Variation in soil carbon stocks and their determinants across a precipitation gradient in West Africa

Running Title: Soil carbon stocks in West Africa

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Abstract

We examine the influence of climate, soil properties, and vegetation characteristics on soil organic carbon (SOC) along a transect of West African ecosystems sampled across a precipitation gradient on contrasting soil types stretching from Ghana (15° N) to Mali (7° N). The pattern in SOC stocks, determined from 1,108 soil cores sampled over 14 permanent plots, reflects the very different climatic conditions which, together with soil properties, also influenced vegetation structure along the latitudinal transect. SOC stocks in the first 2 m of soil ranged from 20 Mg C ha^{-1} for a Sahelian savanna in Mali to over 120 Mg C ha^{-1} for a transitional forest in Ghana with an interdependence between soil bulk density (SBD) and soil properties along the transect highlighted by strong negative relationships between SBD and SOC. Used in combination with a suitable climatic parameter, sand content is a good predictor of SOC stored in highly weathered dry tropical ecosystems with arguably less confounding effects than provided by clay content. A simple predictive function capable of encompassing the effect of climate, soil properties and vegetation type on SOC stocks at different depths showed that available water (W*) and sand content taken together could explain 0.84 and 0.86 of the total variability in SOC stocks observed to 0.3 m and 1.0 m depth respectively. There was an increased contribution of resistant SOC to the total SOC pool for lower rainfall soils, this likely being the result of more frequent fire events in the grassier savannas of the more arid regions. This work provides new insights into the mechanisms determining the distribution of carbon storage in tropical soils and should contribute significantly to the development of robust predictive models of biogeochemical cycling and vegetation dynamics in tropical regions.

Introduction

Soils constitute a major reservoir of carbon at the global scale with about a third of the total SOC stored in tropical regions (Schimel *et al,* 1994; Davidson *et al,* 2000; Amundson, 2001). Although at the global scale the distribution of tropical vegetation and SOC decomposition rates are controlled by climate, edaphic and biotic factors play a fundamental role in affecting the quantity and quality of carbon inputs and decomposition processes at the local scale (Feller & Beare, 1997; Giardina & Ryan, 2000; Wynn *et al,* 2006; Wynn & Bird, 2007) with the SOC inventory in any soil profile being determined by the complex interplay of many factors including climate, soil texture, land use, fire frequency and topography (Bird *et al,* 2001). Soil texture is of paramount importance in controlling SOC storage and strongly influences nutrient availability and water retention, particularly in highly weathered soils (Tiessen *et al,* 1994; Silver *et al,* 2000). In particular, clayeyer soils tend to have higher SOC concentrations due to the formation of passive carbon pools via the adsorption and aggregation of SOM by clay minerals (Schimel *et al,* 1994; Feller & Beare*,* 1997).

Environmental gradients varying systematically in climate or other variables provide an excellent opportunity for both understanding mechanisms of abiotic control on ecosystem processes and study the potential impacts of global change in these ecosystems (Koch *et al,* 1995). The ideal conditions provided by simplified environmental gradients to maximise the interpretation of results are not, however, present in West Africa because of the heterogeneity of soils and the differing frequency of disturbance events such as fire which naturally occur in these ecosystems (Pullan, 1969; White, 1983; Bird *et al,* 2000). However, it is still possible to extract very valuable information about the variation in SOC stocks with a number of soil forming factors in such circumstances (Wynn *et al,* 2006).

The strong climatic gradient existing between the humid environments prevalent near the coast and the arid conditions found in interior continental areas plays a fundamental role on the distribution of vegetation in West Africa (White, 1983; Marks *et al,* 2009) with the heterogeneity of soils also reflecting the large natural diversity of this vast region. Indeed, studies conducted decades ago identified the difficulty of assigning dominant pedogenetic features to any given climate within West Africa (Thomas, 1966; Pullan, 1969). The main reason for this is the lack of unequivocal effect of parent material as a soil formation factor given that West African soils have profiles that may have developed in material of mixed origin and some soils may also have been pre-weathered to a considerable depth. Therefore, the distribution of soils in West Africa cannot be related directly to present climate and vegetation, except perhaps for the nutrient-poor soils of semiarid regions (Pullan, 1969).

A further confounding factor is that the average SOC density in West Africa is significantly lower than the global average as a result of its less favourable agroecological conditions and significant land degradation caused by human activities. Thus the semi-arid and subhumid regions of Africa have been reported by several studies as having the largest potential for carbon sequestration in the World (Batjes, 2001; Marks *et al,* 2009). Many of the soils of these regions are already severely degraded and may be susceptible to further losses with climate change and increasing human pressure on the soil resource (Marks *et al,* 2009). Therefore, there is a clear need for observational data sets of SOC stocks and distribution, to allow for the development and validation of robust biogeochemical cycling models (Bird *et al,* 2001; Wynn *et al,* 2006). Furthermore, while we have moderate understanding about the susceptibility of SOC to degradation in tropical environments, much less is known about how the SOC fraction resistant to decomposition varies along natural precipitation gradients (Cheng *et al,* 2008; Lehmann *et al,* 2008). The assessment of this variation can provide valuable insights into the mechanisms leading to effective carbon sequestration and the likely effects of climate change on SOC pools.

The objectives of the present study are: 1) The estimation of SOC stocks at representative sites over a wide range of relatively undisturbed ecosystems characteristic of West Africa; 2) determination of relative roles of climatic, edaphic and biotic factors in determining SOC stocks; and 3) evaluation of variations in the proportion of the SOC pool resistant to decomposition across the precipitation transect.

Materials and Methods

Description of the West African transect- Sites Characteristics

This study was conducted along a latitudinal transect (15° -7° N) spanning nearly 1,000 km and encompassing a broad array of ecosystems and soil types characteristic of West Africa (Fig. 1a). Measurements were undertaken from August to October 2006 in Ghana, Burkina Faso and Mali. Fourteen study sites, consisting of ten 1 ha plots together with four 0.5 ha plots (BFI sites), were established in areas previously identified as representative of the potential natural vegetation of the region (Table 1). Specific locations were selected because they had some degree of protection from direct human intervention, although fire was not excluded from any of the plots. These included National Parks, Forest Reserves, and other legally protected areas except for the case of the Sahelian sites in Mali, which had no specific conservation status and were subject to varying degrees of grazing pressure, the latter being also the case for the most northern Sudan savanna sites of Burkina Faso. The sites were set out over consistently flat terrain with less than 100 metres of altitudinal variation between them. The northern point of the transect was dominated by Sahelian ecosystems, a very open savanna occurring on nutrient poor arenosols in the Southern border of the Sahara desert (Fig. 1a, Table 1). This ecosystem is characterised by low rainfall with a mean annual precipitation (P_a) typically 200-400 mm a^{-1}, and high rates of potential evaporation. Further south there is a natural progression into more tree-dominated forms of vegetation heavily influenced by the gradual increase in mean annual precipitation (Fig. 1b). The Southern end of transect corresponds to the wettest sites studied (>1200 mm a^{-1}) supporting semi-deciduous tropical forest. The variation in mean annual temperature was less than 4ºC across the transect.

Climatic data for each site was extracted from the WorldClim database with 1 km^2 spatial resolution (Hijmans *et al,* 2005). We made use of a single climatic index effectively used in large scale environmental studies (Berry & Roderick, 2002; Wynn *et al,* 2006). This annual water availability index (W^* in mm a^{-1}) is the difference between P_a and the mean annual amount of water that would be evaporated if all of the global solar radiation received at the surface was used to evaporate water. The index was calculated as:

$$W^* = P_a - (Q_s / \rho_w) L + 4000 \quad \text{(Eq. 1)}$$

; where P_a is mean annual precipitation rate, Q_s is mean annual global solar radiation in J m^{-2} a^{-1}, ρ_w is the density of liquid water (~1000 kg m^{-3} at 25ºC), *and* L is the latent heat of evaporation of water (~2.5 x10^6 J kg^{-1} H_2O at 25ºC). This formulation provides an index of water availability to plants, although it does not take into account runoff, surface albedo, and longwave radiation fluxes into and away from the surface.

The wide range of soil types reported in Table 1 reflect contrasts in geology, climate, and vegetation integrated over extended time periods. Soils were classified according to the World Reference Base (WRB) (IUSS Working Group WRB 2006). For a detailed description of the sites see Domingues *et al,* (2010).

Soil Sampling

To overcome the heterogeneity in amount and stable isotopic signature of SOM in mixed C_3/C_4 environments (where grasses of the C_4 photosynthetic pathway coexist with trees and shrubs of the C_3 photosynthetic pathway) we collected soil samples following a stratified random sampling strategy that has proved well suited to such environments (Bird *et al,* 2004; Wynn *et al,* 2006). This approach consists of taking samples in a stratified manner near trees ('Tree'; T samples at half canopy radius from trunks) and away from trees ('Grass'; G samples at half the maximum distance between trees) to best account for the inherent heterogeneity of SOC characteristic of these ecosystems. At each of these locations surface litter was removed when present and three samples at 0-0.05 m and one sample at 0-0.30 m were taken with the aid of a stainless steel corer 40 mm inner diameter (ø) before being placed in labelled zip-lock bags. This procedure was replicated five times at each site (both for T and G locations). Replicates were subsequently bulked according to location (T versus G) and depth (0-0.05 m and 0-0.30 m) as this procedure has been shown to be a cost effective technique for smoothing out local heterogeneity and for achieving robust regional estimates of SOC inventories (Bird *et al,* 2004; Wynn *et al,* 2006). At some sites, the individual samples were independently analysed and compared against results obtained pooling these samples, which further confirmed the soundness of the bulking procedure.

Using the procedures detailed in Quesada *et al,* (2010), deep soil augering was also carried out within each plot in the near vicinity of 5 of the locations described above and samples taken at 0-0.05 m, 0.05-0.10 m, 0,10-0.20 m, 0,20-0.30 m, 0.30-0.50 m and then every 0.5 m up to 2 m depth (impenetrable layers permitting). These samples were used for determinations of pH, cation exchange capacity (ECEC), and elemental abundance of carbon and nitrogen. For each plot a soil pit was hand-dug up to 2 metres depth to assess soil type and allow for the description of soil characteristics (Quesada *et al,* 2011). In this exposed soil profile, samples were also collected at the same depth intervals as above to allow for analyses of soil colour, consistency, particle size distribution and bulk density. The total number of soil samples collected was 1,108. Samples have been archived at the University of St Andrews (Scotland, UK).

Sample Preparation and Bulk Density Determinations

Samples collected at 0-0.05 and 0-0.30 m using the steel corer were weighed in their sealed bags, clumps broken by hand and then oven dried at 40ºC to constant weight. An aliquot of these samples was then oven dried at 105ºC for four hours which allowed for the calculation of soil bulk density (SBD). Samples were then dry sieved to 2 mm and gravel and root content > 2 mm was determined by weight. The set of samples specifically collected in the soil pit for determination of bulk density were also dried at 105ºC, these having been taken using specifically designed rings (ø = 80 mm). In all cases calculation of SBD included fractions > 2 mm. The impact of including gravel and roots > 2 mm on the calculation of SOC stocks is dealt with separately in this work. Please refer to Supplementary Information.

