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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. This study evaluated the impact of long-term land-use practices, condensed tannins (CT) and soil nutrient status on carbon cycling in arable and permanent systems of a tropical Savannah. 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 19.9 to 36.8 Mg SOC ha^{-1} (mean±sd = 32.9±0.2 Mg ha^{-1}). SOC stocks were lower for grazed-seeded grassland relative to cut-use grass, legume trees and shrubs. Within sown systems, nitrogen availability seemed to be the most critical factor that determines the fate of the SOC stocks, with soil nitrogen (N) concentration and the SOC being highly correlated ($r = 0.90$; $p<0.001$). Accordingly, while converting the native grassland to grazed pastures resulted in mean annual losses of 0.11 Mg C ha^{-1} ($p<0.05$), the conversion to woody legumes resulted in slight (0.03 Mg C ha^{-1}, *ns*) increments. In total, CT, N, P, K and pH (with interaction terms) explained 92 % of variations in the long-term changes of SOC stocks. The regression model showed that improved soil fertility management and the use of tannin-rich plants could promote SOC storage in the Savannah ecological region in the long-run. Our study suggests the cultivation 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

Sequestration of carbon in soils at a rate of 0.4 % per year was 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 carbon 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 carbon (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).

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 input into soils is necessary for increased carbon sequestration. However, the sequestered carbon is sensitive to management and land-use changes, and particularly to grazing, as well as changes in species composition and mineral nutrient availability (Conant et al., 2017). Nevertheless, management practices that increase the supply of quality organic matter could promote carbon 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 on SOC dynamics remains controversial because of its dependence on other parameters such soil pH, tillage and available N in the soil (Khan et al., 2007; Lal, 2008).

As much as increased C input into soils is essential for an increased soil C sequestration, its stabilization in the soil has come into sharp focus. Some SOC stabilization mechanisms that have been proposed include physicochemical 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 belowground 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 examples, 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, belowground 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 carbon, including positive (Reeder and Schuman, 2002), neutral (Shrestha and Stahl, 2008) or negative 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. Therefore, the location of the current study, which is a research exhibition farm cultivated and managed (harvested and weeded to maintain plot purity) since 50 years, with surrounding native and grazed natural grasslands under identical climatic and environmental conditions. Moreover, the location offers unique opportunities to test the long-term effects of converting native grassland to agricultural land on SOC storage. These resources are particularly valuable as long-term experiments designed for this purpose are absent in the sub-Saharan Africa region. The main aim of this study was to assess the impact of long-term land-use practices on soil carbon 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 macronutrients 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 and around a research exhibition 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. The surface lithology is of non-carbonate sedimentary with coarse sandy loam soils belonging to the haplic acrisol group (IUSS, 2014). 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. 1). Thus, the climate is moist semi-arid with a growing period lasting between 120 – 180 days (Ghana Meteorological Services Department, 2018). The land cover is a native tropical grassland Savannah with very limited disturbance. Parts of this native grassland have been converted to different agricultural uses since 1966. The different uses are summarized in Table 1. Briefly, they comprise arable field crops and grazed-seeded grasslands (both at field scales with at least 1 ha), as well as the above mentioned experimental research exhibition farm. The research exhibition farm comprised 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). Each plot was harvested once every year and weeded to maintain species purity, with no other management being conducted. Individual species of each functional group constituted a replicate. Similarly, the different fields under each land-use type constituted a replicate. The management practices associated with the land-use types are summarized in Table 1.

