

Effects of forest conversion into grassland on soil aggregate structure and carbon storage in Panama: evidence from soil carbon fractionation and stable isotopes

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Abstract Land-use and land-cover strongly influence soil properties such as the amount of soil organic carbon (SOC), aggregate structure and SOC turnover processes. We studied the effects of a vegetation shift from forest to grassland 90 years ago in soils derived from andesite material on Barro Colorado Island (BCI), Panama. We quantified the amount of carbon (C) and nitrogen (N) and determined the turnover of C in bulk soil, water stable aggregates (WSA) of different size classes (< 53 μm , 53–250 μm , 250–2000 μm and 2000–8000 μm) and density fractions (free light fraction, intra-aggregate particulate organic matter and mineral associated soil organic C). Total SOC stocks (0–50 cm) under forest (84 Mg C ha⁻¹) and grassland (64 Mg C ha⁻¹) did not differ significantly. Our results revealed that vegetation type did not have an effect on aggregate structure and stability. The investigated soils at BCI did not show higher C and N concentrations in larger aggregates, indicating that organic material is not the major binding agent in these soils to form aggregates.

Based on $\delta^{13}\text{C}$ values and treating bulk soil as a single, homogenous C pool we estimated a mean residence time (MRT) of 69 years for the surface layer (0–5 cm). The MRT varied among the different SOC fractions and among depth. In 0–5 cm, MRT of intra-aggregate particulate organic matter (iPOM) was 29 years; whereas mineral associated soil organic C (mSOC) had a MRT of 124 years. These soils have substantial resilience to C and N losses because the >90% of C and N is associated with mSOC, which has a comparatively long MRT.

Keywords Density fractionation · Forest conversion · Grassland · Mean residence time · Soil organic carbon and nitrogen · Stable carbon isotopes · Tropical soil · Water stable aggregates · Panama

Introduction

Moist tropical forests are important with respect to global C cycle as these forests contain about half of the global forest biomass (Brown and Lugo 1982) and approximately 20% of the global soil C (Jobbagy and Jackson 2000). Further, land-use changes in the tropics are estimated to contribute a considerable amount (about 23%) to human-induced CO₂ emissions (Houghton 2003). The vulnerability of soil organic matter (SOM) to

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climate and land-use change (IPCC 2001) emphasizes the need for understanding SOM dynamics.

Although net deforestation rates have fallen since the 1990–2000 period, around 13 million hectares of the world's forests are still lost each year (FAO 2005). Land-use type and management practices are important factors controlling organic matter storage in soils because they affect the amount and quality of litter input, the litter decomposition rates and the processes of organic matter stabilization in soils. The impact of land-use change on organic carbon pools in the mineral soil depends also on long-term site-specific factors (e.g. climate, topography and parent material) and is often overridden by the high spatial heterogeneity of soil organic carbon.

While forest clear-cutting for pasture in the humid tropics combined with slash removal and/or burning cause significant losses of SOC (Brown and Lugo 1990; Veldkamp 1994), other studies have shown that pasture establishment in the tropics may maintain or even increase the soil organic carbon content especially when grass species with high percentages of below-ground biomass production are used (Feigl et al. 1995). No clear trend in soil C change following the conversion from forest to pasture was shown in a data compilation for the tropics and temperate regions (Murty et al. 2002).

Inconsistent patterns in SOC changes following disturbance may partly be explained by the chemical and physical complexity of SOM. A loss of C in one SOM fraction may be offset by gains in another fraction, leading to no apparent change in bulk SOM. Insights into SOM dynamics may be revealed by using aggregate and density fractionation to distinguish among functionally different SOM fractions (Cambardella and Elliot 1992; Tisdall and Oades 1982). In addition, by separating SOM fractions that are more sensitive than bulk SOM stocks to changes in land-use, management or climate, the detection limit for SOM changes is increased (Six et al. 2002).

Combining SOM fractionation techniques with ^{13}C natural abundance offers an approach to assess quantitative changes of C in different pools and to examine C stability (Jastrow et al. 1996). Differences in the natural stable C isotope

signature between C_3 (average $\delta^{13}\text{C}$ value of -11‰) and C_4 (average $\delta^{13}\text{C}$ value of -27‰ , Smith and Epstein 1971) plants allows to assess soil C dynamics at sites where C_4 grass grows on soils formed under a native C_3 vegetation (Desjardins et al. 1994; Veldkamp 1994).

The Republic of Panama has lost more than 2 million hectares (35%) of its forested area to cropland and agro-pastoral development in the past 50 years (Condit et al. 2001). Although several studies have been published on soil C inventories following forest conversion to pasture in the moist tropics (Trumbore et al. 1995; Veldkamp 1994), data on mean residence times of different C fractions are still rare, especially for Central America. However, to predict future C budgets an understanding of turnover processes and their underlying mechanisms is essential.

This study presents a unique perspective on how changes in vegetation can affect soil processes, independent of other land use changes such as cropping or grazing management. The goal was to examine the long-term effects of forest conversion into grassland on the content and turnover of SOM in bulk soil, water stable aggregates and density fractions. Our specific objectives were (i) to quantify changes in soil carbon and N following a vegetation shift from forest to grassland 90 years ago, (ii) to determine the distribution of C and N in different soil fractions and (iii) to provide insight into C turnover processes using stable isotopes. Our hypotheses for the BCI study are: (1) forest conversion will affect aggregate structure and SOM stocks, (2) aggregate hierarchy will not be found in these soils as mineralogical factors are stronger than biological ones and (3) density fractions are more important in governing C residence time than water stable aggregates.

Study area and methods

Description of the study sites

The study was conducted on Barro Colorado Island (BCI; $9^{\circ}10' \text{ N}$, $79^{\circ}51' \text{ W}$). The island was formed in 1914 with the creation of Lake Gatún as part of the Panama Canal and covers an area of 1,500 ha. The mean annual temperature of the

region is 26°C (STRI, 2006). The island receives an average of 2600 mm of rain per year, with a distinct dry season (approximately from mid-December to the end of April). During the dry season around 285 mm of rain are measured (STRI 2006). The vegetation on BCI is classified as Tropical Moist Forest in the Holdridge life zone system (Leigh et al. 1996). Our study sites were located on the north side of the island close to the Miller lighthouse (UTM-626284 E, 1013458 N). The soils are Oxisols, developed in andesite parent material (Yavitt 2000). X-ray diffractograms (XRD) of bulk soil samples showed no clay minerals besides kaolinite. We selected two different land-use types, undisturbed forest and grassland. Both land-use types are located on a north-facing hill slope of 20 degrees. At the grassland site the forest was cut around 90 years ago to set up a lighthouse for the Panama Canal. During the first half of the 20th century, the grassland was burned to remove the vegetation. In recent years the vegetation has been cut manually several times a year. The residue is left on site. At the time of sampling the vegetation of the grassland site was dominated by wild sugarcane (*Saccharum spontaneum*), a C₄ plant.

