Differences in soil biological activity and soil organic matter status only in the topsoil of Ferralsols under five land uses (Allada, Benin)

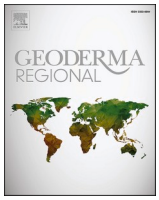
Issiakou Alladé Houssoukpèvi, Tiphaine Chevallier, Hervé Nonwègnon Sayimi Aholoukpè, Murielle Nancy Rakotondrazafy, Demayi Jorès Mauryo Fassinou, Guillaume Lucien Amadji, Lydie Chapuis Lardy

Geoderma Regional 39 (2024) e00865

Contents lists available at ScienceDirect

Geoderma Regional

journal homepage: www.elsevier.com/locate/geodrs



Differences in soil biological activity and soil organic matter status only in the topsoil of Ferralsols under five land uses (Allada, Benin)

Issiakou Alladé Houssoukpèvi [a,b,*], Tiphaine Chevallier [a,*], Hervé Nonwègnon Sayimi Aholoukpè [b,c], Murielle Nancy Rakotondrazafy [a], Demayi Jorès Mauryo Fassinou [b], Guillaume Lucien Amadji [b], Lydie Chapuis-Lardy [a]

[a] UMR Eco&Sols, Université de Montpellier, CIRAD, INRA, IRD, Institut Agro, 34060 Montpellier, France
[b] UR Ecopédologie; Laboratoire de Sciences du sol; Faculté des Sciences Agronomiques, Université d'Abomey-Calavi, BP 526 Cotonou, Benin
[c] Centre de Recherches Agricoles Plantes Pérennes (CRA-PP), Institut National des Recherches Agricoles du Bénin, BP 01 Pobè, Benin

ARTICLE INFO

Keywords:
Soil carbon dynamics
Land management
Tropical soils
Particle size fractionations
POM
MaOM - tea bag index

ABSTRACT

Land use change on the Ferralsols of the Allada Plateau in southern Benin has led to a slight decline in soil organic carbon (SOC) stocks over the last two decades. However, as in many African landscapes, detailed characterisation and quantified data on the SOC stocks and soil biological activity under major land uses are still poorly understood. The aim of this study was to characterise the biological activity and organic matter status of Ferralsols (0–30 cm) under the five major land uses on the Allada Plateau, i.e., forests, tree plantations, young and adult palm groves, and croplands (pineapple, maize). Soil biological activity was assessed using the standardised litter decomposition method (Tea bag index) and soil respiration (during a 28-day soil incubation). Soil organic matter status was characterised by quantifying SOC pools: soil microbial biomass carbon (MB-C), potassium permanganate oxidisable carbon (POX-C), and SOC associated to soil particle-size fractions (e.g. particulate organic matter, POM, and SOC associated to the clay soil fraction). The results indicated that SOC pools and biological activity were lower in tree plantations than in forests. The standardised litter decomposition was also slower in tree plantations than in forest. In croplands and palm groves, SOC pools and soil microbial biomass and respiration were lower than in forests and tree plantations. This high level of biological activity in forests, and at a lesser level in tree plantations, was effective in accumulating carbon in C pools associated to the clay fraction. Agricultural land uses, such as croplands and palm groves decreased all the soil C pools even those associated to the clay fraction, except for POX-C. However, these land-use effects on SOC pools decreased strongly with depth. At 10–30 cm, the differences in SOC pools or soil respiration between the five land uses were no more noticeable. Our results indicated that the amount of organic inputs was an essential factor to sustain high soil biological activity and SOC stabilisation in the clay size fraction, but only in the topsoil. Maintaining forests in the landscape is a priority in order to preserve SOC stocks and soil biological activity, which neither monospecific tree plantations nor cultivation can do at the same level.

1. Introduction

To prevent global warming, recent data clearly show that greenhouse gas emissions must be reduced, but carbon (C) storage strategies must also be developed, particularly in terrestrial ecosystems (IPCC, 2019; UNEP, 2020). Soils are the largest reservoir of C (2300 Gt C in the top 3 m) in terrestrial ecosystems, storing more C than vegetation (650 Gt C) and the atmosphere (860 Gt C) (FAO, 2019; Lorenz and Lal, 2018). Soil organic matter (SOM), which consists of 50–60 % carbon, supports important ecosystem services, including food production, climate regulation, water filtration, erosion control, nutrient cycling, and providing an energy supply for soil organisms (Adhikari and Hartemink, 2016; Lorenz et al., 2019). As a result, carbon sequestration in agricultural soils has been emphasised in recent years for agricultural mitigation and adaptation to climate change as well as for food security (Chevallier et al., 2020; Lal, 2004; Minasny et al., 2017).

Land cover, land use, agricultural or forestry practices affect the SOM dynamics, i.e., its decomposition and stability (Fujisaki et al., 2018;

* Corresponding authors at: UMR Eco&Sols, Université de Montpellier, CIRAD, INRA, IRD, Institut Agro, 34060 Montpellier, France.
E-mail addresses: alladeissiak@gmail.com (I.A. Houssoukpèvi), tiphaine.chevallier@ird.fr (T. Chevallier).

https://doi.org/10.1016/j.geodrs.2024.e00865
Received 19 February 2024; Received in revised form 11 September 2024; Accepted 12 September 2024
Available online 13 September 2024

Wiesmeier et al., 2019). Land use changes have led to a significant decrease in soil organic carbon (SOC) stocks, about −135 Gt C globally in the first metre of soil in 2017 (Lal, 2018). The SOC is more sensitive to land use in the surface horizons (0–30 cm) than in deeper horizons (Buchholz et al., 2014; Harrison et al., 2011). Therefore, a better understanding of the effects of land use and management on the C cycle, especially in the topsoil, is necessary to maintain or even increase SOC stocks (Błonska et al., 2020). However, as in many African landscapes, detailed characterisation and quantified data on SOC stocks and soil biological activity under major land uses have not yet been achieved. The interplay of primary producers, decomposers and soil mineralogy to explain the soil organic matter (SOM) stabilisation (Lehmann and Kleber, 2015) in these environments was still not fully understood. Regional soil information is needed to enrich international databases, raise soil awareness among stakeholders (Razafimbelo et al., 2022), and contribute to the calibration and validation of SOC evolution models at different scales (Le Noë et al., 2023). It is especially important in African areas close to large cities, where high demographic and land pressure is leading to rapid land use changes.

Knowledge of the distribution of C pools is crucial for understanding and modelling the C cycle between terrestrial ecosystems and the atmosphere (Dinakaran et al., 2018), as well as for monitoring the soil ecological functioning. However, most of the studies explore the evolution of land use with the evolution of global SOC stocks (e.g. Grinand et al., 2017; Houssoukpèvi et al., 2023). This global approach does not provide information on SOM decomposition, quality or stabilisation in the long term (Bellamy et al., 2005). Indeed, SOM is a continuum from plant and animal debris to organic matter produced by microbial activities, which could be characterised by conceptual pools (labile, intermediate, and stable/resistant pools) with specific evolutionary mechanisms and turnover rates (Lorenz et al., 2007; Six et al., 2002). Various methods have been proposed in the scientific literature to estimate SOM decomposition and quantify SOC pools. The tea bag index (TBI) uses commercial tea bags as a standardised alternative to estimate SOM decomposition, i.e. the capacity of soil microfauna and microorganisms to transform SOM (Keuskamp et al., 2013). Several physical, biological, and chemical methods are available to quantify SOC pools (Malou et al., 2023): labile pools such as particulate organic matter (POM), readily mineralisable SOC (amount of C-CO_2 emitted by soil respiration), potassium permanganate oxidisable C (POX-C) or more stable pools such as SOC associated with minerals, e.g. associated to clay size fraction. All these C pools, even the stable ones, can be affected by land use and agricultural practices, especially in topsoil (Fonkeng et al., 2024; Malou et al., 2023; Ramesh et al., 2019).

On the Allada plateau, close to Benin's economic capital, population and land use dynamics are rapidly evolving (Brun et al., 2018; Tchibozo, 2020). Aboveground biomass C stocks were highly different between land uses, with much higher stocks in forests than in tree plantations, palm groves and croplands (Houssoukpèvi et al., 2022). The soils of the plateau are mainly Ferrasols and are sandy. The difference in SOC stocks between land uses was noticeable, but much lower than for the aboveground C stocks and concentrated in the topsoil (Houssoukpèvi et al., 2022). The study of SOC and soil biological activity of the major land uses on the Allada plateau will allow us to assess and understand the evolution of SOC pools on Ferralsols, a common soil type in the tropics that covers 750 million hectares under natural vegetation or cultivation (FAO and IIASA, 2023).

The aim of this study was to assess soil biological and organic status of Ferralsols under major land uses of the Allada Plateau, i.e., forests, tree plantations, young palm groves, adult palm groves and cropland (pineapple, maize). The specific objective was to quantify biological activity (litter decomposition and soil respiration) and several SOC pools (microbial biomass, POX-C, POM and SOM associated to soil fractions: 20–50, 2–20 and 0–2 μm) of Ferralsols at two soil depths, 0–10 and 10–30 cm. We hypothesised that (i) land use drives soil biological activity and SOM partitioning into SOC pools especially at 0–10 cm, and that (ii) in cropland and palm groves, microbial biomass, decomposition of standard litter, and amount of SOC associated to any soil size fractions were much lower than in tree plantations and forests.

2. Materials and methods

2.1. Study design

This study was carried out in the Lama region, which comprises three communes, Allada, Toffo, and Zè, on the Allada plateau (6°20′ - 6°50′ N and 2°00′-2°30′E, 3 to 175 m a.s.l.) located in the Atlantic Department in southern Benin. Of the seven communities on the plateau, these three are the most diversified in terms of agricultural practices (Akoegninou et al., 2006; Akouehou et al., 2013). Palm groves, teak plantations, and a wide range of crops such as pineapples, maize, cassava, cowpeas, groundnuts, and tomatoes (Akouehou et al., 2013) dominate the landscape of the Allada plateau. The study area is located in a savannah zone with a tropical wet-dry climate (Aw) according to the Köppen-Geiger climate classification scheme (Rubel and Kottek, 2010). The average monthly temperature ranges from 25 to 29 °C, and the average annual rainfall is 1100 mm (Assogbadjo et al., 2011). The study was carried out on the same plots as in the sampling design in Houssoukpèvi et al. (2022), where it is explained in detail. Briefly, the plots were selected on ferrallitic soils corresponding to Ferralsols in the World Soil Resources Database (IUSS, 2015). These soils are dominant on the Allada Plateau and cover an area of 106,221 ha, representing 70 % of the surface area (Volkoff, 1976). The five main types of land use on these Ferralsols are forests, tree plantations, adult palm groves, young palm groves intercropped with maize or pineapple, and maize or pineapple cultivation (Houssoukpèvi et al., 2022). Two categories of forest were considered together in the present study: (i) sacred forests, which are typically small forest areas protected by the local community, and (ii) classified forests, which are remnants of natural forests under the protection of a public structure. Teak (*Tectona grandis* L.f.) dominates the land use category of tree plantations, which are usually grown without mineral fertilisation. Both state plantations managed by a public structure and private smallholder plantations were considered. The study area is known for its high number of oil palm trees (*Elaeis guineensis* Jacq), mainly managed by smallholders. During the first six years of the plantation, annual crops are grown in the gaps between the young palm trees, making the young palm groves a temporary agroforestry system. The selected young palm groves were associated with maize or pineapple and are nearing the end of their immature phase (*ca* 5 years). The two selected monospecific adult palm groves (10–12 years old) have supported maize and pineapple at tree immature stage. For annual crops, farmers clear the land before each cropping season, often using slash-and-burn techniques. Hoes are used for manual tillage to a maximum depth of 20 cm. For food crops, such as maize, mineral fertilisation is generally low (max. 46 kg N ha^{-1} applied annually as urea). However, for cash crops, such as pineapple, the mineral fertilisation can be significant in the form of urea and NPK fertilisers (14–23-14): approximately 480 kg N ha^{-1}, 70 kg P ha^{-1}, and 93 kg K ha^{-1} in three or four applications over the crop cycle. Some producers return crop residues to the soil after harvest, especially for pineapple. In young palm groves intercropped with maize or pineapple, the oil palms were also fertilised during the immature stage (about 25 kg N ha^{-1} and 30 kg K ha^{-1} when intercropped with pineapple and 50 kg N ha^{-1} and 60 kg K ha^{-1} in total when intercropped with maize) (Koussihouèdé et al., 2020).