Analytical Methods

Determinations of pH values were obtained using a digital pH meter in a 2:1 water soil solution with particle size distributions gravimetrically determined as described by van Reeuwijk (2002). Briefly, 10 g of soil dry sieved to 2 mm was first treated with a chemical dispersant, and then physical and separated by sieving into sand (particle sizes between 0.05 and 2 mm), with the material passing through the sieve subjected to a series of hygrometer readings in a settling soil solution over time in order to determine clay content (particle sizes <0.002 mm). Silt (particle sizes between 0.002 mm and 0.05 mm) were obtained by mass balance from the recorded dry weights.

Cation Exchange Capacity (CEC) was determined by ICP-OES extraction of soils using dilute unbuffered Silver-Thiourea for Al, K, Mg, Ca and Na as described by Quesada *et al,* (2011). Effective cation exchange capacity (ECEC) was calculated as the sum of these bases. Total phosphorous concentration was determined by ICP OES (Perkin Elmer 5300DV) on extracts obtained by acid digestion as described in Tiessen & Moir (1993).

Quantification of Fe and Al elements was done by X-ray fluorescence (XRF) using a Spectro XLAB EDPXRF spectrometer equipped with a Rh anode X-ray tube, with the mineralogy of the Fe and Al oxides present in soil samples determined using X-ray diffractometry (XRD)

(Philips PW1050/Hiltonbrooks DG2) at the University of St Andrews (Scotland). Interpretation and semi-quantitative analysis of the scans was achieved using the Rietveld refinement method built in within the Siroquant software (SIROQUANT Sietronics Pty Ltd Australia).

Sample aliquots were pre-treated with 6N HCl and subsequently analysed for variation in the C content which confirmed the absence of inorganic carbon. Elemental carbon and nitrogen abundances of powdered samples were determined in duplicate using a Costech Elemental Analyzer fitted with a zero-blank auto-sampler coupled via a ConFloIII to a ThermoFinnigan DeltaPlus-XL using Continuous-Flow Isotope Ratio Mass Spectrometry (CF-IRMS) at the University of St Andrews Facility for Earth and Environmental Analysis stable isotope laboratory. Precisions (S.D.) on internal standards for elemental carbon and nitrogen abundances were better than ±0.09% and 0.02% respectively.

We used a modified version of the technique used by Bird & Grocke (1997) to isolate resistant SOC (R_{SOC}). In short, 50 ml of solution made up of 0.1M $K_2Cr_2O_7$ and 2 M H_2SO_4 was added to 500 mg soil samples previously placed in centrifuge tubes. They were then capped and heated to 60°C in a temperature-controlled orbital shaker for 72 hours. The tubes were periodically uncapped to release evolved gases. At the end of the incubation all samples were washed by centrifugation with distilled water thrice and then oven dried at 60°C. The determination of elemental R_{SOC} was as for total SOC (T_{SOC}).

Results

Soil Characteristics

Soils were moderately acid to neutral (4.9 ≤ pH ≤ 7.0) and ranged from medium to coarse texture, with a wide range of fertilities as evidenced by the ECEC varying from 9 to 41 mmol kg^{-1}, [N] ranging from 0.1 to 1.4 mg g^{-1}, and [P] ranging from 0.04 to 0.24 mg kg^{-1} (Table 1).

SBD increased with latitude along the transect (Fig. 2), but with the magnitude of this change depending in soil depth. Northernmost sites had SBD values exceeding 1500 kg m^{-3} at the soil surface (0.0-0.05 m), which more than doubled those observed in forests at the transect southern end. Reflecting the depth-dependent latitudinal gradient the more arid ecosystems towards the north (Sudan/Sahelian savannas) had higher SBD in the first 0.05 m as compared to 0.30 m, while deeper soil samples towards the southern end of the transect had higher SBD than their shallower counterparts.

SBD and SOC showed strong negative relationships across the precipitation transect at both 0.0-0.05 and 0.0-0.3 m intervals. These relationships were best classified on the basis of soil texture (see discussion). Regressions indicated different decreasing patterns in SBD with increasing SOC for each soil depth. While similar rates of change were observed within each depth interval for both textural classes (medium and coarse), analyses of covariance showed these regressions to be significantly different ($P<0.05$; Fig. 3).

The mineralogical composition as derived from XRD analyses revealed the strongly weathered characteristics of the soils as suggested by the large presence of quartz and kaolinite (Table 2). The semi-quantitative XRD analyses provided mineralogical abundances that correlated well with elemental contents obtained from XRF analyses. The imbalance between quantitative XRD and XRF analyses may indicate a significant proportion of amorphous or poorly crystalline material in some of the samples, especially in sites with abundant clay and iron contents (BBI and BDA sites) (Table 2).

- Soil Organic Carbon

There was a large contrast in SOC stocks between sites from the Northern and Southern end of the studied transect (Fig. 4). Sahelian ecosystems contained less than 11 Mg C ha^{-1} in the first 0.3 m of the soil, while transitional dry forests growing in much less water limited sites stored up to ten times that amount. Greater carbon stocks and concentrations were found in the vicinity of trees at all sites compared to those observed in locations away from tree stems 'grass' (Fig.4; Supplementary Information 1). SOC stocks in the first 2 m of the soil ranged from 20 to over 120 Mg C ha^{-1} for a Sahelian and a transitional forest respectively. Overall, the average SOC contained in the first 0.05 m of the soil accounted for roughly 0.3 of that stored in the first 0.3 m. Similarly, the upper 0.3 m of the soil accounted for about 0.3 of the total 2 m OC inventory (Supplementary Information 2). The inclusion of gravel and roots >2 mm had a relatively low impact on the calculation of SOC stocks (Supplementary Information 3).

Although there was an overall discernible increasing pattern of SOC stocks with mean annual precipitation (Fig. 4), this trend was also heavily influenced by the different soil types found along the transect. Simple regressions based on either mean annual precipitation or mean annual temperature could account for only a maximum of 0.52 of the variability in SOC at any depth (analyses not shown) with these fits slightly improving when the available water index (W^*) of Eq. 1 was used as a predictor variable. We did, however, obtained a much better fit when sand content was included along with W^* as predictors of SOC. Taken together these variables explained 0.84 and 0.86 of the total variability in SOC stocks observed to 0.3 and 1.0 m depths respectively (Table 3, Fig. 5).

The relative contribution of R_{SOC} to the T_{SOC} pool declined with increasing precipitation as is shown in Fig 6. Savanna sites showed fractional R_{SOC} contributions larger than 0.18 of the

T_{SOC} while dry forests consistently had lower contributions of R_{SOC} of typically less than 0.1 Absolute R_{SOC} values were lower than 7 Mg C ha^{-1} except for one savanna site with 15 Mg C ha^{-1} (BDA-2) which seemed to have a very intense burning regime (see discussion).

Discussion

- Soil Bulk Density variation along the transect

Calculation of accurate SOC stocks at any given depth relies on the acquisition of SBD and SOC in soil constituents smaller than 2 mm. These variables are interdependent to some degree as it is shown by the latitudinal gradient in SBD, which is primarily the result of the interplay between SOC contents and soil properties at each site (Figs 2-3). Transitional forests at the Southern end of the transect had the lowest values in SBD as a result of having larger content of silts and clays, and the highest SOC values (Table 1, Fig. 3, Supplementary information 1-2). The significance of SOC contents, soil textures and mineral compositions determining SBD along the precipitation transect is highlighted by the fact that large SBD values of the relatively carbon-poor Northern sites were not just exclusive to markedly sandy Sahelian ecosystems (i.e. HOM sites), but also occurred in relatively dry savanna sites with more loamy textures (i.e. BBI and BDA sites) (Table 1). However, the reason behind the relatively high SBD values observed in the savannas with noticeably finer soil textures is very different.

The soils of these Sudan-savannas are characterised by the relatively large content of iron and aluminium oxides with net positive surface charges which have the capacity to form surface coatings on negatively charged clay minerals (Cornell & Schwertmann, 1996; Hien *et al,* 2006). These coated clay particles are cemented by iron, forming sand-sized microaggregates called sesquioxides or pseudo-sands, which feel coarse-textured and result in higher SBD values than those observed in sandier soils at comparable SOC contents (Fig. 3). The strong negative relationships observed between SBD and SOC along the precipitation transect were best classified on the basis of soil texture, a physical property heavily influenced by soil mineral composition.

The relative low amount of OC present in the top soil layer of the most arid ecosystems in this study (Sudan/Sahelian savannas), has direct implications for soil structure and hence the higher bulk density observed at the top layer of these arid sites (Figs. 2-3), a characteristic to which cattle trampling may have also contributed. By contrast, the larger presence of clay particles at depth promoted particle aggregation and consequently the increase in overall pore space, which agrees well with the decrease in SBD observed at these arid sites. However, this pattern in SBD is reversed towards the Southern end of the transect, where deeper soils have higher bulk densities than surface soils (Figs. 2-3).

- *Soil Organic Carbon stocks along the transect*

The range of West African environments studied here show a moderate capacity to store large amounts of organic carbon in the soil with the exception of Sahelian ecosystems and savanna sites growing in markedly sandy soils (sandy and loamy sands textural classes; Table 1). Indeed, where sampling to 1.0 m was possible, sites with finer soil textures invariably showed SOC values exceeding 60 Mg C ha^{-1} (Supplementary information 2), making the soil a much larger carbon reservoir than that of biomass as was also reported by Grace *et al,* (2006) in savanna environments. The SOC stocks observed at different ecosystems agree relatively well with results compiled by Post *et al* (1982) who reported an average of 20, 54, 61, 99 Mg C ha^{-1} at 1 metre depth for tropical desert bush, tropical woodland-savanna, very dry, and dry tropical forests respectively. More specifically, individual studies conducted across West Africa reflect the large degree of variability in SOC stocks for the different types of ecosystems. A study by Woomer *et al* (2004a) report a range of 11-25 Mg C ha^{-1} at 0.4 m in the sahelian transition zone of Senegal, while Roose and Bathès (2001) observed a range of 15-46 Mg C ha^{-1} to 0.3 metres over a rainfall gradient encompassing a Sudano-sahelian savanna in Burkina Faso and a subequatorial forest in Ivory Coast. Moreover, Batjes *et al*

(2001) calculated an average of 42-45 Mg C ha^{-1} for West Africa at 1 metre depth making use of a global soil database. These rates are somewhat lower than the results shown in our work (Supplementary information 2), however that calculation is not just the product of results obtained from relatively low-disturbed natural ecosystems but also from agricultural and more degraded biomes. The loss of SOC by conversion of natural vegetation to agricultural use is widely reported in the literature (Post and Kwon, 2000), and this region is by no means an exception to this trend (Roose and Bathès, 2001; Hien *et al,* 2006). Besides, West Africa is severely affected by other important factors contributing to the decline in SOC stocks including decreases in soil fertility as a result of agricultural mismanagement and overgrazing, persistent droughts and soil erosion (Batjes, 2001; Tschakert *et al*, 2004; Marks *et al*, 2009). Work conducted by Woomer *et al* (2004b) in Senegal, estimated an average annual carbon loss of approximately 0.07% from the first 0.4 m of soil for the period between 1965 and 2000 after adjusting for land use/cover change and the depletion of woody biomass. At the plot scale, the consistently greater SOC stocks observed in locations directly influenced by the presence of trees justifies the use of a stratified sampling design in mixed C_3/C_4 environments, and may reflect both the larger content of OM inputs occurring at tree locations and/or lower decomposition rates of C_3 derived material relative to C_4-derived material (Wynn & Bird, 2007). Furthermore, this aspect is further highlighted by the fact that the largest SOC stock at 0.3 m observed over the entire dataset corresponded to locations that were purposely sampled because of the noticeable presence of clumps of trees growing on abandoned termite mounds (Fig.4). Similarly, in a study conducted on a humid savanna Mordelet *et al,* (1993) reported large SOC concentrations in tree clumps due to greater organic matter input beneath tree canopies.

