Biogeosciences

The influence of C$_3$ and C$_4$ vegetation on soil organic matter dynamics in contrasting semi-natural tropical ecosystems

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Abstract. Variations in the carbon isotopic composition of soil organic matter (SOM) in bulk and fractionated samples were used to assess the influence of C$_3$ and C$_4$ vegetation on SOM dynamics in semi-natural tropical ecosystems sampled along a precipitation gradient in West Africa. Differential patterns in SOM dynamics in C$_3$/C$_4$ mixed ecosystems occurred at various spatial scales. Relative changes in C / N ratios between two contrasting SOM fractions were used to evaluate potential site-scale differences in SOM dynamics between C$_3$- and C$_4$-dominated locations. These differences were strongly controlled by soil texture across the precipitation gradient, with a function driven by bulk δ^{13}C and sand content explaining 0.63 of the observed variability. The variation of δ^{13}C with soil depth indicated a greater accumulation of C$_3$-derived carbon with increasing precipitation, with this trend also being strongly dependant on soil character-

istics. The influence of vegetation thickening on SOM dynamics was also assessed in two adjacent, but structurally contrasting, transitional ecosystems occurring on comparable soils to minimise the confounding effects posed by climatic and edaphic factors. Radiocarbon analyses of sand-size aggregates yielded relatively short mean residence times (τ) even in deep soil layers, while the most stable SOM fraction associated with silt and clay exhibited shorter τ in the savanna woodland than in the neighbouring forest stand. These results, together with the vertical variation observed in δ^{13}C values, strongly suggest that both ecosystems are undergoing a rapid transition towards denser closed canopy formations. However, vegetation thickening varied in intensity at each site and exerted contrasting effects on SOM dynamics. This study shows that the interdependence between biotic and abiotic factors ultimately determine whether SOM dynamics of

C_3- and C_4-derived vegetation are at variance in ecosystems where both vegetation types coexist. The results highlight the far-reaching implications that vegetation thickening may have for the stability of deep SOM.

1   Introduction

A progressive "thickening" of woody vegetation in grasslands and savannas is a global phenomenon that has been widely documented (Archer et al., 2001; Boutton et al., 2009; Guillet et al., 2001; Krull et al., 2005; Liao et al., 2006; Pessenda et al., 1998). Woody thickening is being promoted by climate change, changes in fire regimes and other anthropogenic land use activities (Jackson et al., 2000; Krull et al., 2005; Silva et al., 2008) with increased woody (C_3) plant growth in response to continually increasing atmospheric CO_2 concentrations a likely key driver (Bond and Midgley, 2012; Buitenwerf et al., 2012; Donohue et al., 2013). The impact of these vegetation dynamics on ecosystem biogeochemistry and the global carbon cycle may be highly significant given the large extent of grass-dominated ecosystems, which represent about 30 % of primary production of all terrestrial vegetation and store 10–30 % of all soil organic carbon (SOC; Eswaran et al., 1993; Grace et al., 2006; Hall and Scurlock, 1991). Moreover, despite an increasing number of studies of terrestrial carbon dynamics, improved predictions of the impacts of future climate-driven changes on the tropical SOM pool requires a more detailed understanding of the interactions between vegetation, climate, edaphic and disturbance effects than is currently available (Archer et al., 2001; 2004; Boutton et al., 2009; Jackson et al., 2000).

The use of isotopic techniques in ecological studies broadens the possibilities for better assessing soil carbon dynamics (Bernoux et al., 1998; Bird and Pousai, 1997; Bird et al., 1996; Boutton, 1996; Leifeld and Fuhrer, 2009), the documentation of past vegetation changes (Krull et al., 2005; Liao et al., 2006; Pessenda et al., 1998; Silva et al., 2008), and the reconstruction of earlier environments (Bird et al., 1996; Cerling et al., 2011). The use of the carbon isotope composition of SOM has proven to be a useful tool for investigating the influence of C_3 and C_4 vegetation on SOM dynamics (Wynn and Bird, 2007), and for identifying recent ($\sim$ 100 years) vegetation change patterns that in the past could only be assessed by interpreting historical aerial photography or satellite imagery (Krull et al., 2005). This approach relies on the distinct carbon isotopic (δ^{13}C) values of tropical grasses, employing the C_4 photosynthetic pathway (-14 ‰) compared to the δ^{13}C value of trees and shrubs that utilize the C_3 photosynthetic pathway (-27 ‰; average values from Krull et al., 2007). It is feasible to obtain an integrated measure of the carbon isotopic composition of regional vegetation using SOM, given that this pool integrates the isotopic signature of the precursor biomass, thus serving as a record of changes in

the ratio of tree and grass-derived organic matter input to the soil over different spatiotemporal scales (Bird et al., 2004; Lloyd et al., 2008). However, the simple interpretation of the δ^{13}C value of SOM in a soil profile may not be straightforward because of fractionation effects such as those associated with microbial reprocessing of SOM, differential stabilization of SOM compounds, and the terrestrial "Seuss effect" (Bird et al., 1996; Blagodatskaya et al., 2011; Ehleringer et al., 2000; Rumpel and Kögel-Knabner, 2011). Moreover, the specific characteristics of a soil can fundamentally affect carbon isotopic dynamics through differential physico-chemical protection of SOM as influenced by the chemical, mineralogical, and textural properties of the soil (Krull et al., 2003; Sollins et al., 2009; Veldkamp, 1994).

Physical fractionation of SOM is commonly employed to simplify the complex soil matrix into discrete fractions of similar physico-chemical characteristics, as defined by aggregation, particle size, density, or a combination of these (Crow et al., 2007; Moni et al., 2012; Zimmermann et al., 2007). Each individual technique will result in a specific number of fractions with conceptually different carbon turnover times, although a common feature shared by all methods is the differentiation between mineral-associated organic matter and free particulate organic matter. The latter fraction is predominantly composed of plant-derived material in the early stages of decomposition and is generally reported to mineralise more quickly than physically protected mineral-associated fractions (Six and Jastrow, 2002; Sollins et al., 1996; Zimmermann et al., 2007). The determination of mean residence times (τ) of SOM by radiocarbon (^{14}C) age measurements, combined with δ^{13}C characterisation of vegetation change recorded in SOM has provided strong evidence of the nature and timing of tropical vegetation shifts in the past (Guillet et al., 2001; Krull et al., 2005; 2007; Pessenda et al., 1998). While the use of these techniques yields useful information about SOM dynamics, there are a number of limitations and biases that need to be taken into account when interpreting the results (Creamer et al., 2011; Crow et al., 2007; Trumbore, 2009). Several authors have warned about possible biases related to deep SOM ^{14}C dating, advising that single analyses of bulk SOM would fail to take into account inputs of fresh organic matter from root decomposition and solubilised SOC, which could distort the true age of stabilised SOM at depth (Gaudinski et al., 2001; Herold et al., 2014; Krull et al., 2005; Wurster et al., 2010). This artefact can be minimised by implementing an SOM fractionation procedure, whereby distinct organic matter fractions are independently analysed both for δ^{13}C and ^{14}C at different depths. Nevertheless, it remains a challenge to assess past tropical vegetation dynamics without the confounding effects posed by the interaction of varying climatic and edaphic factors.

Environmental gradients offer great opportunities for both understanding mechanisms of abiotic control on ecosystem processes and to study the potential impacts of global change

(Koch et al., 1995). A good example of such a gradient is the sharp climatic gradient existing between the arid conditions characteristic of West Africa's inner continental regions and the humid environments predominant near its southern coast, which strongly influences the distribution and functioning of the wide range of natural ecosystems currently found across this expansive region (Domingues et al., 2010; Saiz et al., 2012; Schrodt et al., 2015; Veenendaal et al., 2015). However, in addition to climatic factors, SOM dynamics may vary considerably depending on the specific physical and chemical characteristics of the soil (Bruun et al., 2010; Paul et al., 2008; Plante and Conant, 2014). Certainly, West Africa presents a wide variety of soil types not directly related to contemporary climate or vegetation (Pullan, 1969), which combined with increasing anthropogenic pressure and the inherent natural heterogeneity of these ecosystems, makes any attempt to generalise SOM dynamics challenging (Saiz et al., 2012).

Field studies using the stable carbon isotopic composition of SOM can help assess the influence of C_3 and C_4 vegetation on SOM dynamics, enabling a test to determine whether there are differential patterns in their mineralisation potential as previously reported in laboratory-based studies (Wynn and Bird, 2007). The objectives of this study are (1) delineate SOM dynamics across contrasting C_3/C_4 mixed semi-natural tropical ecosystems; (2) investigate any potential variation in tropical vegetation thickening along the precipitation transect; and (3) unambiguously evaluate the effect of vegetation thickening on SOM dynamics in two contiguous but structurally different woodland ecosystems.

2 Materials and methods

2.1 Characteristics of the sites

The description of the sites and sampling methodology used in the present work have been provided in detail in a previous publication focusing on the determinants of SOC stocks (Saiz et al., 2012), with further information provided in Torello-Raventos et al. (2013) and Veenendaal et al. (2015). Hence, a short summary is provided here.

The study was conducted across a latitudinal transect encompassing a wide range of semi-natural ecosystems and soils characteristic of West Africa (Figs. 1, 2). The soil sampling campaign took place in Ghana, Burkina Faso, and Mali from August to October 2006. Fourteen study sites comprised of a total of ten 1 ha and four 0.5 ha plots, were established in locations previously identified as representative of the potential natural vegetation of the region. These included National Parks, Forest Reserves, and other legally protected areas except for the Sahelian sites in Mali, which had no specific conservation status and were subject to varying degrees of grazing pressure, the latter also being the case for the most northern Sudan savanna sites of Burkina Faso.
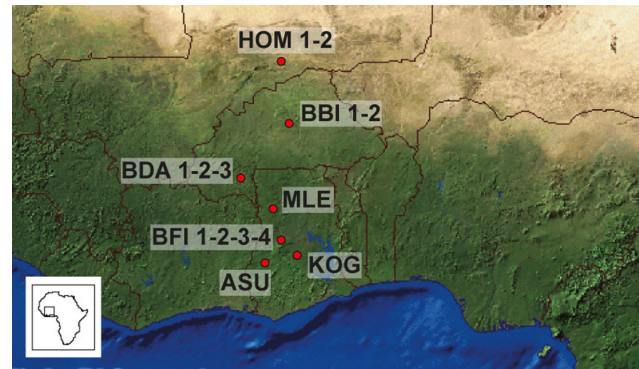

Figure 1. Geographical locations of the studied sites in West Africa. The map interface is adapted from Globalis, a software tool developed by the initiative of the United Nations Association of Norway.

The transect was established on consistently flat terrain with less than 100 m of altitudinal variation between all sites. The northern end of the transect was dominated by Sahelian ecosystems, consisting of grassland savannas (Torello-Raventos et al., 2013) occurring on the relative nutrient-poor Arenosols on the southern border of the Sahara, receiving low mean annual precipitation ($P_A \sim 0.3\,\mathrm{m\,a^{-1}}$) and subject to high rates of potential evaporation (Table A1). Further south there is a natural progression into more woody-dominated savanna forms heavily influenced by a gradual increase in P_A. The southern end of the transect corresponds to the more humid sites supporting semi-deciduous tall forests ($P_A > 1.2\,\mathrm{m\,a^{-1}}$). The variation in mean annual temperature is less than 4 °C across all sites. Saiz et al. (2012) report a wide range of soil types that are the result of the interaction of contrasting geological, climatic, and vegetation factors over extended time periods.