Soil and plant residue sampling

We selected three paired plots at upper, middle, and toe-slope positions in undisturbed forest and grassland. The plots were separated by about 200 m along the slope, and by ~100 m between forest and grassland. At each of the six plots a soil profile was dug in October 2003. From each profile, soil samples were taken at 0–5, 5–10, 10–15, 15–20, 20–30, 30–40 and 40–50 cm. Surface litter and aboveground grass biomass were collected from small quadrates (0.40 × 0.40 m) located near the soil pits.

Bulk density was measured using the core method. Samples were oven-dried (105°C for 48 h) and bulk density was estimated as the mass of oven-dry soil divided by the core volume (100 cm³). Texture of bulk soil (air-dried, sieved, 2 mm) was determined using the hydrometer method (Gee and Or 2002); soil texture classes were identified according to the USDA system (1999). Bulk soil pH (air-dried, sieved, 2 mm) was

measured with a combined electrode (Fisher Scientific, Accumet Basic) on a 1:1 mixture of soil and deionized (DI) water. Clay mineralogy was determined with a XDS 2000 (Scintag Inc., Sunnyvale, CA, USA) automated powder diffraction system on oriented samples before and after glycolation and heating to 300 °C.

Soil texture in both land-use types was sandy clay loam throughout the profile. pH in 0–5 cm depth was 5.7 under forest and 6.6 under grassland. In 40–50 cm we measured a pH of 4.8 for both land-use types.

Separation of water stable soil aggregates

For the separation of water stable aggregates (WSA), field-moist samples were gently passed through an 8-mm sieve and air-dried. Separating soil aggregates into different sizes (2000–8000 µm; 250–2000 µm; 53–250 µm and < 53 µm) was achieved by wet sieving according to Elliot (1986). A 100 g air-dried subsample was immersed in DI water at room temperature on the largest screen (2 mm) for 5 min before sieving commenced. Soils were sieved under water by gently moving the sieve vertically 50 times over a period of 2 min through water contained in a shallow pan. Floatable material in the 2 mm sieve was removed. Material remaining on the sieve was transferred to an aluminum pan and dried at 55°C in a forced-air oven. Soil passing a particular sieve and remaining in the shallow pan was then transferred to the next sieve (250 µm and 53 µm, respectively) and the process repeated. Material < 53 µm (free silt + clay) was allowed to settle, centrifuged (3,000 rpm, 20 min; Sanyo MSE Mistral 3000E, Bensenville, IL, USA), oven dried and weighed. Recoveries from the wet sieving were >97% by weight in all cases. The weight of each WSA fraction was expressed as a proportion of the sum of fraction weights (F_i , in %). Samples were ball-mill ground (Mixer Mill MM 200, Retsch GmbH, Haan, Germany) for C, N and isotope analyses.

Density fractionation of small macroaggregates and microaggregates

Density fractionation was applied to separate mineral-associated organic C (mSOC, < 53 µm)

from particulate organic matter (POM). The latter can be subdivided into free POM (also called free light fraction, free LF), which is located between the soil aggregates and an intra-aggregate particulate organic matter (iPOM) fraction, located within the soil aggregates (Golchin et al. 1995; Six et al. 1998).

Small macroaggregates (250–2000 μm) and microaggregates (53–250 μm) from 0 to 5, 5 to 10, 10 to 15 and 15 to 20 cm were further separated by density according to Six et al. (1998) using sodium polytungstate (SPT) with a density of 1.85 g cm^{-3} . These aggregate classes were chosen because they contained the majority of C in a preliminary analysis. A subsample (8 g) of oven-dried material was put into a 50 ml centrifuge tube and 35–40 ml SPT was added. The centrifuge tube was placed into a vacuum chamber for 10 min to evacuate air entrapped within the aggregates. The suspended samples were then shaken gently until the material was well dispersed. The tubes were centrifuged at 2,500 rpm for 30 min. The floating material (free LF) and SPT were aspirated, filtered through a 20 μm nylon filter, rinsed with DI water, transferred into aluminum tins and dried at 55°C overnight. The remaining material (heavy fraction) in the centrifuge tube was washed with distilled water, followed by centrifugation. After centrifugation the DI was aspirated and discharged. This step was repeated two times. In the final step three drops of 0.25 M CaCl_2 and 0.25 M MgCl_2 were added to settle the clay. The suspension was centrifuged for 60 min (2,500 rpm); the supernatant was discharged. Then two marbles were added and the centrifuge tube was filled with DI water. The suspension was shaken on a reciprocal shaker (60 cycles min^{-1} ; Eberbach Corporation, Ann Arbor, MI, USA) for 24 h. The content was poured onto a 53- μm sieve and washed thoroughly. The material retained on the sieve (iPOM and sand) was oven-dried at 55°C , weighed and ground. Material passing the 53 μm sieve (mSOC and mineral particles) was allowed to settle, centrifuged (3,000 rpm, 20 min), and oven-dried at 55°C . All oven-dry samples were weighed and ground. Sodium polytungstate was recycled according to Six et al. (1999) to avoid cross contamination of C between samples.

Carbon, nitrogen and stable isotope analyses

Soil organic C and N concentration was determined separately for bulk soil, WSA, density fractions and vegetation residue with an elemental analyzer (NCS 2500, CE Elantech, Lakewood, NJ, USA). The precision of the analyzer was $\pm 0.2\%$. Ten percent of all samples were analyzed in duplicate.

Soil organic C and N stocks ($\text{Mg C (or N) ha}^{-1}$) were calculated from bulk soil C and N concentration ($\text{C (or N) kg}^{-1} \text{ soil}$) and bulk density (Mg m^{-3}) for a given depth layer. Stocks were corrected for land-use specific differences in bulk density (Solomon et al. 2002). The C and N concentrations of individual aggregate and density fractions were reported on a per-mass of fraction basis ($\text{g C (or N) kg}^{-1}$ aggregate fraction and g C kg^{-1} density fraction), on a per-mass soil basis for WSA ($\text{g C (or N) kg}^{-1}$ soil) and on a per-mass aggregate basis for density fractions (g C kg^{-1} aggregate).

Because organic matter does not bind well with sand particles it may be necessary to correct for the sand content when comparing the C and N concentrations of WSA aggregates (Elliot et al. 1991). However, we did not perform a sand correction as sand content was less than 5% in both land-use types. Aggregate specific sand content was estimated by taking an 8-g subsample from small macroaggregate and microaggregate fractions which were obtained after wet-sieving. The sample was dispersed in DI water. Two marbles were added and the suspension was shaken for 24 h on a reciprocal shaker.

Natural ^{13}C abundance for bulk soil, WSA, density fractions and plant material, was determined by combusting the samples in an elemental analyzer (NCS 2500, CE Elantech, Lakewood, NJ, USA), and then analyzing the CO_2 with an isotope-ratio mass spectrometer (Isoprime, Micromass, Manchester, U.K.). Results are reported in $\delta^{13}\text{C}$ (‰) relative to the V-PDB standard as:

$$\delta^{13}\text{C}(\text{‰}) = \left(\frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 1000 \quad (1)$$

where R is the $^{13}\text{C}/^{12}\text{C}$ ratio. The precision of the $\delta^{13}\text{C}$ was $\pm 0.2 \text{ ‰}$. Thirty percent of all samples were analyzed in duplicate.