The soils contained about 75 % of sand at 0–30 cm. The pH were comprised between 4.6 and 6.5 (soil:water ratio of 1:2). Soil N and SOC levels (determined after dry combustion and CHN analysis) ranged from 0.4 to 1.8 g N kg^{-1} soil for N and from 4.3 to 18.2 g C kg^{-1} soil for SOC, respectively. The C:N ratio ranged from 11 to 13 at 0–10 cm and to 9 to 12 at 10–30 cm. Plant-available phosphorus (P-Bray; Frank et al., 1998) ranged from 2.8 to 8.4 mg kg^{-1} soil, with high values observed in palm groves and cropland due to soil fertilisation (Houssoukpèvi et al., 2022).

Two sites per land use were selected, for a total of 10 plots (Table 1) separated by 5–10 km of each others. Inside each plots of 0.5 to 75.5 ha, depending of the land use, soil samples were collected with an auger between August and September 2019 at depths of 0–10 cm and 10–30 cm. Sampling was performed in 1 m^2 quadrats randomly established in each plot. In order to take into account the heterogeneity of each plots, the number of quadrats (from 12 in croplands to 35 in Niaouli Forest) depended on the size of the plot (Houssoukpèvi et al., 2022). The individual sampling in quadrats were gathered to form 4 independent composites per plot and per depth. All soil analyses were therefore replicated 8 times (2 plots × 4 independent composites) per land use for a given soil depth. Thus, 80 soil samples (10 plots × 2 depths × 4 composites) were air dried and sieved to 2 mm prior to analysis.

2.2. Decomposition of organic matter by the tea bag index (TBI) approach

The TBI approach is a field-standardised approach to assess the decomposition process by measuring the decomposition rate constant k and the stabilisation factor S of standardised litter during an in situ incubation period of 90 days (Keuskamp et al., 2013). Two standardised materials were used: commercial green tea (considered labile litter; European Article Numbering [EAN] 8,722,700 05552 5) and rooibos tea (considered recalcitrant litter: EAN 8722700 18,843 8) (Lipton, Westervoort, The Netherlands). Eight bags of each tea type were buried at each of the 10 sites (i.e., a total of 160 tea bags), as recommended by Keuskamp et al. (2013); for 90 days, during the short rainy season, the soil depth was 8 cm, with a 2-m gap between two holes. At the end of the incubation period, the tea bags were carefully removed and transported to the laboratory. Tea bags that had been punctured or damaged by invertebrates were removed (25 green and 15 roiboos tea bags in the present study, leaving 120 retained tea bags for analysis). After removing the adhering soil with a brush, the tea bags were dried in an oven at 60 °C for at least 48 h until a constant weight was obtained. The masses of the staple and label of each tea bag were subtracted to obtain the masses of the materials remaining in the dried tea bags. The resulting loss in weight represents the rate of decomposition. The decomposition rate constant k quantifies the mass loss due to early-stage, i.e. short-term, decomposition of the litter. High values of k indicate rapid decomposition of the labile organic compounds in the litter. The S factor measures the amount of hydrolysable compounds in the litter that become recalcitrant. High S values indicate high C storage potential. The k rate constant and S factor were calculated at each site following Keuskamp et al. (2013). Briefly, the stabilisation factor S was calculated based on the decomposable fraction a_g (Eq. (1)) and the hydrolysable fraction Hg (=0.842 g g^{-1} according to Keuskamp et al., 2013) of the green tea after 90 days of incubation in the soil (Eq. (2)):

$$a_g = 1 - Final\_weight\_Green\_Tea / Initial\_Weight\_Green\_Tea \quad (1)$$

$$S = 1 - a_g / H_g \quad (2)$$

The decomposition rate constant k was calculated from the mass loss of the rooibos tea (W) after the incubation period t (90 days), following a double negative exponential regression which describes the degradation of the decomposable fraction a_r at the beginning, then progressively slower, with the recalcitrant fraction (1-a_r) remaining with time (Eq. (3)):

$$W(t) = a_r e^{-kt} + (1 - a_r) \quad (3)$$

The decomposable fraction of rooibos tea (a_r) was determined by its hydrolysable fraction Hr (=0.552 g g^{-1} according to Keuskamp et al., 2013) and the stabilisation factor S (Eq. (4)):

$$a_r = H_r \times (1 - S) \quad (4)$$

2.3. Microbial biomass and activity

Soil respiration was assessed by incubating the samples in the laboratory under controlled conditions at 28 °C and a soil water potential (−0.03 MPa) corresponding to 80 % of the soil's water holding capacity (i.e. a soil water content of ca.10 % for such sandy soils). These samples were incubated for 28-days as this period has been shown to be appropriate for tropical sandy soils with low soil OM content (Malou et al., 2023). The CO_2 emissions were trapped as sodium carbonate (Na_2CO_3) in an alkaline solution (NaOH, 1 N). On days 3, 7, 14, 21 and 28, Na_2CO_3 was precipitated as barium carbonate ($BaCO_3$) by the addition of barium chloride ($BaCl_2$) (Gorissen, 1996). The excess sodium hydroxide was titrated with normal hydrochloric acid (HCl, 1 N) to pH 8.6 using a Titrino plus 848 titrator. Soil respiration was represented in this study only by the cumulative CO_2 emitted during the 28-day incubation, expressed as C-CO_2 in mg C-CO_2 kg^{-1} soil.

Soil microbial biomass was measured after the soil incubation on the same soil samples. After 28 days of incubation, soil microbial biomass (MB) was determined using the chloroform fumigation extraction method. Microbial biomass C (MB-C) was calculated as the difference between the organic C extracted with a K_2SO_4 solution (0.025 mol/L) applied to chloroform-fumigated and non-fumigated soils (Ross, 1990; Vance et al., 1987a). The amount of C extracted in K_2SO_4 was determined using a total dissolved organic carbon analyser (TOC-V_{CSH} Shimadzu, Kyoto, Japan). MB-C is proportional to microbial C (Brookes, 2001). A typical extraction efficiency of 0.45 was applied to account for non-extractable biomass and to convert microbial C to MB-C (mg C_{MB} kg^{-1} soil) (Vance et al., 1987b; Wu and Brookes, 2005).

Three indicators based on the MB-C concentration and soil respiration (after the 28-d incubation) were further determined to assess microbial activity and SOC bioavailability, i.e. a readily mineralisable SOC pool. The microbial metabolic quotient (qCO_2), which is the microbial respiration per unit of biomass per unit of time, was calculated on the cumulative CO_2 emissions and microbial biomass after 28 days and is expressed in µg C-CO_2 mg^{-1} MB-C. Increased or decreased qCO_2 is associated with shifts in microbial metabolism (Anderson and Domsch, 2010). The microbial quotient (q_{mic}) is the ratio of MB-C to SOC (Santos

Table 1
Information on the 10 studied sites.

Land use	Description	Site	Area (ha)	Municipality	Land use age (years)	Practices age (years)
Forests	Classified forests, sacred forests	Classified forest of Niaouli	75.5	Allada	>50	–
		Sacred forest of Damè	11	Toffo	>50	–
Tree plantations	Monospecific teak plantations.	State teak plantation	24	Zè	65	21
		Private teak plantation	0.5	Toffo	–	10
Adult palm groves[§]	Oil palm groves (>10 years)	Maize	1	Allada	–	10
		Pineapple	3	Zè	–	12
Young palm groves[§§]	Immature palm trees associated with a crop	Maize	0.5	Toffo	–	<5
		Pineapple	1	Zè	–	<5
Croplands	Annual or biennial crops	Maize	0.8	Zè	–	4
		Pineapple	1.5	Toffo	–	5

[§] Adult palm trees were associated with Maize or Pineapple at their young stage,
[§§] Young palm trees are currently associated with Maize or Pineapple.

et al., 2012; Sparling, 1992). The q_{mic} indicates the amount of SOC as microbial biomass and thus reflects the bioavailability of SOC. In addition, the bioavailability of SOC has also been assessed by the relative C mineralisation rate, expressed as the ratio between the C-CO_2 produced and the SOC content in g C-CO_2 100 g^{-1} SOC (Chevallier et al., 2010; Wang et al., 2003).

2.4. Permanganate-oxidisable carbon (POX-C)

A 2.5 g sample of dried soil sieved to 2 mm was added to 20 mL of potassium permanganate solution ($KMnO_4$ 0.02 mol/L), shaken for exactly 2 min at 240 oscillations min^{-1} according to the protocol described by Weil et al. (2003), and allowed to decant for 10 min. The supernatant (0.5 mL) was diluted with deionised water (49.5 mL), and the absorbance was measured at 565 nm using a spectrometer (SpectroVis Plus Go Direct, GDX SVIS+). The concentration of POX-C was calculated using Eq. (5):

$$\mathrm{POXC} = \left[0.02\ \mathrm{mol\ L^{-1}} - (\mathrm{a} + \mathrm{b\ Abs})\right] \times \left(9000\ \mathrm{mg\ C\ mol^{-1}}\right) \times \left(\frac{0.02\ \mathrm{L_{solution}}}{\mathrm{W_t}}\right) \quad (5)$$

where *0.02 mol/L* is the initial concentration of the $KMnO_4$ solution, *a* is the intercept of the calibration curve, *b* is the slope of the calibration curve, *Abs* is the absorbance of the unknown soil sample, *9000 mg* is the amount of C oxidised by 1 mol of MnO_4 with reduction of Mn^{7+} to Mn^{4+}, *0.02* $L_{solution}$ is the volume of the KMnO solution$_4$, i.e., 20 mL reacted with the soil, and W_t is the amount of soil used in the reaction (kg).

2.5. Particle size fractionation of SOM

The analysis was performed according to the methods described by Gavinelli et al. (1995) and Balesdent et al. (1998). Soil samples (20 g) were first soaked overnight at 4 °C in 300 mL of deionised water supplemented with 10 mL of sodium hexametaphosphate (50 g/L). The suspensions were then shaken with 5-mm diameter agate beads using a rotary shaker at 43 rpm for 6 h. Successive sieving in water separated the soil fractions into the following size classes: > 200 μm and 50–200 μm. The solution containing particles <50 μm was subjected to ultrasonic waves for 10 min to disperse soil aggregates smaller than 50 μm using a probe-type ultrasonic device (Fisher Bioblock Scientific, Illkirch, France) with a power of 600 W at a frequency of 20 kHz and a on/off intervals of 0.7/0.3. The 20–50 μm fraction was recovered by sieving the sonicated suspension. The 2–20 μm and 0–2 μm fractions were separated by sedimentation. All the fractions were then dried in an oven at 40 °C, weighed (except for the 2–20 μm fraction estimated by subtraction), ground (< 200 μm) and analysed with an elemental analyser (Thermo flash 2000 CN analyser, Milan, Italy). In our study, fractions >200 μm and 50–200 μm were grouped together after analysis. The particulate organic matter (POM), i.e. the light and organic fractions >50 μm, was separated from the mineral particles >50 μm by flotation in water (Gavinelli et al., 1995). The C content of the mineral fraction >50 μm was analysed (average 0.37 ± 0.03 mg C g^{-1} fraction) to determine whether it contained mostly minerals and very little carbon. The fraction <50 μm has recently been referred to in the scientific literature as the MaOM fraction (e.g., Cotrufo et al., 2013). Because different particle sizes were separated in our study, we preferred to refer to these mineral-associated OM fractions as the F0–2, F2–20 μm and F20–50 μm fractions based on their size.

2.6. Statistical analysis

For the tea bag index (TBI) approach, a general linear mixed model, with land use and tea type as fixed factors and replication as a random factor, was used to test for differences between the remaining tea masses after incubation. The general linear mixed effects model was also used to test the difference between land use types as a function of soil depth (0–10 vs. 10–30 cm) for the other parameters studied. The normality of the residuals was tested using the Shapiro-Wilk test and the Breusch-Pagan test to check the homogeneity of the residual variance. Post hoc comparison tests of means were performed for the independent factor (land use) using the Tukey HSD test at the 0.05 probability level. Pearson correlation coefficients between SOC pools were also calculated. Seven SOC pools were considered: microbial biomass pool (MB-C), readily mineralisable SOM (C-CO_2, the cumulative CO_2 from soil respiration in 28 days), permanganate oxidisable carbon (POX-C) and the 4 organic particle size fractions (POM, F20–50 μm, F2–20 μm and 0–2 μm). All analyses were performed using R software version 3.6.3 (R Development Core, 2020).