Estimates of the fractional vegetation cover of woody vegetation (FC_w) were obtained as described in Veenendaal et al. (2015), while estimates of the fractional vegetation of the axylale vegetation (FC_a) are as in Torello-Raventos et al. (2013). In short, the canopy area index (C), which is defined as the sum of individual canopy projected area divided by the ground area, was estimated separately for three woody strata. These strata are distinguished on the basis of stem diameter (D) at breast height (1.3 m), and individual tree height (H). The upper (u) stratum consists of trees with $d > 0.1$ m, all of which were individually measured at each plot. The mid (m) stratum consists of woody vegetation of $0.1 > d > 0.025$ m, which was quantified through measurements made along ten 50 m long transects. The subordinate (s) or lower stratum is made up of trees and shrubs with $d < 0.025$ m and $H > 1.5$ m, which were quantified in the same way as the mid-stratum. Subsequently, stand-level canopy projected area for each stratum (Cu, Cm, Cs) was estimated according to site-specific allometric equations presented in Torello-Raventos et al. (2013). Therefore, assum-
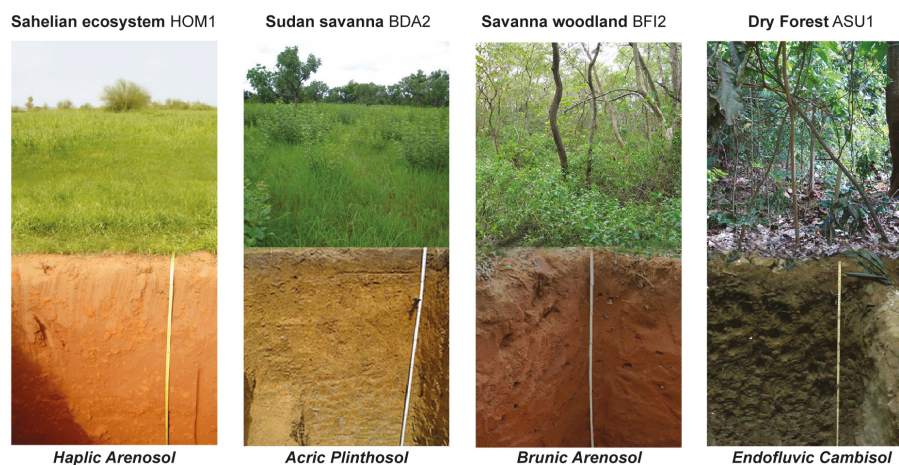
Figure 2. Selected examples of ecosystem types and soil profiles occurring over the precipitation gradient.

ing a random distribution of trees and/or shrubs, the fraction of ground covered by crowns (including within-crown light gaps), which we refer here as the FC of woody vegetation (FC_w) can be estimated as

$$FC_w = 1 - \exp(-Cu - Cm - Cs), \qquad (1)$$

FC_a was visually recorded along a series of transects with a sampling intensity of $110 \times 1\,m^2$ quadrants per plot.

2.2 Soil sampling

We made use of a stratified sampling strategy employed by Bird et al. (2004) and Wynn et al. (2006) that has been proven to be well suited for both studying the inherent spatial heterogeneity of SOM that is typically exhibited in mixed C_3/C_4 environments, and achieving robust regional estimates of SOC inventories. This sampling 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.

Surface litter was removed when present at each sampling location and three soil samples were taken at 0–0.05 m and one sample at 0–0.30 m with the aid of a stainless steel corer 40 mm inner diameter (ø). All the samples were placed in labelled zip-lock bags. Three replicate samples were collected at 0–0.05 m to smooth out local heterogeneity, which is generally more pronounced closer to the soil surface compared to deeper locations. 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 and 0–0.30 m). In addition, a soil pit was hand-dug up to 2 m depth at each plot to assess soil type, provide an estimate of root biomass, and allow for the description of soil characteristics (Quesada et al., 2011). Samples were taken at 0–0.05, 0.05–0.30, 0.30–0.50 m and then every 0.5 up to 2 m depth (impenetrable layers permitting).

2.3 SOM fractionation procedure

Soil samples were fractionated using a combination of physical sieving and density separation following a procedure that has been described in detail by a number of publications (Dondini et al., 2009; Wurster et al., 2010; Zimmermann et al., 2007). Briefly, thirty grams of dry-sieved soil (< 2 mm) was added to 161 mL of ultrapurified water (Milli-Q, Millipore Corp., Massachusetts, USA), and dispersed using a calibrated ultrasonic probe-type (VC 750, Sonics & Materials Inc., Newtown, CT, USA) with an output-energy of $22\,J\,mL^{-1}$. The soil solution was then wet sieved through a 53 µm mesh until the rinsing water was clear, and the size fractions were subsequently dried at 40 °C. All the particulate material passing the 53 µm mesh sieve corresponded to the silt and clay fraction (s+c). The material > 53 µm containing sand and water stable aggregates (heavy fraction - HF) was separated from the light fraction (LF) by means of static dense media separation (Wurster et al., 2010) prepared at $1.87\,g\,cm^{-3}$ using sodium polytungstate (Sometu-Europe™, Berlin, Germany). All the resultant fractions were then washed and filtered at 0.45 µm with ultrapure water to remove any traces of salt, dried at 40 °C, and the weight of each fraction was determined before further analysis.

2.4 Analytical methods and calculations

Stable isotope composition and elemental abundances of carbon and nitrogen were determined in duplicate in powdered samples 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 (U.K.). Precisions (S.D.) on internal standards for elemental carbon and nitrogen abundances and

stable carbon isotopic composition were better than 0.09 % and 0.2 ‰ respectively.

The relative change in C / N ratios (Rc) for the very stable (s+c) fraction in relation to the relatively fresh particulate organic matter represented by the light fraction (LF) was determined for each sampling location (-G and -T) according to the following equations:

$$\mathrm{Rc_G} = 1 - (\mathrm{C/N_{s+c_G}}/\mathrm{C/N_{LF_G}}) \quad (2)$$

$$\mathrm{Rc_T} = 1 - (\mathrm{C/N_{s+c_T}}/\mathrm{C/N_{LF_T}}), \quad (3)$$

where $\mathrm{C/N_{s+c}}$ and $\mathrm{C/N_{LF}}$ are the C / N ratios of the s+c and LF fractions respectively, and the subscripts (-G or -T) indicate the sampling location.

Subsequently, the difference in the relative change in C / N ratios for the two contrasting SOM fractions between both sampling locations ($\Delta\mathrm{C/N^*_{G-T}}$) was calculated for each site according to Eq. (3):

$$\Delta\mathrm{C/N^*_{G-T}} = \mathrm{Rc_G} - \mathrm{Rc_T}. \quad (4)$$

Radiocarbon analyses were conducted at the Accelerator Mass Spectrometry facility managed by the Australian Nuclear Science and Technology Organisation (ANSTO) in Kirrawee, NSW, Australia. [14]C measurement efforts were concentrated at the two transitional sites (BFI-02 and 04) on depth intervals where δ^{13}C values of bulk SOM showed a significant shift (0.3–0.5 m), and also in the deepest studied interval (1.5–2.0 m) in order to determine the τ of mineral-bound deep SOM fractions. Here we use radiocarbon age of each fraction as a proxy for its average τ. Radiocarbon ages were calculated according to Stuiver and Polach (1977). Calculation of τ for samples classified as "Modern" (pMC > 100 %) was determined making use of the model presented by Harkness et al. (1986). The reference [14]CO$_2$ atmospheric data for the Northern Hemisphere in 2006 (date of collection) are those published in Hua and Barbetti (2004) and Levin et al. (2008). Simple interpolation was used to quantify the τ where the data fell between two points on the model. Furthermore, soil texture, pH, and effective cation exchange capacity (ECEC) were determined for different depth intervals to help explain potential variations in τ between the two transitional sites (BFI-02 and 04). Particle size distribution was determined gravimetrically as described by Reeuwijk (2002). Soil pH was measured using a digital pH meter in a 2 : 1 water:soil solution. The CEC was determined by inductively coupled plasma optical emission spectrometry (ICP-OES) extraction of soils using dilute unbuffered Silver-Thiourea for Al, K, Mg, Ca and Na as described by (Quesada et al., 2011), and ECEC was calculated as the sum of these bases.

3 Results

3.1 Stable carbon isotopic composition of SOM across the precipitation transect

Associated with the gradual shift in vegetation from the relatively open savannas found in the interior of the continent in Mali to the dense forests near the Atlantic coast of Ghana (Figs. 1, 2), were changes in the carbon stable isotopic composition of SOM along the transect (Fig. 3a). Shallow soil samples (0–0.05 m) showed distinctly high δ^{13}C values in grass-dominated environments of the north, in contrast with the lower δ^{13}C values observed in the forest ecosystems occurring in the more moist, southern end of the transect. Within each sampling site, higher δ^{13}C values were consistently obtained at -G sampling locations. The difference between -T and -G sampling locations at each site was consistently larger at savanna sites compared to the difference observed in forests (Fig. 3a). Nonetheless, it is worth noting the strong effect of tree clumping in δ^{13}C at sites BDA 01-02, as well as the relatively large difference observed between the two sampling locations at the KOG-01 site, which reflects the vegetation composition of the southernmost savanna site sampled. SOC contents and δ^{13}C values ranged from 1.5 mg C g^{-1} and -13.7 ‰, respectively, in one of the Sahelian sites (HOM-01), to 55.5 mg C g^{-1} and -28.5 ‰ in the semideciduous dry forest (ASU-01) at the south end of the transect (Fig. 4). Carbon contents were generally higher at -T locations, compared to -G locations, while the opposite was true for δ^{13}C values.

3.2 Variation in δ^{13}C values and C / N ratios in bulk soil and SOM fractions

Analyses of bulk soil samples showed that dry forests and woody savannas typically had lower C / N ratios than grass-dominated ecosystems (Fig. 5a). Likewise, for the LF the relationship between δ^{13}C and C / N ratios showed lower C / N values being associated with woodier ecosystems (Fig. 5b); though with the notable exception of the most northerly Sahelian grassland savannas occurring in very sandy soils (HOM sites), which were characterised by very low C / N ratios. Consistently higher C / N ratios were observed in -T compared to -G sampling locations, with the differences between them becoming larger as δ^{13}C values became more positive.

The stable s+c fraction consistently exhibited lower C / N ratios compared to LF at each site (data not shown). However, the relative difference in C / N ratios for these two contrasting SOM fractions generally differed between the (-G and -T) sampling locations at each site (Fig. 6a). Sites showing positive $\Delta\mathrm{C/N^*_{G-T}}$ values indicate that "Grass" sampling locations had a greater relative reduction in C / N ratios than their "Tree" counterparts, while the opposite was true for negative $\Delta\mathrm{C/N^*_{G-T}}$ values. The datum with the low-
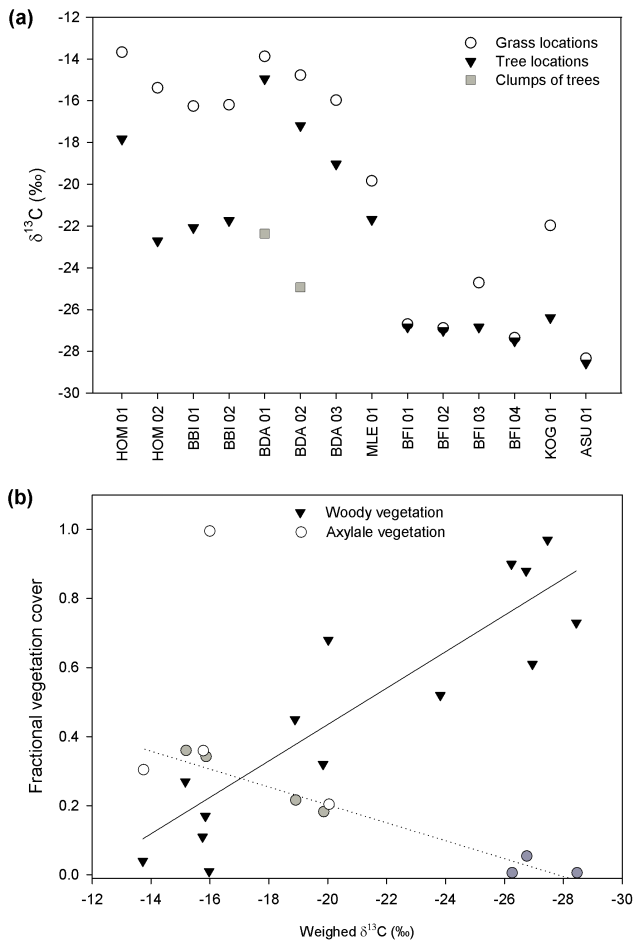
Figure 3. (a) Stable carbon isotope composition of soil samples taken from the 0–0.05 m interval at different sampling locations (i.e. Grass, Tree, and Clumps of trees). Sites are ordered by decreasing latitude; **(b)** relationship between the weighted average stable carbon isotopic composition of all sample locations and both the fractional vegetation cover (FC) of all woody vegetation taller than 1.5 m, and the axylale vegetation (grass and herbs). The gradation intensities of the axylale symbols correspond to the relative contribution of C_4 species over the total axylale vegetation. Accordingly, white, grey and dark-grey symbols represent > 0.66, 0-66-0.33, and < 0.33 of that contribution respectively. Regressions have the form FC $= a + b \times (\delta^{13}C)$ and the regression coefficients (r^2) are 0.81 and 0.93 for the woody (solid line) and axylale (dotted line) vegetation respectively; $p < 0.05$ in both regressions. The pure grassland stand (BDA-03) was not included in the regressions.