Calculation of new carbon

The proportion of soil C derived from grassland was calculated according to Balesdent and Mariotti (1996).

$$F_{\text{new}}(\%) = \left(\frac{\delta_{\text{grassland}} - \delta_{\text{forest}}}{\delta_{\text{vegetation}} - \delta_{\text{forest}}} \right) \quad (2)$$

where F_{new} is the proportion (in %) of new (grassland derived) C, $\delta_{\text{grassland}}$ is the $\delta^{13}\text{C}$ value of soil C under grassland at a given depth, δ_{forest} is the $\delta^{13}\text{C}$ value of soil C under forest at the corresponding depth and $\delta_{\text{vegetation}}$ is the $\delta^{13}\text{C}$ value from the grassland residue ($\delta^{13}\text{C} = -16.2 \pm 4.2\text{‰}$). The proportion of C derived from the forest (old C) is $100 - F_{\text{new}}$ at a given depth. The proportion of new and old C, variances, error propagation and confidence intervals were calculated using the single isotope option in the program ISOERROR 1.04 (Phillips and Gregg 2001). Calculations were done separately for bulk soil, WSA and density fractions and each soil depth.

Estimating the mean residence time for soil organic carbon

The mean residence time (MRT) of C derived from the original vegetation (forest derived C) was estimated by using a first-order decay model (Six and Jastrow 2002). MRT (years) is an inverse function of the turnover rate k (1 year^{-1}).

$$\text{MRT} = \frac{1}{k} = -\frac{t}{\ln\left(\frac{C_t}{C_0}\right)} \quad (3)$$

where t is the time since conversion (here 90 years), C_t is the content (in Mg C ha^{-1} , g C kg^{-1} aggregate fraction, g C kg^{-1} density fraction) of remaining forest derived C (old C) in the grassland soil at the time of sampling, and C_0 is the C content present under the forest at the time of sampling. Mean residence time was calculated separately for bulk soil, WSA and density fractions.

Statistical analyses

The significance of differences in properties among aggregates and density fractions, depths

and land-use types was assessed by ANOVA and post-hoc Tukey HSD. We used Pearson product-moment correlation to identify relationships among parameters. For all data, differences that are reported in the text were considered significant at $P < 0.05$. All statistical analyses were done using STATISTICA 7.1 (StatSoft Inc., Tulsa, OK, USA).

Results

Characteristics of bulk soil and plant residue

We did not find a significant effect of slope position on bulk density ($P = 0.43$), C ($P = 0.27$), N ($P = 0.33$) or stable isotopes of soil C ($P = 0.44$). Thus, all parameters were averaged across the slope. The bulk density ($0.85\text{--}0.99 \text{ Mg m}^{-3}$) did not differ significantly among depths or between land-use types. Surface (0–5 cm depth) soil C stock was ~50% higher under forest ($22.4 \pm 5.6 \text{ Mg C ha}^{-1}$) than under grassland ($15.3 \pm 1.1 \text{ Mg C ha}^{-1}$). However, the differences were not significant ($P = 0.12$). Forest and grassland soil (0–5 cm) contained $1.7 \pm 0.3 \text{ Mg N ha}^{-1}$ and $1.5 \pm 0.1 \text{ Mg N ha}^{-1}$, respectively ($P = 0.09$) (Table 1). Under both land-use types, C and N stocks decreased significantly with depth. In 40–50 cm depth, we found $6 \pm 1.4 \text{ Mg C ha}^{-1}$ ($1.1 \pm 0.1 \text{ Mg N ha}^{-1}$) under grassland and $7.2 \pm 1.5 \text{ Mg C ha}^{-1}$ ($1.1 \pm 0.2 \text{ Mg N ha}^{-1}$) under forest (Table 1). The amount of C and N stored in the profile (0–50 cm) was 84 Mg C ha^{-1} (9 Mg N ha^{-1}) under forest and 64 Mg C ha^{-1} (8 Mg N ha^{-1}) under grassland.

Mean C:N ratios in bulk soil did not reveal significant differences between grassland and natural forest, except for the uppermost layer (0–5 cm) where the C:N ratio under forest was wider (13.0 ± 1.4) than under grassland (9.9 ± 0.2) (Table 1). The C:N ratios under both land-use types decreased significantly with depth (Table 1).

Land-use affected the $\delta^{13}\text{C}$ values of litter and bulk soil. The average $\delta^{13}\text{C}$ value of litter from the forest floor was $-30.1 \pm 0.5 \text{‰}$, indicating $\delta^{13}\text{C}$ signatures characteristic of C_3 vegetation. Plant residue collected from the grassland had a significantly higher $\delta^{13}\text{C}$ value ($-16.2 \pm 4.2\text{‰}$). The

Table 1 Soil organic carbon concentration, C:N ratios, soil organic carbon stock, proportion of new carbon and mean residence time (MRT) of bulk soil under forest (F) and grassland (GL), BCI, Panama

Depth (cm)	Carbon concentration (g C kg ⁻¹ soil)		C:N		Carbon stock (Mg C ha ⁻¹)		New carbon (%)	MRT (year)
	F	GL	F	GL	F	GL	GL	GL
0–5	56.0Aa (15.2)	38.2Aa (4.6)	13.0Aa (1.4)	9.9Ba (0.2)	22.4Aa (5.6)	15.3Aa (1.1)	59.9 a (4.7)	69 a (12)
5–10	32.4Aa (12.1)	29.5Aa (3.5)	10.8Aab (1.3)	10.4Aa (0.1)	14.6Aa (4.3)	12.5Aa (0.6)	44.0 b (3.0)	123 b (25)
10–15	24.4Ab (10.0)	18.4Ab (4.7)	9.2Ab (1.5)	9.4Aa (0.6)	11.1Ab (5.3)	8.3Ab (2.7)	31.8 c (4.9)	134 b (39)
15–20	19.4Ab (8.7)	14.1Ab (2.6)	8.4Ab (1.6)	8.7Aa (0.3)	8.6Ab (4.0)	6.2Ac (1.3)	31.7 b,c (9.9)	128 b (28)
20–30	12.4Ab (3.1)	10.1Ab (2.1)	7.8Ab (1.6)	7.5Ab (0.8)	11.2Ab (2.6)	9.1Ab (1.6)	23.8 c (6.9)	187 b (47)
30–40	10.2Ab (1.3)	7.7Ab (2.4)	6.9Abc (0.7)	6.8Ab (1.0)	8.7Ab (1.0)	6.5Ac (1.6)	16.4 c (9.7)	191 b (58)
40–50	8.3Ab (1.6)	6.9Ab (1.4)	6.6Abc (1.0)	6.5Ab (1.1)	7.2Ab (1.5)	6.0Bc (1.4)	21.2 c (10.2)	211 b (71)

Values are means of three replicates. Standard deviation is given in parentheses. Different capital letters indicate significant differences between forest and grassland and different lower-case letters indicate differences among depths ($P < 0.05$)

bulk soil $\delta^{13}\text{C}$ values in the surface layer also differed significantly between grassland and forest (Fig. 3). Mean $\delta^{13}\text{C}$ (0–5 cm depth) was $-21.2 (\pm 0.6)$ ‰ under the 90-year-old grassland and $-28.7 (\pm 0.4)$ ‰ under forest. The $\delta^{13}\text{C}$ signature tended to decrease with depth under grassland (-23.0 ± 1.7 ‰; 40–50 cm), but increased significantly under forest (-24.8 ± 1.2 ‰; 40–50 cm) (Fig. 3).