Although there was an overall discernible increasing pattern in SOC stocks with increasing precipitation (Fig. 4), this trend was heavily influenced by the different soil types existing along the transect (Table 1). Indeed, simple regressions based on either mean annual precipitation or mean annual temperature could just account for up to 0.52 of the variability in SOC at any depth (analyses not shown). These results are comparable to other studies that have used linear relationships driven by single climatic or soil variables to explain SOC stocks across extensive tropical semi-arid regions (Jones, 1973; Bird *et al,* 2004; Wynn *et al,* 2006). The relatively low explanatory power of these functions, which typically explain less than 0.50 of the total variation, suggest a complex interplay of multiple factors driving the storage dynamics of SOC.

It is well established that fine textured soils have a strong effect on SOC decomposition processes by means of physically protecting SOM, which increases both SOC content and carbon residence time (Schimel *et al,* 1994; Silver *et al,* 2000). In this study, soils very sandy in nature (sandy and loamy sand textures), consistently had the lowest SOC stocks regardless of climate because of the low nutrient and water retention capacity as well as the poor soil structure characteristic of these soils, while the opposite was true for soils with finer textural classes (Table 1; Fig. 4).

In addition to the influence of climate and soil properties on SOC stocks, the type of vegetation existing at a given location has a strong effect on the amount and quality of organic inputs returning to the soil, thus greatly influencing its carbon storage potential (Post *et al,* 1982). Within this context, it is worth considering the role of soil fertility in determining the type of vegetation across the transect. Overall, the soils studied here presented relatively low ECEC rates commonly observed in strongly weathered tropical ecosystems (Marques *et al,* 2004). Indeed ECEC, defined as the sum of the exchangeable cations that a soil can adsorb, is an important chemical property commonly used for assessing the fertility of a given soil (Brady & Weil, 2002; Sankaran *et al,* 2005). Nonetheless, the role of soil nitrogen (N) and phosphorous (P) in available forms to plants should also have important implications for plant productivity and ecosystem functioning (Domingues *et al*, 2010; Quesada *et al*, 2010). The irregular pattern in ECEC rates observed along the transect, with some Sudan savannas showing the highest values (Table 1), demonstrates that soil fertility was not the main limiting factor behind the type of vegetation occurring at a given location, except perhaps for the forests existing in the wetter end of transect where we observed larger concentrations in soil N and P compared to savannas. Therefore precipitation, or rather the amount of water available for plant growth, may be the main factor influencing the type of vegetation occurring along the transect, which has direct implications for site productivity, and consequently for soil structure, SBD, and SOC storage. A good example of the complex interplay of factors determining the impact that soils have on vegetation and their capacity to store carbon is offered by the Sudan savannas studied in Burkina Faso. These sites had comparatively large SOC contents because of the physical protection provided by the nature of their soils (Tables 1-2). The presence of sesquioxides greatly affected soil structure and consequently their water retention capacity, since these particles promote large inter-aggregate pores capable of draining water at the same soil water potentials as sands of comparable size, whereas the intra-aggregate micropores hold water at very high tensions (Santos *et al,* 1989). The consequence of this is that less water will be available for plant growth given that these soils have relatively few pores in the size range that contains water accessible for plants (Nitzsche *et al,* 2008), which undoubtedly influence the type of vegetation that can be sustained. While the amount of water available for plant growth can be reasonably considered as the main determinant for the type of vegetation observed along this precipitation transect, there are more factors other than soil fertility, which may influence this distribution. These factors include both natural and anthropogenic disturbances (fire, grazing pressure), and soil physical constraints for plant growth. Such is the case of BDA-3, a grassland site growing on hardened plinthite crust occurring at less than

0.2 m from the surface (Table 1). In such circumstances root penetration by woody plants is strongly diminished and only herbaceous vegetation may develop.

- *Functions predicting Soil Organic Carbon stocks*

In view of the contrasting soil characteristics observed over the wide range of vegetation existing across the precipitation gradient, we established a relatively simple predictive function to predict SOC stocks at different depths driven by a combination of climate and quantifiable soil variables capable of effectively encompassing the effect of climate, soil properties and vegetation type on SOC storage.

A large number of studies have reported strong correlation between SOC and clay contents, and indeed most process-based models simulating SOM dynamics make use of this relationship as the role of clays in soil physiochemical processes has been proved fundamental (Spain, 1990; Schimel *et al*, 1994; Sollins *et al*, 1996; Feller & Beare, 1997). However, it is difficult to find unequivocal evidence on the role of clays stabilising SOC, given that clay may be correlated with other factors and it is not clear which ones are causative (Oades *et al*, 1988). Moreover, there are also studies that have found weak correlations between SOC and clay contents in contrasting ecosystems (Percival *et al*, 2000; Silver *et al*, 2000; Bricklemyer *et al*, 2007). The effect of clay on SOC stocks is also dependent on the clay mineralogy of the soil (Spain, 1990, Bruun *et al*, 2010). Therefore, caution should be exerted when generalising about the role played by clay content in SOC stabilization.

Most tropical systems, with the exception of those occurring in mountainous regions, wetlands or recent volcanic deposits, usually contain soils that have undergone significant heavy weathering for prolonged periods of time. Consequently, their soil matrixes are mainly made up of minerals with high resistance to weathering (Table 2). As discussed above, the association of clays with aluminium and iron oxides may result in the formation of sesquioxides in certain tropical soils conferring the soil a sand-like texture, which strongly affects its water retention capacity and result in the unusual high SBD values observed for medium-textured soils (Fig. 3). Thus, these particles may exert a strong influence on these two soil properties which are essential factors in determining SOC stocks. However, a large proportion of the constituents of sesquioxides will be accounted for as clay fraction in laboratory analyses, which may limit to some extent the predictive power of regressions driven by clay content (Table 3). In this study, a function combining sand content and available water index (W*) explained 0.84 and 0.86 of the total variability in SOC stocks observed at 0.0-0.3 and 0.0-1.0 m respectively (Table 3, Fig. 5). Used in combination with a suitable climatic parameter, sand content was a good predictor of SOC stored in highly weathered dry tropical ecosystems with arguably less confounding effects than that provided by clay content.

- *Resistant Soil Organic Carbon variation along the transect*

The soil sampling strategy we used in this study allowed for the comparison of soil properties at systematically defined locations. The fact that we used 'Grass' locations in the assessment of R_{SOC} had a double advantage; on the one hand, it excludes the possibility of confounding effects derived from any preferential sampling of woody biomass, while on the other hand, sampling at a mid distance from trees allows for the relative unbiased account of the effect of contrasting woody covers. However, failure to determine R_{SOC} at 'Tree' locations may result in an underestimation of its overall absolute value for a particular site.

Several studies using strong acid treatments to isolate R_{SOC} have shown that poorly crystalline and amorphous mineral components are left relatively untouched (Siregar *et al*, 2004; Kleber *et al*, 2005; Mikutta *et al*, 2006), thus supporting the idea that the most important determinants controlling mineral associated R_{SOC} in heavily weathered soil systems may not be significantly affected by the use of acid treatments. The analytical procedure we chose to isolate the R_{SOC} fraction has already been used as a proxy for pyrogenic carbon (Bird & Grocke, 1997), although we purposefully chose not remove the mineral component by HF dissolution prior to oxidation to include OC protected by mineral associations, given that dissolution of mineral phases previous to oxidation with treatments like HF hydrolysis has been shown to release significant amounts of OC from soils containing large contents of mineral-bound OM (Kaiser *et al*, 2002; Gonçalvez *et al*, 2003).

The physicochemical protection of SOC conferred by soil minerals may be an important factor contributing to R_{SOC}, indeed the presence of sesquioxides promoting stable aggregates may have contributed to the relatively large R_{SOC} contribution observed in the savannas of Burkina Faso (Tables 1-2; Fig. 6). It has been reported that the lability of SOC in tropical ecosystems when compared across contrasting soils types is significantly influenced by clay mineralogy and content of Fe and Al (hydr-) oxides but not by clay content (Bruun *et al*, 2010). On the other hand, Plante *et al* (2006) showed in a study conducted over two widely-ranged textural gradients that biochemically protected OC in whole soil samples increased with clay content. Even though the range of textures covered in our study is much narrower than that of the abovementioned work, the role of texture influencing the rates of mineral-protected SOC, particularly in soils presenting similar mineralogy, cannot be ignored.

Chemically recalcitrant carbon compounds are also known to be significant contributors to the abundance of R_{SOC} (Cheng *et al*, 2008; Lehmann *et al*, 2008). The mechanisms of stabilization of OM in forest subsoils were investigated by Mikutta *et al* (2006) who reported an average contribution of 27% of the total stable SOC attributable to chemically recalcitrance of OC. However, that study was not conducted in fire-prone savannas which have been shown to present a relatively large presence of recalcitrant substances derived from incomplete combustion of biomass (i.e. charcoal) (Bird and Grocke, 1997; Lehmann *et al*, 2008). Aromatic substances like lignin have traditionally been considered as important controlling factors over the formation and stabilization of SOC, however recent studies have challenged this view (Thevenot *et al*, 2010). In particular, mechanisms behind their stabilization and turnover in soils remain open to debate. Furthermore, there are a limited number of studies dealing with lignin dynamics in dry tropical ecosystems, and those reported show relatively low lignin contents compared to other systems such as agricultural and temperate forests (Guggenberger *et al*, 1995; Thevenot *et al*, 2010). Hence, we hypothesize that the role of lignin determining the amount of R_{SOC} in these ecosystems is far less significant than that of pyrogenic carbon. The savanna site with the highest R_{SOC} contribution to T_{SOC} provided good evidence for fire being the main factor behind the high content of R_{SOC} observed in savanna environments not only because of the noticeably low numbers of trees that were able to reach maturity (Table 1), but also because this site had an extraordinary large presence of *Cochlospermum planchonii*, a pyrophyllic shrub associated with very frequent fires (Devineau *et al,* 2010). Therefore, we postulate that the decreasing trend in the contribution of R_{SOC} to T_{SOC} with increasing precipitation is mainly the result of more frequent fire events characteristic of savanna ecosystems (Sankaran *et al,* 2005; Grace *et al,* 2006; Furley *et al,* 2008), which is in agreement with the higher abundance of macroscopic charcoal fragments we noted in the soils of these ecosystems.