est δ^{13}C and a neutral $\Delta C/N^*_{G\text{-}T}$ value corresponds to a dry semideciduous forest with no C_4 vegetation (ASU-01). The relatively large variation in $\Delta C/N^*_{G\text{-}T}$ values across the transect appeared to be strongly controlled by soil textural characteristics (Fig. 6a) with a function driven by sand content and the weighted soil δ^{13}C explaining 0.63 of this variation (Fig. 6b). Here the weighted soil δ^{13}C was calculated

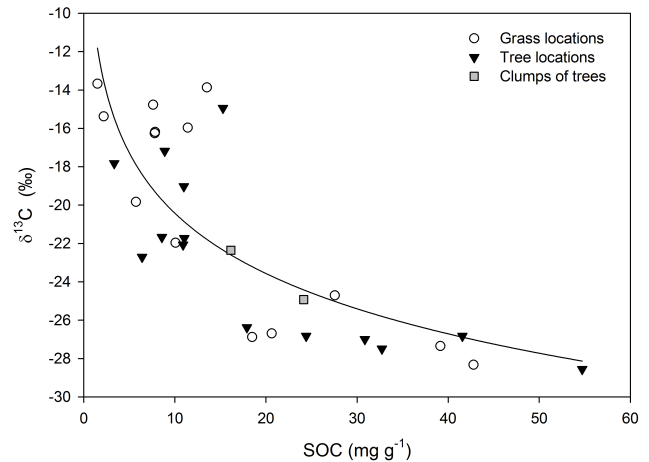**Figure 4.** Relationship between δ^{13}C values and SOC content for the 0–0.05 m depth interval at different sampling locations. The regression has the form: $\delta^{13}C = -4.536 \times \ln (\text{mg g}^{-1} \text{ SOC}) - 9.981$; $r^2 = 0.61$; $p < 0.05$.

for each site according to woody fractional vegetation cover shown in Fig. 3b.

3.3 Stable carbon isotopic composition of SOM with depth across the transect

The differences in δ^{13}C values between samples collected within the 0.05–0.3 m depth interval and the topmost soil layer (0–0.05 m) were relatively small for most sites across the precipitation gradient (< 2 ‰ ; Fig. 7). The exception to this trend occurred at transitional sites, which exist on the boundary between naturally occurring forest and savannas at the wettest end of the transect (KOG-01 and BFI sites). Similarly, the differences in δ^{13}C between the 0.3–0.5 m depth interval and the topmost soil layer (0–0.05 m) were also the largest in these transitional ecosystems. These differences were consistently positive along the transect, except for the case of the Sahelian ecosystems (HOM sites) and KOG-01, a savanna woodland occurring on a very sandy soil. Figure 8 shows the variation of δ^{13}C values in soil profiles spanning 2 m depth for four selected sites, which illustrates the range of past changes in vegetation that may have occurred at some sites across the transect. A slight ^{13}C enrichment with depth is observed in the semideciduous forest at the wettest end of the transect (ASU-01, Fig. 1). Both BFI-02 and BFI-04 show a very large increase in δ^{13}C values with depth. By contrast, a Sahelian site (HOM-01) showed a gradual decrease in δ^{13}C values with soil depth.

3.4 Shifts in δ^{13}C and ^{14}C with depth in SOM fractions in two contrasting transitional ecosystems

Figure 9 shows δ^{13}C values of bulk and fractionated SOM at different depths for two contrasting transitional ecosystems
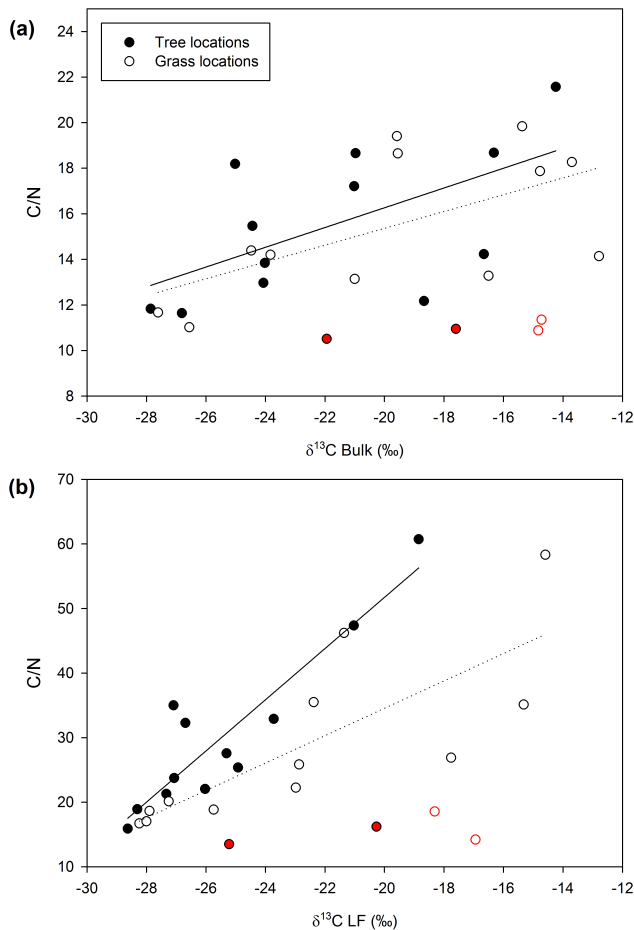
Figure 5. Relationship between δ^{13}C and C/N values across the gradient at both "Tree" and "Grass" sampling locations for **(a)** bulk soil samples, and **(b)** the light fraction (LF). Solid and dotted regression lines denote "Tree" and "Grass" sampling locations respectively. In red are the Sahelian ecosystems (HOM sites), which have not been included in the regressions. All samples derive from the 0–0.3 m depth interval. The regressions have the form C/N $= a + b \times (\delta^{13}$C) and the regression coefficients (r^2) are 0.3 and 0.37 for the Tree and Grass locations respectively for bulk soil samples (5a); while r^2 are 0.83 and 0.63 for the Tree and Grass locations respectively for LF samples (5b); $p < 0.05$ in all regressions.

Figure 6. (a) Relationship between the weighted average soil δ^{13}C calculated for each site and the difference in the relative change in C/N values for two contrasting SOM fractions (see text for details) between -G and -T sampling locations (ΔC/N$^*_{G-T}$). The size of each data point is proportional to sand content. Grey dots denote transitional sites (Saiz et al., 2012; Fig. 7). **(b)** Measured and predicted ΔC/N$^*_{G-T}$ as a function of weighted average δ^{13}C and sand content (sc). The regression takes the form ΔC/N$^*_{G-T} = 0.441 + 0.011$ (δ^{13}C) $- 0.410$ (sc); $r^2 = 0.63$, $P < 0.05$, $n = 13$.

(BFI-02 and BFI-04). Both sites display varying degrees of increase in SOM δ^{13}C values with soil depth. The low δ^{13}C values observed in the top soil layers (0–0.05 m) agree well with the current presence of nearly closed canopy woodlands in which C$_4$ vegetation is either absent (BFI-04), or virtually absent (BFI-02). There were, however, differences in the extent to which δ^{13}C increased with soil depth at each site, although both ecosystems showed a sharp increase in δ^{13}C values within the first 0.5 m. This trend was most acute for the woodland savanna (BFI-02), which exhibited values as high as -18.2 ‰ at 0.3–0.5 m, representing an absolute difference of more than 4 ‰ for that depth interval between the
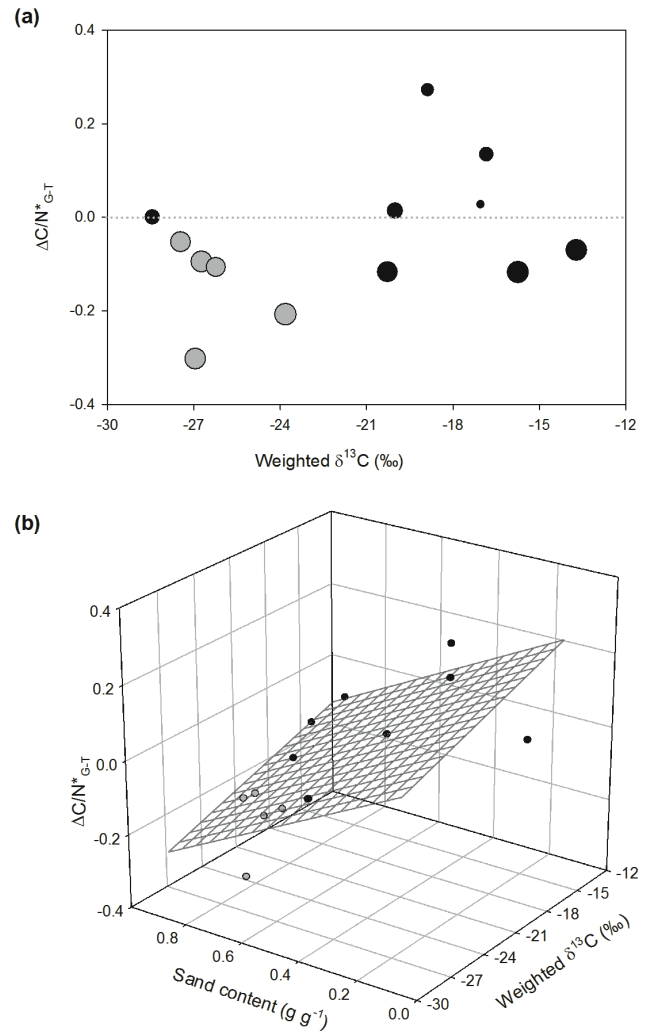
two sites. At deeper locations δ^{13}C was relatively invariant for the dry forest, while there was a gradual change in δ^{13}C towards lower values in the woodland savanna, nearly matching the trend exhibited by the dry forest.

Our results show that SOC contents, root biomass, and C/N ratios decreased with depth (Table 1). Moreover, radiocarbon analyses confirmed that high C/N ratios observed near the surface represented relatively young (with three out of four dates reflecting the contribution of modern carbon fixed after nuclear weapons testing in the late 1950s; Table A2). Furthermore, as is shown in Figure A1 there was
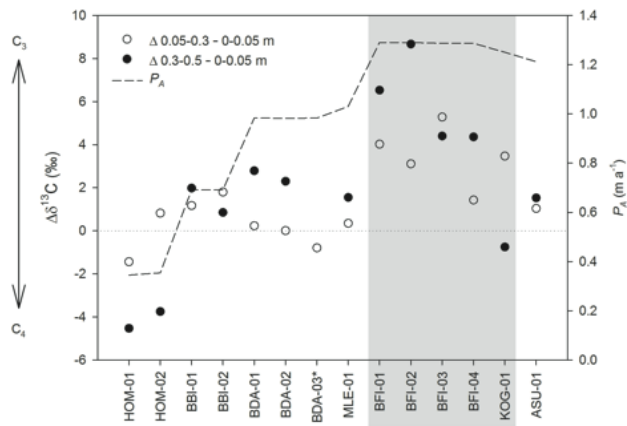
Figure 7. Differences in soil $\delta^{13}C$ values between both the 0.05–0.3 and 0.3–0.5 m depth intervals and the topmost soil layer (0–0.05 m) across the precipitation gradient. The dashed line represents mean annual precipitation (P_A). Sites are ordered by decreasing latitude. The shaded region contains the transitional sites. The asterisk at BDA-3 denotes that soil sampling was limited to 0.19 m only.