The mixing model revealed that 90 years after forest conversion ~60% of the existing C in the in the top 5 cm was derived from new C (grassland derived C). The remaining 40% of the bulk soil C in this layer was attributed to old C (forest derived C). The proportion of new C decreased significantly with depth. On average less than 25% of the SOC below 20 cm was new C (Table 1). The total amount of new C in the profile was 24 Mg C ha^{-1} ($=0.27 \text{ Mg C ha}^{-1} \text{ year}^{-1}$). Based on $\delta^{13}\text{C}$ values and treating bulk soil as a single, homogenous pool (one-pool model) (Eq. 2), we calculated a mean residence time of 69 years for the surface layer (0–5 cm) and 120 years below 20 cm (Table 1).

Distribution and characteristics of water stable aggregates

Land use did not significantly alter the mass distribution of WSA fractions. Throughout the profiles, small macroaggregates (250–2000 μm) accounted for 60 to 80% of the total sample mass under forest and grassland (Fig. 1). A substantial percentage (~20–40%) of large macroaggregates

(2000–8000 μm) was found in the top 15 cm under both land-use types. Microaggregates (53–250 μm) and free silt + clay (< 53 μm) contributed less than 10% to the sample weight in the upper soil. Especially under the grassland the proportion of large macroaggregates decreased below 15 cm depth whereas the contribution of microaggregates (53–250 μm) and free silt + clay (< 53 μm) increased ($P > 0.05$) (Fig. 1).

Change in vegetation type also did not significantly alter the C and N concentrations in WSA (Table 2). Soil organic C and N concentrations (g C (or N) kg⁻¹ aggregate fraction) in all WSA fractions were closely correlated with bulk soil C and N concentrations ($r^2 > 0.96$) (Table 1 and 2). Similar to bulk soil, soil C and N concentrations in all WSA decreased significantly with depth under grassland and forest (Table 2). For the top 20 cm of both land-use types we did not find significant differences in C and N concentrations among WSA (Table 2). In contrast, below 20 cm (under forest) and below 30 cm (under grassland) large macroaggregates had a significantly lower C concentration as compared to small macroaggregates, microaggregates and free silt + clay (Table 2).

When expressed on a per-mass of soil basis (g C (or N) kg⁻¹ soil), the sum of small and large macroaggregates (>250 μm) contained most of soil C and N which can mainly be explained by the amount of soil in these aggregate size classes. Under forest and grassland around 80% of C and N was associated with macroaggregates throughout the profiles (Fig. 2 a,b).

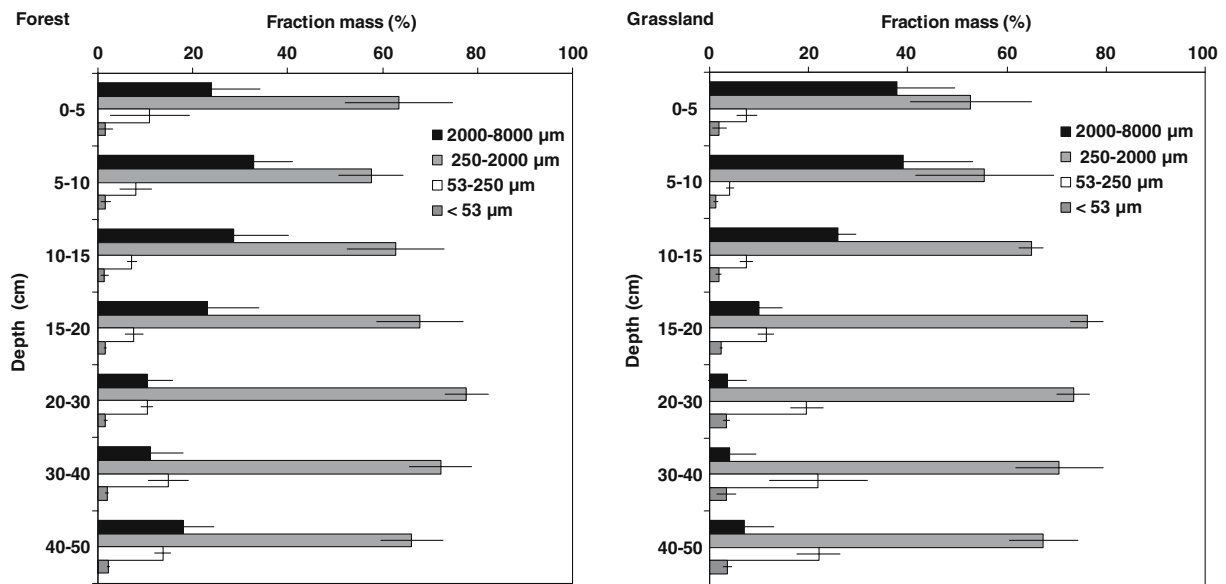


Fig. 1 Soil mass distribution of water stable aggregate fractions over depth under forest and grassland, BCI, Panama. Bars represent standard deviation of three replicates

Although not significant, C:N ratios in 0–5 cm depth under forest tended to be slightly higher (10.2–11.8) as compared to grassland (9.4–10.7) (Table 2). In contrast, below 5 cm C:N ratios under forest were slightly lower as compared to grassland ($P > 0.05$) (Table 2). In general, C:N decreased with depth (Table 2). Under both land-use types C:N ratios were similar in all WSA of the same depth, except for the 10–15 cm layer under grassland (Table 2).

The $\delta^{13}\text{C}$ values did not differ significantly among WSA, neither under forest nor grassland (Fig. 3 a,b; left panel). Average $\delta^{13}\text{C}$ values in 0–5 cm ranged from -25.9 to -26.5‰ (forest) and from -19.8 to -20.6‰ (grassland). Under forest, $\delta^{13}\text{C}$ values of all WSA throughout the profile were 2 to 4‰ higher ($P < 0.05$) as compared to $\delta^{13}\text{C}$ bulk soil values (Fig. 3a; left panel). Under grassland no consistent and statistically significant differences were observed between $\delta^{13}\text{C}$ values of WSA and bulk soil. Large macroaggregates tended to have lower $\delta^{13}\text{C}$ values as compared to bulk soil (Fig. 3b; left panel). With increasing depth, WSA $\delta^{13}\text{C}$ values increased under forest (-22.8 to -23.5‰ ; 40–50 cm) and tended to decrease under grassland (-21.4 to -23.4‰ ; 40–50 cm) (Fig. 3a,b; left panel).