3. Results

3.1. Soil biological activity

3.1.1. Standardised tea bag litter decomposition indicators

Irrespective to the land use, the remaining tea mass after 90 days of incubation in the field was greater for rooibos tea (on average, 64.4 ± 8.2 %) than for green tea (32.4 ± 9.1 %) (Fig. 1). The remaining rooibos tea masses were similar between the different land use types (Fig. 1). The results of the general linear mixed model were presented in the Appendix A. The remaining green tea mass was affected by land use ($p < 0.05$), significantly lower in forests and tree plantations than in croplands (Fig. 1).

The variability in the decomposition rate constants *k* and stabilisation factors *S* measured within the same land use was high (Fig. 2). However, general linear mixed model revealed a significant variation in the decomposition rate constant *k* between the different land use types ($p < 0.05$). The highest value was found in forest soils (Fig. 2). Surprisingly, the decomposition rate constant *k* was significantly higher in cropland than in tree plantations or palm groves. In contrast, the stabilisation factor *S* did not differ significantly between land use types ($p > 0.05$) (Fig. 2).

3.1.2. Soil respiration

The results of the general linear mixed model are presented in the Appendices A and B. The CO_2 released by the soil microbial respiration over 28 days under controlled conditions varied significantly ($p < 0.05$) according to the land use at a depth of 0–10 cm (Fig. 3). In contrast, at a depth of 10–30 cm, land use did not significantly ($p > 0.05$) influence the cumulative CO_2 emissions from the soil (Fig. 3). At a depth of 0–10 cm, the cumulative CO_2 emissions from forest soils (1700 ± 319 mg C kg^{-1} soil) and tree plantations (1611 ± 91 mg C kg^{-1} soil) were significantly higher than those from other land uses. Cumulative CO_2 emissions from cropland (1226 ± 36 mg C kg^{-1} soil) were not significantly different from those from adult palm groves (1306 ± 131 mg C kg^{-1} soil) (Fig. 3).

Soil respiration accounted for a greater proportion of total SOC (C-CO_2:SOC ratio) at the 10–30 cm soil depth than at the soil surface, regardless of the land use type (Table 2). At 0–10 cm, the C-CO_2:SOC ratio was significantly affected by land use ($p < 0.05$), with lower values in the forest than in the other land use types (Table 2). The C-CO_2:SOC ratios were similar under tree plantations, palm groves - either adult or young - and cropland. At 10–30 cm, the C-CO_2:SOC ratio was still lower in the forest treatment than in the other land use types, but no significant difference was found between the forest and adult palm groves (Table 2).

3.1.3. Soil microbial biomass and related ratios

Land use had a significant effect on microbial indicators, except for q_{mic} at 10–30 cm depth (Table 2).

Microbial biomass carbon concentration (MB-C) was significantly affected by depth ($p < 0.05$), with significantly higher values at the soil

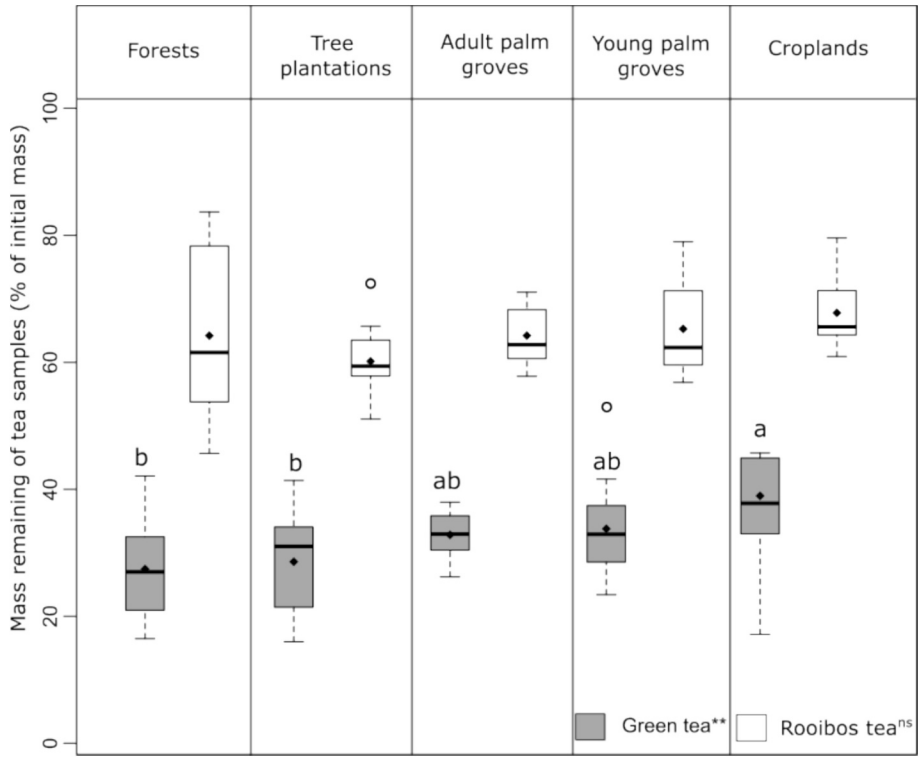


Fig. 1. Remaining mass (% of initial mass) of green tea and rooibos tea materials 90 days after burying bags in Ferralsols, according to land use.
The lines inside the boxes indicate the median and the diamonds inside the boxes indicate the mean (n = 8); the boxes define the 25th and 75th percentiles; and the whiskers define the highest and lowest values excluding outliers. Circles represent outliers. Different letters indicate a significant difference ($p < 0.05$) between land use types for the green tea treatment (** $p < 0.01$). The roiboos tea has undergone no significant effect (ns; $p > 0.05$).

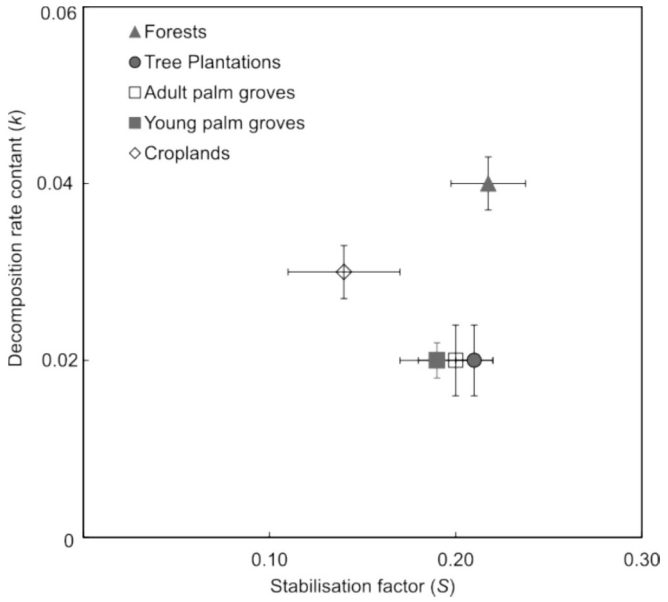


Fig. 2. Decomposition rate constant k and stabilisation factor S based on rooibos tea and green tea respectively, according to land use ($n = 8$; means ± SD).

surface (0–10 cm) than at 10–30 cm depth. In the 0–10 cm soil layer, MB-C under forest was about 2 times higher than under tree plantations, 4 times higher than under palm groves, and 6 times higher than under cropland (Table 2). The MB-C under adult palm groves, young palm groves and cropland did not differ significantly. At the 10–30 cm depth, the MB-C was also significantly higher in forest than in adult palm groves, young palm groves, and cropland, but not significantly different ($p > 0.05$) between forest and tree plantations.

Microbial biomass C represents 0.5 to 1.1 % of the total SOC. This microbial quotient (q_{mic}) was not significantly different between the two depths studied (Table 2). However, significant differences between land use types were observed in the 0–10 cm soil layer. At 0–10 cm, the proportion of microbial biomass to total SOC was significantly higher in forests or tree plantations than in palm groves or cropland (0.9–1.1 vs. 0.5–0.7 mg MB-C 100 mg^{-1} SOC).

The metabolic quotient (qCO_2) was sensitive to soil depth and land use. It was significantly greater at 10–30 cm depth than in the topsoil for a given land use. In contrast to q_{mic}, qCO_2 was greater in the croplands (Table 2). In the 0–10 cm soil layer, qCO_2 increased from forest to cropland, from 11.9 ± 3.7 to 39.9 ± 6.8 µg C-CO_2 mg^{-1} MB-C. The qCO_2 was almost 2 to 3 times higher under palm groves and cropland, with no difference between these two land use types, than under forest. The qCO_2 was not significantly different between the palm groves and the tree plantations. At 10–30 cm, the differences in qCO_2 between land uses remained significant and were marked between forests and other land uses (Table 2).

3.2. Soil organic carbon pools

3.2.1. Soil organic carbon contents

For all depths the SOC content ranged from 4.0 to 18.2 g C kg^{-1} soil (Table 3). At all depths, SOC contents varied significantly according to the land use (Table 3). At a depth of 0–10 cm, the SOC content was significantly higher in forests than in the other land use types. Cropland was the land use type with the lowest SOC content (Table 3). The SOC content of croplands was 2.5 times lower than that of forests and 1.5 times lower than that of tree plantations (Table 3). SOC contents decreased with depth. At a depth of 10–30 cm, there were no significant differences between forests, tree plantations, adult palm groves, and croplands.

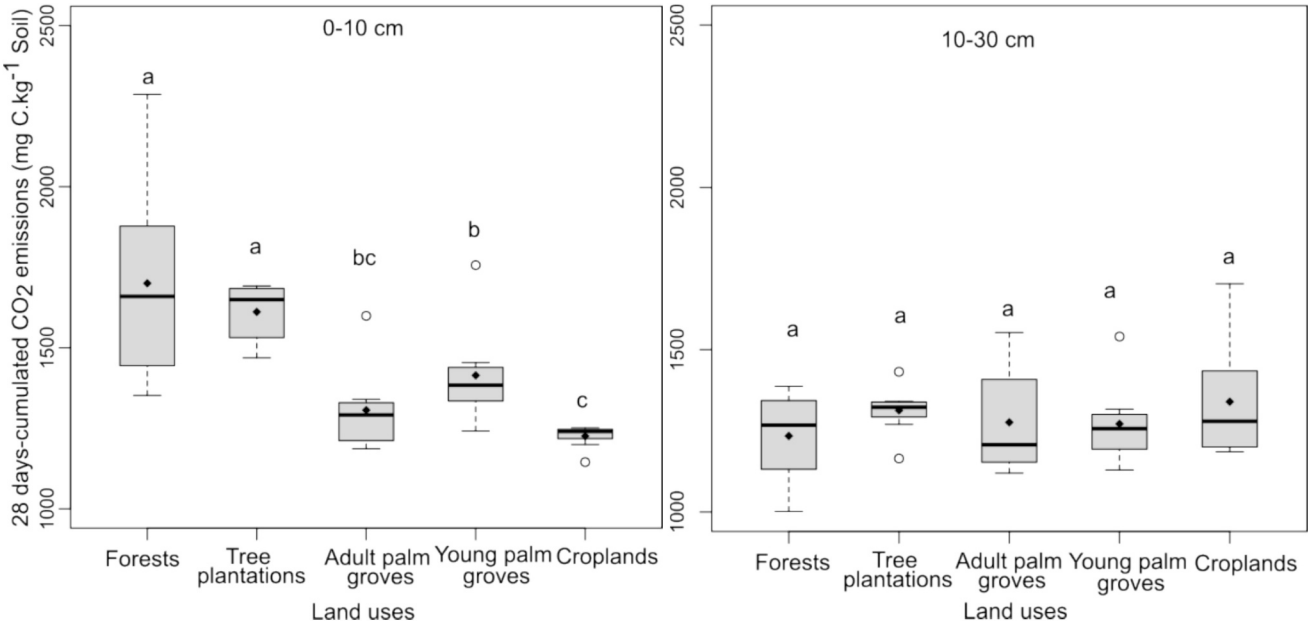


Fig. 3. Cumulative CO_2 emissions over a 28-days incubation of soil layers collected at 0–10 cm and 10–30 cm deep according to land use.
Lines within boxes indicate median and diamonds within boxes indicate mean (n = 8); boxes define 25th and 75th percentiles; whiskers define highest and lowest values excluding outliers and circles represent outliers. Different letters indicate a significant difference ($p < 0.05$) between land use types for a given soil depth.

Table 2
Soil microbial indicators (mean ± standard deviation; n = 8 per soil layer) as depicted per land use and soildepths.