Figure 8. Variation in soil $\delta^{13}C$ values with depth for selected ecosystems demonstrating distinctive vegetation dynamics across the precipitation gradient.

a strong positive correlation between ^{14}C activity (pMC) and observed C / N ratios across the various SOM fractions. The sand-size aggregate fraction ($>53\,\mu m$ HF) consistently presented younger ^{14}C ages than the most comminuted fraction ($<53\,\mu m$ s+c) within the same site and depth interval.

4   Discussion

4.1   Stable carbon isotopic composition of SOM across the precipitation transect

The broad range of biotic and abiotic conditions present across the precipitation gradient was reflected in a wide diversity of vegetation structural formation types (Fig. 2). Besides climate, the inherent characteristics of the soil play a dominant role in determining both plant nutrient availability and the amount of water available for plant growth, making it one of the most important factors controlling the type of vegetation at a given site (Bloomfield et al., 2014; Quesada et al., 2012; Saiz et al., 2012). In turn, vegetation type strongly controls the quantity and quality of organic inputs returning to the soil, thus exerting a strong influence on its carbon storage potential (Post et al., 1982; Wynn and Bird, 2007). The gradual depletion in ^{13}C associated with increasing P_A reflects current vegetation patterns well, with high $\delta^{13}C$ values corresponding to grass-dominated savannas (Fig. 3a), showing an axylale (herbs and grasses) layer containing a variable mixture of C_3 and C_4 species (Fig. 3b; see also Torello-Raventos et al. 2013).

The relationship between $\delta^{13}C$ and SOC content in mixed C_3/C_4 systems has been reported to be linear by several local studies (Bird et al., 2004, 2000), with this attributed to differences in the input rates and turnover times of woody
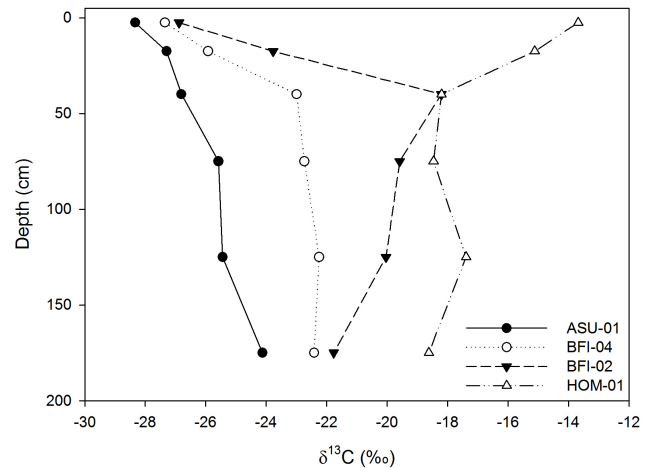
and grass-derived carbon. In the present work the relationship was, however, non-linear (Fig. 4), suggesting that one or several additional factors may have been involved in generating the observed pattern at a broad scale. In our study, the northern arid sites are heavily limited by low water availability with a rainy season of less than 4 months (Schrodt et al., 2015) which undoubtedly not only reduces organic inputs into the soil but likely the rate of OM decomposition as well. The latter is confirmed by previous research conducted over broad latitudinal gradients, which has shown SOM turnover rates to be heavily controlled by climate (Bird and Pousai, 1997; Bird et al., 1996). Besides climatic factors, the contrasting characteristics of the soils studied have been shown to have a strong influence on the potential preservation of SOM (Saiz et al., 2012). It is therefore plausible that the contrasting textural and mineralogical characteristics of these soils may have a major effect on both the physical protection of particulate carbon and the chemical stabilization of ^{13}C enriched microbial metabolites (Dümig et al., 2013; Šantrůčková et al., 2000). Such a strong influence would explain the comparatively high $\delta^{13}C$ and SOC values observed in the iron-rich, silty loams of the BDA sites in particular (Saiz et al., 2012).

4.2   Differential patterns in SOM dynamics across contrasting C_3/C_4 mixed ecosystems

Savannas in their natural state are generally less productive than forests due to a myriad of reasons, which include characteristically lower precipitation, the existence of periods of drought of varying severity, discrete seasonal productivities, and an overall net reduction of annual productivity due to fire (Grace et al., 2006). Studies conducted in West African savannas show that more than half of the net primary productivity of these ecosystems is attributable to C_4 grasses (Menaut

Table 1. Soil properties determined for different depth intervals at both studied sites. Numbers in brackets denote standard deviation from the means ($n = 5$). Analyses were conducted on dry samples sieved to 2 mm.

Site	Depth (m)	Sand (g g^{-1})	Clay (g g^{-1})	pH	eCEC (mmol kg^{-1})	Root density[a] (kg m^{-2})	C (mg g^{-1})	N (mg g^{-1})	C/N	C/N soil fractions[b] Bulk	s+c	HF	LF
	0.00–0.05	0.67	0.15	6.3	12.2 (6.4)	0.4 (0.2)	13.2 (2.1)	1.1 (0.2)	12.5 (1.8)				
	0.05–0.30	0.69	0.09	5.1	12.2 (5.7)	2.3 (3.6)	6.2 (1.5)	0.5 (0.2)	12.3 (2.0)				
BFI 2	0.30–0.50	0.80	0.18	5.2	5.1	2.3 (3.3)	4.3 (1.1)	0.4 (0.1)	11.4 (2.1)	13.5	12.6	21.6	29.7
	0.50–1.00	0.36	0.06	5.4	8.0	0.4 (0.3)	4.1 (0.7)	0.5 (0.1)	9.4 (1.6)				
	1.00–1.50	0.49	0.39	5.6	15.9	0.2 (0.2)	2.7 (0.8)	0.3 (0.1)	8.5 (2.0)				
	1.50–2.00	0.45	0.38	5.6	10.1	0.1 (0.1)	2.8 (0.8)	0.3 (0.1)	8.7 (2.8)	9.1	10.8	9.3	28.9
	0.00–0.05	0.75	0.10	6.4	30.5 (15.7)	0.8 (0.5)	22.3 (12.2)	2.2 (0.9)	11.6 (3.1)				
	0.05–0.30	0.63	0.03	6.8	32.1 (8.8)	0.8 (0.7)	9.0 (7.0)	1.1 (0.6)	10.5 (4.5)				
BFI 4	0.30–0.50	0.73	0.08	6.5	23.6	0.9	1.9	0.2	9.3	12.3	9.6	17.4	30.3
	0.50–1.00	0.57	0.31	4.7	27.6	0.7	2.8	0.4	6.7				
	1.00–1.50	0.43	0.55	4.6	25.7	0.0	2.5	0.3	7.1				
	1.50–2.00	0.43	0.42	4.3	17.3	0.0	1.9	0.2	8.3	9.9	9.5	7.4	20.1

[a] Abundance of root fragments < 0.02 m was assessed over the total dry mass of each individual sample prior to any sieving. [b] Soil fractions were obtained from a composite sample made up from all five individual samples at each depth interval. Bulk: composite sample subject to fractionation; $s + c$: fraction < 53 μm associated to silt and clay; HF: Heavy fraction > 53 μm and > 1.87 g cm^{-3}; LF: Light fraction < 1.87 g cm^{-3}.

and Cesar, 1979), a fact further supported by the pantropical productivity estimates for savannas reported by Lloyd et al. (2008).

In order to facilitate the study of heterogeneous C$_3$/C$_4$ environments, we adopted a soil sampling strategy that allowed for the comparison of soil properties at systematically defined locations. This approach allows for the relative unbiased accounting of the effect of woody cover, thus minimising the potential confounding effects derived from preferential sampling of either grass or woody-dominated areas across all study sites. Indeed, there was considerable variation in carbon isotope composition of surface soil samples at the individual plot scale, as demonstrated by the large differences in δ^{13}C values between -T and -G sampling locations in ecosystems where C$_3$/C$_4$ species coexist (Fig. 3). Similarly, carbon contents were generally higher in -T locations than in their -G counterparts across all sites (Fig. 4). This, especially as it has been reported by some earlier studies (Bird et al., 2000; 2004; Wynn and Bird, 2007), suggests that such variation could be mainly related to differences in the input rates and turnover times of tree and grass-derived carbon. However, both the large temporal and spatial variability in OM inputs and turnover rates, as well as the potentially large time lag between production and decomposition processes, make any comprehensive characterisation of SOM dynamics very challenging, especially under field conditions. Indeed, it is characteristically difficult to make sound generalizations of even the most fundamental properties of natural ecosystems. Such is the case for plant biomass C/N ratios, a feature considered to be highly relevant in SOM decomposition processes (Brady and Weil, 2007; Kirschbaum et al., 2008; Tian et al., 1992).

Plant C/N ratio is greatly dependent on a number of factors that include the type and age of the tissue, sampling season, and the specific characteristics of the species being sampled (i.e. drought tolerant, contents of polyphenol and lignin, etc; Abbadie et al., 2006). Large spatial variability in OM inputs is inherent in commonly heterogeneous tropical environments (Mordelet and Menaut, 1995), and while an adequate assessment of aboveground litter may be relatively straightforward, it is certainly much more difficult to obtain accurate information on the quality, quantity, and spatiotemporal variability of belowground litter dynamics (Gignoux et al., 2006). Hence, it is highly problematic to establish an unambiguous relationship between the properties of the precursor biomass and that of SOM. Figure 5 shows that dry forests and woody savannas typically had lower C/N ratios than grass-dominated ecosystems. The latter environments may also present relatively high C/N values as influenced by their comparatively larger amounts of pyrogenic carbon (Saiz et al., 2012). The exception to such a trend were the Sahelian ecosystems (HOM-01-02) which had very low C/N ratios as a result of their very low biomass (Aranibar et al., 2004), the occurrence of dominant, albeit sparse, nitrogen fixing species (i.e. Acacia sp, Zornia sp.; Hiernaux et al., 2009b), and the external nitrogen inputs from domestic grazers (Saiz et al., 2012). The LF or particulate organic matter is the soil fraction that best reflects recent organic inputs to the soil, as it includes contributions from both aboveground and belowground biomass. This fraction is widely referred to as a very labile SOM component with characteristically high C/N ratios, mainly composed of recent OM inputs that have not yet been physically protected by the soil matrix (Marin-Spiotta et al., 2009; Zimmermann et al., 2007).