In the top layer (0–5 cm) the proportion of new C under grassland varied between 55 and 65%. There were no significant differences in new C percentages among WSA. The contribution of C from grassland vegetation decreased with depth. In the subsoil (40–50 cm) on average 22% of new C was found in the aggregates, except for the large macroaggregates which contained only 10% new C (Table 3). The average MRT of SOC in the uppermost layer ranged between 66 and 93 years; whereas in 40–50 cm the MRT was estimated to be longer than 190 years (Table 3).

Distribution and characteristics of density fractions

Under both vegetation types, free LF within small macroaggregates and microaggregates contributed less than 2% to the total aggregate soil mass of these aggregate classes. In contrast, the mineral-associated SOC (mSOC) fraction amounted to over 93% to total aggregate soil mass of small macroaggregates and microaggregates (Table 4).

In 0–5 and 5–10 cm depths, the iPOM C concentration (g C kg^{-1} density fraction) under forest was considerably higher than iPOM C concentration under grassland. In contrast, free

Table 2 Soil organic carbon concentration and C:N ratios of water stable aggregates under forest (F) and grassland (GL), BCI, Panama

Depth (cm)	Soil organic carbon concentration (g C kg ⁻¹ aggregate fraction)														
	Forest						Grassland								
	C		N		C:N		C		N		C:N				
	2000–8000	250–2000	53–250	< 53	2000–8000	250–2000	53–250	< 53	2000–8000	250–2000	53–250	< 53			
0–5	44.2A	50.2A	47.3A	43.7A	37.9A	39.1a	33.0a	31.8a	11.1A	11.8A	11.0A	10.2A	10.5a	10.3ab	9.4b
5–10	25.1A	30.5A	28.7A	29.7A	27.3a	29.1a	24.1a	26.2a	9.8A	9.4A	9.3A	9.1A	9.8a	10.1a	9.3a
10–15	18.8A	22.9A	21.3A	21.8A	21.0a	19.1a	18.1a	17.1a	8.3A	8.5A	8.4A	8.2A	9.3a	10.4b	9.5ab
15–20	15.6A	18.8A	16.1A	17.2A	15.0a	13.8a	12.3a	14.2a	7.9A	7.7A	7.5A	7.6A	9.1a	9.1a	8.3a
20–30	4.5A	13.3B	11.9B	11.4B	8.0a	10.7a	9.6a	10.8a	6.5A	7.0A	6.8A	6.3A	7.1a	8.5a	8.3a
30–40	3.8A	10.7B	9.9B	9.8B	3.5a	8.0b	7.4b	8.4b	5.1A	6.8A	5.9A	5.8A	5.6a	7.7a	8.4a
40–50	2.5A	8.8B	7.3B	6.7B	1.5a	7.4b	6.5b	7.5b	nd	5.7A	5.1A	7.3A	7.0a	6.9a	6.4a

Different upper-case letters indicate differences among WSA under forest. Different lower-case letters indicate differences among WSA under grassland

nd = not determined

LF under grassland contained more C than free LF under forest (Table 4). Carbon concentrations of mSOC were low (10–29 g C kg⁻¹ density fraction) and did not differ between forest and grassland (Table 4).

When expressed on a per-mass of aggregate basis (g C kg⁻¹ aggregate) differences in C amounts were much smaller. At 0–5 and 5–10 cm iPOM C amounts were 7.2 vs. 4.8 g C kg⁻¹ aggregate and 2.0 g C kg⁻¹ vs. 2.3 g C kg⁻¹ aggregate under forest vs grassland, respectively (Table 4). Although free LF C concentration at 0–5 cm was higher under grassland than under forest (211 g C kg⁻¹ vs 172 g C kg⁻¹ density fraction), free LF C on a per-mass of aggregate basis was smaller under grassland than under forest (1.6 g C kg⁻¹ vs 2.7 g C kg⁻¹ aggregate) due to differences in fraction weight (0.8 vs 1.5%) (Table 4). For all density fractions combined, between 74 and 96% of C was associated with mSOC.

Under forest, free LF tended to have the lowest $\delta^{13}\text{C}$ values (–29.2 to –31.6‰) (Fig. 3a; right panel). In contrast, under grassland, $\delta^{13}\text{C}$ values of iPOM (–16.9 to –19.8‰) showed ^{13}C enrichment as compared to free LF (–21.4 to –23.6‰) and mSOC (–21.6 to –24.7‰) (Fig. 3b; right panel).

The proportion of new C under grassland was highest in iPOM (71–94%), followed by free LF (47–61%) and mSOC (13–50%). The MRT of C in iPOM (20–50 years) was significantly lower than in free LF (112–211 years) and mSOC (120–306 years) (Table 3).

Discussion

Natural ^{13}C abundance and turnover of C in bulk soil

While forest conversion did not result in a significant loss of bulk soil C and N stocks at our study site, natural ^{13}C abundance did indicate land-use related changes. These changes must be interpreted in view of the variations in $\delta^{13}\text{C}$ in the undisturbed forest. The mean $\delta^{13}\text{C}$ value for forest leaf litter in this study was –30.1 (± 0.5)‰, which falls within the range of –24 to –34‰ found for C₃