Conclusions

We assessed the influence of climate, soil properties, and vegetation characteristics on soil organic carbon (SOC) storage in a key geographical area with considerable potential for SOC sequestration. The soil sampling strategy used in this study allowed for the comparison of soil properties at systematically defined locations. The strong control by vegetation at the plot level was shown by the contrasting values in SOC contents observed between sampling locations. The large observed variation in SOC stocks reflects the very different climatic conditions existing along the transect, which together with soil properties, strongly determined the contrasting type of vegetation occurring at those sites. The degree of interdependence between SBD and soil properties for the range of soils covered in this work is highlighted by the strong negative relationships observed between SBD and SOC along the transect. Early studies dealing with SOC in tropical ecosystems usually reported soil carbon abundances without information on SBD (e.g. Jones, 1973; Kadeba, 1978). Therefore, it has not been possible to convert those results to inventories. However, provided that information on the basic textural characteristics of those soils is available, one can make use of the SOC-SBD relationships reported here in order to ascertain SBD for the range of mineral soils included in the present study. This can be achieved within a reasonable degree of accuracy since at least 0.84 of the variability gets explained. Therefore, the use of these relationships may allow the calculation of SOC stocks for those studies, which may provide really useful baselines for research work dealing with changes in SOC stocks over time.

Used in combination with a suitable climatic parameter, such as available water, sand content is a reliable predictor of SOC stored in highly weathered dry tropical ecosystems with arguably less confounding effects than are associated with the use of clay content as a predictor. The presence of sesquioxides at some of the studied sites resulted in an ‘apparently coarse' texture which strongly influenced both the high SBD values observed and the amount of water available to plants. The latter played a fundamental role influencing the type of vegetation occurring along the transect, which has direct implications for the amount and quality of organic inputs returning to the system, and consequently on soil structure, SBD, and SOC storage. Factors influencing the type of vegetation observed along this precipitation transect included soil fertility, soil physical constraints for plant growth and both natural and anthropogenic disturbances (e.g. grazing pressure, fire).

We suggest that the observed decreasing trend in the contribution of resistant SOC to total SOC pool with increasing precipitation was mainly the result of more frequent fire events characteristic of savanna ecosystems. Global coupled climate carbon cycle model simulations predict net losses in SOC stocks in West Africa as a result of increased heterotrophic soil respiration and reduced precipitation (Friedlingstein *et al,* 2010). These models have identified that SOC losses will be more significant in humid coastal regions, while SOC pools will show lower susceptibility in more arid regions. The greater relative proportion of R_{SOC} in savannas further confirms that the resilience of these ecosystems to SOC loss is larger than that of forests. While the present study stresses the relevance of West African soil properties in SOC storage, our findings reinforce the view that semi-arid ecosystems offer a significant opportunity for soil carbon sequestration because of their large area and relatively low human populations (Tschakert *et al*, 2004; Marks *et al,* 2009). This work will contribute to the development of robust predictive models of biogeochemical cycling and vegetation dynamics in semi-arid tropical regions.

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References

Amundson R (2001) The carbon budget in soils. *Annual Review of Earth and Planetary Sciences,* **29**, 535-562.

Batjes NH (1996) Total carbon and nitrogen in the soils of the world. *European Journal of Soil Science* ,**47**, 151-163.

Batjes NH (2001) Options for increasing carbon sequestration in West African soils: An exploratory study with special focus on Senegal. *Land Degradation & Development,* **12**, 131-142.

Berry SL, Roderick ML (2002) Estimating mixtures of leaf functional types using continental-scale satellite and climatic data. *Global Ecology and Biogeography,* **11**, 23-39.

Bird MI and Grocke DR (1997) Determination of the abundance and carbon isotope composition of elemental carbon in sediments. *Geochimica et Cosmochimica Acta*, **61**, 3413-3423.

Bird MI, Veenendaal EM, Moyo C, Lloyd J and Frost P (2000) Effect of fire and soil texture on soil carbon in a sub-humid savanna (Matopos, Zimbabwe). *Geoderma,* **94**, 71-90.

Bird MI, Lloyd J and Santruchkova H (2001) Global soil organic carbon In *Global Biogeochemical Cycles in the Climate System*. pp 185-199. Academic Press, New York.

Bird MI, Veenendaal EM and Lloyd J (2004) Soil carbon inventories and $\delta^{13}C$ along a moisture gradient in Botswana. *Global Change Biology,* **10**, 342-349.

Brady NC and Weil RR (2002) *The nature and properties of soils*. Prentice Hall, Inc., NJ. pp. 960.

Bricklemyer RS, Miller PR, Turk PJ, Paustian K, Keck T and Nielsen GA (2007) Sensitivity of the Century Model to scale-related soil texture variability. *Soil Science Society of America Journal,* **71**, 784–792.

Bruun TB, Elberling B and Christensen BT (2010) Lability of soil organic carbon in tropical soils with different clay minerals. *Soil Biology & Biochemistry*, **42**, 888-895.

Cheng CH, Lehmann J, Thies JE and Burton SD (2008) Stability of black carbon in soils across a climatic gradient. *Journal of Geophysical Research-Biogeosciences* **113**, 10.

Cornell R and Schwertmann U (1996) *The Iron Oxides: Structure, Properties, Reactions, Occurrence and Uses*. VHC Verlag, Weinheim.

Davidson EA, Trumbore SE and Amundson R (2000) Biogeochemistry - Soil warming and organic carbon content. *Nature,* **408**, 789-790.

Devineau JL, Fournier A and Nignan S (2010) Savanna fire regimes assessment with MODIS fire data: Their relationship to land cover and plant species distribution in western Burkina Faso (West Africa). *Journal of Arid Environments,* **74**, 1092-1101.

Domingues TF, Meir P, Feldpausch TR, Saiz G, Veenendaal EM, Schrodt F, Bird M, Djagbletey G, Hien F, Compaore H, Diallo A, Grace J and Lloyd J (2010) Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. *Plant Cell and Environment,* **33**, 959-980.

Feller C and Beare MA (1997) Physical control of soil organic matter dynamics in the tropics. *Geoderma*, **79**, 69-116.

Friedlingstein P, Cadule P, Piao SL, Ciais P and Sitch S (2010) The African contribution to the global climate-carbon cycle feedback of the 21st century. *Biogeosciences*, **7**, 513–519.

Furley PA, Rees RM, Ryan CM and Saiz G (2008) Savanna burning and the assessment of long-term fire experiments with particular reference to Zimbabwe. *Progress in Physical Geography*, **32**, 611-634.

Giardina CP and Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858-861.

Gonçalves CN, Dalmolin RSD, Dick DP, Knicker H, Klamt E and Kögel-Knabner I (2003) The effect of 10% HF treatment on the resolution of CPMAS ^{13}C NMR spectra and on the quality of organic matter in Ferralsols. *Geoderma*, **116**, 373–392.

Grace J, San Jose J, Meir P, Miranda HS and Montes RA (2006) Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography,* **33**, 387-400.

Guggenberger G, Zech W and Thomas RJ (1995) Lignin and carbohydrate alteration in particle-size separates of an oxisol under tropical pastures following native savanna. *Soil Biology & Biochemistry*, **27**, 1629-1638.

Hien E, Ganry F and Oliver R (2006) Carbon sequestration in a savannah soil in southwestern Burkina as affected by cropping and cultural practices. *Arid Land Research and Management*, **20**, 133-146.

Hijmans RJ, Cameron SE, Parra JL, Jones PG and Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

IUSS (International Union of Soil Science) Working Group WRB (2006) *World Reference Base for Soil Resources 2006: A Framework for International Classification, Correlation and Communication*. World Soil Resources Report 103, FAO, Rome.

Jones MJ (1973) Organic matter content of savanna soils of West-Africa. *Journal of Soil Science*, **24**, 42-53.

Kadeba O (1978) Organic matter status of some savanna soils of Northern Nigeria. *Soil Science*, **125**, 122-127.

Kaiser K, Eusterhues K, Rumpel C, Guggenberger G and Kögel-Knabner I (2002) Stabilization of organic matter by soil minerals - investigations of density and particle-size fractions from two acid forest soils. *Journal of Plant Nutrition* and *Soil Science*, **165**, 451–459.

Kleber M, Mikutta R, Torn MS and Jahn R (2005) Poorly crystalline mineral phases protect organic matter in acid subsoil horizons. *European Journal of Soil Science*, **56**, 717-725.

Koch GW, Vitousek PM, Steffen WL and Walker BH (1995) Terrestrial transects for global change research. *Vegetatio*, **121**, 53-65.

Lehmann J, Skjemstad J, Sohi S, Carter J, Barson M, Falloon P, Coleman K, Woodbury P and Krull E (2008) Australian climate-carbon cycle feedback reduced by soil black carbon. *Nature Geoscience*, **1**, 832-835.

Marks E, Aflakpui GKS, Nkem J, Poch RM, Khouma M, Kokou K, Sagoe R and Sebastia MT (2009) Conservation of soil organic carbon, biodiversity and the provision of other ecosystem services along climatic gradients in West Africa. *Biogeosciences*, **6**, 1825-1838.

Marques JJ, Schulze DG, Curi N and Mertzman SA (2004) Major element geochemistry and geomorphic relationships in Brazilian Cerrado soils. *Geoderma*, **119**, 179-195.

Mikutta R, Kleber M, Torn MS, Jahn R (2006) Stabilization of soil organic matter: Association with minerals or chemical recalcitrance?. *Biogeochemistry*, **77**, 25-56.

Mordelet P, Abbadie L and Menaut JC (1993) Effects of ree clumps on soil characteristics in a humid savanna of West Africa (Lamto, Cote d'Ivoire). *Plant and Soil,* 153, 103-111.

Nitzsche RP, Percival JB, Torrance JK, Stirling JAR and Bowen JT (2008) X-ray diffraction and infrared characterization of Oxisols from central and southeastern Brazil. *Clay Minerals*, **43**, 549-560.

Oades JM (1988) The retention of organic matter in soils. *Biogeochemistry,* **5**, 35–70.

Percival HJ, Parfitt RL and Scott NA (2000) Factors controlling soil carbon levels in New Zealand grasslands: is clay content important?. *Soil Science Society of America Journal,* **64**, 1623–1630.