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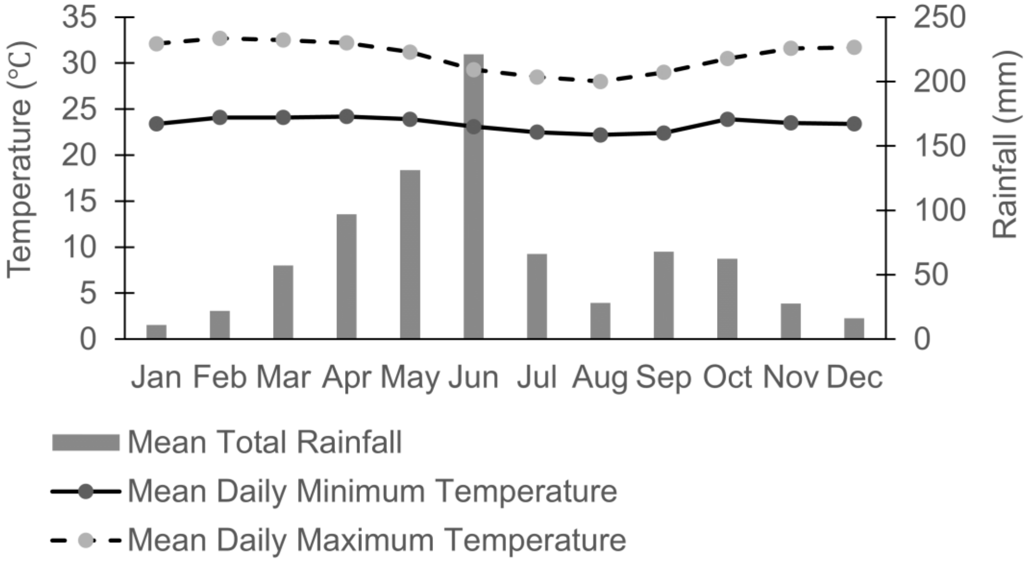

Fig.1. Climate (30-year average) of the study area (Data source: Ghana Meteorological Services Department 2018)

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

Land-use type	Description
Native grassland (field) (NG)	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 (about five livestock units per ha); above-ground biomass yield is 5.7 – 7.2 t/ha (Timpong-Jones et al., 2013)
Arable food crop production (AFC) (field)	*Manihot esculenta*, *Arachis hypogea*, *Zea mays* and *Vigna unguiculata* were food crops cultivated; tillage and fertiliser application practised
Grazed-seeded grasslands (GSG) (field)	Single-species pastures -*Brachiaria brizantha*, *B. ruziziensis* and *Digitaria decumbens*; grazed by sheep and cattle; annual stocking rates above ten livestock units per ha.
Cut–use forage production (plots)	Monoculture (25-30 m^2); 38, 11, 7 and 3 species of grasses (C-G), legume herbs (C-LH), legume trees/shrubs (C-LTS) and non-legume trees/shrubs (C-NLTS), respectively, no soil amendments. Plots were harvested and weeded to maintain plot purity.

2.2 Soil sampling, preparation and analyses

The sampling procedure adopted in this study followed recommendations by Saiz and Albrechts (2016). For each sampling plot or field, four replicates of soil samples were taken (0–30 cm depth). Replicate samples obtained were bulked, thoroughly mixed, and a representative sample taken into a zipped polythene bag for analyses. For the estimation of soil bulk density, four sets of soil samples were taken from each experimental unit (plots/fields) using a stainless-steel core sampler at depths of 0 – 5 cm, 5 – 10 cm, 10 – 15 cm, 15 – 20 cm and 20–25 cm. 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 (TN) 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 phosphorus (P) and exchangeable potassium (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.).

2.3 Plant sampling and proanthocyanidin analyses

Plant samples for CT determination were taken from soil sampling sites in January 2018 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). 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) at 4°C overnight. The samples were then centrifuged for 10 minutes (14000 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 sodium dodecyl sulphate (SDS) and 50 g/L 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 90oC for 90 minutes, cooled on ice and transferred to a spectrophotometer (Libra S22, Biochrom) and analyzed at 550 nm to determine the CT concentrations. For the fiber-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^{o}C, before being cooled on ice to room temperature, centrifuged for 1 min and then measured in the spectrophotometer at 550 nm. Total CT (TCT) was calculated as the sum of ECT, PCT and FCT for each candidate species. 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).

2.4 Calculations and statistics

Soil bulk density and C stock were estimated according to methods by Guo and Gifford (2002). Change in soil C stock as a result of the land-use change was estimated as the difference between soil C stock of native vegetation (natural baseline) and the land use type under consideration (FAO, 2019). Annual changes in soil C stock were estimated by dividing each difference by the number of years (50 years) since the native grassland was converted. To analyse the effect of the different land-use types on soil properties, we performed a one-way ANOVA, followed by Tukey's post hoc tests to permit pairwise comparisons of means ($p<0.05$). In cases where data normality (Shapiro-Wilks) or the equality of error variances (Levene's test) required for ANOVA were not confirmed per data set, a non-parametric test (Kruskal-Wallis) was used, followed by Dunnett T3's post hoc tests to permit pairwise comparisons of means (Table S2). 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 using linear mixed-effect modelling, with species as a "random factor". Non-normal data were transformed before analyses of variance (Table S3). Means with significant differences were separated using Tukey.