We therefore made use of the relative change in C/N ratios between two contrasting SOM fractions (LF and s+c) in order to assess potential differences in SOM dynamics in grass- and tree-dominated sampling locations. Figure 6 shows a relatively large variation in ΔC/N*$_{G-T}$ values across the transect, which appears to be strongly controlled by soil textural characteristics. Negative ΔC/N*$_{G-T}$ values were observed for relatively coarse-textured soils across
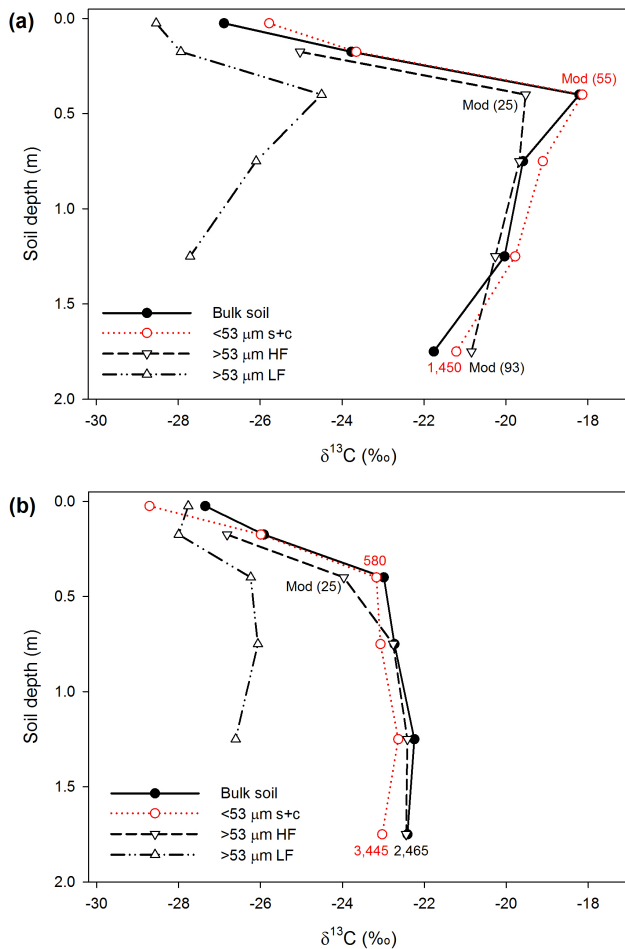
Figure 9. Stable carbon isotope composition of bulk and fractionated SOM, and mean residence times (τ) for two transitional ecosystems in central Ghana; **(a)** savanna woodland (BFI-02), **(b)** semi-deciduous dry forest (BFI-04). Bulk soil is defined as < 2000 µm; < 53 µm is the fraction associated to silt and clay; HF is the heavy fraction > 53 µm (specific density > 1.87 g cm^{-3}); LF is the light fraction > 53 µm (specific density < 1.87 g cm^{-3}). τ of selected SOM fractions are shown adjacent to the fractions and denote conventional radiocarbon ages and, in between brackets, calculated τ derived from radiocarbon analyses presented in Table A2.

through fire and/or overgrazing (Saiz et al., 2015), which have an adverse impact on the amount of fresh organic inputs returned to the soil, an aspect that may be particularly severe in grass-dominated locations (Abbadie and Bismarck Nacro, 2006). These factors, together with the comparably higher SOM contents observed in tree-dominated locations (Fig. 3a), may all result in the persistence of suitable environmental conditions further promoting the activities of SOM decomposers at these localities.

In addition to growing on relatively coarse-textured soils, the transitional sites had a much lower abundance of C$_4$ vegetation (Fig. 3b) which seems is progressively being replaced by newly established C$_3$ plants as a result of woody thickening (the reader is referred to the next section for more details). This might result in low C / N_LF$_G$ values, and consequently an overall negative ΔC/N*$_{G-T}$. On the other hand, positive ΔC/N*$_{G-T}$ values were only evident in open grass-dominated ecosystems occurring on fine-textured soils. Besides maintaining the herbaceous cover for longer than Sahelian ecosystems (HOM sites), these soils also have a greater water retention capacity compared to sites on coarse-textured soils, which may diminish the role of trees as key factors for maintaining suitable conditions for the activities of SOM decomposers.

Further to site-specific soil stabilization mechanisms and differences in the C / N composition of the precursor biomass, it is also likely that differences in the organic biochemical composition of C$_3$ and C$_4$-derived litter represent an inherent primary control on their respective decomposition rates (Meentemeyer, 1978; Melillo et al., 1982). Indeed, the recalcitrance of plant biomass to degradation is a function of how polymers (e.g. lignin and cellulose) crosslink and aggregate within cell walls (McCann and Carpita, 2008), and it is well recognised that the composition of cell walls of grasses greatly differs from those of most other angiosperms (Carpita and Gibeaut, 1993). Abbadie and Bismarck Nacro (2006) showed the preponderant role that grass root mineralisation plays in primary production for savannas where the axylale layer was almost exclusively composed of C$_4$ grass perennials, which also provides support for the grass component being very dynamic. Recent work suggests litter carbon chemistry is a key factor controlling litter decay through its effect on microbial substrate use efficiency (Cotrufo et al., 2013). While the latter is not the focus of the present work, our findings broaden the possibilities for further research to be conducted on preferential substrate utilisation of grass-derived carbon by microbial communities in mixed C$_3$/C$_4$ ecosystems.

Laboratory-based work has reported different turnover times for tree and grass-derived carbon in soils from mixed C$_3$/C$_4$ ecosystems (Bird and Pousai, 1997; Wynn and Bird, 2007). However, the findings of such studies cannot be universally extrapolated given that these controlled experiments could not account for the contrasting environmental conditions likely experienced by "Grass" and "Tree" sampling lo-

the wide range of ecosystems studied, indicating that "Tree" sampling locations exhibited a greater relative change in C / N ratios between the two contrasting SOM fractions than their 'Grass' counterparts. This implies that, at those sites, the processing of SOM was potentially faster in tree-dominated locations compared to those dominated by grass. The role of trees in preserving soil water on coarse-textured soils in semi-arid environments may be very relevant at the canopy level due to their provision of shade and the funnelling of precipitation with associated improvements in soil water availability (Abbadie et al., 2006; Mordelet et al., 1993; Ong and Leakey, 1999). Moreover, these ecosystems traditionally suffer from a recurrent loss of herbaceous cover

cations that usually occur in real field settings. On the other hand, the work by Wynn and Bird (2007) agrees well with our view that, under comparable (site-scale) environmental conditions, C_4-derived SOM decomposes faster than SOM derived from woody biomass in mixed C_3/C_4 ecosystems. Our results further suggest that soil textural properties exert a strong influence on SOM dynamics across the ecosystems examined along the transect. We postulate that the interdependence between biotic and abiotic factors ultimately determine whether SOM dynamics of C_3- and C_4-derived vegetation differ from each other in ecosystems where both vegetation types coexist.

4.3 Vegetation shifts along the precipitation transect

The differences in $\delta^{13}C$ values between the surface (0–0.05 m) and the 0.3–0.5 m interval provide evidence of recent vegetation shifts across the precipitation gradient (Fig. 7). Even after considering the relatively small ^{13}C enrichment with depth typically observed in semi-arid soils (Bird et al., 2004; Krull et al., 2005), our results suggest a significant increase in woody vegetation at the wetter sites along the transect. The trend in isotope composition with depth is also heavily dependant on the characteristics of the soils, which have also been identified as one of the main determinants of vegetation type observed at each site (Saiz et al., 2012). Vegetation thickening reached its maximum in the transitional ecosystems (BFI sites; Fig. 2), which constitute the natural border between savanna and dry forests on the transect. The vegetation dynamics occurring at each end of the precipitation gradient were quite different (Fig. 8). On the one hand, the wettest end of the transect corresponded to a semideciduous dry forest (ASU-01) showing quite a stable $\delta^{13}C$ composition of SOM with depth, which agrees well with the long-term persistence of a closed canopy ecosystem. On the other hand, the arid Sahelian ecosystems studied (HOM sites) may have experienced a relatively recent reduction in woody cover as evidenced from the large enrichment in ^{13}C towards the surface. There may be several reasons behind this potential thinning of woody biomass at the driest sites, with a combination of overgrazing, fuel harvesting, fires, and above all the severe droughts suffered over the past few decades, being the most likely causes (Krull et al., 2007). However, Sahelian ecosystems are known to have a large resilience to drought and grazing, to the extent that woody plant population dynamics can largely vary between nearby sites as a result of contrasting substrates, grazing intensities, land use history, and species composition (Hiernaux et al., 2009a; Mougin et al., 2009).

Vegetation shifts at a given site may alter the quantity and quality of OM inputs into the soil, as different vegetation types are likely to have distinct biochemical and physiological characteristics. Therefore, these vegetation dynamics will have significant impacts on the total production and allocation of biomass and on its mineralization potential (Melillo

et al., 1982; Wynn and Bird, 2007). Moreover, fundamental differences in $\delta^{13}C$ fractionation dynamics have been reported for different soils and types of organic matter (Krull and Skjemstad, 2003), and it is therefore of paramount importance to unambiguously evaluate the impact that vegetation shifts may have exerted on SOM dynamics in the past.

4.4 Effect of vegetation thickening on SOM dynamics in two neighbouring transitional ecosystems

As has been previously discussed, it is difficult to assess past vegetation dynamics in isolation from the confounding effects posed by the interactions between climatic and edaphic factors. However, a Natural Reserve in central Ghana provided the ideal conditions to study potential shifts in vegetation in two structurally different ecosystems occurring under the same climatic conditions given that the sites are < 1 km from each other. The two sites are classified as transitional ecosystems, each with vegetation widely divergent from the other (Table 1). BFI-02 is a savanna woodland with a relatively sparse tree canopy cover (0.6) that allows the development of a thin grass stratum. BFI-04 is a semideciduous dry tall forest with an almost complete tree canopy closure (0.8). For a detailed floristic composition of these sites, refer to Domingues et al. (2010) and Torello-Raventos et al. (2013).

The detailed study of these two sites revealed a close concordance in $\delta^{13}C$ values along the soil profile between bulk SOM and the fractions associated with silt and clay (s+c), and to a lesser degree to sand-size aggregates (HF; Fig. 9). The only obvious exception to this general trend was the surface layer (0–0.05 m), where a significant proportion of the OM may not be associated with mineral phases. The observed decrease in both SOC contents and C / N ratios with depth at both sites (Table 1) is a commonly reported observation indicating that deep SOM is usually highly processed by microbes (Rumpel and Kögel-Knabner, 2011). It is also worth noting the large differences in C / N ratios between LF and the rest of the fractions, which confirm their contrasting degrees of decomposition.

Fractionation of OM down soil profiles has previously been used to isolate fresh OM inputs derived from current vegetation (Krull et al., 2005; Marin-Spiotta et al., 2009). Indeed, the LF had significantly lower $\delta^{13}C$ values compared to the bulk soil, with this difference increasing with depth at both sites. This is consistent with higher contemporary C_3 vegetation input throughout the soil profile than was the case at some time in the past. On the other hand, the increasing $\delta^{13}C$ values with soil depth is another commonly reported feature that may be explained by a combined effect of several factors, which include OM decomposition processes (i.e., progressive significance of microbial and fungal decay to the SOM pool), the influence of carbon fixed from the higher $\delta^{13}C$ atmosphere that existed prior to significant fossil fuel burning, and stabilization mechanisms influenced by specific properties of a given soil (Bird et al., 1996; Ehleringer et al.,

2000; Krull et al., 2003). However, the magnitude of the increase in $\delta^{13}C$ values, and more specifically the large differences observed in $\delta^{13}C$ between fresh organic matter (LF) and other fractions, are critical indicators that the vegetation at these sites is undergoing significant change (Krull et al., 2005).

It is worth reflecting on the very different τ observed between the two sites. Both ecosystems present highly dynamic SOM processes, highlighted by the relatively short τ of sand-size aggregates ($> 53\,\mu m$ HF) even at considerable depth (1.5–2.0 m; Fig. 9). Interestingly, the most stable SOM fraction associated with silt and clay ($< 53\,\mu m$ s+c) has a shorter radiocarbon age in the savanna woodland (1450 y BP) than in the pure C_3 dry forest site (3445 y BP). The main reason for the contrasting τ observed in comparable fractions between the two sites may be the different input rates of belowground OM. There is increasing evidence that SOM turnover is mainly controlled by its availability to decomposers (Don et al., 2013; Dungait et al., 2012). These sites are characterised by a low abundance of SOM, particularly at depth, and it is likely that woody encroachment has led to an increase in recent organic matter inputs below the topmost soil as a result of the larger/deeper root systems characteristic of woody vegetation (Boutton et al., 2009). This process may have been more pronounced in the savanna woodland (BFI-02 site) with the previously more abundant grassland stratum being gradually replaced with woody vegetation, as demonstrated by the large shift in $\delta^{13}C$ values towards the surface (Fig. 9). While both sites show a strong reduction in root biomass with depth, this trend is more obvious in the case of the dry tall forest (BFI-04), which shows a lower belowground biomass content over the entire soil profile compared to the savanna woodland (BFI-02; Table 1). This observation is in agreement with findings reported by Lawson et al. (1970, 1968) in work conducted in a savanna and a tropical deciduous forest in Ghana. Butler et al. (2012) also compared two structurally contrasting savannas, and found that the more open canopy savanna had a proportionally higher carbon investment belowground. Recent findings reported by Don et al. (2013) show that any increase in the carbon concentration down the soil profile decreases the distance between decomposer and substrate, which may increase accessibility and SOM turnover. Therefore, the enhanced contribution in belowground organic matter inputs in the savanna woodland as a result of woody encroachment could largely explain its comparatively shorter τ across all soil fractions compared to the dry forest (Figs. 9, A1).