Microbial indices	Forests	Tree plantations	Adult palm groves	Young palm groves	Croplands
MB-C (mg C_{MB} Kg^{-1} soil)					
0–10 cm	232.4 ± 50.9 Aa	107.4 ± 13.5 Ab	57.7 ± 8.6 Ac	59.7 ± 6.0 Ac	35.8 ± 4.6 Ac
10–30 cm	55.8 ± 9.9 Ba	38.5 ± 8.8 Bab	28.1 ± 4.9 Bb	24.2 ± 4.3 Bb	25.6 ± 4.3 Bb
q_{mic} (mg MB-C 100 mg^{-1} SOC)					
0–10 cm	1.1 ± 0.2 Aa	0.9 ± 0.1 Aab	0.6 ± 0.1 Ac	0.7 ± 0.0 Abc	0.5 ± 0.1 Ac
10–30 cm	0.8 ± 0.1 Aa	0.8 ± 0.2 Aa	0.6 ± 0.1 Aa	0.6 ± 0.1 Aa	0.5 ± 0.1 Aa
qCO_2 (µg C-CO_2 mg^{-1} MB-C)					
0–10 cm	11.9 ± 3.7 Bc	16.3 ± 1.6 Bbc	26.8 ± 4.8 Bab	25.5 ± 2.7 Bb	39.9 ± 6.8 Ba
10–30 cm	29.8 ± 6.9 Ab	52.4 ± 11.9 Aa	55.4 ± 8.7 Aa	60.9 ± 7.4 Aa	68.2 ± 15.4Aa
C-CO_2:SOC ratio (g C-CO_2 100 g^{-1} SOC)					
0–10 cm	9.1 ± 1.1 Bb	15.0 ± 1.4 Ba	13.7 ± 1.1 Ba	17.2 ± 1.4 Ba	17.6 ± 1.5 Ba
10–30 cm	20.8 ± 2.0 Ab	33.9 ± 4.2 Aa	28.3 ± 1.9 Aab	32.9 ± 2.2 Aa	29.9 ± 4.7 Aa

MB-C: Microbial biomass carbon; q_{mic}: microbial quotient; qCO_2: metabolic quotient; C-CO2:SOC ratio: relative mineralisation rate. Means with different capital letters indicate a significant difference ($p < 0.05$) between soil depths for a given land use. Means with different lowercase letters indicate a significant difference between land use types for a given soil depth ($p < 0.05$).

3.2.2. *Permanganate-oxidisable carbon (POX-C)*

The amount of POX-C varied significantly with land use, independent of the soil depth (Table 3).

Overall, POX-C was slightly higher at the surface than at depth (0.4 to 1.2 vs. 0.2 to 1.0 g C kg^{-1} soil, respectively). The differences in POX-C between the different land uses were small regardless of depth. For both soil depths, POX-C was significantly lower ($p < 0.05$) in soils under tree plantations than under other land uses, and POX-C under forest was lower than POX-C under palm groves and cropland, without being significantly different from the POX-C measured under cropland at 0–10 cm (Table 3).

The POX-C:SOC ratio was significantly higher at depth than at the surface, except in soils under tree plantations (Table 3). This indicator was sensitive to land use at both depths studied. For both depths, this ratio was significantly greater in soils under palm groves (adult or young) or cropland than in soils under forests and tree plantations (Table 3), with 12–16 vs. 4–5 g POX-C 100 g^{-1} SOC at 0–10 cm and 23–26 vs. 4–11 g POX-C 100 g^{-1} SOC at 10–30 cm.

3.2.3. *Organic carbon distribution in the soil particle size fractions*

The average mass recovery after soil fractionation was 99 % at both depths, and the average carbon yield was upper to 87 % at 0–10 cm and upper to 83 % at 10–30 cm (Appendix C). Land use had a significant effect on the C content of the soil fractions (g C kg^{-1} soil) regardless of the soil depth (Fig. 4).

At the 0–10 cm depth, the C content of all the SOM fractions was significantly higher in the forests than in the other land use types (Fig. 4). For example, the C content of the POM fractions in soils under forests (8.4 ± 2.9 g C kg^{-1} soil) was significantly higher than that in soils under tree plantations, adult palm groves, young palm groves, and cropland (2.6–3.7 g C kg^{-1} soil) (Fig. 4). The C contents of POM, F 20–50 µm, and F 2–20 µm were not significantly different in the soils

Table 3
Soil organic carbon and the POX-C pools in the different land uses (mean ± standard deviation; n = 8 per soil layer).

Soil properties	Forests	Tree plantations	Adult palm groves	Young palm groves	Croplands
SOC (g C kg^{-1} soil)					
0–10 cm	18.2 ± 2.3 Aa	11.4 ± 1.0 Ab	10.0 ± 1.0 Ab	8.6 ± 0.7 Ab	7.2 ± 0.5 Ac
10–30 cm	6.4 ± 0.7 Ba	4.3 ± 0.5 Bab	4.6 ± 0.3 Bab	4.0 ± 0.4 Bb	5.2 ± 0.8 Bab
POX-C (g POX-C kg^{-1} soil)					
0–10 cm	0.9 ± 0.11 Ab	0.4 ± 0.06 Ac	1.2 ± 0.03 Aa	1.2 ± 0.02 Aa	1.1 ± 0.09 Aab
10–30 cm	0.6 ± 0.18 Ab	0.2 ± 0.02 Bc	1.0 ± 0.01 Ba	1.0 ± 0.02 Ba	1.0 ± 0.03 Aa
POX-C : SOC (g POX-C 100 g^{-1} SOC)					
0–10 cm	5.1 ± 0.9 Bb	3.8 ± 0.4 Ab	12.4 ± 1.1 Ba	14.6 ± 1.0 Ba	15.6 ± 1.9 Ba
10–30 cm	11.5 ± 3.9 Ab	4.4 ± 0.6 Ab	23.0 ± 1.4 Aa	26.1 ± 1.8 Aa	22.8 ± 3.2 Aa

Means with different capital letters indicate a significant difference ($p < 0.05$) between soil depths for the same land use. Means with different lowercase letters indicate a significant difference between land use types for the same soil depth ($p < 0.05$).

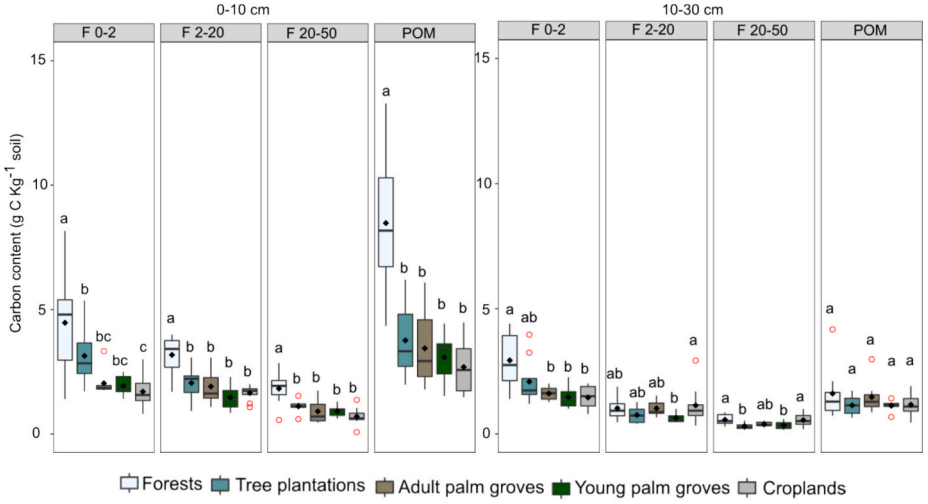


Fig. 4. SOC associated with each soil fraction as a function of land use at 0–10 cm and at 10–30 cm depth.
Lines within boxes indicate the median and diamonds within boxes indicate the mean (n = 8); boxes define the 25th and 75th percentile; whiskers define highest and lowest values excluding outliers and circles represent outliers. Different letters indicate a significant difference ($p < 0.05$) between land use types for a given soil depth and fraction. POM: Particulate Organic Matter >50 μm, F = organo-mineral fractions with 0–2, 2–20, and 20–50 as the corresponding particle size (μm).

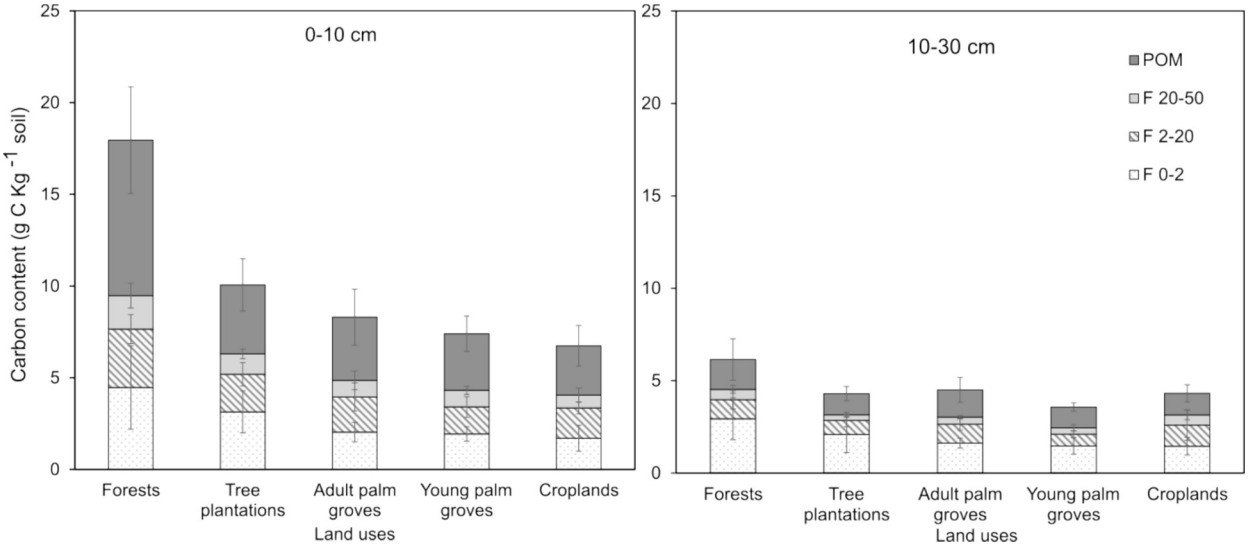


Fig. 5. Distribution of SOC content between soil particle-size fractions according to land use.

under tree plantations, adult palm groves, young palm groves, or cropland (Fig. 4). For the finest fraction (F 0–2 µm), there were three groups with significantly different values, which gradually decreased from forests (4.5 ± 2.3 g C kg^{-1} soil), plantations, tree or palm grove plantations (3.1 to 1.9 g C kg^{-1} soil), and cropland (1.7 ± 0.7 g C kg^{-1} soil) (Fig. 4).

At the 10–30 cm depth, the C content of POM did not vary significantly ($p > 0.05$) according to the land use (Fig. 4). In the F 2–20 and F 20–50 µm fractions, the differences in C content between land uses were very small. However, the C content of the fine fraction (F 0–2 µm) varied significantly ($p < 0.05$), with higher contents occurring in forests (2.9 ± 1.1 g C kg^{-1} soil) than in adult palm groves, young palm groves, or cropland (i.e., 1.5–1.6 g C kg^{-1} soil) (Fig. 4). The C contents of the fine fraction under forests and under tree plantations were not significantly different due to the large heterogeneity in the results for the forests.

The distribution of SOC between the particle size fractions varied with depth. POM represented on average 40 % of the total SOC at 0–10 cm on average, whereas it represented for 29 % of the total SOC at 10–30 cm, irrespective of the land use (Fig. 5, Appendix D). The fine fractions F0–2 µm or F0–20 µm (i.e., F0–2 + F2–20 µm) represented respectively 25 % and 50 % of the total SOC at 0–10 cm and 40 % and 60 % at 10–30 cm (Fig. 5, Appendix D). The F 20–50 µm fraction represented very little C, about 10 % of the total SOC at both soil depths.

3.2.4. Relationships between the different soil C pools

At 0–10 cm, Pearson correlation coefficients between the different SOC pools showed strong positive relationships between readily mineralisable C (C-CO_2), MB-C, and SOC associated to POM, F 20–50 µm and F 0–2 µm ($R > 0.5$ and $p < 0.05$) (Table 4). POX-C was negatively correlated with C-CO_2 and the amount of SOC associated with the F0–2, F2–20, and F20–50 particle size fractions. At the 10–30 cm depth, in contrast to the soil surface, there was no relationship between C-CO_2 and the other C pools (Table 4). However, at the surface and at 10–30 cm, there was a strong positive correlation between the MB-C and C associated with POM and with the F0–2 fraction. At 10–30 cm, POX-C was not correlated with most other C pools, except weakly and negatively for MB-C and F 0–2 ($p < 0.05$; Table 4).

