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Glucose decomposition and its incorporation into soil microbial biomass depending on land use in Mt. Kilimanjaro ecosystems

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A R T I C L E   I N F O

A B S T R A C T

Land use change can affect terrestrial C stocks, resulting in increased CO_2 flux from soil to the atmosphere. In Africa, conversion of natural ecosystems to agricultural lands is the most common land use change. This study investigated the effects of six land use types occurring in Mt. Kilimanjaro ecosystems i.e. (1) lower montane forest (2) grassland and (3) savannah (natural ecosystems) (4) Chagga homegardens (semi-natural ecosystem) and (5) maize fields and (6) coffee plantation (agroecosystems) on microbial biomass carbon (MBC) and dynamics of ^{14}C labelled glucose added into soil. Decomposition of ^{14}C labelled glucose and its incorporation into microbial biomass in surface soils (0–10 and 10–20 cm) were determined. MBC decreased significantly with increased intensity of land use. Mineralization of the ^{14}C labelled glucose occurred in two phases with contrasting rates: 0–10 days (6–18% of ^{14}C d^{-1}) and 15–65 days (<0.1% of ^{14}C d^{-1}). Land use intensification in agroecosystems led to an average increase of glucose decomposition of 14%. The decay rates of the labile C pool in intensively used agricultural lands were up to three times higher compared to natural ecosystems. The incorporation of ^{14}C glucose into microorganisms ranged between 1 and 7% of ^{14}C input in all soils, and was highest in savannah. Agricultural intensification decreased C content in soil through increased mineralization of organic substances and negatively impacted the upper soil layer more compared to the lower one. Based on these results we conclude that semi-natural ecosystems (e.g. Chagga homegardens) are more sustainable in Mt. Kilimanjaro ecosystems compared to intensive agroecosystems.

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1. Introduction

Terrestrial ecosystems play an important role in the global carbon (C) cycle. Soil-vegetation systems can act as a sink or source of atmospheric CO_2 depending on the mineralization and formation of soil organic carbon (SOC) [66]. Terrestrial biosphere-atmosphere exchanges are affected by both anthropogenic disturbances, e.g. clearing of land for crop production and conversion of forest to pasture, as well as natural disturbances, e.g. wild fires. Such land use changes affect C stocks in soil [44] and atmospheric greenhouse-gas emissions [64]. Generally, losses of up to 50% of SOC have been reported after 30–50 years of crop production [52]. Conversion of natural ecosystems to agricultural land in Africa has led to a decrease in C stocks [41,48]. Whereas the trend of organic matter (OM) loss due to land use change is well known, the effect of land use changes on specific ecosystems functions, e.g. C and N cycles, decomposition and nutrient mineralization, microbial biomass content, are less known [45], especially in the terrestrial tropical and sub-tropical ecosystems.

Tropical ecosystems are known to influence global climate and biogeochemical cycles, especially C turnover and sequestration [56]. At the same time they are very sensitive to the changes because the cycles of C and nutrients in tropics are much faster compared to temperate ecosystems [71]. Nevertheless, C stocks dynamics in differing land use types in tropical Africa remain widely unknown [42,50]. Expansion of land area for crop production is widely regarded as one of the most important human alterations of the global environment [45]. The conversion of natural ecosystems to intensively used agricultural lands causes a significant decrease in terrestrial C stocks, resulting in changes in CO_2 fluxes [56].

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Carbon emissions from deforestation and forest degradation have been estimated to account for about 20% of global anthropogenic CO_2 emissions [64]. These emissions have generally increased in tropical and sub-tropical ecosystems since the 1950s [56]. There is still a large uncertainty as to C stocks and CO_2 fluxes following deforestation, so making accurate estimates of greenhouse gas emissions from deforestation in the tropics remains difficult. Therefore, adaptive management of terrestrial ecosystems and soil C sequestration is a new challenge in the context of climate change mitigation [23].