It is well established that the physical protection of SOM by aggregation mechanisms plays a fundamental role in soil carbon stabilisation (Denef et al., 2001; Six et al., 2004). Root-derived particulate organic matter has a significant control on aggregate dynamics (Six et al., 2004) as the stabilization and de-stabilization of macroaggregates in soils is strongly linked to the incorporation and biodegradation of fresh plant debris (Puget et al., 2000). This fresh OM is even-

tually redistributed among aggregate classes through their destruction and re-formation. Compared to grasses, the comparatively more recalcitrant OM input from woody vegetation can promote lower microbial substrate use efficiency, which may have a negative effect on aggregate stability (Cotrufo et al., 2013). Furthermore, a combination of $\delta^{13}C$ and ^{14}C measurements has shown that even very stable soil structures, such as iron nodules containing occluded carbon, do not act as closed systems with respect to organic carbon exchange (Bird et al., 1994). These observations together with the findings presented in this study, further suggest that carbon transfers within the soil matrix are highly dynamic, especially if impacted by recent shifts in vegetation type (Guidi et al., 2014). It is therefore highly likely that the different τ observed between the two sites is strongly influenced by vegetation-related factors, especially when considering that there are only minor differences in soil physical properties (i.e. texture, mineralogy – cf. Table 1 in Saiz et al., 2012), which are, by themselves, insufficient to explain such contrasting τ between the two sites. Therefore, making the reasonable assumption that both stands have been exposed to comparable deposition and erosion regimes; our results strongly suggest that both ecosystems are undergoing a rapid transition from open woodlands to denser canopy formations. However, such vegetation thickening varies in intensity at each site, and this exerts contrasting effects on their SOM dynamics (Fig. A1).

5 Conclusions

The first objective of this study was to assess the influence of C_3 and C_4 vegetation on SOM dynamics in semi-natural tropical ecosystems sampled along a precipitation gradient in West Africa. This work shows that the interdependence between biotic and abiotic factors ultimately determine whether SOM dynamics of C_3- and C_4-derived vegetation are at variance in ecosystems where both vegetation types coexist. Our results suggest that soil textural properties exert a strong influence on the contrasting SOM dynamics observed across the precipitation gradient. Accordingly, C_4-derived SOM decomposes faster than SOM derived from woody biomass in mixed C_3/C_4 ecosystems, provided comparable (site-scale) environmental conditions exist. This is in agreement with previous research conducted under controlled environmental conditions (Wynn and Bird, 2007). Moreover, studies conducted in West African savannas as well as pantropical productivity estimates both show that more than half of the net primary productivity of these ecosystems is attributable to C_4 grasses (Lloyd et al., 2008; Menaut and Cesar, 1979). This agrees well with the notion that, at least in non-coarse textured soils, SOC sequestration potential per unit productivity must be inherently lower for C_4 dominated locations, which is further confirmed by the comparatively lower SOC

concentrations observed at grass-dominated locations (Saiz et al., 2012).

The second objective of our study was to investigate potential variations in tropical vegetation shifts along the precipitation transect. Vegetation thickening was significant at the more humid sites, in the zones of tension where forest and savanna formations coexist. Our findings reveal that current environmental conditions favour the expansion of C_3 species over their C_4 counterparts in the more mesic savanna ecosystems of West Africa. Such vegetation dynamics pose significant impacts not only on the total production and allocation of biomass, but also on its mineralization potential.

The third objective was to unambiguously evaluate the effect of vegetation thickening on SOM dynamics in two contiguous but structurally contrasting transitional ecosystems occurring on comparable soils. Such a setting was chosen to minimise confounding effects posed by climatic and edaphic factors as fundamental differences in δ^{13}C fractionation dynamics have been reported for different soils and types of organic matter (Krull and Skjemstad, 2003). Radiocarbon dating of SOM fractions together with the vertical variation in δ^{13}C values strongly suggest that both ecosystems are undergoing a rapid transition towards denser closed canopy formations. However, vegetation thickening varied in intensity at each site and exerted contrasting effects on SOM dynamics. This study further highlights the far-reaching implications that vegetation thickening has for the stability of deep SOC, which has been shown to be heavily controlled by fresh organic inputs (Fontaine et al., 2007). It also confirms that SOM pools that have been stabilized for centuries to millennia may be susceptible to abrupt change when soils cross pedogenic thresholds associated with rapid shifts in vegetation (Trumbore, 2009).

Our findings have significant implications for a lot of carbon cycle science that exploits the carbon isotopic difference of C_3/C_4 photosynthetic pathways. This includes research work that uses the variation in soil δ^{13}C values to unravel past vegetation shifts and their impact on SOC storage, paleoenvironmental interpretations, and modelling of ecosystem carbon budgets (Lloyd et al., 2008; Saiz et al., 2015; Wynn and Bird, 2007).

Appendix A

Table A1. General characteristics of the sites.

Site	Lat. (N)	Lon. (W)	MAP (m)	MAT (°C)	Regional classification of vegetation	Soil type WRB	Textural class FAO (USDA)
HOM-1	15.344	1.468	0.34	29.9	Open Sudan savanna (Sahel)	Haplic Arenosol	Coarse (Sandy)
HOM-2	15.335	1.547	0.35	30.0	Open Sudan savanna (Sahel)	Haplic Arenosol	Coarse (Sandy)
BBI-1	12.731	1.165	0.69	28.3	Open Sudan savanna	Haplic Luvisol	Medium (Clay Loam)
BBI-2	12.733	1.163	0.69	28.3	Open Sudan savanna	Pisolithic Plinthosol	Medium (Loam)
BDA-1	10.940	3.149	0.98	27.8	Open Savanna woodland	Haplic Fluvisol	Medium Fine (Silty loam)
BDA-2	10.940	3.154	0.98	27.9	Open Savanna woodland	Acric Stagnic Plinthosol	Medium (Silty loam)
BDA-3	10.865	3.073	0.98	27.6	Open Savanna grassland	Epipetric Stagnic Plinthosol	n/a
MLE-1	9.304	1.858	1.03	27.9	Open Savanna woodland Guinea	Brunic Arenosol	Coarse (Loamy sand)
BFI-1	7.714	1.694	1.29	25.4	Savanna woodland Transition zone	Haplic Alisol	Coarse (Sandy loam)
BFI-2	7.715	1.692	1.29	25.4	Savanna woodland Transition zone	Brunic Arenosol	Coarse (Sandy loam)
BFI-3	7.705	1.696	1.29	25.4	Semideciduous dry forest Transition zone	Haplic Nitosol	Medium (Sandy clay loam)
BFI-4	7.708	1.698	1.29	25.4	Semideciduous dry forest Transition zone	Haplic Nitosol	Medium (Sandy Loam)
KOG-1	7.302	1.180	1.25	26.3	Savanna woodland Transition zone	Haplic Arenosol	Coarse (Loamy sand)
ASU-1	7.137	2.447	1.21	26.0	Semideciduous dry forest	Endofluvic Cambisol	Medium (Loam)

MAP and MAT stand for mean annual precipitation, and mean annual temperature respectively. For the regional classification of vegetation the reader is referred to Domingues et al. (2010). The soil textural classes are based on the 0.0–0.30 m interval, except for BDA-3 which had a 0.19 m average maximum depth.

Table A2. Radiocarbon results (AINSE Grant 12/030; RUN 393; Fink et al., 2004) and calculated mean residence times (τ).

ANSTO code	Sample ID	$\delta^{13}C$ (‰)	Percent Modern Carbon (pMC)	Conventional radiocarbon age (y BP)	Calculated τ (y)
OZP675	BFI-02 30–50 < 53	-18.1 ± 0.2	113.06 ± 0.37	Modern	55
OZP676	BFI-02 150–200 < 53	-20.4 ± 0.1	83.48 ± 0.30	1450 ± 30	
OZP677	BFI-02 30–50 HF	-21.2 ± 0.1	122.81 ± 0.45	Modern	25
OZP678	BFI-02 150–200 HF	-21.0 ± 0.2	108.88 ± 0.39	Modern	93
OZP679	BFI-04 30–50 < 53	-22.4 ± 0.1	93.06 ± 0.37	580 ± 35	
OZP680	BFI-04 150–200 < 53	-22.6 ± 0.1	65.12 ± 0.27	3445 ± 35	
OZP681	BFI-04 30–50 HF	-24.3 ± 0.1	122.07 ± 0.41	Modern	25
OZP682	BFI-04 150-200 HF	-21.9 ± 0.1	73.59 ± 0.27	2465 ± 30	

$\delta^{13}C$ values relate solely to the graphite derived from the fraction that was used for the radiocarbon measurement. Results from both percent modern carbon (pMC) and conventional radiocarbon age are reported with 1σ errors ($\pm$) attached.
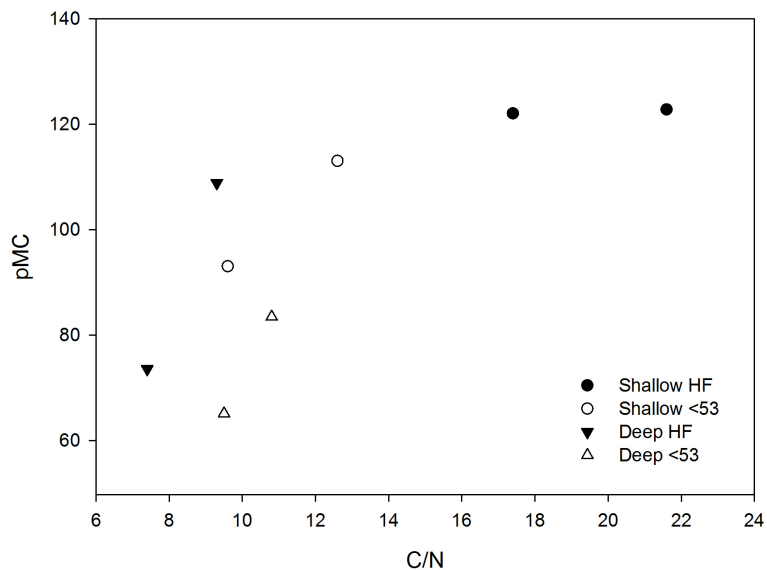
Figure A1. Comparison of ^{14}C data (pMC) and C / N ratios presented in Table 1 for the fractionated SOM samples. Circles indicate shallow samples (0.3–0.5 m) and triangles denote deep samples (1.5–2.0 m). < 53 μm is the fraction associated to silt and clay; HF is the heavy fraction > 53 μm (specific density > 1.87 g cm^{-3}). The largest C / N value of each paired symbol consistently represents BFI-02.

References

Abbadie, L. and Bismarck Nacro, H.: Soil carbon and organic matter dynamics, in: Lamto, structure, functioning, and dynamics of a savanna ecosystem, edited by: Abbadie, L., Gignoux, J., Roux, X., and Lepage, M., Springer, New York, USA, 179, 201–214, 2006.

Abbadie, L., Gignoux, J., Roux, X., and Lepage, M.: Lamto: structure, functioning, and dynamics of a savanna ecosystem, Springer, New York, USA, 2006.

Aranibar, J. N., Otter, L., Macko, S. A., Feral, C. J., Epstein, H. E., Dowty, P. R., Eckardt, F., Shugart, H. H., and Swap, R. J.: Nitrogen cycling in the soil–plant system along a precipitation gradient in the Kalahari sands, Glob. Change Biol., 10, 359–373, 2004.

Archer, S., Boutton, T. W., and Hibbard, K. A.: Trees in Grasslands: Biogeochemical Consequences of Woody Plant Expansion, in: Global Biogeochemical Cycles in the Climate System, edited by: Schulze, E.-D., Heimann, M., Harrison, S., Holland, E., Lloyd, J., Prentice, I. C., and Schimel, D., 115–137, Academic Press, San Diego, 2001.