4. Discussion

4.1. Land use affects soil biological activity

4.1.1. Standard litter decomposition highly variable but slightly higher in forests

The difference in the residual litter mass between green tea and roiboos showed that the soil microbial colonisation of tea litter was likely substrate-selective, with no significant effect on the more recalcitrant litter. The constant *k* reflects the rate at which the labile fraction of the litter decomposes and serves as an indicator of early decomposition (Fanin et al., 2020; Keuskamp et al., 2013). The lower the remaining mass of green tea, the greater the litter decomposition (k-value), with greater soil respiration and microbial biomass in forests than in other land uses (Figs. 1, 2, 3; Table 2).These results show that soil biological activity and labile organic residue dynamics were strongly influenced by land use, particularly in the topsoil (Fig. 3). These results are consistent with the literature describing the high activity of soil organisms in forests (Duddigan et al., 2020; Kagezi et al., 2016) and the larger *k*-decomposition constant in undisturbed forests than in disturbed systems (Attignon et al., 2004; Becker and Kuzyakov, 2018). Compared to that in tree plantations, the faster OM decomposition in forests may be a consequence of the vegetation structure of forests with a high diversity of tree and plant species, which probably leads to a more diversified litter quality (Hättenschwiler et al., 2005; Sauvadet et al., 2021) and a more efficient food web than in a monospecific tree plantation with only teak (Sauvadet et al., 2019). This activity, combined with an increase in soil microbial biomass (Table 2) and possibly in the diversity of soil microbial populations (Hansen, 2000; Nilsson and Wardle, 2005; Tresch et al., 2019) should promote litter decomposition (Daebeler et al., 2022). The lower *k*-constant of standardised litter in agricultural soils and plantations is probably a consequent of reduced plant diversity, mineral fertilisation practices, and low organic inputs to soils (Houssoukpèvi et al., 2022), which has led to a reduction in microbial biomass (Table 2) and probably in microbial diversity (Kagezi et al., 2016; Zang et al., 2016).

In the tree plantation and in the palm grove plantation, the remaining mass of green tea was similar, but the *k* decomposition rate was lower than that in the forest soil. Surprisingly, the *k* value was lower in monospecific plantations (teak or palm grove) than in cropland, while cropland had the lowest values of the stabilisation factor *S*. *S* reflects the proportion of the undecomposed, hydrolysable labile fraction remaining after field incubation and thus reflects long-term carbon stability (Keuskamp et al., 2013). This result seems to show that plant diversity in space, as in forests, or to a lesser extent in time through rotation, as in cropland, improves the *k*-decomposition rate constant of a standardised labile litter, i.e., "how fast" the labile litter fraction is decomposed independent of the soil microbial biomass in soil (Barel et al., 2019; Fanin et al., 2020). Furthermore, the slight decrease in S, which reflects "how much" of the labile litter fraction is stabilised, was observed in cropland compared to forests and plantations and may reflect the high turnover of organic inputs in tropical sandy agricultural soils (Malou et al., 2023). Contrary to the literature (Becker and Kuzyakov, 2018; Duddigan et al., 2020; Saint-Laurent and Arsenault-Boucher, 2020), our study did not show a greater sensitivity of the stabilisation factor *S* compared to the *k*-decomposition rate constant to changes in edaphic conditions in response to agricultural practices. Our highly variable results need to be confirmed by a complementary tea bag decomposition experiment, extending the time periods to account for possible seasonal effects (Daebeler et al., 2022) and by studying decomposer communities associated with different land uses.

4.1.2. Both microbial biomass and activity higher in forests

The high microbial biomass and soil respiratory CO_2 emissions under forests and tree plantations compared to cropland are in line with the literature. Microbial biomass and soil respiration are strongly influenced by the soil-climate conditions created by land use (Wang et al., 2013) and by the availability of organic resources (Colman and Schimel, 2013; Sowerby et al., 2000), which could also be exudates and root debris from trees (Dennis et al., 2010). Mineralisation of organic matter is usually high in forests and plantations, where litter is much more available than in other land uses (Houssoukpèvi et al., 2022) and is frequently renewed, creating favourable physicochemical and resource conditions for the activity of heterotrophic microorganisms (Bertolino et al., 2010; Gu and Riley, 2010; Yiqi and Zhou, 2010). In a previous study, we noticed that the soil C:N ratios were rather similar in the five land uses with differences less than 1.5 units with slightly higher C/N ratios (≈13) under forest and tree plantations than in croplands and palm groves (≈11) (Houssoukpèvi et al., 2022). These differences were not significantly different except in adult palm groves (data not shown) and could hardly explain the difference of soil biological activity observed.

Table 4
Pearson correlation coefficient between the different SOC pools.

		C-CO_2	MB-C	POX-C	POM	F 20-50	F 2-20	F0-2	
C-CO_2			0.08	-0.11 .	-0.06	0.25	0.1	0.09	
MB-C		0.55**		-0.33*	0.53**	0.4*	0.23	0.72**	
POX-C		-0.35*	-0.38*		0.28	0.14	0.24	-0.50**	
POM	0-10 cm	0.55**	0.80**	-0.14		0.42*	0.45*	0.14	10-30 cm
F 20-50		0.59**	0.53**	-0.30*	0.66**		0.47*	0.38*	
F 2-20		0.44*	0.78**	-0.32*	0.78**	0.63**		0.21	
F 0-2		0.50**	0.86**	-0.34*	0.86**	0.53**	0.80**		

MB-C: Microbial biomass carbon; POX-C permanganate oxidisable carbon; POM = organic fraction >50 µm, F = organo-mineral fraction. 0–2, 2–20 and 20–50 represent particle size (µm). "*": significant relationship $p < 0.05$.

Soil microbial biomass and soil respiration were greater in the forest than in the tree plantation, as explained above, probably due to the greater amount and diversity of organic inputs in the forest, but the monospecific teak plantations also had much greater microbial biomass and soil respiration than did the monospecific palm grove plantations. Even in the mature phase (10–12 years old), the palm groves had a much lower soil microbial biomass and soil respiration than did the teak plantations, with values close to those of cropland (Fig. 3, Table 2). The higher litter inputs in the adult palm plantation than in the teak plantation (23.9 ± 1.7 Mg ha^{-1} vs. 7.6 ± 0.7 Mg ha^{-1}, respectively), in Houssoukpèvi et al., 2022, did not compensate for the soil degradation at the establishment of the palm grove or the low root biomass and probably C inputs from root turnover between the palm groves and teak. The amount of organic inputs seemed to be a major driver of the microbial activity.

4.1.3. Greater microbial efficiency and SOC stabilisation in forests

Soil microbial activity, assessed by microbial indicators such as the microbial quotient (q_{mic}) or the metabolic quotient (qCO_2), was clearly influenced by land use, as previously reported (e.g. Kaschuk et al., 2011). A lower microbial activity per unit of microbial biomass, i.e., the metabolic quotient qCO_2, measured in the forest indicated a higher efficiency of microbial metabolism in these soils (Table 2). The lower qCO_2 values reflect a lower energy requirement to maintain the microbial community in forests and on the soil surface of tree plantations compared to palm groves and cropland. In contrast, the high qCO_2 observed in croplands suggests that the conversion of carbon into microbial biomass is less efficient under these land use conditions (Anderson and Domsch, 2010; Dinesh and Ghoshal Chaudhuri, 2013; Fterich et al., 2014). In croplands, low substrate availability, low pH (Table 3) and shallow tillage could induce microbial stress, i.e., microorganisms diverting their energy from growth to maintenance (Anderson and Domsch, 2010; Hungria et al., 2009; Kaschuk et al., 2011; Mangalassery et al., 2015). Low qCO_2 in forests and plantations tended to indicate a low turnover rate of the microbial biomass, with a tendency for C to accumulate or stabilise under forest or tree plantation conditions, at least at the soil surface where the biological activity was high. This is consistent with the lower *S* value of the TBI experiment on cropland than on other land uses. Similarly, high microbial quotients (q_{mic}) and a low relative mineralisation rate (C-CO_2:SOC ratio) in forests (Table 2) indicated better growth of microbial populations, i.e., a high proportion of SOC in microbial form and less CO_2 loss or better SOC stabilisation. Under palm groves or cropland, the low proportion of organic C in microbial form could be explained by cultivation and/or agricultural practices (low organic root input, slash-and-burn and/or tillage) that did not favour the formation of a large microbial pool. In croplands, teak plantations and palm groves, the high C-CO_2:SOC ratios measured may be related to intense microbial activity with limited labile and available OM pools (Xu et al., 2011) and reduced SOC stabilisation against soil microbial activity (Wang et al., 2003). The croplands and palm groves appear to have the most fragile soil ecosystems due to their lower q_{mic}, higher qCO_2 (Kaschuk et al., 2011) and higher C-CO_2:SOC ratio. Unfortunately, these land uses, as shown in our study, are under a great agronomic pressure (Kaschuk et al., 2011). There were intermediate values for tree plantations, which were probably less dynamic than those of palm groves.

4.1.4. A microbial activity concentrated in the soil surface

The soil biological activity of the sandy Ferralsol is concentrated on the soil surface and seems low in relation to soil microbial biomass. The microbial quotient, q_{mic}, values usually range from 1 to 4 g MBC 100 g^{-1}C soil (Sparling, 1992). In the soils studied, the q_{mic} values measured under forests and tree plantations were at the lower end of the value range observed by Sparling even in the topsoil. The values measured under palm groves and cropland were even lower (0.5 to 0.7 mg MB-C 100 mg^{-1}C soil). This could be explained by the low C and sandy nature of the Ferralsols studied. However, the values of the microbial indicators confirmed that the microbial communities in these soils were still efficient indicators of C turnover as they remained influenced by land use (Rodrigues et al., 2015).

The effects of land use on tea litter decomposition and soil microbial biomass and activity were much smaller at 10–30 cm than at 0–10 cm (Tables 2 and 3). These results are well documented in the literature (e.g., Banerjee et al., 2006; Maharjan et al., 2017) and were explained by lower organic inputs at depth than at the surface. This decrease with depth was particularly pronounced in forest and tree plantation soils. Consequently, the effect of land use on microbial biomass was much lower at 10–30 cm than at 0–10 cm and was no longer significant for microbial respiration at 10–30 cm (Figs. 3, 4–5). In these sandy Ferralsols, the main biological activity and SOC turnover seemed to be concentrated at the soil surface and were little affected by land use at the 10–30 cm depth.

4.2. Land use affects soil organic carbon pools

4.2.1. Land use affects soil organic carbon contents mainly in topsoil

As in Houssoukpèvi et al. (2022), SOC content decreased from forest to tree plantations, palm groves and cropland and is concentrated in the topsoil. The difference in SOC content between land uses could be due to the larger amounts of litter and organic inputs from plant biomass and dead roots available in forests than in tree plantations (Houssoukpèvi et al., 2022), which are much younger than forest sites (Table 1), palm groves and croplands. Also in the forests, the higher plant diversity could also enrich the soil with a variety of organic carbon inputs, helping to favour the SOC stocks compared to tree plantations (N'Gbala et al., 2017). No difference in the C/N ratio of the total soil were noticeable between the soils under forest and tree plantation to explain difference in SOM mineralisation.

4.2.2. Permanganate oxidable carbon pool higher in croplands and palm groves

The high POX-C pools, as well as the high POX-C:SOC and C-CO_2:SOC ratios (Tables 2 and 3), in croplands and palm groves compared to those in forests and tree plantations could be the result of rapid conversion of organic debris into extractable organic matter. The nature and biological origin of the POX-C pool remain unclear in the scientific literature, and our results provide little guidance. Our results showed no correlation with SOC pools known as labile organic C pools (POM, C-CO_2 emissions), as in Malou et al. (2023) in other tropical sandy soils, and only negative weak correlations with SOC pools known as stable organic C pools (e.g., F0–2; Table 4).

Under croplands, this rapid microbial transformation resulting in a higher POX-C:SOC ratio was consistent with the results of previous studies (Thapa et al., 2018), the low stabilisation factor (S) and the high *k* decomposition rate constant (Fig. 2). However, the POX-C and POX-C:SOC ratios were similar under croplands and palm groves, and there was no similar position for these two land uses in the *k* vs. *S* plots in Fig. 2. The high POX-C and especially POX-C:SOC ratios in croplands and palm groves at 10–30 cm could be explained by lower amounts of OM available for microorganisms (Thapa et al., 2018) with high microbial activity, as indicated by the high qCO_2 under these land uses and at greater depths (Table 2). Our results tended to show that in these Ferrasols, the POX-C pools indicated rapid transformation of OM without significant accumulation of C in stable C pools.