Plante AF, Conant RT, Stewart CE, Paustian K and Six J (2006) Impact of soil texture on the distribution of soil organic matter in physical and chemical fractions. *Soil Science Society of America Journal*, **70**, 287-296.

Post WM, Emanuel WR, Zinke PJ and Stangenberger AG (1982) Soil carbon pools and world life zones. *Nature*, **298**, 156-159.

Post WM and Kwon KC (2000) Soil carbon sequestration and land-use change: processes and potential. *Global Change Biology*, **6**, 317-327.

Pullan RA (1969) The soil resources of West Africa. In Environment and land use in Africa. Ed. Thomas and G.W. Whittington. pp 147-172. Methuen, London.

Quesada CA, Lloyd J, Anderson LO, Fyllas NM, Schwarz M and Czimczik CI (2011) Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences,* **8**, 1415–1440.

Quesada CA, Lloyd J, Schwarz M, Patiño S, Baker TR, Czimczik C, Fyllas NM, Martinelli L, Nardoto GB, Schmerler J, Santos AJB, Hodnett MG, Herrera R, Luizão FJ, Arneth A, Lloyd G, Dezzeo N, Hilke I, Kuhlmann I, Raessler M, Brand WA, Geilmann H, Moraes Filho JO, Carvalho FP, Araujo Filho RN, Chaves JE, Cruz Junior OF, Pimentel TP and Paiva R (2010) Variations in chemical and physical properties of

Amazon forest soils in relation to their genesis. *Biogeosciences*, **7**, 1515–1541, doi:10.5194/bg-7-1515- 2010.

Roose E and Bathès B (2001) Organic matter management for soil conservation and productivity restoration in Africa: a contribution from Francophone research. *Nutrient Cycling* in *Agroecosystems*, **61**, 159–170.

Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F, Ardo J, Banyikwa F, Bronn A, Bucini G, Caylor KK, Coughenour MB, Diouf A, Ekaya W, Feral CJ, February EC, Frost PGH, Hiernaux P, Hrabar H, Metzger KL, Prins HHT, Ringrose S, Sea W, Tews J, Worden J and Zambatis N (2005) Determinants of woody cover in African savannas. *Nature*, **438**, 846-849.

Santos MCD, Mermut AR and Ribeiro MR (1989) Submicroscopy of clay microaggregates in an oxisoil from Pernambuco, Brazil. *Soil Science Society of America Journal*, **53**, 1895-1901.

Schimel DS, Braswell BH, Holland EA, McKeown R, Ojima DS, Painter TH, Parton WJ and Townsend AR (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles*, **8**, 279-293.

Silver WL, Neff J, McGroddy M, Veldkamp E, Keller M and Cosme R (2000) Effects of soil texture on belowground carbon and nutrient storage in a lowland Amazonian forest ecosystem. *Ecosystems*, **3**, 193-209.

Siregar A, Kleber M, Mikutta R and Jahn R (2005) Sodium hypochlorite oxidation reduces soil organic matter concentrations without affecting inorganic soil constituents. *European Journal of Soil Science*, **56**, 481-490.

Sollins P, Homann P, and Caldwell BA (1996) Stabilization and destabilization of soil organic matter: Mechanisms and controls. *Geoderma*, **74**, 65–105.

Spain AV (1990) Influence of environmental conditions and some soil chemical properties on the carbon and nitrogen contents of some tropical Australian rainforest soils. *Australian Journal of Soil Research*, **28**, 825–839.

Thevenot M, Dignac MF and Rumpel C (2010) Fate of lignins in soils: A review. *Soil Biology & Biochemistry*, **42**, 1200-1211.

Thomas MF (1966) Some Geomorphological Implications of Deep Weathering Patterns in Crystalline Rocks in Nigeria. Transactions of the Institute of British Geographers, 173-193.

Tiessen H, Cuevas E, and Chacon P (1994) The role of soil organic matter in sustaining soil fertility. *Nature*, **371**, 783–785.

Tiessen H and Moir JO (1993) Total and Organic Carbon in: Soil Sampling and Methods of Analysis, edited by: Carter, MR, Leis Publ., Boca Raton, FL, 187–199.

Tschakert P, Khouma M and Sène M (2004) Biophysical potential for soil carbon sequestration in agricultural systems of the Old Peanut Basin of Senegal. *Journal of Arid Environments*, **59**, 511-533.

van Reeuwijk L.P. (ed.) Procedures for soil analysis / International Soil Reference and Information Centre.-(Technical Paper / International Soil Reference and Information Centre. -Wageningen ISSN 0923-3792 : no. 9.

White F (1983) The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa. UNESCO, Paris, France. pp. 356.

Woomer PL, Tieszen LL, Tappan G, Touré A and Sall M (2004a) Land use change and terrestrial carbon stocks in Senegal. *Journal of Arid Environments*, **59**, 625–642.

Woomer PL, Touré A and Sall M (2004b) Carbon stocks in Senegal' Sahel Transition Zone. *Journal of Arid Environments*, **59**, 499–510.

Wynn JG, Bird MI, Vellen L, Grand-Clement E, Carter J and Berry SL (2006) Continental-scale measurement of the soil organic carbon pool with climatic, edaphic, and biotic controls. *Global Biogeochemical Cycles*, **20**, -.

Wynn JG and Bird MI (2007) C4-derived soil organic carbon decomposes faster than its C3 counterpart in mixed C3/C4 soils. *Global Change Biology*, **13**, 2206-2217.

Table 1: Characteristics of the sites.

Site	Regional Classification of Vegetation	Canopy Cover	Soil Type WRB	Textural Class FAO (USDA)	Clay content $kg\ kg^{-1}$	Sand content $kg\ kg^{-1}$	pH	ECEC $mmol\ kg^{-1}$	N $mg\ g^{-1}$	P $mg\ g^{-1}$	Fe $mg\ g^{-1}$	Al $mg\ g^{-1}$
HOM-1	Open Sudan savanna (Sahel)	0.01	Haplic Arenosol	Coarse (Sandy)	0.03	0.89	6.4	9.6 (1.7)	0.11	0.05	7.0	9.5
HOM-2	Open Sudan savanna (Sahel)	0.05	Haplic Arenosol	Coarse (Sandy)	0.01	0.93	6.7	11.9 (3.8)	0.12	0.05	4.9	9.0
BBI-1	Open Sudan savanna	0.28	Haplic Luvisol	Medium (Clay Loam)	0.39	0.31	5.8	39.4 (5.0)	0.30	0.08	23.8	52.9
BBI-2	Open Sudan savanna	0.51	Pisolithic Plinthosol	Medium (Loam)	0.18	0.49	6.1	27.6 (3.4)	0.43	0.11	22.4	55.0
BDA-1	Open Savanna woodland	0.162	Haplic Fluvisol	Medium Fine (Silty loam)	0.25	0.11	5.8	41.0 (10.7)	0.60	0.11	44.1	40.2
BDA-2	Open Savanna woodland	0.03	Acric Stagnic Plinthosol	Medium (Silty loam)	0.1	0.39	5.6	26.3 (12.7)	0.32	0.07	45.5	24.3
BDA-3	Open Savanna grassland	0.00	Epipetric Stagnic Plinthosol	n/a			5.6	8.7 (6.4)	0.68	0.17	65.0	30.2
MLE-1	Open Savanna woodland Guinea	0.24	Brunic Arenosol	Coarse (Loamy sand)	0.04	0.81	6.1	16.8 (5.2)	0.20	0.05	7.0	11.6
BFI-1	Savanna woodland Transition Zone	0.30	Haplic Alisol	Coarse (Sandy loam)	0.11	0.72	7.0	26.5 (5.4)	0.70	0.13	16.1	23.3
BFI-2	Savanna woodland Transition Zone	0.60	Brunic Arenosol	Coarse (Sandy loam)	0.09	0.71	5.3	12.2 (5.7)	0.67	0.12	15.4	22.8
BFI-3	Semideciduous dry forest Transition Zone	0.72	Haplic Nitosol	Medium (Sandy clay loam)	0.2	0.61	5.7	38.0 (5.3)	1.40	0.19	22.4	41.8
BFI-4	Semideciduous dry forest Transition Zone	0.80	Haplic Nitosol	Medium (Sandy Loam)	0.05	0.65	6.7	31.8 (8.8)	1.42	0.24	14.7	30.7
KOG-1	Savanna woodland Transition Zone	0.42	Haplic Arenosol	Coarse (Loamy sand)	0.03	0.77	5.3	9.1 (6.3)	0.24	0.04	2.8	4.2
ASU-1	Semideciduous dry forest	0.50	Endofluvic Cambisol	Medium (Loam)	0.17	0.43	4.9	29.9 (8.8)	1.31	0.15	18.2	27.0

All soil related values are based on the 0.0 - 0.30 m interval, except for BDA-3 which had a 0.19 m average maximum depth. For the regional classification of vegetation and calculation of canopy covers the reader is referred to Domingues *et al,* (2010). Numbers in brackets within the ECEC column are standard deviations from the mean (n=5).

Table 2: Relative abundance of main minerals present in the soil (<2 mm) extracted from x-ray diffraction (XRD) analysis for the different sites across the transect. Absolute differences in Fe and Al contents (mg g^{-1}) between x-ray fluorescence (XRF) and (XRD) analyses are also shown to assess the presence of amorphous or poorly crystalline mineral phases and test the accuracy of the XRD-rietveld-determined elemental contents.

Site	Quartz SiO_2	Kaolinite $Al_2Si_2O_5(OH)_4$	Hematite Fe_2O_3	Goethite $FeO(OH)$	K-Feldspar $KAlSi_3O_8$	Absolute difference between XRF-XRD (mg g^{-1})	
						Fe	Al
HOM-1	0.94	0.04	0.01	0.00	0.01	0.0	0.2
HOM-2	0.95	0.04	0.00	0.00	0.01	4.9	-0.3
BBI-1	0.65	0.28	0.01	0.00	0.04	16.8	-11.6
BBI-2	0.72	0.23	0.01	0.00	0.04	15.4	3.0
BDA-1	0.74	0.18	0.02	0.02	0.03	17.5	-1.4
BDA-2	0.85	0.1	0.01	0.03	0.01	19.6	2.4
BDA-3	0.79	0.15	0.02	0.02	0.01	38.5	-3.2
MLE-1	0.94	0.05	0.00	0.00	0.01	7.0	0.2
BFI-1	0.87	0.11	0.02	0.00	0.00	2.1	0.3
BFI-2	0.87	0.11	0.02	0.00	0.00	1.4	-0.2
BFI-3	0.76	0.21	0.03	0.00	0.00	1.4	-2.1
BFI-4	0.85	0.13	0.02	0.00	0.00	0.7	3.5
KOG-1	0.97	0.02	0.00	0.00	0.01	2.8	-0.9
ASU-1	0.84	0.12	0.01	0.00	0.02	11.2	-1.1

Other minerals present in rather small concentrations include those bearing Ti, Ca, and Na (i.e. rutile, plagioclase, etc) which are not shown here. Amorphous minerals not detected by XRD are also not shown. Mineral contents determined by the XRD-rietveld approach was converted to elemental composition (i.e. Fe and Al) using factors derived from the ideal chemical formulae of minerals shown above.