Full correlations and multiple linear regressions were conducted to establish relationships between the measured variables and changes in SOC stock (ΔSOC). A full hierarchical model was fitted to each of the two datasets (Table 5) to assess the extent to which the measured variables could predict the observed changes in SOC stocks. The backward elimination procedure (based on the lowest contributing variable) was used to generate a total of 17 candidate models (Table S4). Due to differences in sample size, Akaike's Information Criterion with small-sample bias adjustment (AIC_C) and respective AIC weights (Akaike, 1985; Burnham et al., 2011) was estimated and used to narrow the models down to the best model (model with the highest AIC weight) per each dataset. Finally, the model with the highest coefficient of determination (R^2) and lowest error term was selected as the best equation (Eq. 1):

$$\Delta SOC(Mg\ SOC\ ha^{-1}yr^{-1}) = -1.74 - 0.073TCT + 0.967N + 7.57P - 2.31K + 0.174pH - (0.12N * pH) + (0.433K * pH) - (2.87N * P) + (0.006TCT * N) - (0.054TCT * P)\ , \tag{1}$$

where TCT is total condensed tannins (mg kg^{-1} DM), *N* is total soil nitrogen (Mg ha^{-1}), *P* is plant-available phosphorus (Mg ha^{-1}), *K* is exchangeable potassium (Mg ha^{-1}), and *pH* is soil acidity or alkalinity. All statistical analyses were done using the R statistical platform (R Core team, 2019).

3 Result

3.1 Land-use change and soil C stocks

Land use types impacted soil C stocks in the upper soil layer (0–30 cm), with the group means ranging from 19.9 to 36.8 Mg C ha^{-1} and with a standard deviation of ±10.2 Mg $ha^{-1.}$ SOC stocks were 85 % and 78 % lower ($p<0.01$) for grazed-seeded grassland relative to cut-use trees/shrubs and grasses, respectively (Fig. 2A). Among the cut-use forage systems, SOC stocks were 77 % higher for grasses compared to legume herbs ($p<0.01$). Converting the native grassland to agricultural land-uses resulted in changes in SOC, ranging from -309 – 43 kg ha^{-1} yr^{-1}, with a mean annual loss of -16 % (Fig. 2B). The most considerable negative change of 44 % occurred in grazed-seeded grasslands, being significantly higher ($p<0.05$) than the losses observed in soils of cut-use grasses in legume trees/shrub fields. Also, SOC losses in soils of cut-use legume herbs were 26 % greater than in soils of cut-use grasses ($p<0.05$).

3.2 Land use change and soil chemical attributes

The land-use types caused variations in the soil properties, with a mean(±sd) soil organic matter, total nitrogen, available P and exchangeable K of 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, varying most within each land-use type (coefficient of variation > 30 %). Soil total N (TN) was generally low, yet lowest for grazed-seeded grasslands and non-legume tree/shrub, compared to cut-use grasses and legume tree/shrubs (Table 2). For the tree/shrub species (deep-rooted), the legumes had 56 % higher ($p<0.01$) TN relative to the non-legumes. For the shallow-rooted species, cut-use grasses had 52 % more N compared legume herbs (Table 2). Plant available P only differed between grazed-seeded grasslands and non-legume tree/shrubs ($p<0.05$), which was five-fold higher for non-legume tree/shrubs (Table 2). Exchangeable K differed only between cut-use grasses and legume herbs ($p<0.05$), although it was almost three times higher in food crop soils compared to the soils of other land-use types (Table 2). CN-ratio was lower ($p<0.05$) for grazed-seeded grasslands compared to cut-use grasses, legume herbs and legume trees/shrubs. Meanwhile, CN-ratio was not affected by plant

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functional grouping. Soil pH ranged from moderately acidic to neutral and was affected by the land-use types. The cut-use legume herb soils were more acidic compared to cut-use grasses (*p*<0.05), but not the others (Table 2). 190