4.2.3. Greater amount of C in all the soil particle size fractions in forest topsoil

The availability of soil litter between land uses could explain the greater amount of OC in all the soil fractions, from the POM to even the smallest soil fraction, F0–2 μm, especially at 0–10 cm (Fig. 4). At 0–10 cm, the higher POM content in forests compared to other land uses is attributed to aboveground and root litter inputs, which are greater in

forests (Błońska et al., 2017; Sainepo et al., 2018; Vanguelova et al., 2013). The difference in POM amounts between forests and monospecific tree plantations could be explained by differences in litter inputs. Similarly, the low amount of crop residues returned to the soil in cropland (Houssoukpèvi et al., 2022) likely explains the lower POM content observed. As the POM pool accounts for 40 % of the total SOC content at 0–10 cm, which is quite common in sandy soils (Fujisaki et al., 2018), the difference in POM content between land uses explains much of the difference in total SOC content, especially in the 0–10 cm soil layer.

The SOC pools associated with the fine fractions (F 0–2 μm) were larger in the forest plots than in the other plots at both 0–10 and 10–30 cm. This could be explained by the age of the forests studied, which were established for more than 50 years and benefited from regular organic inputs of aboveground and belowground plant C. Tree plantations and palm groves were more frequently rotated or cut (Table 1, Houssoukpèvi et al., 2022). The C associated with fine fractions originated from dissolved organic matter (Rubino et al., 2010; Sanderman et al., 2014), root exudation, and microbial compounds derived from biological activity (Mambelli et al., 2011; Rossi et al., 2020; Vidal et al., 2018), and was therefore lower in land uses with lower soil biological activity and C inputs. Furthermore, strong correlations were found between MB-C and F0–2 μm (Table 4), which could indicate the accumulation of microbial products in the fine fraction of the soil. This accumulation of SOC associated with the fine soil fractions should reinforce a stable SOC pool, as SOC associated with the mineral matrix has a slow renewal rate due to its inaccessibility to soil microorganisms (Christensen, 2001; Six et al., 2002).

The correlations between C-CO_2, MB-C and all the SOM fractions (Table 4) illustrated the microbial activity that progressively incorporates plant biomass into microbial biomass (Cotrufo et al., 2013). The greater quantity and diversity of plant residues in forests increases the substrate diversity of microbial communities and the efficiency of microbial communities in converting these substrates into microbial biomass (see q_{mic} in Table 4, Bonner et al., 2018; Fanin and Bertrand, 2016), promoting the association of SOC with the mineral matrix. This is particularly true at 10–30 cm, where F0–2, representing 60 % of the SOC, was highly correlated with MB-C and was the only SOM fraction affected by land use. The high POX-C:SOC and the high C-CO_2:SOC ratios at 10–30 cm could also highlight the rapid transformation of OM in this soil layer, probably because there is little SOC input available to microorganisms. The rapid decomposition and mineralisation of plant litter and SOC in sandy Ferralsols could explain why C accumulated only in small amounts and was associated with the smallest fine fraction (F0–2) at depth. Our results also confirmed the value of separating SOC pools of different sizes (0–2, 2–20, and 20–50 μm class sizes instead of only one 0–50 μm class size) to highlight the influence of land use on SOC distribution and stabilisation.

5. Conclusion

This study showed the effect of land use on the decomposition, mineralisation and stabilisation of SOM in the five major land uses on the Ferralsols of the Allada plateau. The results showed that high biological activity in forests, or to a lesser extent in tree plantations, seems to be effective in accumulating carbon in SOC pools associated to the clay size fraction. Furthermore, agricultural land uses as croplands and palm groves decreased all SOC pools, including those associated to the clay size fraction, except the POX-C. However, forests and tree plantations were not similar. The SOC pools and soil microbial properties remained lower in tree plantations, resulting in lower C accumulation. Our results indicated that the amount of organic inputs was a main factor to explain the organic and biological status of the soils with higher soil biological activity and SOM stabilisation in the clay size fraction in forest than in tree plantations or crops, but only in the topsoil. The diversity of tree, litter and probably organic inputs in the forests could not be exploited in this study. Further studies on litter and soil microbial diversity are needed to understand the variability observed between forests and plantations and the specific role of the diversity litter on C cycle. Protecting forests in the landscape remains a priority to maintain SOC stocks and soil biological activity that neither monospecific tree plantations nor cultivation could have achieved. Our results also support initiatives to promote agricultural or land management practices that improve the availability of organic matter and C inputs through diverse litter.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This study was funded by the BNP Paribas Foundation through its 2017 Climate Initiative and the SoCa project (BeyonD Climate, Soil C Sequestration to sustain Family Farming in the Tropics) and the French National Research Institute for Sustainable Development (IRD) for the doctoral fellowship (i.e., Allocation de Recherche pour une Thèse au Sud-ARTS) awarded to I.A. Houssoukpèvi. The authors are grateful to the farmers, landowners, and public authorities for allowing access to the plots.

Appendix A. Appendix

Table A
Results of GLM, depicting effects of land use according to depth on the studied variables using F statistic and *p* value (degree of freedom = 4).

Studied indicators	Soil depth (cm)	F statistic	Pr (>F)
Remaining mass of green tea	–	4.62	3.3E-03
Remaining mass of red tea	–	1.39	0.25
S	–	1.79	0.14
K	–	7.56	2.05E-04
C-CO_2	0–10	10.58	1.4E-05
	10–30	0.65	0.63
MB-C	0–10	10.78	1.2E-05

(*continued on next page*)

Table A (*continued*)

Studied indicators	Soil depth (cm)	F statistic	Pr (>F)
q_{mic}	10–30	3.78	1.2E-02
	0–10	5.53	1.6E-03
	10–30	2.75	4.5E-02
qCO_2	0–10	6.30	7.3E-04
	10–30	2.01	0.13
C-CO_2:SOC ratio	0–10	6.37	8.9E-04
	10–30	2.78	0.06
SOC	0–10	12.00	4.5E-06
	10–30	3.01	0.03
POX-C	0–10	18.63	5.3E-08
	10–30	20.39	1.9E-08
POX-C:SOC ratio	0–10	22.10	7.8E-09
	10–30	13.83	1.2E-06
POM	0–10	15.06	5.02E-07
	10–30	0.96	0.5
F 20–50	0–10	8.16	0.0001
	10–30	3.81	0.012
F 2–20	0–10	8.79	6.6E-05
	10–30	1.36	0.27
F 0–2	0–10	7.19	3.01E-04
	10–30	5.53	0.002

Appendix B. Appendix

Table B
Results of GLM, depicting the effects of depth on the variables studied using F statistic and *p* value (degree of freedom = 1).

Dependent variable	F statistic	Pr(>F)
C-CO_2	15.47	1.9E-4
MB-C	24.67	4.6E-06
q_{mic}	1.78	0.19
qCO_2	34.53	1.24E-07
C-CO2:SOC ratio	90.37	4.8E-14
SOC	78.86	3.9E-13
POX-C	13.32	4.9E-4
POX-C:SOC ratio	32.67	2.3E-07
POM	59.23	1.3E-10
F 20–50	47.95	2.63E-09
F 2–20	53.92	5.5E-10
F 0–2	9.791	0.003

Appendix C. Appendix

Table C
Quality of particle size fractionation of MOS.

Land use	Mass recovery (%)		Carbon recovery (%)	
	0–10 cm	*10–30 cm*	*0–10 cm*	*10–30 cm*
Forests	100 ± 1.9	99 ± 0.91	88 ± 0.1	96 ± 0.1
Tree plantations	100 ± 0.6	100 ± 0.5	88 ± 0.1	100 ± 0.1
Adult palm groves	100 ± 0.4	99 ± 0.7	87 ± 0.1	100 ± 0.2
Young palm groves	99 ± 0.7	99 ± 0.2	88 ± 0.1	87 ± 0.2
Croplands	99 ± 0.4	99 ± 0.8	94 ± 0.1	83 ± 0.1

Appendix D. Appendix

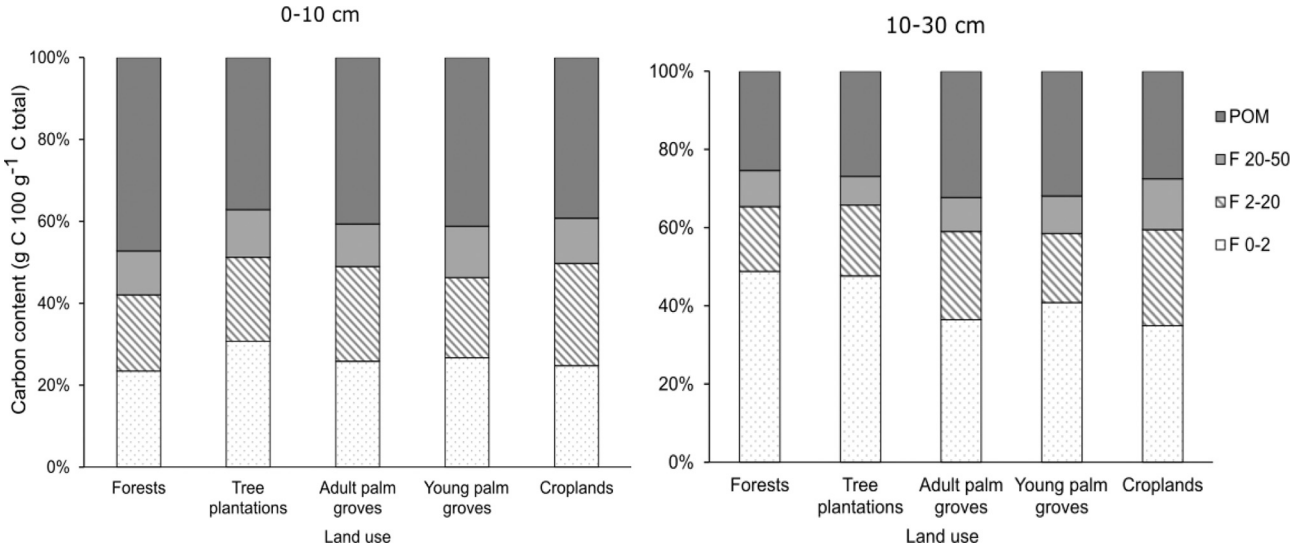


Fig. D. Contribution of soil particle-size fractions to SOC content (g 100 g^{-1}).

References

Adhikari, K., Hartemink, A.E., 2016. Linking soils to ecosystem services - a global review. Geoderma 262, 101–111. https://doi.org/10.1016/j.geoderma.2015.08.009.

Akoegninou, A., van der Burg, W., LJG, van der M., 2006. In: Adjakidjè, V., Essou, J.P., Sinsin, B., Yédomonhan, H. (Eds.), Flore Analytique du Bénin. Backhuys Publ Cotonou Wageningen, pp. 50–62.

Akouehou, G.S., Assogba, D., Houndonougbo, A., Sinsin, A., 2013. Diversité floristique, sécurisation foncière et gestion des systèmes agroforestiers à palmier à huile (Elaeis guineensis) en zones périurbaines et rurales du Département de l'Atlantique au Sud du Bénin. Int. J. Biol. Chem. Sci. 7, 1180. https://doi.org/10.4314/ijbcs.v7i3.24.

Anderson, T.H., Domsch, K.H., 2010. Soil microbial biomass: the eco-physiological approach. Soil Biol. Biochem. 42, 2039–2043. https://doi.org/10.1016/j.soilbio.2010.06.026.

Assogbadjo, A.E., Kakaï, R.G., Edon, S., Kyndt, T., Sinsin, B., 2011. Natural variation in fruit characteristics, seed germination and seedling growth of Adansonia digitata L. in Benin. New For. 41, 113–125.

Attignon, S.E., Weibel, D., Lachat, T., Sinsin, B., Nagel, P., Peveling, R., 2004. Leaf litter breakdown in natural and plantation forests of the Lama forest reserve in Benin. Appl. Soil Ecol. 27, 109–124. https://doi.org/10.1016/j.apsoil.2004.05.003.

Balesdent, J., Besnard, E., Arrouays, D., Chenu, C., 1998. The dynamics of carbon in particle-size fractions of soil in a forest-cultivation sequence. Plant Soil 201, 49–57.