Archer, S., Boutton, T. W., and McMurtry, C.: Carbon and nitrogen accumulation in a savanna landscape: field and modeling perspectives, Global environmental change in the ocean and on land, Terrapub, Tokyo, 359–373, 2004.

Bernoux, M., Cerri, C. C., Neill, C., and de Moraes, J. F.: The use of stable carbon isotopes for estimating soil organic matter turnover rates, Geoderma, 82, 43–58, 1998.

Bird, M. I. and Pousai, P.: Variations of δ13C in the surface soil organic carbon pool, Global Biogeochem. Cy., 11, 313–322, 1997.

Bird, M. I., Quade, J., Chivas, A. R., Fifield, L. K., Allan, G. L., and Head, M. J.: The carbon isotope composition of organic matter occluded in iron nodules, Chem. Geol., 114, 269–279, 1994.

Bird, M. I., Chivas, A. R., and Head, J.: A latitudinal gradient in carbon turnover times in forest soils, Nature, 381, 143–146, 1996.

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

Bird, M. I., Veenendaal, E. M., and Lloyd, J. J.: Soil carbon inventories and δ13C along a moisture gradient in Botswana, Glob. Change Biol., 10, 342–349, 2004.

Blagodatskaya, E., Yuyukina, T., Blagodatsky, S., and Kuzyakov, Y.: Turnover of soil organic matter and of microbial biomass under C 3–C 4 vegetation change: Consideration of 13 C fractionation and preferential substrate utilization, Soil Biol. Biochem., 43, 159–166, 2011.

Bloomfield, K. J., Domingues, T. F., Saiz, G., Bird, M. I., Crayn, D. M., Ford, A., Metcalfe, D. J., Farquhar, G. D., and Lloyd, J.: Contrasting photosynthetic characteristics of forest vs. savanna species (Far North Queensland, Australia), Biogeosciences, 11, 7331–7347, doi:10.5194/bg-11-7331-2014, 2014.

Bond, W. J. and Midgley, G. F.: Carbon dioxide and the uneasy interactions of trees and savannah grasses, Philos. T. R. Soc. B, 367, 601–612, 2012.

Boutton, T. W.: Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change, in: Mass spectrometry of soils, edited by: Boutton, T. W. and Yamasaki, I. S., Marcel Dekker Inc., New York, USA, 47–82, 1996.

Boutton, T. W., Liao, J. D., Filley, T. R., and Archer, S. R.: Belowground carbon storage and dynamics accompanying woody plant encroachment in a subtropical savanna, in: Soil Carbon Sequestration and the Greenhouse Effect, edited by: Lal, R. and Follett, R., Soil Sci. Soc. Am., Madison, WI, 181–205, 2009.

Brady, N. C. and Weil, R. R.: The nature and properties of soils, 14 ed., Prentice Hall, Inc., New Jersey, USA, 506–511, 2007.

Bruun, T. B., Elberling, B., and Christensen, B. T.: Lability of soil organic carbon in tropical soils with different clay minerals, Soil Biol. Biochem., 42, 888–895, doi::10.1016/j.soilbio.2010.01.009, 2010.

Buitenwerf, R., Bond, W. J., Stevens, N., and Trollope, W.: Increased tree densities in South African savannas: > 50 years of data suggests CO_2 as a driver, Glob. Change Biol., 18, 675–684, 2012.

Butler, A., Meir, P., Saiz, G., Maracahipes, L., Marimon, B. S., and Grace, J.: Annual variation in soil respiration and its component parts in two structurally contrasting woody savannas in Central Brazil, Plant Soil, 352, 129–142, 2012.

Carpita, N. C. and Gibeaut, D. M.: Structural models of primary cell walls in flowering plants: consistency of molecular structure

with the physical properties of the walls during growth, Plant J., 3, 1–30, 1993.

Cerling, T. E., Wynn, J. G., Andanje, S. A., Bird, M. I., Korir, D. K., Levin, N. E., Mace, W., Macharia, A. N., Quade, J., and Remien, C. H.: Woody cover and hominin environments in the past 6 [thinsp] million years, Nature, 476, 51–56, 2011.

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., and Paul, E.: The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter?, Glob. Change Biol., 19, 988–995, 2013.

Creamer, C. A., Filley, T. R., Boutton, T. W., Oleynik, S., and Kantola, I. B.: Controls on soil carbon accumulation during woody plant encroachment: Evidence from physical fractionation, soil respiration, and delta C-13 of respired CO$_2$, Soil Biol. Biochem., 43, 1678–1687, doi:10.1016/j.soilbio.2011.04.013, 2011.

Crow, S., Swanston, C., Lajtha, K., Brooks, J. R., and Keirstead, H.: Density fractionation of forest soils: methodological questions and interpretation of incubation results and turnover time in an ecosystem context, Biogeochemistry, 85, 69–90, doi:10.1007/s10533-007-9100-8, 2007.

Denef, K., Six, J., Paustian, K., and Merckx, R.: Importance of macroaggregate dynamics in controlling soil carbon stabilization: short-term effects of physical disturbance induced by dry–wet cycles, Soil Biol. Biochem., 33, 2145–2153, 2001.

Domingues, T. F., Meir, P., Feldpausch, T. R., Saiz, G., Veenendaal, E. M., Schrodt, F., Bird, M., Djagbletey, G., Hien, F., Compaore, H., Diallo, A., Grace, J., and Lloyd, J.: Colimitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands, Plant Cell Environ., 33, 959–980, doi:10.1111/j.1365-3040.2010.02119.x, 2010.

Don, A., Rödenbeck, C., and Gleixner, G.: Unexpected control of soil carbon turnover by soil carbon concentration, Environ. Chem. Lett., 11, 407–413, 2013.

Dondini, M., Hastings, A., Saiz, G., Jones, M. B., and Smith, P.: The potential of Miscanthus to sequester carbon in soils: comparing field measurements in Carlow, Ireland to model predictions, Glob. Change Biol., 1, 413–425, doi:10.1111/j.1757-1707.2010.01033.x, 2009.

Donohue, R. J., Roderick, M. L., McVicar, T. R., and Farquhar, G. D.: Impact of CO$_2$ fertilization on maximum foliage cover across the globe's warm, arid environments, Geophys. Res. Lett., 40, 3031–3035, 2013.

Dungait, J. A., Hopkins, D. W., Gregory, A. S., and Whitmore, A. P.: Soil organic matter turnover is governed by accessibility not recalcitrance, Glob. Change Biol., 18, 1781–1796, 2012.

Dümig, A., Rumpel, C., Dignac, M.-F., and Kögel-Knabner, I.: The role of lignin for the δ13C signature in C$_4$ grassland and C$_3$ forest soils, Soil Biol. Biochem., 57, 1–13, 2013.

Ehleringer, J. R., Buchmann, N., and Flanagan, L. B.: Carbon isotope ratios in belowground carbon cycle processes, Ecol. Appl., 10, 412–422, 2000.

Eswaran, H., Van Den Berg, E., and Reich, P.: Organic carbon in soils of the world, Soil Sci. Soc. Am. J., 57, 192–194, 1993.

Fink, D., Hotchkis, M., Hua, Q., Jacobsen, G., Smith, A. M., Zoppi, U., Child, D., Mifsud, C., van der Gaast, H., Williams, A., and Williams, M.: The ANTARES AMS facility at ANSTO, Nucl.Instrum. M. B , 223, 109–115, 2004.

Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B., and Rumpel, C.: Stability of organic carbon in deep soil layers controlled by fresh carbon supply, Nature, 450, 277–280, 2007.

Gaudinski, J., Trumbore, S., Davidson, E., Cook, A., Markewitz, D., and Richter, D.: The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon, Oecologia, 129, 420–429, 2001.

Gignoux, J., Mordelet, P., and Menaut, J. C.: Biomass cycle and primary production, in: Lamto, Structure, Functioning, and Dynamics of a Savanna Ecosystem, vol. Ecological Studies 179, edited by: Abbadie, L., Gignoux, J., Roux, X., and Lepage, M., 115–137, Springer, New York, 2006.

Grace, J., José, J. S., Meir, P., Miranda, H. S., and Montes, R. A.: Productivity and carbon fluxes of tropical savannas, J. Biogeogr., 33, 387–400, 2006.

Guidi, C., Magid, J., Rodeghiero, M., Gianelle, D., and Vesterdal, L.: Effects of forest expansion on mountain grassland: changes within soil organic carbon fractions, Plant Soil, 385, 373–387, 2014.

Guillet, B., Achoundong, G., Happi, J., Beyala, V., Bonvallot, J., Riera, B., Mariotti, A., and Schwartz, D.: Agreement between floristic and soil organic carbon isotope (C-13/C-12, C-14) indicators of forest invasion of savannas during the last century in Cameroon, J. Trop. Ecol., 17, 809–832, 2001.

Hall, D. O. and Scurlock, J.: Climate change and productivity of natural grasslands, Annals Bot., 67, 49–55, 1991.

Harkness, D. D., Harrison, A. F., and Bacon, P. J.: The temporal distribution of "bomb" ^{14}C in a forest soil, Radiocarbon, 28, 328–337, 1986.

Herold, N., Schöning, I., Michalzik, B., Trumbore, S., and Schrumpf, M.: Controls on soil carbon storage and turnover in German landscapes, Biogeochemistry, 119, 435–451, 2014.

Hiernaux, P., Diarra, L., Trichon, V., Mougin, E., Soumaguel, N., and Baup, F.: Woody plant population dynamics in response to climate changes from 1984 to 2006 in Sahel (Gourma, Mali), J. Hydrol., 375, 103–113, 2009a.

Hiernaux, P., Mougin, E., Diarra, L., Soumaguel, N., Lavenu, F., Tracol, Y., and Diawara, M.: Sahelian rangeland response to changes in rainfall over two decades in the Gourma region, Mali, J. Hydrol., 375, 114–127, 2009b.

Hua, Q. and Barbetti, M.: Review of tropospheric bomb ^{14}C data for carbon cycle modeling and age calibration, Radiocarbon, 46, 1273–1298, 2004.

Jackson, R. B., Schenk, H. J., Jobbagy, E. G., Canadell, J., Colello, G. D., Dickinson, R. E., Field, C. B., Friedlingstein, P., Heimann, M., Hibbard, K., Kicklighter, D. W., Kleidon, A., Neilson, R. P., Parton, W. J., Sala, O. E. ,and Sykes, M. T.: Belowground Consequences of Vegetation Change and Their Treatment in Models, Ecol. Appl., 10, 470–483, 2000.

Kirschbaum, M. U., Guo, L. B., and Gifford, R. M.: Why does rainfall affect the trend in soil carbon after converting pastures to forests?: A possible explanation based on nitrogen dynamics, Forest Ecol. Manag., 255, 2990–3000, 2008.

Koch, G. W., Vitousek, P. M., Steffen, W. L., and Walker, B. H.: Terrestrial transects for global change research, Vegetatio, 121, 53–65, 1995.

Krull, E. S. and Skjemstad, J. O.: δ 13 C and δ 15 N profiles in 14 C-dated Oxisol and Vertisols as a function of soil chemistry and mineralogy, Geoderma, 112, 1–29, 2003.

Krull, E., Skjemstad, J., Graetz, D., Grice, K., Dunning, W., Cook, G., and Parr, J.: C-13-depleted charcoal from C4 grasses and the role of occluded carbon in phytoliths, Org. Geochem., 34, 1337–1352, doi:10.1016/S0146-6380(03)00100-1, 2003.

Krull, E., Skjemstad, J., Burrows, W., Bray, S., Wynn, J., Bol, R., Spouncer, L., and Harms, B.: Recent vegetation changes in central Queensland, Australia: Evidence from delta C-13 and C-14 analyses of soil organic matter, Geoderma, 126, 241–259, doi:10.1016/j.geoderma.2004.09.012, 2005.

Krull, E., Bray, S., Harms, B., Baxter, N., Bol, R., and Farquhar, G.: Development of a stable isotope index to assess decadal-scale vegetation change and application to woodlands of the Burdekin catchment, Australia, Glob. Change Biol., 13, 1455–1468, doi:10.1111/j.1365-2486.2007.01376.x, 2007.