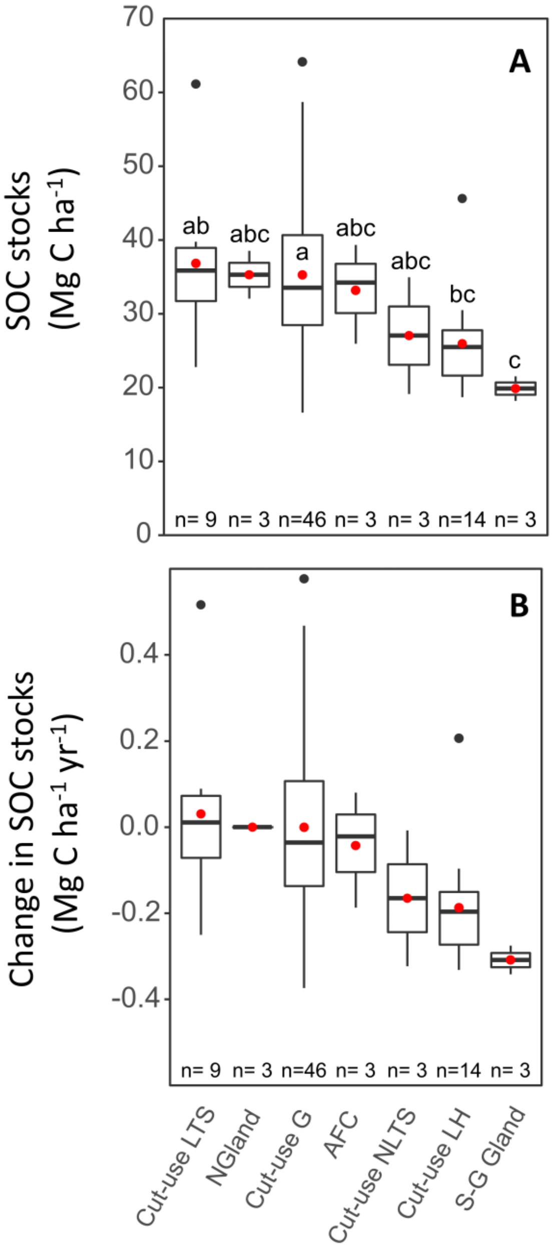

Fig. 2. Barplots (with error bars) of SOC stocks (A) and changes in SOC stocks (B) due to native grassland conversion under different land-use scenarios. Numbers in parenthesis indicate per cent change. Different lowercase letters indicate significant differences between the land-use types (p<0.05). [C-LTS= cut-use legume trees/shrubs; NG= native grassland; C-G= cut-use grasses; AFC= arable food crops; C-NLTS=Cut-use non-legume trees/shrubs; C-LH= cut-use legume herbs; GSG = grazed-seeded grasslands]

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Table 2. Impact of different long-term land uses on residual soil macro-nutrients and other chemical traits (mean±sd)

Soil chemical trait	Native grassland	Arable food crops	Grazed-seeded grassland	Cut-use forage production			
				Grass	Legume herb	Legume trees/shrub	Non-legume tree/shrubs
TN, Mg/ha	2.52±0.54^{abc}	2.48±0.75^{abc}	1.75±0.10^{c}	2.66±0.84^{a}	1.94±0.62^{bc}	2.57±0.52^{ab}	1.65±0.22^{c}
Av. P, kg/ha	89.59±79.3^{ab}	184.73±162^{ab}	15.00±8.00^{a}	37.82±68.3^{ab}	28.11±11.8^{ab}	105.14±82.5^{ab}	82.45±18.7^{b}
K, Mg/ha	6.96±3.67^{ab}	16.6±8.38^{ab}	3.34±2.58^{ab}	7.42±4.57^{a}	4.45±2.31^{b}	7.03±3.70^{ab}	5.12±1.63^{ab}
C: N ratio	14.4±1.80^{ab}	13.6±1.44^{ab}	11.3±0.30^{b}	13.5±2.05^{a}	13.6±1.36^{a}	14.3±2.38^{a}	16.0±2.63^{ab}
Soil pH	5.69±0.45^{ab}	5.80±0.65^{ab}	4.71±0.64^{ab}	5.35±0.32^{a}	4.79±0.47^{b}	5.42±0.51^{ab}	5.02±0.20^{ab}

TN= soil total nitrogen; P= plant-available phosphorus; K= soil potassium. ^{abc}Mean values in the same horizontal row with different letters are significantly different (*p*< 0.05)

3.3 Plant secondary metabolites

Extractable CT (ECT) ranged between 0.1 – 3.0 %; protein-bound CT (PCT) ranged between 0.1–1.7 % fiber-bound CT (FCT) between 0.04 – 2.0 % and total CT (TCT) between 0.2–5.7 % of dry matter (DM). The concentration of the tannins was affected by plant functional group (p<0.001). In both leaves and leaf stalks, ECT, PCT, FCT and total CT were lower in cut-use legume herbs compared with legume trees/shrubs (*p*<0.001) but not non-legume trees/shrubs (Table 3). Total CT was about four-fold in legume trees/shrubs compared with levels in the legume herbs (Table 3). However, the condensed tannins were not affected by the part of the plant analyzed (Table 3). Both leaves and leaf stalks contained similar levels of ECT, PCT, FCT and TCT (*p*> 0.05).