Banerjee, B., Aggarwal, P.K., Pathak, H., Singh, A.K., Chaudhary, A., 2006. Dynamics of organic carbon and microbial biomass in alluvial soil with tillage and amendments in rice-wheat systems. Environ. Monit. Assess. 119, 173–189.

Barel, J.M., Kuyper, T.W., Paul, J., de Boer, W., Cornelissen, J.H.C., De Deyn, G.B., 2019. Winter cover crop legacy effects on litter decomposition act through litter quality and microbial community changes. J. Appl. Ecol. 56, 132–143. https://doi.org/10.1111/1365-2664.13261.

Becker, J.N., Kuzyakov, Y., 2018. Teatime on Mount Kilimanjaro: assessing climate and land-use effects on litter decomposition and stabilization using the tea bag index. Land Degrad. Dev. 29, 2321–2329. https://doi.org/10.1002/ldr.2982.

Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., Kirk, G.J.D., 2005. Carbon losses from all soils across England and Wales 1978–2003. Nature 437, 245–248.

Bertolino, A.V.F.A., Fernandes, N.F., Miranda, J.P.L., Souza, A.P., Lopes, M.R.S., Palmieri, F., 2010. Effects of plough pan development on surface hydrology and on soil physical properties in southeastern Brazilian plateau. J. Hydrol. 393, 94–104.

Błońska, E., Lasota, J., Gruba, P., 2017. Enzymatic activity and stabilization of organic matter in soil with different detritus inputs. Soil Sci. Plant Nutr. 63, 242–247. https://doi.org/10.1080/00380768.2017.1326281.

Błonska, E., Lasota, J., da Silva, G.R.V., Vanguelova, E., Ashwood, F., Tibbett, M., Watts, K., Lukac, M., 2020. Soil organic matter stabilization and carbon-cycling enzyme activity are affected by land management. Ann. For. Res. 63, 71–86. https://doi.org/10.15287/afr.2019.1837.

Bonner, M.T.L., Shoo, L.P., Brackin, R., Schmidt, S., 2018. Relationship between microbial composition and substrate use efficiency in a tropical soil. Geoderma 315, 96–103.

Brookes, P., 2001. The soil microbial biomass: concept, measurement and applications in soil ecosystem research. Microbes Environ. 16, 131–140. https://doi.org/10.1264/jsme2.2001.131.

Brun, L.E., Gaudence, D.J., Gibigaye, M., Tente, B., 2018. Dynamique de l'occupation du sol dans les zones humides de la commune d'Allada au Sud-Benin (Sites Ramsar 1017 et 1018). Eur. Sci. Journal, ESJ 14, 59. https://doi.org/10.19044/esj.2018.v14n12p59.

Buchholz, T., Friedland, A.J., Hornig, C.E., Keeton, W.S., Zanchi, G., Nunery, J., 2014. Mineral soil carbon fluxes in forests and implications for carbon balance assessments. GCB Bioenergy 6, 305–311.

Chevallier, T., Woignier, T., Toucet, J., Blanchart, E., 2010. Organic carbon stabilization in the fractal pore structure of andosols. Geoderma 159, 182–188. https://doi.org/10.1016/j.geoderma.2010.07.010.

Chevallier, T., Loireau, M., Courault, R., Chapuis-Lardy, L., Desjardins, T., Gomez, C., Grondin, A., Guérin, F., Orange, D., Pélissier, R., Serpantié, G., Durand, M.H., Derioz, P., Gildas Laruelle, G., Schwoob, M.H., Viovy, N., Barrière, O., Blanchart, E., Blanfort, V., Brossard, M., Demenois, J., Fargette, M., Heulin, T., Mahe, G., Manlay, R., Podwojewski, P., Rumpel, C., Sultan, B., Chotte, J.L., 2020. Paris climate agreement: promoting interdisciplinary science and stakeholders' approaches for multi-scale implementation of continental carbon sequestration. Sustainability 12. https://doi.org/10.3390/SU12176715.

Christensen, B.T., 2001. Physical fractionation of soil and structural and functional complexity in organic matter turnover. Eur. J. Soil Sci. 52, 345–353.

Colman, B.P., Schimel, J.P., 2013. Drivers of microbial respiration and net N mineralization at the continental scale. Soil Biol. Biochem. 60, 65–76.

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The M icrobial E fficiency-M atrix S tabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Glob. Chang. Biol. 19, 988–995.

Daebeler, A., Petrová, E., Kinz, E., Grausenburger, S., Berthold, H., Sandén, T., Angel, R., 2022. Pairing litter decomposition with microbial community structures using the tea bag index (TBI). Soil Discuss. 2021, 1–20.

Dennis, P.G., Miller, A.J., Hirsch, P.R., 2010. Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiol. Ecol. 72, 313–327.

Dinakaran, J., Chandra, A., Chamoli, K.P., Deka, J., Rao, K.S., 2018. Soil organic carbon stabilization changes with an altitude gradient of land cover types in central Himalaya, India. Catena 170, 374–385. https://doi.org/10.1016/j.catena.2018.06.039.

Dinesh, R., Ghoshal Chaudhuri, S., 2013. Soil biochemical/microbial indices as ecological indicators of land use change in mangrove forests. Ecol. Indic. 32, 253–258. https://doi.org/10.1016/j.ecolind.2013.03.035.

Duddigan, S., Alexander, P.D., Shaw, L.J., Sandén, T., Collins, C.D., 2020. The tea bag index-UK: using citizen/community science to investigate organic matter decomposition rates in domestic gardens. Sustainability 12. https://doi.org/10.3390/SU12176895.

Fanin, N., Bertrand, I., 2016. Aboveground litter quality is a better predictor than belowground microbial communities when estimating carbon mineralization along a land-use gradient. Soil Biol. Biochem. 94, 48–60.

Fanin, N., Bezaud, S., Sarneel, J.M., Cecchini, S., Nicolas, M., Augusto, L., 2020. Relative importance of climate, soil and plant functional traits during the early decomposition stage of standardized litter. Ecosystems 23, 1004–1018. https://doi.org/10.1007/s10021-019-00452-z.