Lawson, G. W., Armstrong Mensah, K. O., and Hall, J. B.: A catena in tropical moist semi-deciduous forest near Kade, Ghana, Journal of ecology, 58, 371–398, 1970.

Lawson, G. W., Jenik, J., and Armstrong Mensah, K. O.: A study of a vegetation catena in Guinea savanna at Mole Game Reserve Ghana, J. Ecol., 56, 505–522, 1968.

Leifeld, J. and Fuhrer, J.: Long-term management effects on soil organic matter in two cold, high-elevation grasslands: clues from fractionation and radiocarbon dating, Eur. J. Soil Sci., 60, 230–239, doi:10.1111/j.1365-2389.2008.01111.x, 2009.

Levin, I., Hammer, S., Kromer, B., and Meinhardt, F.: Radiocarbon observations in atmospheric CO_2: Determining fossil fuel CO_2 over Europe using Jungfraujoch observations as background, Sci. Total Environ., 391, 211–216, 2008.

Liao, J. D., Boutton, T. W., and Jastrow, J. D.: Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland, Soil Biol. Biochem., 38, 13–13, doi:10.1016/j.soilbio.2006.04.003, 2006.

Lloyd, J., Bird, M. I., Vellen, L., Miranda, A. C., Veenendaal, E. M., Djagbletey, G., Miranda, H. S., Cook, G., and Farquhar, G. D.: Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate, Tree Physiol., 28, 451–468, 2008.

Marin-Spiotta, E., Silver, W. L., Swanston, C. W., and Ostertag, R.: Soil organic matter dynamics during 80 years of reforestation of tropical pastures, Glob. Change Biol., 15, 1584–1597, 2009.

McCann, M. C. and Carpita, N. C.: Designing the deconstruction of plant cell walls, Current opinion in plant biology, 11, 314–320, 2008.

Meentemeyer, V.: Macroclimate and lignin control of litter decomposition rates, Ecology, 59, 465–472, 1978.

Melillo, J. M., Aber, J. D., and Muratore, J. F.: Nitrogen and lignin control of hardwood leaf litter decomposition dynamics, Ecology, 63, 621–626, 1982.

Menaut, J.-C. and Cesar, J.: Structure and Primary Productivty of Lamto Savannas, Ivory Coast, Ecology, 1197–1210, 1979.

Moni, C., Derrien, D., Hatton, P.-J., Zeller, B., and Kleber, M.: Density fractions versus size separates: does physical fractionation isolate functional soil compartments?, Biogeosciences, 9, 5181–5197, doi:10.5194/bg-9-5181-2012, 2012.

Mordelet, P. and Menaut, J. C.: Influence of trees on above-ground production dynamics of grasses in a humid savanna, J. Veg. Sci., 6, 223–228, 1995.

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

Mougin, E., Hiernaux, P., Kergoat, L., Grippa, M., De Rosnay, P., Timouk, F., Le Dantec, V., Demarez, V., Lavenu, F., and Arjounin, M.: The AMMA-CATCH Gourma observatory site in Mali: Relating climatic variations to changes in vegetation, surface hydrology, fluxes and natural resources, J. Hydrol., 375, 14–33, 2009.

Ong, C. K. and Leakey, R.: Why tree-crop interactions in agroforestry appear at odds with tree-grass interactions in tropical savannahs, Agrofor. Sys., 45, 109–129, 1999.

Paul, S., Martinson, G. O., Veldkamp, E., and Flessa, H.: Sample Pretreatment Affects the Distribution of Organic Carbon in Aggregates of Tropical Grassland Soils, Soil Sci. Soc. Am. J., 72, 500–506, doi:10.2136/sssaj2007.0052N, 2008.

Pessenda, L. C. R., Gomes, B. M., Aravena, R., Ribeiro, A. S., Boulet, R., and Gouveia, S. E. M.: The carbon isotope record in soils along a forest-cerrado ecosystem transect: implications for vegetation changes in the Rondonia state, southwestern Brazilian Amazon region, The Holocene, 8, 599–603, 1998.

Plante, A. and Conant, R. T.: Soil Organic Matter Dynamics, Climate Change Effects, in: Global Environmental Change, edited by: Freedman, B., 317–323, Springer, Dordrecht, Netherlands, 2014.

Post, W. M., Emanuel, W. R., Zinke, P. J., and Stangenberger, A. G.: Soil carbon pools and world life zones, Nature, 298, 156–159, doi:10.1038/298156a0, 1982.

Puget, P., Chenu, C., and Balesdent, J.: Dynamics of soil organic matter associated with particle-size fractions of water-stable aggregates, Eur. J. Soil Sci., 51, 595–605, 2000.

Pullan, R. A.: The soil resources of West Africa, in Environment and land use, in: Africa, edited by: Thomas, M. F. and Whittington, G. W., 147–191, Methuen, London, 1969.

Quesada, C. A., Lloyd, J., Anderson, L. O., Fyllas, N. M., Schwarz, M., and Czimczik, C. I.: Soils of Amazonia with particular reference to the RAINFOR sites, Biogeosciences, 8, 1415–1440, doi::10.5194/bg-8-1415-2011, 2011.

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., Fyllas, N. M., Hodnett, M. G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, A., Arroyo, L., Chao, K. J., Dezzeo, N., E rwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E. M., Killeen, T., Lezama, A. T., Lloyd, G., López-González, G., Luizão, F. J., Malhi, Y., Monteagudo, A., Neill, D. A., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M. C., Peña Cruz, A., Pitman, N., Priante Filho, N., Prieto, A., Ramírez, H., Rudas, A., Salomão, R., Santos, A. J. B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh, J., and Lloyd, J.: Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate, Biogeosciences, 9, 2203–2246, doi:10.5194/bg-9-2203-2012, 2012.

Reeuwijk, L. V.: Procedures for soil analysis, Technical Paper, International Soil Reference and Information Centre, Wageningen ISSN 0923-3792, 9, 2002.

Rumpel, C. and Kögel-Knabner, I.: Deep soil organic matter – a key but poorly understood component of terrestrial C cycle, Plant Soil, 338, 143–158, 2011.

Saiz, G., Bird, M. I., Domingues, T., Schrodt, F., Schwarz, M., Feldpausch, T. R., Veenendaal, E., Djagbletey, G., Hien, F., and Com-

paore, H.: Variation in soil carbon stocks and their determinants across a precipitation gradient in West Africa, Glob. Change Biol., 18, 1670–1683, 2012.

Saiz, G., Wynn, J. G., Wurster, C. M., Goodrick, I., Nelson, P. N., and Bird, M. I.: Pyrogenic carbon from tropical savanna burning: production and stable isotope composition, Biogeosciences, 12, 1849–1863, doi:10.5194/bg-12-1849-2015, 2015.

Schrodt, F., Domingues, T. F., Feldpausch, T. R., Saiz, G., Quesada, C. A., Schwarz, M., Ishida, F. Y., Compaore, H., Diallo, A., Djagbletey, G., Hien, F., Sonké, B., Toedoumg, H., Zapfack, L., Hiernaux, P., Mougin, E., Bird, M. I., Grace, J., Lewis, S. L., Veenendaal, E., and Lloyd, J.: Foliar trait contrasts between African forest and savanna trees: genetic versus environmental effects, Funct. Plant Biol., 42, 63–83, 2015.

Silva, L. C. R., Sternberg, L., Haridasan, M., Hoffmann, W. A., Miralles-Wilhelm, F., and Franco, A. C.: Expansion of gallery forests into central Brazilian savannas, Glob. Change Biol., 14, 2108–2118, doi:10.1111/j.1365-2486.2008.01637.x, 2008.

Six, J. and Jastrow, J. D.: Organic matter turnover, in Encyclopedia of soil science, edited by W. Chesworth, Marcel Dekker Inc., New York, USA, 936–942, 2002.

Six, J., Bossuyt, H., Degryze, S., and Denef, K.: A history of research on the link between (micro) aggregates, soil biota, and soil organic matter dynamics, Soil Till. Res., 79, 7–31, 2004.

Sollins, P., Homann, P., and Caldwell, B. A.: Stabilization and destabilization of soil organic matter: mechanisms and controls, Geoderma, 74, 65–105, 1996.

Sollins, P., Kramer, M. G., Swanston, C., Lajtha, K., Filley, T., Aufdenkampe, A. K., Wagai, R., and Bowden, R. D.: Sequential density fractionation across soils of contrasting mineralogy: evidence for both microbial-and mineral-controlled soil organic matter stabilization, Biogeochemistry, 96, 209–231, 2009.

Šantrůčková, H., Bird, M. I., and Lloyd, J.: Microbial processes and carbon-isotope fractionation in tropical and temperate grassland soils, Funct. Ecol., 14, 108–114, 2000.

Stuiver, M. and Pollach, H.A.: Discussion: Reporting of ^{14}C data, Radiocarbon, 19, 355–363, 1977.

Tian, G., Kang, B. T., and Brussaard, L.: Biological effects of plant residues with contrasting chemical compositions under humid tropical conditions—decomposition and nutrient release, Soil Biol. Biochem., 24, 1051–1060, 1992.

Torello-Raventos, M., Feldpausch, T. R., Veenendaal, E., Schrodt, F., Saiz, G., Domingues, T. F., Djagbletey, G., Ford, A., Kemp, J., Marimon, B. S., and Lloyd, J.: On the delineation of tropical vegetation types with an emphasis on forest/savanna transitions, Plant Ecol. Divers., 6, 101–137, 2013.

Trumbore, S.: Radiocarbon and soil carbon dynamics, Annu. Rev. Earth Planet. Sci., 37, 47–66, 2009.

Veenendaal, E. M., Torello-Raventos, M., Feldpausch, T. R., Domingues, T. F., Gerard, F., Schrodt, F., Saiz, G., Quesada, C. A., Djagbletey, G., Ford, A., Kemp, J., Marimon, B. S., Marimon-Junior, B. H., Lenza, E., Ratter, J. A., Maracahipes, L., Sasaki, D., Sonké, B., Zapfack, L., Villarroel, D., Schwarz, M., Yoko Ishida, F., Gilpin, M., Nardoto, G. B., Affum-Baffoe, K., Arroyo, L., Bloomfield, K., Ceca, G., Compaore, H., Davies, K., Diallo, A., Fyllas, N. M., Gignoux, J., Hien, F., Johnson, M., Mougin, E., Hiernaux, P., Killeen, T., Metcalfe, D., Miranda, H. S., Steininger, M., Sykora, K., Bird, M. I., Grace, J., Lewis, S., Phillips, O. L., and Lloyd, J.: Structural, physiognomic and above-ground biomass variation in savanna-forest transition zones on three continents – how different are co-occurring savanna and forest formations?, Biogeosciences, 12, 2927–2951, doi:10.5194/bg-12-2927-2015, 2015.

Veldkamp, E.: Organic carbon turnover in three tropical soils under pasture after deforestation, Soil Sci. Soc. Am. J., 58, 175–180, 1994.

Wurster, C. M., Saiz, G., Calder, A., and Bird, M. I.: Recovery of organic matter from mineral-rich sediment and soils for stable isotope analyses using static dense media, Rapid Commun. Mass Spectrom., 24, 165–168, doi:10.1002/rcm.4358, 2010.

Wynn, J. G. and Bird, M. I.: C$_4$-derived soil organic carbon decomposes faster than its C$_3$ counterpart in mixed C$_3$ / C$_4$ soils, Glob. Change Biol., 13, 2206–2217, doi:10.1111/j.1365-2486.2007.01435.x, 2007.

Wynn, J. G., Bird, M. I., Vellen, L., Grand Clement, E., Carter, J., and Berry, S. L.: Continental-scale measurement of the soil organic carbon pool with climatic, edaphic, and biotic controls, Global Biogeochem. Cy., 20, doi:10.1029/2005GB002576, 2006.

Zimmermann, M., Leifeld, J., Schmidt, M. W. I., Smith, P., and Fuhrer, J.: Measured soil organic matter fractions can be related to pools in the RothC model, Eur. J. Soil Sci., 58, 658–667, doi:10.1111/j.1365-2389.2006.00855.x, 2007.