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

Bivariate regressions showed positive correlations between changes in SOC and all tested soil properties (r= 0.13 – 0.9; *p*<0.05), except CN, with correlations of SOC and TN, K and pH being significant (Table 4). The impact of N on SOC storage or loss was highest among the soil properties. The response size of changes in SOC to changes in N content was larger in legume trees/shrubs (slope = 15) compared to response size in the grasses (with a slope = 11) and the legume herbs (slope = 10; Fig. 3). All the CTs (ECT, PCT, FCT and total CT) correlated positively and significantly (p<0.05) with changes in SOC stock, with the highest impact from PCT (Table 3). Full multiple regression analyses showed that the soil chemical variables (N, P, K and pH), including interaction terms, explained 82 % of the variations in SOC stocks when the native grassland was converted to agriculture. However, including TCT (and interactions with soil chemical traits) in the models explained an additional 10 % of the variations in SOC stocks as affected by land-use types (Supplementary Table S-2), hence improving the predictability of SOC changes, and raising the adjusted coefficient of determination to 0.92 (*Eq.* 1). Table 5 shows details (ANOVA) of the best model explaining changes in SOC stock due to native grassland conversion. Soil N, exchangeable K and plant-available P concentration in soils had a significant impact ($p<0.05$) on the observed changes in SOC stock at the site.

Table 3. Condensed tannins (g/kg DM in forages) from three plant functional groups and the two-way ANOVA (functional group: plant part).

Functional group	Plant-part	ECT	PCT	FCT	TCT
Legume trees/shrubs	leaves	11.36±11.6^{b}	9.64±8.03^{a}	6.84±4.54^{b}	27.84±18.8^{b}
	leaf stalk	8.81±8.45^{b}	6.08±3.40^{a}	4.41±3.33^{b}	19.30±8.38^{b}
Legume herbs	leaves	2.19±3.12^{a}	2.71±3.70^{b}	2.58±4.46^{a}	7.48±9.92^{a}
	leaf stalk	3.62±6.20^{a}	2.35±0.99^{b}	3.22±5.66^{a}	9.20±12.49^{a}
Non-legume trees/shrubs	leaves	5.71±4.19^{ab}	3.38±1.69^{ab}	5.77±5.96^{ab}	14.37±8.97^{ab}
	leaf stalk	6.05±0.81^{ab}	2.95±1.35^{ab}	2.84±2.66^{ab}	11.83±4.59^{ab}
ANOVA					
Functional group (F)	*F*-value	15.53	29.05	20.21	32.43
	P-value	<0.001	<0.001	<0.001	<0.001
Plant part (P)	*F*-value	0.035	0.171	3.178	0.519
	P-value	>0.05	>0.05	>0.05	>0.05
F x P	*F*-value	1.372	2.044	3.675	1.019
	P-value	>0.05	>0.05	>0.05	>0.05

ECT= extractable condensed tannins; PCT= protein-bound condensed tannins; FCT= fibre-bound condensed tannins; TCT= total condensed tannins (ECT+PCT+FCT); By plant functional groups, values in a same column with different letters are significantly different.

4 Discussion

4.1 Land use change and carbon stocks

Our study reported a differential distribution of SOC across the land-use types. This observation affirms the claim by previous authors (Amézquita et al., 2008; Stahl et al., 2016) that the type of land use affects soil C cycling and determines the ultimate C storage potential of soils. The range of SOC stocks observed in the current study largely agrees with previously reported ranges of 10 – 50 Mg C 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), we observed that converting native grassland to seeded grassland or arable land resulted in both positive and negative responses by soil C dynamics with a mean net loss of 16 % within 50 years.