Tropical and subtropical ecosystems are very sensitive to land use changes, because much higher temperature lead to decomposition rates of organic substrates that are much higher compared to temperate ecosystems [27]. Therefore, there is considerable concern that land-use change from natural ecosystems to agricultural land lead to a depletion of soil C and subsequent increases in CO_2 levels in the atmosphere [48]. Conversion of natural ecosystems to intensive agricultural used ecosystems (among others: maize and coffee) is common in East Africa. However, the Chagga homegardens in Tanzania well exemplify a traditional sustainable land use system with many ecosystem services [61]. The Chagga homegardens are characterised by an integration of numerous trees (e.g. *Grevillea robusta*, *Cordia abyssinica* and *Albizia schimperiana*), coffee shrubs, and food crops (e.g. banana, maize, beans, potato, sweet potato and tomato) on the same agroecosystem [18,61]. The shading effect of the crown layer of the trees, higher precipitation and cooler annual average temperature of about 19 °C provides cooler micro-climate which supports the thriving of a larger microbial population than entirely agroecosystems located at a lower elevation.

Natural ecosystems are continually being converted to agricultural land. Therefore, there is an urgent need to improve the management of organic inputs and soil organic matter (SOM) dynamics in tropical land-use systems [40]. Input of organic substances such as crop residues and litter, play a critical role in the tropical and sub-tropical ecosystems because they provide both a short-term supply of nutrients and substrate for synthesis of SOM in the long-term [17]. Although decomposition of plant litter and its physical and chemical processes remain a major determinant of nutrient cycles of most terrestrial ecosystems, there is still little understanding for the management of organic C inputs in tropical ecosystems.

In order to understand and quantify C-dynamics in tropical soils depending on land use, decomposition of ^{14}C-labelled glucose and its incorporation into microbial biomass was investigated in an incubation experiment with soils from different land use systems. Glucose is the most common easily available substrate because it represents simple monosaccharaides [12] that will be produced during decomposition of e.g. cellulose, present in plant residue and will be released as root exudates [13,15].

The objectives of this study were to (1) evaluate the effect of land use change on mineralization of easily available substrates and (2) assess glucose stabilization in soil by incorporation into microbial biomass. This study focused on two hypotheses: (1) increased agricultural intensification will increase mineralization of easily available substrates; and (2) increased agricultural intensification will decrease the contents of MBC as well as the incorporation of simple organic substrates into MB.

2. Materials and methods

2.1. Study area

This study was conducted using soils from the southern slopes of Mt. Kilimanjaro, Tanzania (3°4′33″S 37°21′12″E). The diverse climatic differences at Mt. Kilimanjaro create a high diversity of ecosystems [34] and vegetational zonation [24,70]. The vegetation in Mt. Kilimanjaro is described in detail by Ref. [24]. Rainfall pattern is seasonal and varies with altitude. The long rains extend from March to June and the short rains between November and December. The southern slopes at 700 m a.s.l. receive an annual rainfall of 800–900 mm and slopes at 1500 m a.s.l. receive 1500–2000 mm. The forest belt lies between 2000 and 2300 m a.s.l [26]. The mean annual temperature varies between 10 and 21 °C and Zech (2006) described the soils from Mt. Kilimanjaro as Andosols.

2.2. Description of study sites and soil sampling

Soils were sampled at 0–10 cm and 10–20 cm depths from six ecosystems i.e., lower montane forest, grassland and savannah (natural), homegardens (semi-natural), and coffee plantations and maize fields (agroecosystems). Two sites representing each land use type were sampled. These ecosystems are located at different elevations (Fig. 1). A brief description of the study sites is given in Table 1.

The natural ecosystems have been altered through collection of firewood and occasional mowing. Due to the high demand of building material, firewood and farmland, lower montane forests have also been converted to grassland, which subsequently could be converted to coffee plantations. Moreover, the continued demand and expansion of agricultural land has resulted to the clearing of savannah woodlands characterized by *Acacia* trees for maize cultivation [50]. Intensively used agricultural ecosystems i.e. maize fields and coffee plantations are characterized by considerable disturbances through mechanization, use of pesticides and relatively frequent fertilization. The Chagga homegardens can be classified as agrisilvicultural system [25] and have been developed through anthropogenic influence on the lower montane forest [25,50]. The Chagga farming system has often been described as a model sustainable land use system and has evolved over more than five centuries [61]. However, the farming system has not changed much over the last decades compared to land uses in lower elevations [25]. After removing visible plant debris and roots, soil was sieved through a 2.0 mm mesh screen and stored under moist field conditions at 5 °C until analysis.