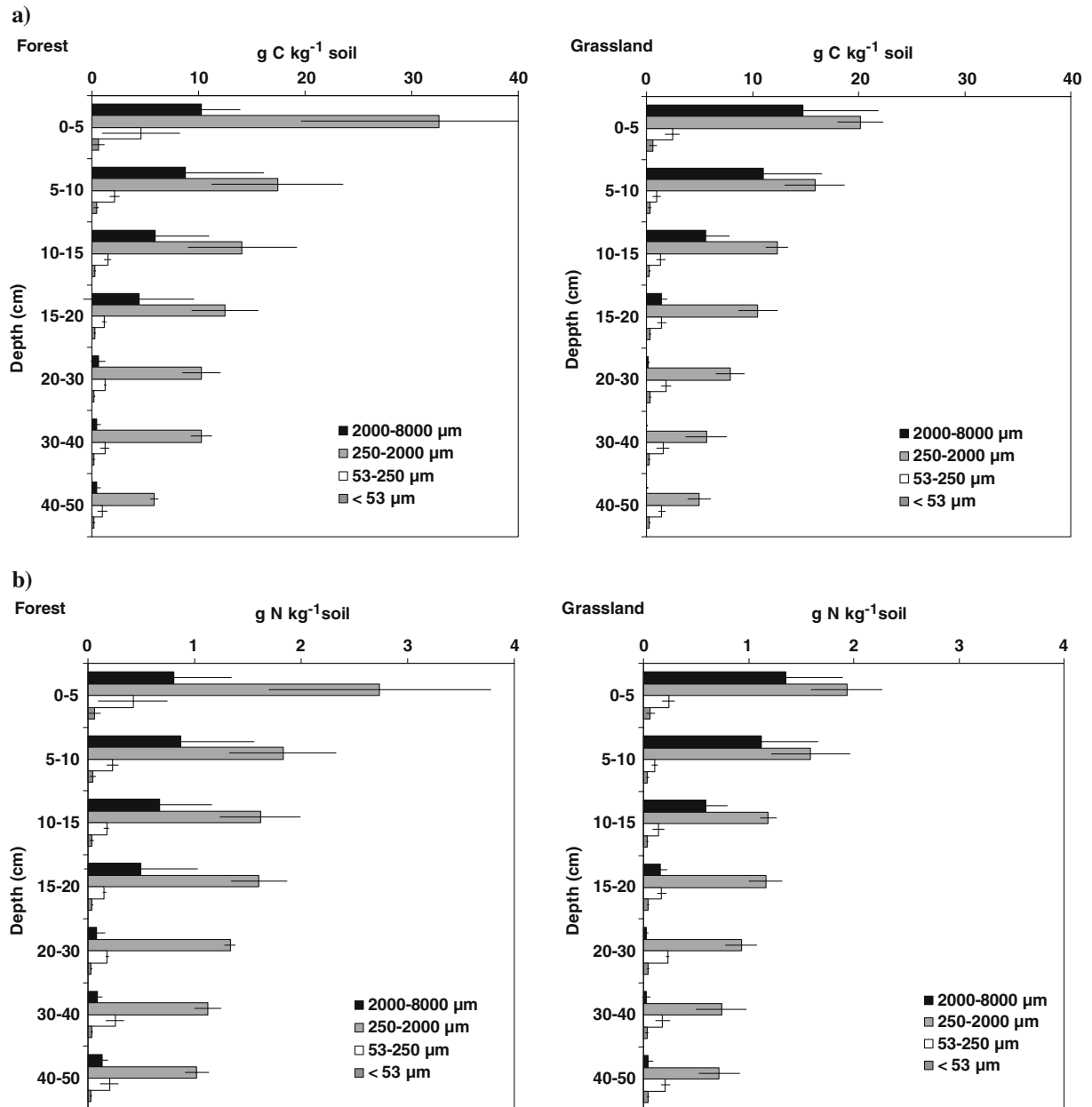


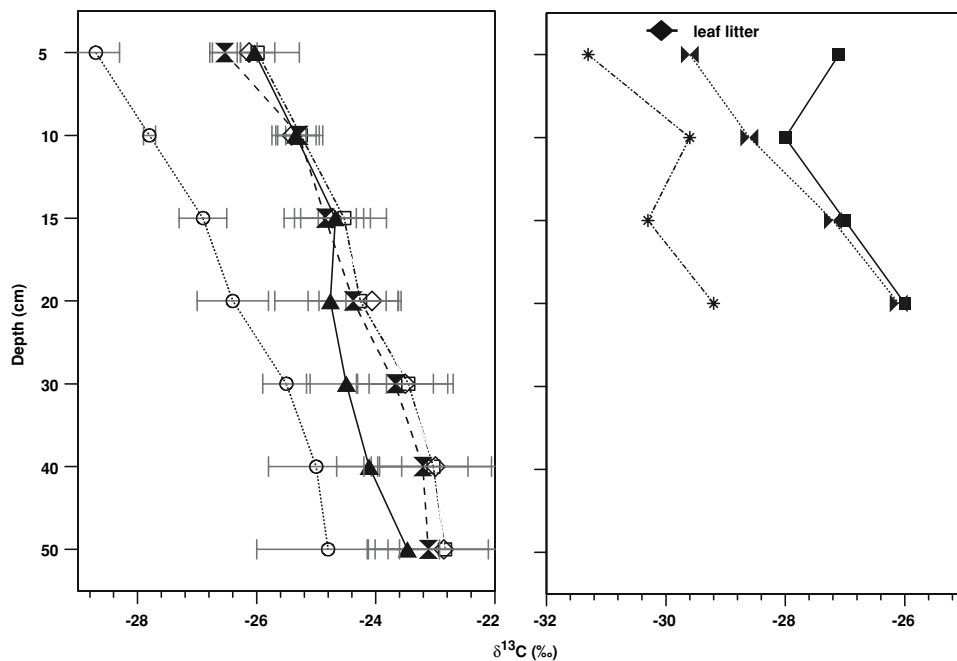
Fig. 2 Amount of soil organic carbon (a) and nitrogen (b) of individual water stable aggregate fractions on a per-mass of soil basis (g C kg^{-1} soil) over depth under forest

and grassland, BCI, Panama. Bars represent standard deviation of three replicates

plants (Smith and Epstein 1971). The bulk soil $\delta^{13}\text{C}$ value of the 0–5 cm depth resembled that of the leaf litter input. In the forest soil, $\delta^{13}\text{C}$ increased from -28.7‰ in the surface layer to -24.8‰ at 50-cm depth. The increase of $\delta^{13}\text{C}$ with depth is consistent with results from other soil profiles under forest in the tropics (e.g. Desjardins et al. 1994; Volkoff and

Cerri 1987). One explanation for the increase in $\delta^{13}\text{C}$ with depth is microbial discrimination against heavy C isotopes during decomposition (Balesdent and Mariotti 1996; Nadelhoffer and Fry 1988). Another factor that can also account for depth dependent changes in SOC $\delta^{13}\text{C}$ values is the decrease in the $\delta^{13}\text{C}$ value of atmospheric CO_2

a) Forest



b) Grassland

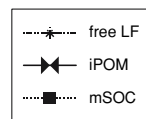
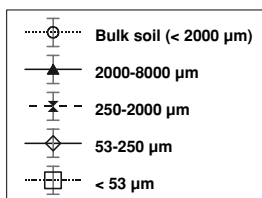
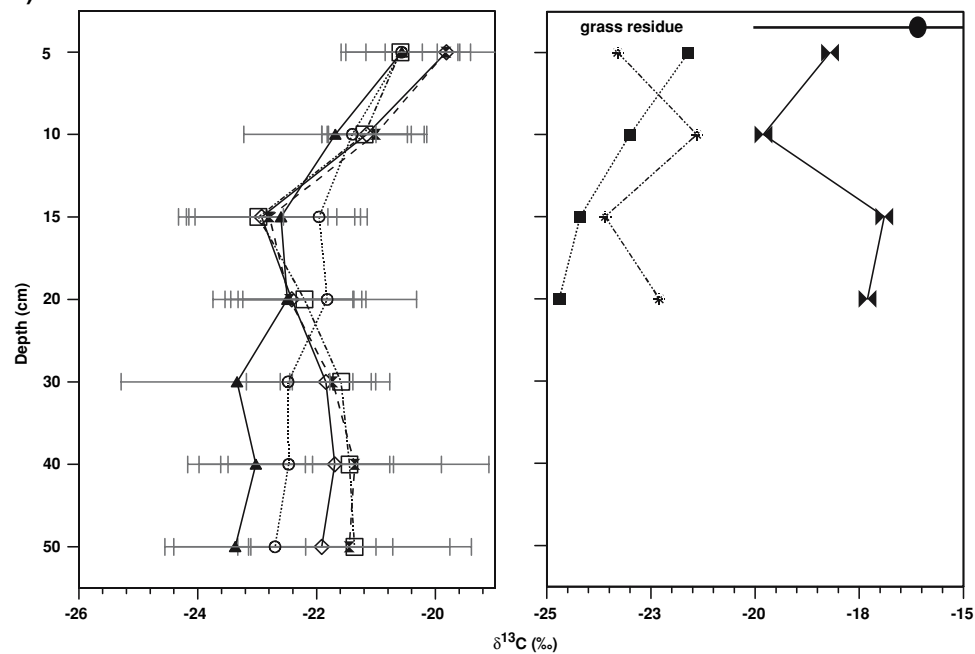