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Table 4: Bivariate relationship between SOC stock changes and variables considered in the final structural equation models predict changes in SOC stock

Predictor	se	df	n	*F*-value	*p*-value	Correlation Coefficient	Significance	Transformation
TN	0.043	111	109	460	0.000	0.899	***	log
P	0.033	111	109	2.54	0.114	0.151	ns	log
K	0.068	111	109	9.00	0.003	0.276	**	log
pH	0.051	111	109	42.1	0.000	0.528	***	
CN	3.143	111	109	1.80	0.182	-0.128	ns	1/(x)
TCT	0.042	52	54	12.9	0.001	0.45	***	log
FCT	0.039	52	54	9.12	0.004	0.39	**	log
ECT	0.033	52	54	6.94	0.011	0.34	*	log
PCT	0.047	52	54	16.5	0.000	0.49	***	log

The response and predictor variables are listed along with their correlation coefficients, standard errors (se), degrees of freedom (df), sample size (n), F values, p-values, significance levels, and transformations. Significance symbology is as follows: $0.05<p<0.1$=ns, $0.01<p<0.05$=*, $0.001<p<0.01$=**, $p<0.001$=***. ECT= extractable condensed tannins; PCT= protein-bound condensed tannins; FCT= fibre-bound condensed tannins; TCT= total condensed tannins (ECT+PCT+FCT); TN= soil total nitrogen; P= plant available phosphorus; K= soil potassium. TN, P and K (Mg/ha); ECT, PCT, FCT and TCT (mg/kg DM).

Table 5: ANOVA of the best model explaining variations in SOC stock changes after converting native tropical grassland

Source	Type III sum of squares	*df*	*F-value*	*p-value*
Model	0.057	43	63.39	0.000
Intercept	0.040	1	12.37	0.001
Total condensed tannins (TCT)	0.062	1	19.34	0.000
Total soil nitrogen (N)	0.071	1	22.27	0.000
Plant available phosphorus (P)	0.136	1	42.35	0.000
Exchangeable potassium (K)	0.020	1	6.296	0.014
Soil pH (pH)	0.010	1	3.161	0.082
N x pH*	0.033	1	10.15	0.003
K x pH	0.018	1	5.523	0.023
N x P	0.120	1	37.37	0.000
TCT x N	0.123	1	38.35	0.000
TCT x P	0.037	1	11.63	0.001
Error	0.138	43		