FAO, 2019. Recarbonization of global soils: A tool to support the implementation of the Koronivia joint work on agriculture. Rome.
FAO, IIASA, 2023. Harmonized World Soil Database Version 2.0. Food and Agriculture. https://doi.org/10.4060/cc3823en.
Fonkeng, E.E., Chevallier, T., Sauvadet, M., Enock, S., Rakotondrazafy, N., Chapuis-Lardy, L., Takoutsing, B., Fritz, O.T., Harmand, J.-M., 2024. Dynamics of soil organic carbon pools following conversion of savannah to cocoa agroforestry systems in the Centre region of Cameroon. Geoderma Reg. 36, e00758.
Frank, K., Beegle, D., Denning, J., 1998. Phosphorus. In: Brown, J.R. (Ed.), Recommended Chemical Soil Test Procedures for the North Central Region, pp. 21–29. North Central Regional Publ. 221 (revised). Publ. SB 1001. Missouri Exp. Stn., Columbia. Phosphorus. p. 21–29. JR Brown Recomm. Chem. soil test Proced. North Cent. Reg. North Cent. Reg. Publ. 221 (revised). Publ. SB 1001. Missouri Exp. Stn., Columbia.
Fterich, A., Mahdhi, M., Mars, M., 2014. The effects of acacia tortilis subsp. raddiana, soil texture and soil depth on soil microbial and biochemical characteristics in arid zones of Tunisia. Land Degrad. Dev. 25, 143–152. https://doi.org/10.1002/ldr.1154.
Fujisaki, K., Chapuis-Lardy, L., Albrecht, A., Razafimbelo, T., Chotte, J.L., Chevallier, T., 2018. Data synthesis of carbon distribution in particle size fractions of tropical soils: implications for soil carbon storage potential in croplands. Geoderma 313, 41–51. https://doi.org/10.1016/j.geoderma.2017.10.010.
Gavinelli, E., Feller, C., Larré-Larrouy, M.C., Bacye, B., Djegui, N., Nzila, J.D., 1995. A routine method to study soil organic matter by particle-size fractionation: examples for tropical soils. Commun. Soil Sci. Plant Anal. 26, 1749–1760.
Gorissen, A., 1996. ESPAS - an advanced phytotron for measuring carbon dynamics in a whole plant-soil system. Plant Soil 179, 81–87. https://doi.org/10.1007/BF00011645.
Grinand, C., Le Maire, G., Vieilledent, G., Razakamanarivo, H., Azafimbelo, T., Bernoux, M., 2017. Estimating temporal changes in soil carbon stocks at ecoregional scale in Madagascar using remote-sensing. Int. J. Appl. Earth Obs. Geoinf. 54, 1–14. https://doi.org/10.1016/j.jag.2016.09.002.
Gu, C., Riley, W.J., 2010. Combined effects of short term rainfall patterns and soil texture on soil nitrogen cycling—a modeling analysis. J. Contam. Hydrol. 112, 141–154.
Hansen, R.A., 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology 81, 1120–1132. https://doi.org/10.1890/0012-9658(2000)081[1120,EOHCAC]2.0.CO;2.
Harrison, R.B., Footen, P.W., Strahm, B.D., 2011. Deep soil horizons: contribution and importance to soil carbon pools and in assessing whole-ecosystem response to management and global change. For. Sci. 57, 67–76.
Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst. 36, 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932.
Houssoukpèvi, I.A., Aholoukpè, H.N.S., Fassinou, D.J.M., Rakotondrazafy, M.N., Amadji, G.L., Chapuis-Lardy, L., Chevallier, T., 2022. Biomass and soil carbon stocks of the main land use of the Allada plateau. Carbon Manag. 13, 249–265. https://doi.org/10.1080/17583004.2022.2074314.
Houssoukpèvi, I.A., le Maire, G., Aholoukpè, H.N.S., Fassinou, D.J.M., Amadji, G.L., Chapuis-Lardy, L., Chevallier, T., 2023. Effect of land use change on carbon stocks in an agricultural region of southern Benin. Land Degrad. Dev. 34, 1447–1463. https://doi.org/10.1002/ldr.4545.
Hungria, M., Franchini, J.C., Brandao-Junior, O., Kaschuk, G., Souza, R.A., 2009. Soil microbial activity and crop sustainability in a long-term experiment with three soil-tillage and two crop-rotation systems. Appl. Soil Ecol. 42, 288–296.
IPCC, 2019. 2019 Refinement to the 2006 IPCC Guidelines for National Greenhouse gas Inventories.
IUSS, 2015. World reference base for soil resources 2014. International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. Rome.
Kagezi, G.H., Kaib, M., Nyeko, P., Bakuneeta, C., Schädler, M., Stadler, J., Brandl, R., 2016. Impacts of land-use intensification on litter decomposition in western Kenya. Web Ecol. 16, 51–58. https://doi.org/10.5194/we-16-51-2016.
Kaschuk, G., Alberton, O., Hungria, M., 2011. Quantifying effects of different agricultural land uses on soil microbial biomass and activity in Brazilian biomes: inferences to improve soil quality. Plant Soil 338, 467–481. https://doi.org/10.1007/s11104-010-0559-z.
Keuskamp, J.A., Dingemans, B.J.J., Lehtinen, T., Sarneel, J.M., Hefting, M.M., 2013. Tea bag index: a novel approach to collect uniform decomposition data across ecosystems. Methods Ecol. Evol. 4, 1070–1075. https://doi.org/10.1111/2041-210X.12097.
Koussihouèdé, H., Aholoukpè, H., Adjibodou, J., Hinkati, H., Dubos, B., Chapuis-Lardy, L., Barthès, B.G., Amadji, G., Clermont-Dauphin, C., 2020. Comparative analysis of nutritional status and growth of immature oil palm in various intercropping systems in southern Benin. Exp. Agric. 56, 371–386. https://doi.org/10.1017/S0014479720000022.
Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. Science 304, 1623–1627.
Lal, R., 2018. Digging deeper: a holistic perspective of factors affecting soil organic carbon sequestration in agroecosystems. Glob. Chang. Biol. 24, 3285–3301. https://doi.org/10.1111/gcb.14054.
Le Noë, J., Manzoni, S., Abramoff, R., Bölscher, T., Bruni, E., Cardinael, R., Ciais, P., Chenu, C., Clivot, H., Derrien, D., 2023. Soil organic carbon models need independent time-series validation for reliable prediction. Commun. Earth Environ. 4, 158.
Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature 528, 60–68.
Lorenz, K., Lal, R., 2018. In: Lorenz, K., Lal, R. (Eds.), Soil Carbon Stock BT - Carbon Sequestration in Agricultural Ecosystems. Springer International Publishing, Cham, pp. 39–136. https://doi.org/10.1007/978-3-319-92318-5_2.
Lorenz, K., Lal, R., Preston, C.M., Nierop, K.G.J., 2007. Strengthening the soil organic carbon pool by increasing contributions from recalcitrant aliphatic bio(macro) molecules. Geoderma 142, 1–10. https://doi.org/10.1016/j.geoderma.2007.07.013.
Lorenz, K., Lal, R., Ehlers, K., 2019. Soil organic carbon stock as an indicator for monitoring land and soil degradation in relation to United Nations' Sustainable Development Goals. Land Degrad. Dev. 30, 824–838. https://doi.org/10.1002/ldr.3270.
Maharjan, M., Sanaullah, M., Razavi, B.S., Kuzyakov, Y., 2017. Effect of land use and management practices on microbial biomass and enzyme activities in subtropical top-and sub-soils. Appl. Soil Ecol. 113, 22–28. https://doi.org/10.1016/j.apsoil.2017.01.008.
Malou, O.P., Chevallier, T., Moulin, P., Sebag, D., Rakotondrazafy, M.N., Badiane-Ndour, N.Y., Thiam, A., Chapuis-Lardy, L., 2023. Measuring the stability of soil organic carbon in Arenosols in the Senegalese Groundnut Basin. J. Arid Environ. 213, 104978.
Mambelli, S., Bird, J.A., Gleixner, G., Dawson, T.E., Torn, M.S., 2011. Relative contribution of foliar and fine root pine litter to the molecular composition of soil organic matter after in situ degradation. Org. Geochem. 42, 1099–1108. https://doi.org/10.1016/j.orggeochem.2011.06.008.
Mangalassery, S., Mooney, S.J., Sparkes, D.L., Fraser, W.T., Sjögersten, S., 2015. Impacts of zero tillage on soil enzyme activities, microbial characteristics and organic matter functional chemistry in temperate soils. Eur. J. Soil Biol. 68, 9–17.
Minasny, B., Malone, B.P., McBratney, A.B., Angers, D.A., Arrouays, D., Chambers, A., Chaplot, V., Chen, Z.S., Cheng, K., Das, B.S., Field, D.J., Gimona, A., Hedley, C.B., Hong, S.Y., Mandal, B., Marchant, B.P., Martin, M., McConkey, B.G., Mulder, V.L., O'Rourke, S., Richer-de-Forges, A.C., Odeh, I., Padarian, J., Paustian, K., Pan, G., Poggio, L., Savin, I., Stolbovoy, V., Stockmann, U., Sulaeman, Y., Tsui, C.C., Vågen, T.G., van Wesemael, B., Winowiecki, L., 2017. Soil carbon 4 per mille. Geoderma 292, 59–86. https://doi.org/10.1016/j.geoderma.2017.01.002.
N'Gbala, F.N.G., Guéi, A.M., Tondoh, J.E., 2017. Carbon stocks in selected tree plantations, as compared with semi-deciduous forests in Centre-West Côte d'Ivoire. Agric. Ecosyst. Environ. 239, 30–37. https://doi.org/10.1016/j.agee.2017.01.015.
Nilsson, M.-C., Wardle, D., 2005. Understory vegetation as a forest ecosystem driver. Ecol. Soc. Am. 3, 421–428.
R Development Core, T., 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
Ramesh, T., Bolan, N.S., Kirkham, M.B., Wijesekara, H., Kanchikerimath, M., Srinivasa Rao, C., Sandeep, S., Rinklebe, J., Ok, Y.S., Choudhury, B.U., Wang, H., Tang, C., Wang, X., Song, Z., Freeman, O.W., 2019. Soil organic carbon dynamics: impact of land use changes and management practices: a review. Adv. Agron. 156, 1–107. https://doi.org/10.1016/bs.agron.2019.02.001.
Razafimbelo, T., Albrecht, A., Becquer, T., Bernard, L., Chevallier, T., Erktan, A., Chapuis-Lardy, L., Trap, J., Andriamananjara, A., Rabenarivo, M., 2022. Priorities for soil research and sustainable management in Madagascar. Geoderma Reg 29, e00518.
Rodrigues, R.C., Araújo, R.A., Costa, C.S., Lima, A.J.T., Oliveira, M.E., Cutrim, J.A.A., Santos, F.N.S., Araújo, J.S., Santos, V.M., Araújo, A.S.F., 2015. Soil microbial biomass in an agroforestry system of Northeast Brazil. Trop. Grasslands-Forrajes Trop. 3, 41–48. https://doi.org/10.17138/TGFT(3)41-48.
Ross, D.J., 1990. Estimation of soil microbial c by a fumigation-extraction method: influence of seasons, soils and calibration with the fumigation-incubation procedure. Soil Biol. Biochem. 22, 295–300. https://doi.org/10.1016/0038-0717(90)90103-7.
Rossi, L.M.W., Mao, Z., Merino-Martín, L., Roumet, C., Fort, F., Taugourdeau, O., Boukcim, H., Fourtier, S., Del Rey-Granado, M., Chevallier, T., Cardinael, R., Fromin, N., Stokes, A., 2020. Pathways to persistence: plant root traits alter carbon accumulation in different soil carbon pools. Plant Soil 452, 457–478. https://doi.org/10.1007/s11104-020-04469-5.
Rubel, F., Kottek, M., 2010. Observed and projected climate shifts 1901-2100 depicted by world maps of the Köppen-Geiger climate classification. Meteorol. Z. 19, 135–141. https://doi.org/10.1127/0941-2948/2010/0430.
Rubino, M., Dungait, J.A.J., Evershed, R.P., Bertolini, T., De Angelis, P., D'Onofrio, A., Lagomarsino, A., Lubritto, C., Merola, A., Terrasi, F., 2010. Carbon input belowground is the major C flux contributing to leaf litter mass loss: evidences from a 13C labelled-leaf litter experiment. Soil Biol. Biochem. 42, 1009–1016.
Sainepo, B.M., Gachene, C.K., Karuma, A., 2018. Assessment of soil organic carbon fractions and carbon management index under different land use types in Olesharo Catchment, Narok County, Kenya, Carbon Balance Manag. https://doi.org/10.1186/s13021-018-0091-7.
Saint-Laurent, D., Arsenault-Boucher, L., 2020. Soil properties and rate of organic matter decomposition in riparian woodlands using the TBI protocol. Geoderma 358. https://doi.org/10.1016/j.geoderma.2019.113976.
Sanderman, J., Maddern, T., Baldock, J., 2014. Similar composition but differential stability of mineral retained organic matter across four classes of clay minerals. Biogeochemistry 121, 409–424.
Santos, V.B., Araújo, A.S.F., Leite, L.F.C., Nunes, L.A.P.L., Melo, W.J., 2012. Soil microbial biomass and organic matter fractions during transition from conventional to organic farming systems. Geoderma 170, 227–231. https://doi.org/10.1016/j.geoderma.2011.11.007.
Sauvadet, M., Van den Meersche, K., Allinne, C., Gay, F., de Melo Virginio Filho, E., Chauvat, M., Becquer, T., Tixier, P., Harmand, J.-M., 2019. Shade trees have higher impact on soil nutrient availability and food web in organic than conventional coffee agroforestry. Sci. Total Environ. 649, 1065–1074.

Sauvadet, M., Trap, J., Damour, G., Plassard, C., Van den Meersche, K., Achard, R., Allinne, C., Autfray, P., Bertrand, I., Blanchart, E., 2021. Agroecosystem diversification with legumes or non-legumes improves differently soil fertility according to soil type. Sci. Total Environ. 795, 148934.

Six, J., Callewaert, P., Lenders, S., De Gryze, S., Morris, S.J., Gregorich, E.G., Paul, E.A., Paustian, K., 2002. Measuring and understanding carbon storage in afforested soils by physical fractionation. Soil Sci. Soc. Am. J. 66, 1981–1987. https://doi.org/10.2136/sssaj2002.1981.

Sowerby, A., Blum, H., Gray, T.R.G., Ball, A.S., 2000. The decomposition of Lolium perenne in soils exposed to elevated CO2: comparisons of mass loss of litter with soil respiration and soil microbial biomass. Soil Biol. Biochem. 32, 1359–1366.

Sparling, G.P., 1992. Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. Aust. J. Soil Res. 30, 195–207. https://doi.org/10.1071/SR9920195.

Tchibozo, E.A.M., 2020. Modélisation de la dynamique spatio – temporelle de l'occupation du sol et analyse des changements du territoire de la Lama au Bénin. Eur. Sci. J. ESJ 16, 500–524. https://doi.org/10.19044/esj.2020.v16n6p499.

Thapa, V.R., Ghimire, R., Mikha, M.M., Idowu, O.J., Marsalis, M.A., 2018. Land use effects on soil health in semiarid drylands. Agric. Environ. Lett. 3, 180022. https://doi.org/10.2134/ael2018.05.0022.

Tresch, S., Frey, D., Le Bayon, R.C., Zanetta, A., Rasche, F., Fliessbach, A., Moretti, M., 2019. Litter decomposition driven by soil fauna, plant diversity and soil management in urban gardens. Sci. Total Environ. 658, 1614–1629. https://doi.org/10.1016/j.scitotenv.2018.12.235.

UNEP, 2020. Emissions Gap Report 2020- Executive Summary. Nairobi. Nairobi, Kenya.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987a. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707. https://doi.org/10.1016/0038-0717(87)90052-6.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987b. Microbial biomass measurements in forest soils: determination of kC values and tests of hypotheses to explain the failure of the chloroform fumigation-incubation method in acid soils. Soil Biol. Biochem. 19, 689–696. https://doi.org/10.1016/0038-0717(87)90050-2.

Vanguelova, E.I., Nisbet, T.R., Moffat, A.J., Broadmeadow, S., Sanders, T.G.M., Morison, J.I.L., 2013. A new evaluation of carbon stocks in B ritish forest soils. Soil Use Manag. 29, 169–181.

Vidal, A., Hirte, J., Bender, S.F., Mayer, J., Gattinger, A., Höschen, C., Schädler, S., Iqbal, T.M., Mueller, C.W., 2018. Linking 3D soil structure and plant-microbe-soil carbon transfer in the rhizosphere. Front. Environ. Sci. 6, 9.

Volkoff, B., 1976. Notice explicative n°66 (2) de la caarte pédologique de reconnaissance de la République Populaire du Bénin à 1/200.000 - Feuille d'Abomey (2).

Wang, W.J., Dalal, R.C., Moody, P.W., Smith, C.J., 2003. Relationships of soil respiration to microbial biomass, substrate availability and clay content. Soil Biol. Biochem. 35, 273–284. https://doi.org/10.1016/S0038-0717(02)00274-2.

Wang, Q., Zhong, M., He, T., 2013. Home-field advantage of litter decomposition and nitrogen release in forest ecosystems. Biol. Fertil. Soils 49, 427–434. https://doi.org/10.1007/s00374-012-0741-y.

Weil, R.R., Islam, K.R., Stine, M.A., Gruver, J.B., Samson-Liebig, S.E., 2003. American Journal of Alternative Agriculture Estimating active carbon for soil quality assessment: a simplified method for laboratory and field use estimating active carbon for soil quality assessment: a simplified method for laboratory and field use. Am. J. Altern. Agric. 18, 3–17. https://doi.org/10.1079/AJAA200228.

Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., Von Lützow, M., Marin-spiotta, E., Van Wesemael, B., Rabot, E., Ließ, M., Garcia-franco, N., Wollschläger, U., Vogel, H., Kögel-knabner, I., 2019. Soil organic carbon storage as a key function of soils - a review of drivers and indicators at various scales. Geoderma 333, 149–162. https://doi.org/10.1016/j.geoderma.2018.07.026.

Wu, J., Brookes, P.C., 2005. The proportional mineralisation of microbial biomass and organic matter caused by air-drying and rewetting of a grassland soil. Soil Biol. Biochem. 37, 507–515. https://doi.org/10.1016/j.soilbio.2004.07.043.

Xu, M., Lou, Y., Sun, X., Wang, W., Baniyamuddin, M., Zhao, K., 2011. Soil organic carbon active fractions as early indicators for total carbon change under straw incorporation. Biol. Fertil. Soils 47, 745–752.

Yiqi, L., Zhou, X., 2010. Soil Respiration and the Environment. Elsevier.

Zang, H., Wang, J., Kuzyakov, Y., 2016. N fertilization decreases soil organic matter decomposition in the rhizosphere. Appl. Soil Ecol. 108, 47–53. https://doi.org/10.1016/j.apsoil.2016.07.021.