Fig. 3 Carbon isotope composition of soil organic carbon under (a) forest and (b) grassland, BCI, Panama. The left hand panel showing $\delta^{13}\text{C}$ values in bulk soil and water stable aggregates. The right hand panel shows the $\delta^{13}\text{C}$ values for density fractions. Bars represent standard deviation of three replicates. Note different scales for each panel

because of the combustion of ^{13}C depleted fossil fuel (Friedli et al. 1986).

The plant residue from the grassland had a significantly higher $\delta^{13}\text{C}$ signature ($-16.2 \pm 4.2\text{‰}$) than forest litter, indicating a somewhat variable mixture of the dominant C_4 grass *Saccharum spontaneum* plus residue from C_3 vegetation. The uppermost soil layer in the 90-year-old grassland was surprisingly depleted (-21.2‰). This might be explained by: (i) an important fraction of recalcitrant, forest derived C, (ii) a relatively important C_3 component throughout much of its land-use history, and/or (iii) a high proportion of charcoal debris left after biomass burning. Krull et al. (2003) showed that $\delta^{13}\text{C}$ values of C_4 derived chars from natural burns were depleted by up to 8‰ . Although we did not measure charcoal, the low $\delta^{13}\text{C}$ values of free LF, comparatively high pH values and the presence of charred particles in the free LF fraction corroborate the latter possibility. The $\delta^{13}\text{C}$ values of SOC under grassland decreased with soil depth, because in deeper layers the contribution of C_3 (forest C) is more dominant as it is not yet substituted by as much new (grassland) C. Deeper soil C may be dominated by forest C because of low grass C inputs and/or refractory C with longer residence times than in the top 5 cm.

Nonetheless, our results indicate significant inputs of C derived from grassland vegetation. In the uppermost layer, the grassland site contained 60% of new carbon formed by grassland residue. However, compared to other studies the proportion of grassland derived C is low, especially considering its 90-year age. Choné et al. (1991) found in an 8-year-old pasture (clayey Oxisol) near Manaus 68% of the C stock of the 0–3 cm upper layer was derived from pasture. In an 81-year-old pasture (sandy Ultisol) in Rondonia, the relative contribution of pasture derived C in bulk soil (0–5 cm) was 80% (Neill et al. 1996). In

Table 3 Proportion of new carbon and mean residence time (MRT) of water stable aggregates and density fractions under grassland, BCI, Panama

Depth (cm)	New C (%)		MRT (year)																										
	Water stable aggregate fractions (μm)					Density fractions					Water stable aggregate fractions (μm)					Density fractions													
	2000–8000	250–2000	53–250	< 53	mSOC	free LF	iPOM	mSOC	2000–8000	250–2000	53–250	< 53	free LF	iPOM	mSOC	2000–8000	250–2000	53–250	< 53	free LF	iPOM	mSOC							
0–5	55.6	65.0	63.6	55.2	47.6	85.0	50.4	93	69	66	80	80	203	29	124	43.2	47.1	46.2	44.9	61.3	71.4	47.0	*	132	113	125	211	50	227
5–10	32.1	23.8	21.2	18.6	47.5	94.0	26.2	*	198	224	202	202	141	20	173	34.3	23.5	21.0	25.5	52.9	89.4	13.7	*	154	180	184	112	39	306
10–15	24.2	26.1	22.7	25.7	nd	nd	nd	*	173	191	261	nd	nd	nd	nd	20–30	26.4	19.2	23.3	nd	nd	nd	*	151	176	215	nd	nd	
15–20	10.6	24.1	20.2	22.3	nd	nd	nd	*	196	271	649	nd	nd	nd	nd	30–40	20.7	26.4	19.2	23.3	nd	nd	*	151	176	215	nd	nd	
20–30																40–50													

nd = not determined

*Calculation results in unrealistic values as the fraction of old carbon in the grassland is higher than under forest

Table 4 Soil mass distribution, carbon concentration and carbon amount of density fractions under forest (F) and grassland (GL), BCI, Panama

Depth (cm)	Fraction mass distribution (%)						C concentration (g C kg ⁻¹ density fraction)						C amount (g C kg ⁻¹ aggregate)					
	Forest			Grassland			Forest			Grassland			Forest			Grassland		
	free LF	iPOM	mSOC	free LF	iPOM	mSOC	free LF	iPOM	mSOC	free LF	iPOM	mSOC	free LF	iPOM	mSOC	free LF	iPOM	mSOC
0–5	1.5	2.6	95.8	0.8	5.9	93.4	172.1	271.3	28.9	211.0	82.6	28.3	2.7	7.2	27.7	1.6	4.8	26.4
5–10	0.6	2.0	97.4	0.8	3.9	95.4	147.0	104.7	17.0	247.6	60.2	21.5	0.9	2.0	16.5	1.9	2.3	20.6
10–15	0.4	1.3	98.4	0.2	2.0	97.8	216.9	24.4	13.7	218.5	24.7	11.1	0.8	0.3	13.5	0.5	0.1	10.8
15–20	0.4	3.7	96.0	0.2	1.5	98.3	157.3	10.6	12.7	149.6	10.2	10.9	0.6	0.4	12.1	0.3	0.2	10.7

contrast, in 23-year-old pastures (clayey Oxisol) in Eastern Amazonia, Trumbore et al. (1995) found that only 21% of C (0–10 cm) was made up of C from the pasture. Trumbore et al. (1995) explained this low proportion of pasture derived C by the significant inputs of C derived from C₃ weeds. Further, care should be taken when using the ¹³C of modern standing vegetation as an end-member to constrain the long-term $\delta^{13}\text{C}$ value of the C added to the soil surface, because the abundance of C₃ and C₄ plants might have changed over time (Bird et al. 2003). Although *Saccharum spontaneum* was introduced to Panama only in 1970 (Hammond 1999), native C₄ grasses were probably important during much of the grassland's history.