2.3. Incubation and ^{14}C glucose labelling

The incubation was conducted in closed vessels, in the dark at room temperature for 65 days. Four replicates, for each ecosystem
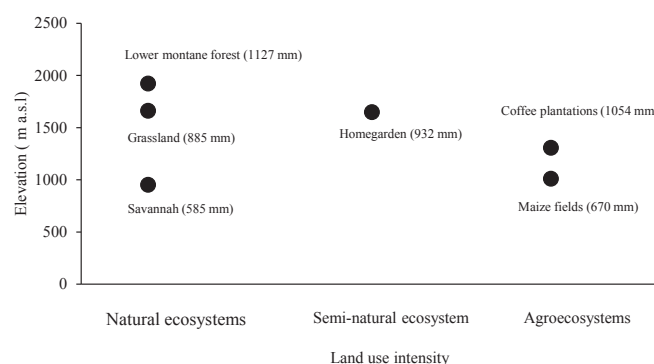

Fig. 1. Elevation (m a.s.l), annual rainfall (mm yr^{-1}) and land use intensities categories of the investigated ecosystems of Mt. Kilimanjaro.

Table 1
Site characteristics of investigated ecosystems of the southern slopes of Mt. Kilimanjaro, Tanzania.

Ecosystem	Land use	Bulk density	pH (H_2O)	Phosphorus (mg P g^{-1} soil)	CEC (mmol kg^{-1})	Management strategies	
						Fertilizer use	Pesticide use
Lower montane forest	Natural	0.34 ± 0.09	6.09 ± 0.07	3.47	175.92	Nil	Nil
Grassland	Natural	0.51 ± 0.01	6.36 ± 0.04	2.60	59.05	Nil	Nil
Home gardens	Semi-natural	0.77 ± 0.04	6.68 ± 0.03	1.60	227.18	Moderate	Moderate
Coffee plantation	Agricultural	1.02 ± 0.06	5.35 ± 0.02	2.33	113.33	High	High
Maize fields	Agricultural	1.21 ± 0.03	6.61 ± 0.01	1.13	69.92	High	High
Savannah	Natural	0.83 ± 0.05	6.71 ± 0.01	3.59	317.60	Nil	Nil

and depth, each weighing 20 g, were prepared and weighed into 250 ml glass. Initial MBC content was estimated using the chloroform-fumigation-extraction method (see below). [14]C labelled glucose (2.56 kBq) corresponding to about 50% of initial MBC was added uniformly to the soil as 1 ml aqueous solution. Small vials with 3 ml of 1.0 M NaOH solution were placed in the vessels to trap CO_2. The soil moisture was maintained at 70% of water holding capacity and the CO_2 traps were changed periodically throughout the incubation period. In addition to the incubated soil samples, four empty vessels containing only CO_2 traps served as control.

2.4. Total carbon, total nitrogen and ^{14}C analyses

Total C and N contents in soil were determined by dry combustion with Elementar Vario EL analyzer (Elementar Analysensysteme GmbH, Germany). Since the carbonate contents of the soils is negligible, total C content was accepted as soil organic C.

[14]C activity in 1 ml aliquots of the [14]CO_2 enriched NaOH from the CO_2 traps mixed with 3 ml of the scintillation cocktail Rotiszint Eco Plus (Carl Roth Company, Germany) was measured using a Beckman LS 6500 Liquid Scintillation Counter (Beckman Coulter Inc., USA).