Table 3: Regression values for the functions predicting T_{SOC} using Water availability index-*W** (mm a^{-1}, *x*), and sand and clay content (kg kg^{-1}, *y*) respectively at two different depths.

Depth	0.30 m			1.00 m		
Sand	n=13	r^2 0.84	P <0.0001	n=12	r^2 0.86	P <0.0001
f = y_o+a*x+b*y	y_o	a	b	y_o	a	b
Coefficient	16.063	0.010	-27.056	57.918	0.019	-72.901
St Error coeff	6.410	0.002	5.703	16.694	0.006	14.281
t	2.506	4.721	-4.744	3.469	3.273	-5.105
P value	0.031	0.001	0.001	0.007	0.010	0.001
Clay	n=13	r^2 0.70	P=0.0025	n=12	r^2 0.63	P=0.0114
f = y_o+a*x+b*y	y_o	a	b	y_o	a	b
Coefficient	-8.971	0.012	45.779	-12.679	0.0268	65.417
St Error coeff	7.008	0.003	17.363	19.278	0.009	36.807
t	-1.280	3.920	2.637	-0.658	3.026	1.777
P value	0.229	0.003	0.025	0.527	0.014	0.109

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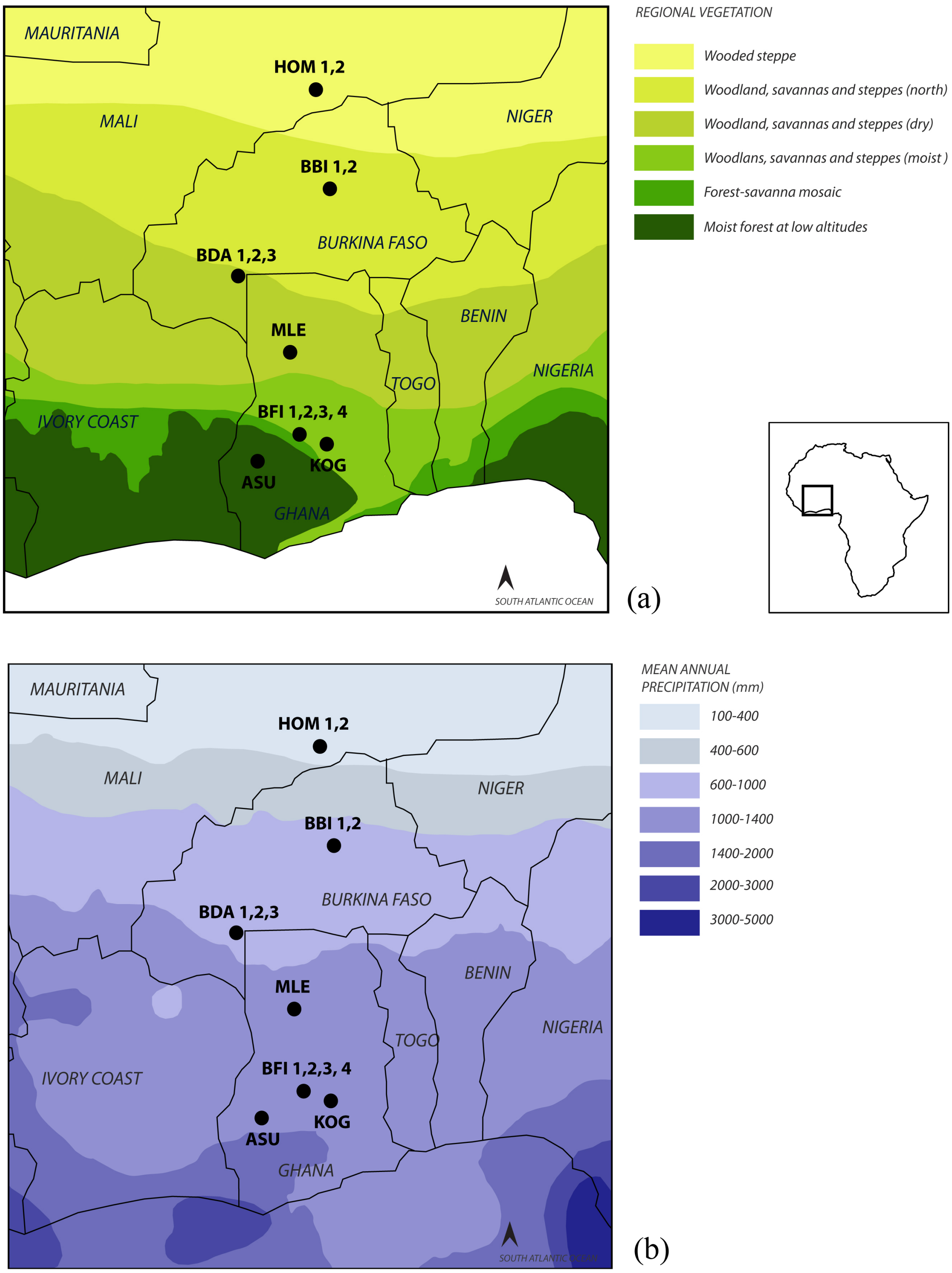
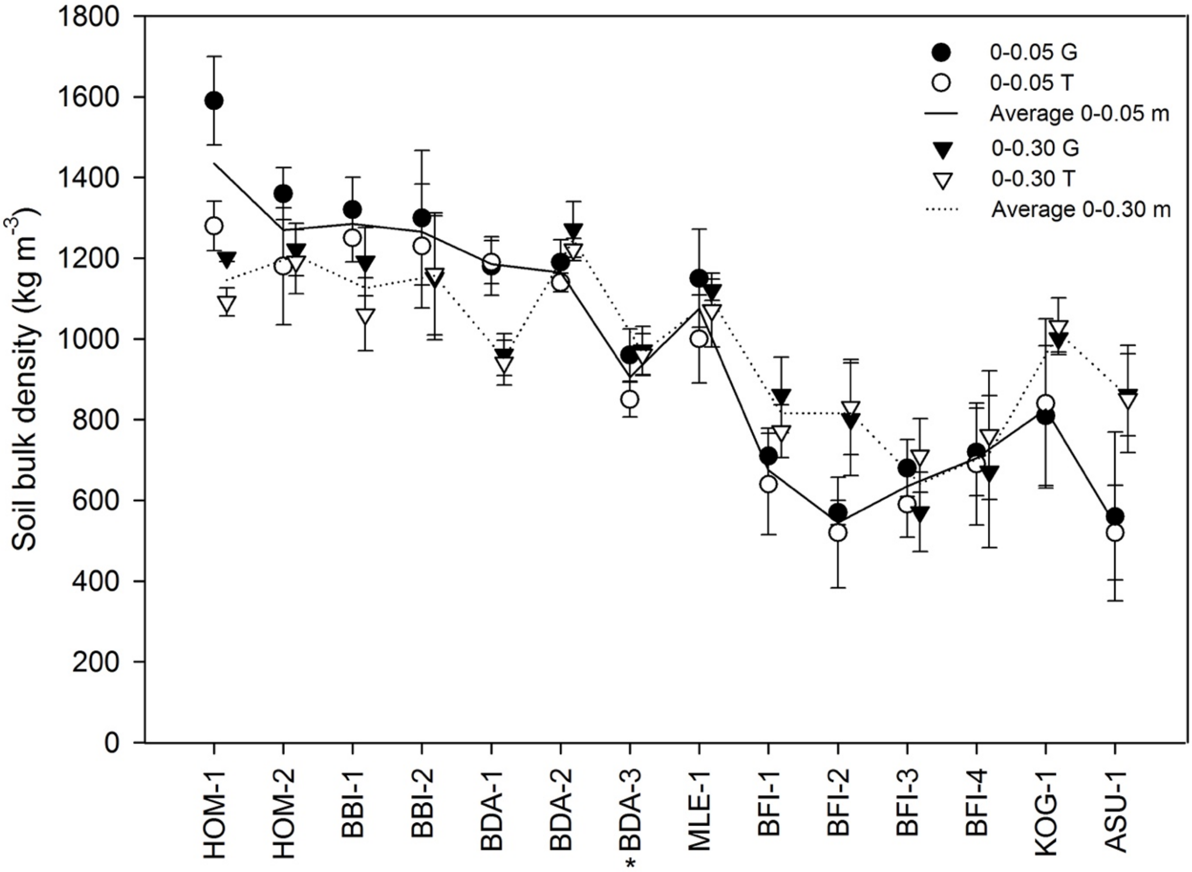
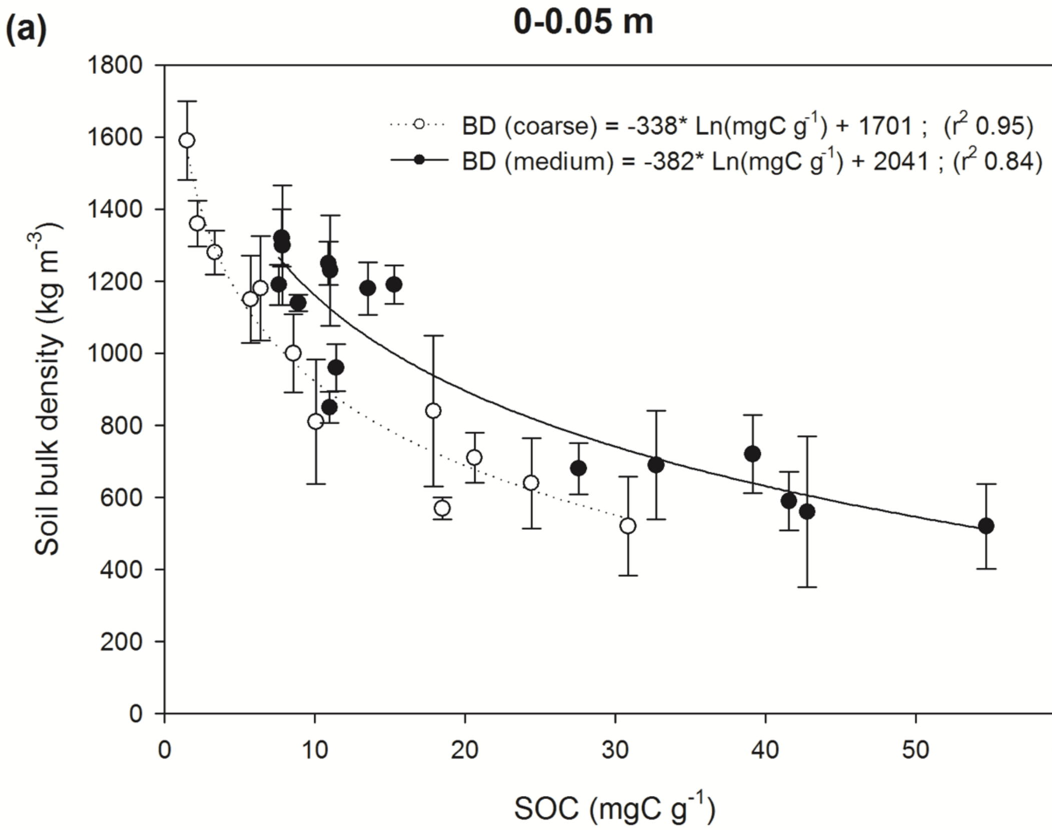
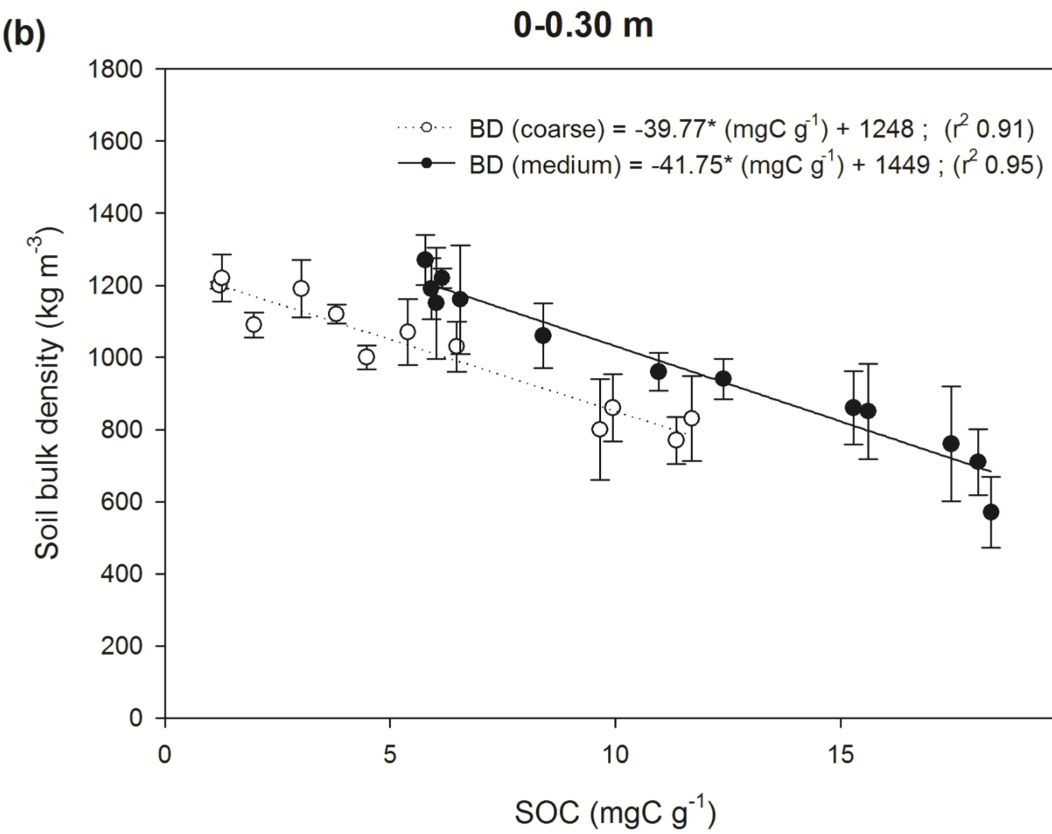
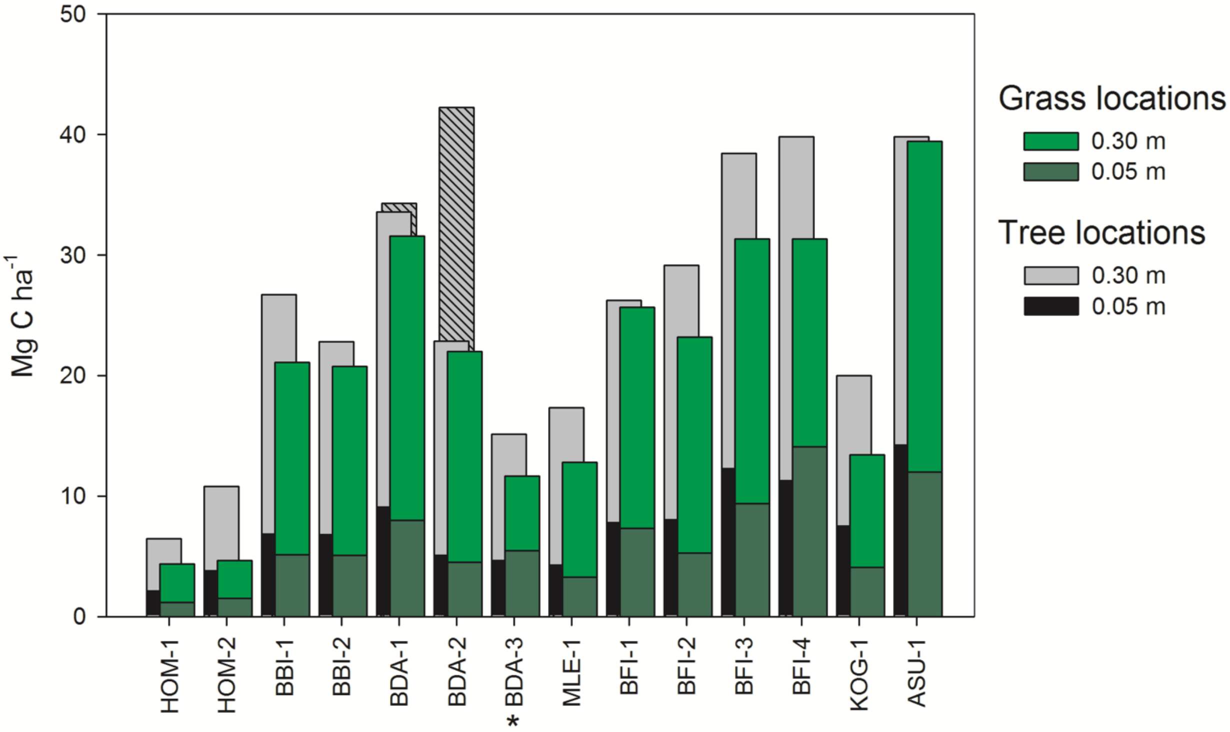