Adjusted R^2*=0.92;* *= interaction terms, *df* = degrees of freedom

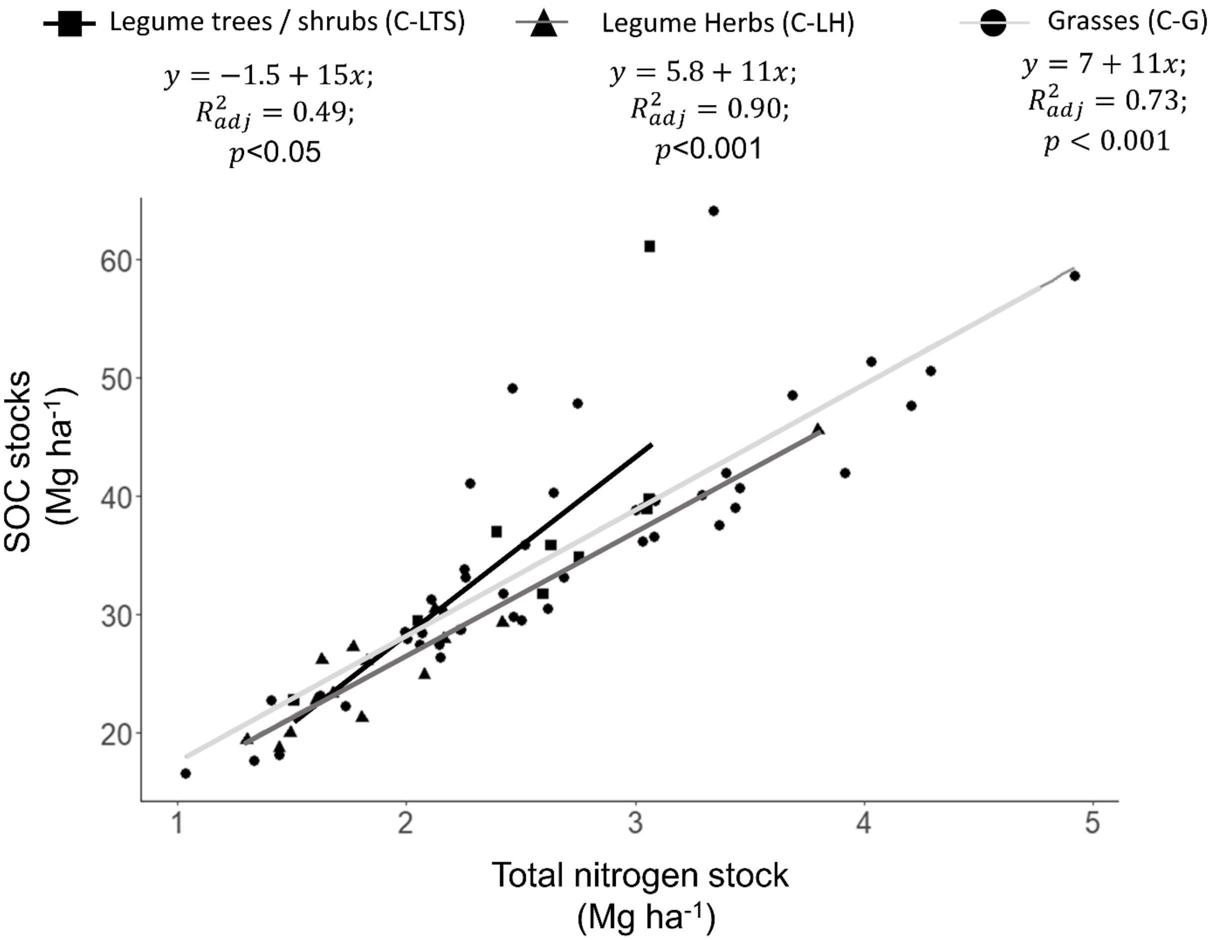

Fig.3. Relationships between SOC and soil total N as affected by plant type

Under different climate change scenarios, Tan et al. (2009) projected -4 to -23 % (2000 to 2100) change in soil C stocks of cultivated savannahs of Ghana. Thus, the magnitude of change in SOC stocks (-16 %) due to land-use change in 50 years observed in our current study could be considered high. However, we observed an indication of C sequestration (31 kg C ha^{-1} year^{-1}) 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. Thus, the type of land-use system adopted after converting native grasslands may have a significant influence on soil C dynamics. 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). These causative factors are discussed in the subsequent paragraphs.

4.2 Grazing intensity and soil carbon storage

The low SOC stock in grazed-seeded grasslands was half (20 vs 35 t SOC ha^{-1}) that of native grassland, suggesting a utilization effect. This observation is consistent with earlier studies (McSherry and Ritchie, 2013) which reported that the effect size of grazing on SOC stocks might be dependent on the interactions of several factors, including grazing intensity. Although this study could not obtain adequate information about the stocking rate of the grazing fields, the low nutrient profile of the soils (Table 2) suggests a degradation and overuse of soils. 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 aboveground herbaceous biomass, thus reducing the potential of CO_2 fixation in photosynthetic tissue and reduction in belowground 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 above-ground biomass of grasslands but also improve soil texture to enhance the accumulation of organic C (Xu et al., 2018). In this instance, the relatively low nutrient concentration observed in the grazed-seeded grasslands matches the low C stocks.

4.3 Species composition and carbon stocks

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 organic matter input, and for that matter, C sequestration in the soil. Dry matter productivity is an essential factor that influences the accumulation of soil C. Although we could not obtain information on above-ground biomass production of the various plants encountered, earlier reports indicated higher above-ground biomass production for grasses compared to legume herbs under an extensive system in West Africa (Barnes and Addo-Kwarfo, 1996; Adjolohoun et al., 2008).

Moreover, grasslands containing more C4 grass species were reported to store more SOC compared to 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, nitrogen 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

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tissue in C4 plants limit organic matter decomposition, thus producing more recalcitrant organic carbon (Yang et al., 2019). 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). Moreover, C4 plants have a higher concentration of amino acids and organic acids in their root exudates compared to C3 plants (Nabais et al., 2011); the organic acids 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.

The higher SOC stocks observed under legume trees/shrubs compared with legume herbs could be partly attributed to the higher ability of legume trees/shrubs to produce relatively high biomass (Barnes and Addo-Kwarfo, 1999), maintain soil fertility (as shown in Table 2), control runoff soil erosion (Franzel et al., 2014) and to maintain SOM. Moreover, higher CT content (Table 3) in legume trees/shrubs might slow the decomposition rate of soil organic matter (Dong et al., 2016) to promote SOC accumulation. The rate of change of SOC to changes in total soil N was higher in legume trees/shrubs, relative to grasses and herbs (Fig. 3).