2.5. Microbial biomass carbon and water extractable organic carbon

Soil microbial biomass C (MBC) was determined by chloroform fumigation-extraction method [65] in modification of [7]. Ethanol-free $CHCl_3$ was used to fumigate 4 g of moist soil for 24 h in an exsiccator at room temperature. Soluble C from fumigated and non-fumigated soil samples was extracted with 30 ml of 0.05 M K_2SO_4 via shaking on an orbital shaker (60 min, 120 rotations min^{-1}) and filtered. Extracts were analysed for total organic C using the 'multi N/C 2100' (Analytik Jena, Jena). C content in K_2SO_4 extracts from unfumigated soil samples was accepted as water extractable organic carbon (WOC) [7]. Since not the entire microbial C can be extracted by K_2SO_4, a k_{EC} factor of 0.45 [30] was used to convert microbial C flush into MBC. [14]C activity in microbial biomass was measured as described above.

2.6. Estimation of labile and stabile C pools and ^{14}C glucose depletion

The decomposition rate of the ^{14}C-labelled glucose was estimated by the double exponential model as described by Ref. [37] (Eq. (1)),

$$^{14}CO_2(t) = C_a \cdot (1 - \exp(-ka \cdot t)) + C_b \cdot (1 - \exp(-kb \cdot t)) \quad (1)$$

where [14]CO_2(t) is the cumulative amount of [14]CO_2 released (in % of input ^{14}C) by time t, C_a and C_b are the sizes of the labile and refractory C pools, respectively, ka and kb are mineralization rate constants for the respective pool and t is the incubation time in days.

In this study, ka was assumed to correspond to the mineralization rate of glucose added to soil and since microbial uptake of low molecular weight organic substances outcompete all other processes in soil [20], kb was seen to reflect mineralization of glucose metabolites.

The half-life ($t_{1/2}$) of the glucose and microbial biomass in the soils can be determined from [14]CO_2 evolution. The corresponding $t_{1/2}$ of the solution glucose pool (C_{lab}) and (C_{MB}) can be represented by Eq. (2).

$$t_{1/2} = \ln(2)/k \quad (2)$$

2.7. Statistical analysis

A non-linear least-square regression analysis was used to estimate the parameters from cumulative [14]CO_2 originated from glucose mineralization (Eq. (1)) (Software STATISTICA 10.0, StatSoft Inc.). Decomposition parameters were compared between the land-use types and soil depths. The decomposition parameters, incorporation of ^{14}C labelled glucose in MB, cumulative [14]CO_2 efflux at day 64, MBC, WOC, TOC, TN of bulk soil were analysed using two-way ANOVA to test for significant differences between treatments. Fischer's LSD *post hoc* test was used to separate significant differences at $P < 0.05$ significance level. Since the incubation was done with four replicates, all displayed results represent arithmetic means $\pm$ standard error (SE).

3. Results

3.1. Total C and N content

Soils from the lower montane forest at 0–10 cm depth had the highest total C content (161 mg C g^{-1} soil). Intensively used maize fields had very low C content in both the 0–10 cm and 10–20 cm depths with a content of 12.5 mg C g^{-1} soil (Fig. 2). Total C content in the upper and lower soil layers differed significantly only in lower montane forest ecosystem (Fig. 2). Similar to total C, lower montane forest soil contained significantly higher total N content (10.6 mg N g^{-1} soil) in the 0–10 cm depth compared to all the other ecosystems. The lowest N content in both the 0–10 cm and 10–20 cm depths were found under intensively used maize fields (1.0 mg N g^{-1} soil). Differences in total N content in the upper and lower soil layers were significant only in lower montane forest soils (as above Fig. 2).

The highest C:N ratio of 17 was found in the upper 0–10 cm of savannah soils while the lowest C:N ratio of 10 was found in the lower 10–20 cm of coffee plantation soils.