MAURITANIA
MALI
NIGER
BURKINA FASO
BENIN
NIGERIA
TOGO
IVORY COAST
GHANA
HOM 1,2
BBI 1,2
BDA 1,2,3
MLE
BFI 1,2,3, 4
KOG
ASU
SOUTH ATLANTIC OCEAN
REGIONAL VEGETATION
Wooded steppe
Woodland, savannas and steppes (north)
Woodland, savannas and steppes (dry)
Woodlans, savannas and steppes (moist)
Forest-savanna mosaic
Moist forest at low altitudes
(a)
MEAN ANNUAL
PRECIPITATION (mm)
100-400
400-600
600-1000
1000-1400
1400-2000
2000-3000
3000-5000
(b)

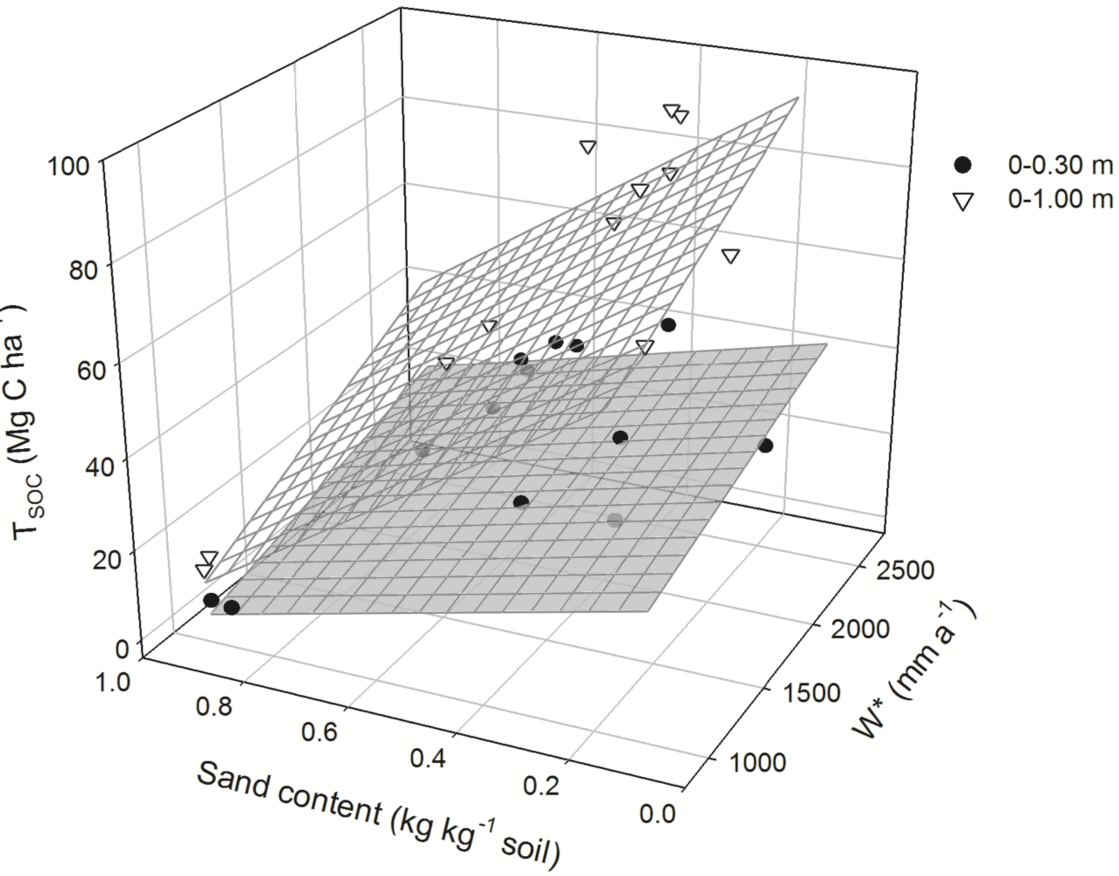

1800
1600
1400
1200
1000
800
600
400
200
0
Soil bulk density (kg m-3)
0-0.05 G
0-0.05 T
Average 0-0.05 m
0-0.30 G
0-0.30 T
Average 0-0.30 m
HOM-1
HOM-2
BBI-1
BBI-2
BDA-1
BDA-2
* BDA-3
MLE-1
BFI-1
BFI-2
BFI-3
BFI-4
KOG-1
ASU-1


(a)
0-0.05 m
BD (coarse) = -338* Ln(mgC g-1) + 1701 ; (r2 0.95)
BD (medium) = -382* Ln(mgC g-1) + 2041 ; (r2 0.84)
Soil bulk density (kg m-3)
SOC (mgC g-1)
0
200
400
600
800
1000
1200
1400
1600
1800
0
10
20
30
40
50
60

