for primary plant productivity and ecosystem functioning (Post et al., 2012; Marques et al., 2016). However, most Ghanaian soils are inherently infertile (Bationo et al., 2018) as result of leaching, soil erosion by rainfall (0.6–0.9 t ha-1) and the fact that nutrients removed by crop harvest are not replaced by the corresponding amount of plant nutrients (Bonsu, 1979; Bationo et al., 2018). Consequently, the low concentration of soil nutrients across the fields may partly explain the low SOC stocks observed for soils in the study site. These fragile soils would require sustainable forms of agricultural land-use systems to ensure higher below-ground net primary productivity (NPP) for increased C stocks.

The forage legume herbs showed lowest yields (Table 1), indicating low bioactivity in comparison to grasses while the legume shrubs had the highest yields and thus captured a lot of N from the biomass. In addition to that soils under the shrubs contained similar *t*N compared with grasses, suggesting that most of the tested forage legume herbs were not suitable with regards to biomass yield for forage and soil carbon sequestration. Legume shrubs should be preferred as they provide more forage and ecosystem services. Invariably, our findings further extend the benefits of cut-use trees/shrubs as they already contribute to food security, incomes and livelihoods in Africa. These plants are deep-rooted, resistant to drought and maintain high protein levels during the dry season when high-quality feed is scarce (Wambugu et al., 2011).

5.0 Conclusion

We tested the hypothesis that the conversion of native grasslands can cause considerable losses in soil C stocks of sub-Sahara Africa. Although SOC stocks under in the agricultural soils did not differ statistically from the native grassland soils, most of the land transformations resulted in declining SOC stocks, questioning the potential of such farms to achieve the 4-permille target. However, the observed wide range of SOC stocks suggests an enormous potential for SOC storage in the area. Our findings further extend the benefits of cut-use trees/shrubs as they already contribute to food security, incomes and livelihoods in Africa. The inclusion of cut-use shrubs/trees or their integration with grass fodder production could be researched further as they show a potential to store more C. All the measured soil chemical properties correlated positively and significantly with SOC, endorsing the fact that soil chemicals are essential drivers of NPP in ecosystems. Hence a boost in productivity is also most likely to result in a boost in SOC. Condensed tannins were positively associated with SOC and could be explored further to harness their potential to extend the residence time of SOC in soils. Discrepant pasture management, such as improper livestock stocking rate, grazing or forage harvest, species selection and nutrient management, could affect the transformation efficiency of plant CT to soil CT. We hypothesize that sustainable soil management practices, coupled with the adoption of CT-rich forages, might improve SOC storage capacity of livestock production systems in this ecological region of Ghana.

Data availability

All data used in the analysis, tables and figures are made available at https://doi.org/10.6084/m9.figshare.12016158.v1.

Author contribution

J. K. Nyameasem acquired funding to carry out the study, J. K. Nyameasem, C. S. Malisch and T. Reinsch conceptualized the research experiment and the hypotheses; J. K. Nyameasem, C. Y. F. Domozoro and E. Marfo-Ahenkora carried out the data collection, J. K. Nyameasem performed the soil and plant analyses, as well as developed the model code and performed the data analysis; J. K. Nyameasem, C. Malisch, and T. Reinsch and I. Emadodin prepared the manuscript with contributions from all co-authors; F. Taube provided oversight and took leadership responsibility for the research activity planning and execution.

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Competing interests

The authors declare that they have no competing interests.

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