Mean residence time of bulk soil estimated by ¹³C natural abundance was lowest in the uppermost soil horizon (69 years). Our data are within the range reported by Six et al. (2002), who reviewed MRT studies based on approaches similar to ours. The authors found a high variability in MRT for tropical (13–108 years) and temperate soils (14–141 years). On BCI, MRT increased with depth, indicating that the stability of bulk SOC was higher at depth. This was also reported by Trumbore (1993) who compared MRT's in tropical and temperate soil using radiocarbon measurements.

Aggregate structure and the role of water stable aggregates and density fractions on carbon turnover

Aggregate and density fractionation did not reveal significant land-use effects on soil structure at BCI. Studies have shown that conversion of forest into pasture leads to a decline in macroaggregates (Conant et al. 2004; Garcia-Oliva et al. 2006). In contrast, our data revealed a slightly higher proportion of macroaggregates in the 0–5-cm layer under grassland as compared to the forest. Thus, grassland vegetation may increase aggregate size, while grazing may decrease it, suggesting the importance of separating components of management techniques to understand effects on ecosystem properties.

We did not observe a significant increase in C and N concentration (g C (or N) kg⁻¹ aggregate

fraction) with increasing aggregate size class (free silt + clay < microaggregates < small macroaggregates). This is in contrast with the concept of aggregate hierarchy (Tisdall and Oades 1982) which states that with increasing aggregate size class the C concentration increases as larger aggregates are composed of smaller aggregates plus organic binding agents. However, aggregate hierarchy is only observed where organic material is the major binding agent to form aggregates (Six et al. 2002). The lack of a pronounced increase in C concentration with aggregate size at BCI might be explained by the high variability among sites and the mineralogy. In soils with a considerable content of 1:1 clay minerals (e.g. Kaolinites), oxides and other binding agents are the dominant stabilizing agents and thus prevent the formation of aggregate hierarchy caused by organic materials (Oades and Waters 1991). Those soils do not show higher C concentrations in larger aggregates (Six et al. 2000).

Under forest we did not observe significant differences in $\delta^{13}\text{C}$ values among WSA. However, SOC of all WSA and mSOC had higher $\delta^{13}\text{C}$ values as compared to bulk soil $\delta^{13}\text{C}$ throughout the soil profile (Fig. 3a; left panel). Higher $\delta^{13}\text{C}$ values relative to those in bulk soil indicates that SOC in macroaggregates, microaggregates and free silt + clay is more decomposed and contains more refractory C. In several studies from soils under C_3 vegetation it was found that C associated with finer particles has higher $\delta^{13}\text{C}$ values than C in coarser size fractions (Balesdent and Mariotti 1996; Feigl et al. 1995; Solomon et al. 2002). A compilation revealed that C associated with finer particles (< 2 μm) had on average 1–2‰ higher $\delta^{13}\text{C}$ values than C coarse size fractions (200–2000 μm) (Bird et al. 2003).

Under grassland, $\delta^{13}\text{C}$ values in bulk soil were higher than under forest owing to incorporation of C_4 -C, and WSA showed further enrichment of ^{13}C relative to the bulk soil (Fig. 3b; left panel). This could indicate a higher proportion of grassland derived C in WSA as compared to bulk soil and/or a higher state of decomposition in WSA. Apparently, enrichment in ^{13}C is associated with WSA as C is incorporated from bulk soil in both grassland and forest soils. The lower $\delta^{13}\text{C}$ values of mSOC compared to bulk soil suggest that

mSOC under grassland contained a higher proportion of residual forest C (C_3). This is supported by its long MRT. The $\delta^{13}\text{C}$ signature of iPOM isolated from the grassland was closest to the $\delta^{13}\text{C}$ value of the current vegetation, reflecting most clearly the inputs of C_4 derived C. Surprisingly, $\delta^{13}\text{C}$ values of free LF under grassland were lower than iPOM. Three hypotheses might explain this result: (i) free LF consisted not only of recent C_4 plant residue but also contained older C_3 material, (ii) free LF was primarily derived from roots residue ($\delta^{13}\text{C}$ of -24.7‰ , unpublished data) and (iii) free LF contained charcoal particles. The occurrence of charcoal in free LF and iPOM is common under sites where frequent vegetation burning was done (Cadisch et al. 1996; Skjemstad et al. 1990). Brodowski et al. (2006) measured black carbon in aggregate and density fractions of grassland soils, and found that the highest amount of charred plant material is accumulated in the occluded POM fraction (< 1.6 g cm^{-3}).

Isotopic methods confirm that grassland-derived C is incorporated in all fractions (Table 3). Differences in the proportion of new C among WSA were small and non-significant. However, inputs of grassland derived C in the upper 20 cm were slightly higher in the small macroaggregates than in the microaggregates and silt + clay. This is in accordance with other studies where pasture-derived C was incorporated more rapidly in coarse than fine SOM fractions (Desjardins et al. 2004; Feller and Beare, 1997). The fastest turnover was calculated for iPOM (< 50 years). This indicates that iPOM at this site on BCI contains easily degradable compounds and/or is physically less protected. This is in contrast to other studies where iPOM was reported to be physically and chemically more stable than free LF (Cambardella and Elliott 1992; Golchin et al. 1995). The mSOC fraction is stable and contains a large proportion of C and N, providing resilience of these soils to C and N losses. Note that the expression MRT with respect to soil organic fractions is misleading as the first order decay model does not account for the transfer of C between size classes fractions (John et al. 2005; Six et al. 1998). Aggregate formation is a dynamic process and C within micro- and macro-aggregates

might have been incorporated in other fractions before entering aggregates. Our MRT was calculated assuming that no C transfer occurred among fractions.

Conclusions

Contrary to our hypothesis forest conversion into grassland did not result in a significant loss of C and N throughout the profile. Despite the high losses in C and N the number of replicate was insufficient to demonstrate significant differences. Aggregate separation revealed that the shift in vegetation did not have a pronounced effect upon the aggregate stability. Under both land-use types around 80% of the C and N were associated with macroaggregates. Further, most C in small macroaggregates and microaggregates was stored in mSOC. Our research suggests that simply altering the vegetation cover may not be sufficient to alter aggregate structure or C stocks. Soil aggregate structure and organic carbon content may have changed more drastically if the land-use/vegetation change was coupled with intensive grazing or cropping.

Soil fractionation combined with stable isotope techniques provided insight into C turnover processes. The iPOM had the highest proportion of new C and in turn the lowest MRT (<50 years). This finding indicates that iPOM can serve as an early indicator for total C changes. In our study, free LF was depleted in ^{13}C relative to the vegetation input and iPOM. This resulted in a small proportion of new C and a comparatively long mean residence time (100–200 years). We hypothesized that free LF contained a high proportion of charcoal debris due to biomass burning. In addition, mSOC also had long MRT. Since this fraction contained a large portion of C and N it helps explain the non-significant changes in soil C and N. This points out that the evaluation of density fractions was an important step that provided more information on C storage and turnover than WSA for these soils.

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