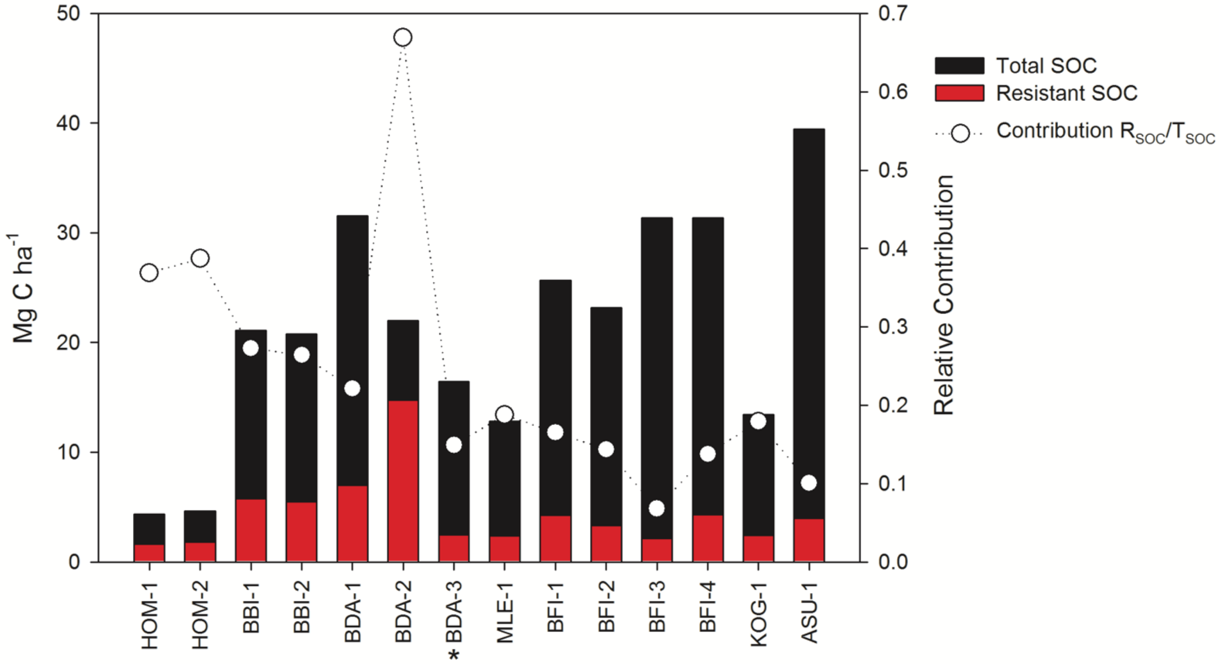

(b)
0-0.30 m
BD (coarse) = -39.77* (mgC g-1) + 1248 ; (r2 0.91)
BD (medium) = -41.75* (mgC g-1) + 1449 ; (r2 0.95)
Soil bulk density (kg m-3)
SOC (mgC g-1)
0
200
400
600
800
1000
1200
1400
1600
1800
0
5
10
15
20



50
40
30
20
10
0
Mg C ha-1
Grass locations
0.30 m
0.05 m
Tree locations
0.30 m
0.05 m
HOM-1
HOM-2
BBI-1
BBI-2
BDA-1
BDA-2
* BDA-3
MLE-1
BFI-1
BFI-2
BFI-3
BFI-4
KOG-1
ASU-1



100
80
60
40
20
0
T_SOC (Mg C ha-1)
1.0
0.8
0.6
0.4
0.2
0.0
Sand content (kg kg-1 soil)
1000
1500
2000
2500
W* (mm a-1)
0-0.30 m
0-1.00 m


Mg C ha-1
Relative Contribution
Total SOC
Resistant SOC
Contribution RSOC/TSOC
HOM-1
HOM-2
BBI-1
BBI-2
BDA-1
BDA-2
* BDA-3
MLE-1
BFI-1
BFI-2
BFI-3
BFI-4
KOG-1
ASU-1
0
10
20
30
40
50
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7

Supplementary Information 1: SOC densities (mg C g^{-1} soil) for the 0.0-0.05 and 0.0-0.30 m depth intervals at two sampling locations across the transect.

Site	Latitude (N)	Longitude (W)	n	0.05 m		n	0.30 m	
				Tree	Grass		Tree	Grass
HOM-1	15.344	1.468	5	3.34	1.50	5	1.98	1.21
HOM-2	15.335	1.547	5	6.40	2.19	5	3.03	1.27
BBI-1	12.731	1.165	5	10.91	7.79	5	8.40	5.91
BBI-2	12.733	1.163	5	11.03	7.83	5	6.56	6.02
BDA-1	10.940	3.149	5	15.28	13.52	5	12.40	10.96
BDA-2	10.940	3.154	5	8.89	7.61	5	6.16	5.78
BDA-3	10.865	3.073	5	10.98	11.41	5	6.74*	9.06*
MLE-1	9.304	1.858	5	8.57	5.73	5	5.40	3.81
BFI-1	7.714	1.694	5	24.42	20.63	5	11.35	9.94
BFI-2	7.715	1.692	5	30.85	18.48	5	11.69	9.66
BFI-3	7.705	1.696	5	41.57	27.56	5	18.05	18.34
BFI-4	7.708	1.698	5	32.73	39.15	5	17.45	15.59
KOG-1	7.302	1.180	5	17.90	10.08	5	6.48	4.48
ASU-1	7.137	2.447	5	54.71	42.78	5	15.61	15.28

Supplementary Information 2: SOC stocks (Mg C ha^{-1}) for the different soil depths across the transect.

Site	n	0.05 m		n	0.30 m		n	0.50 m	n	1.00 m	n	1.50 m	n	2.00 m
		Tree	Grass		Tree	Grass								
HOM-1	5	2.14	1.19	5	6.47	4.35	5	7.63 (0.22)	5	11.64 (0.60)	5	15.81 (0.60)	5	18.73 (0.59)
HOM-2	5	3.78	1.49	5	10.82	4.64	5	9.99 (0.23)	5	14.61 (2.32)	5	19.01 (0.70)	5	22.19 (0.70)
BBI-1	5	6.82	5.14	5	26.71	21.10	5	35.31 (4.37)	4	56.86 (2.12)	3	70.01 (4.50)		
BBI-2	5	6.78	5.09	5	22.82	20.78	5	33.63 (1.41)						
BDA-1	5	9.09	7.98	5	34.96	31.56	5	50.07 (3.76)	5	71.92 (5.61)	5	89.68 (5.44)		
BDA-2	5	5.07	4.53	5	22.53	22.01	5	36.67 (4.43)	5	71.85 (19.10)				
BDA-3	5	4.67	5.48	5	15.27*	16.44*								
MLE-1	5	4.29	3.29	5	17.32	12.81	5	21.62 (1.32)	5	34.93 (1.57)	5	44.56 (0.91)	4	52.20 (2.09)
BFI-1	5	7.81	7.32	5	26.23	25.65	5	35.95 (0.93)	4	61.28 (2.15)	4	84.80 (5.90)	1	101.71
BFI-2	5	8.02	5.27	5	29.12	23.18	5	40.03 (3.02)	4	74.20 (5.69)	4	98.21 (5.99)	4	119.04 (5.32)
BFI-3	5	12.26	9.37	5	38.44	31.35	1	54.31	1	87.96	1	111.73	1	126.06
BFI-4	5	11.29	14.09	5	39.79	31.34	1	52.39	1	77.59	1	96.96	1	113.21
KOG-1	5	7.52	4.08	5	20.01	13.44	5	23.41 (4.30)	5	33.60 (5.45)	5	45.06 (7.05)	1	60.46
ASU-1	5	14.22	11.98	5	39.81	39.43	5	58.52 (12.65)	3	80.77 (25.61)	2	86.02 (0.62)		

Numbers in brackets are standard deviations from the mean. In the case of 0.05 and 0.30 m intervals values were calculated from pooling five individual samples in both sampling locations (T-G). They are reported here as they are likely to cover a representative range of SOC stocks at each site. Asterisks in BDA-3 0.30 m sample denote a 0.19 m average sampling depth.

Supplementary Information 3: Proportion of soil mass (w/w) attributed to the fraction >2 mm separated in gravel and roots, over the whole bulk soil for the 0.0-0.05 and 0.0-0.30 m depth intervals. Relative differences in SOC stocks (%) are calculated using whole soil samples compared to the classical approach that makes use of the < 2 mm fraction only. Results are shown for calculations made using gravel alone and gravel and roots fractions combined.

Site		0.05 m				0.30 m			
		(w/w)		Relative difference in SOC stocks (%)		(w/w)		Relative difference in SOC stocks (%)	
	n	Gravel	Roots	Gravel	Gravel & Roots	Gravel	Roots	Gravel	Gravel & Roots
HOM-1	5	0.000	0.003	-0.3	0.0	0.000	0.001	-0.1	-0.1
HOM-2	5	0.000	0.003	-0.3	-0.1	0.000	0.001	-0.1	-0.1
BBI-1	5	0.006	0.000	-0.7	-0.6	0.014	0.003	-1.8	-1.3
BBI-2	5	0.083	0.002	-9.0	-7.9	0.099	0.002	-10.7	-9.0
BDA-1	5	0.003	0.001	-0.4	-0.4	0.019	0.001	-2.1	-2.0
BDA-2	5	0.020	0.020	-4.2	0.8	0.105	0.004	-11.6	-7.5
BDA-3	5	0.173	0.002	-20.4	-18.0	0.167	0.001	-19.0	-17.9
MLE-1	5	0.006	0.003	-1.0	-0.7	0.027	0.002	-3.0	-2.3
BFI-1	5	0.002	0.006	-0.8	-0.7	0.004	0.003	-0.7	-0.6
BFI-2	5	0.000	0.002	-0.2	-0.2	0.000	0.008	-0.8	-0.5
BFI-3	5	0.003	0.017	-2.0	-1.4	0.001	0.006	-0.7	-0.6
BFI-4	5	0.003	0.005	-0.8	-0.8	0.006	0.003	-0.9	-0.9
KOG-1	5	0.000	0.003	-0.3	-0.3	0.000	0.002	-0.2	-0.2
ASU-1	5	0.041	0.013	-5.7	-4.9	0.082	0.004	-9.3	-8.0

Gravel fraction is estimated to have a bulk density of 1.65 kg m^{-3} and contain an average of 2.5 mg C g^{-1} soil. Roots are estimated to have a bulk density of 0.5 kg m^{-3} and contain an average of 450 mg C g^{-1} root. We note that the amount of carbon contained in very stable aggregates > 2 mm might be quite variable and caution should be exercised in soils likely to contain significant amounts of sesquioxides such as those occurring in BBI and BDA sites. Therefore the differences presented for those sites should be considered as preliminary only.