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). Additionally, fodder trees /shrubs provide by-products such as stakes, firewood, bees and seeds. The high CT content of cut-use legume trees/shrubs helps to reduce methane emissions per unit of output and reduce carbon emissions by substituting for commercially manufactured concentrates (Franzel et al., 2014). The positive effects of tannins on ruminant nutrition, particularly on enteric methane emission and reduced urine N excretion, have been well reported (Hristov et al., 2013; Nyameasem et al., 2017). CTs may have both positive and negative effects on livestock, depending on the concentration of CT in the plants. This nutritional implication is particularly vital with tropical shrubs and tree species where high CTs are known to impair protein availability (Jayanegara et al., 2018). Compared with other tropical forage species, the TCT 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 will be required to give reliable estimates of digestibility.

4.4 Drivers of carbon storage at the micro-level

4.4.1 Soil properties

The mean nutrient concentrations in the soils suggest the soils are highly depleted of N and organic C. Although legumes are known to fix atmospheric N in soils, we observed higher N concentration in cut-use grass fields compared to legume herb fields. 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} year^{-1} atmospheric N, respectively (Hassen et al., 2017). 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. 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 belowground (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 higher TN in legume trees/shrubs compared to non-legume trees/shrubs is attributed to biological nitrogen fixation, which seems to have been more efficient in the woody legumes than in the legume herbs, potentially due to better compatibility with prevalent rhizobia strains.

While P and K levels were moderate in arable food 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). The soils were generally acidic, a common feature 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). Apart from the arable crop fields, the pasture fields/plots received no nutrient replenishment during the period under consideration.

Soil nutrients have implications for plant primary 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 explains the low potential of the soils to store SOC. These fragile soils, therefore, require sustainable forms of agricultural land-use systems to ensure higher below-ground NPP for increased C stocks.

4.4.2 Condensed tannins concentration in aboveground biomass

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). 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).

A previous study by Mudau et al. (2007) demonstrated that regardless of season, application of nitrogenous, P and K fertilizers increased the total polyphenols in a quadratic manner in bush tea, suggesting that N, P and K limitation might affect the synthesis of CTs by the plants and for that matter SOC storage. The low nutrients in soils could partly explain the lower concentration of CTs in the forages encountered compared to earlier reports on similar species (Jackson et al., 1996; Rosales, 1999; Pereira et al., 2018). Thus, increased soil fertility might have some implications for CT concentration in forages. The proportion of extractable CTs and bound CTs, even within species, may change with plant maturity and environmental conditions (Jackson et al., 1996) and may influence the feeding value of the forage.

4.4.3 Regression analyses

Soil macronutrient concentration and polyphenol content were significant factors that drove organic C dynamics (Table 5), confirming our hypothesis that the chemical status of soils might be influential in C storage or loss in extensive land-use systems. We observed a close relationship between soil C and N, suggesting N as an essential factor in the soil C cycle. However, the relationship is ambiguous in the literature, and evidence of different responses of soil CO_2 fluxes to N levels in soils exists (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 inadequate 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.

Interaction effects between N and P, N and pH and K and pH had significant ($p<0.05$) impact on the models, suggesting that the effect of N on SOC sequestration might be dependent on the other variables. The associative effect of N and P was also reported by an earlier study (Bradford et al., 2008) where P and N additions led to 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 biomass and 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. It appears that the relative proportions of soil nutrients impact SOC storage. Thus, soils deficient in P and cations (Ca^{2+}, Mg^{2+}) may not be able to use N efficiently, resulting in increased N losses by gaseous emissions and leaching, and depletion of SOC pools. The theoretical basis, according to linear mixed-effects regression models (Table 5), shows that associative effects of CT and soil chemical properties may predict changes in SOC stocks in tropical sand soils.

Conclusion

Our study tested the hypothesis that the conversion of native grasslands can cause considerable losses in soil C stocks of sub-Sahara Africa. Most transformations resulted in declining SOC stocks; however, the degree of loss varied according to land-use types and the management system adopted after the native grassland was converted. The observed wide range of SOC stocks, however, suggests an enormous potential for SOC storage in the area. The inclusion of cut-use shrubs/trees in pastoral systems of the area is recommended due to their potential to store more C as well as their ability to supply feed even during dry periods. 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. 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. However, 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 suggest that sustainable soil management practices, coupled with the adoption of CT-rich forages, could improve the 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 in (Nyameasem et al., 2020).

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 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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