3.2. Microbial biomass carbon and water extractable organic carbon

The MBC content was higher in natural and semi-natural ecosystems compared to agricultural ecosystems. Significantly higher
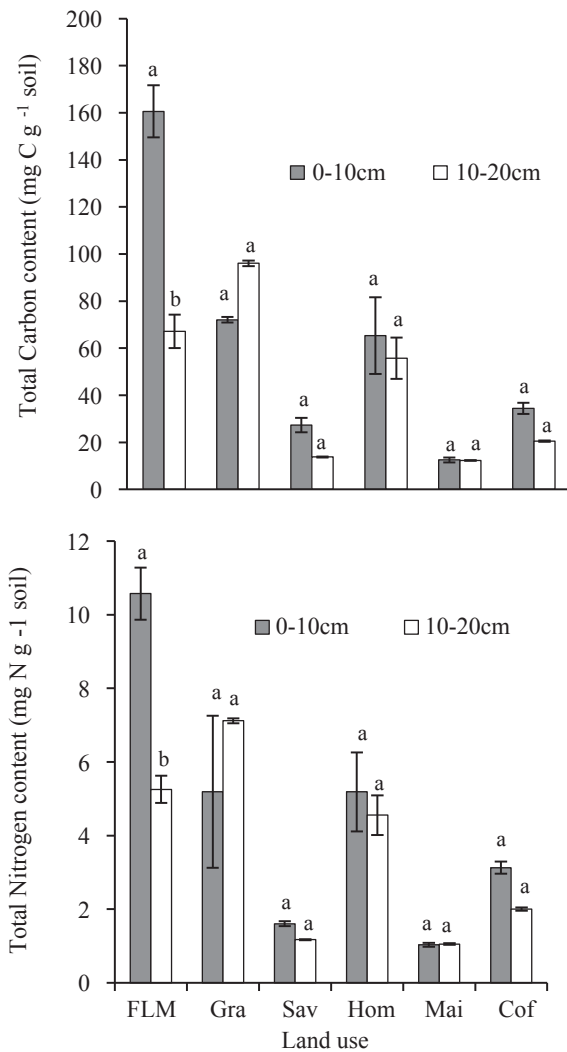
Fig. 2. Total Carbon (top) and total N content (bottom) depending on soil depth and land use intensity: Natural (FLM-Lower Montane Forest, Gra-Grassland and Sav-Savannah); sustainable use/semi natural (Hom-Homegardens) and intensive use (Mai-Maize fields and Cof-Coffee Plantation). Error bars represent the standard error of means ($n = 4$). Soil depths in an ecosystem followed by the same letters are not significantly different at $P = 0.05$.

MBC content was found in lower montane forest soils located at the highest elevation (Fig. 3). Intensively used soils under coffee plantation contained the least MBC (Fig. 3). The MBC in the natural ecosystems was between 3 and 6-fold higher than in intensively used agricultural soils (Fig. 3).

Higher water extractable organic carbon (WOC) content was observed in ecosystems at higher elevations compared to those at lower elevation. At a depth of 0−10 cm lower montane forest soils had significantly higher WOC content compared to all the other ecosystems. Lower elevated and intensively cultivated maize fields and savannah soils had very little WOC content. Similar to MBC content, the WOC content in the upper and lower soil layers was significantly different only in soils under lower montane forest and coffee plantations. WOC in lower montane forest soils showed a strong negative trend with depth whereas a strong positive trend with depth was observed in soils from coffee plantations (Fig. 3). The highest MBC/WOC ratio was observed in savannah soils (1.13 at 0−10 cm depth), whereas coffee plantation showed the lowest MBC/WOC ratio at (0.04 at 10−20 cm depth).

3.3. Decomposition of ^{14}C-labelled glucose

To compare the glucose decomposition in soils with different organic carbon (SOC) content, the $^{14}CO_2$ efflux rates are presented as percentage of ^{14}C input. Mineralization of glucose occurred in 2 phases. The first phase between day 0 and 10 was characterized with high mineralization rates, the maximum being observed within the first 24 h. The maximal mineralization rates (%) occurred in the natural lower montane forest, whereas the lowest mineralization rates during the same time period were recorded in soils from intensively used maize fields. After one day, 9−24% of the ^{14}C input from the glucose was mineralized to $^{14}CO_2$ in all ecosystems. The rapid initial mineralization phase (first 10−15 days) accounted for 35−50% of added glucose. In comparison to the first period, the decomposition after 15 days was slow at the end of the 65 days incubation period, mineralization rates ranged from 0.07% to 0.1% of ^{14}C input per day in all soils (Fig. 4).

Cumulative $^{14}CO_2$ emissions from the lower 10−20 cm depth were higher compared to the upper layers in ecosystems at higher elevations: lower montane forest, grassland and Chagga
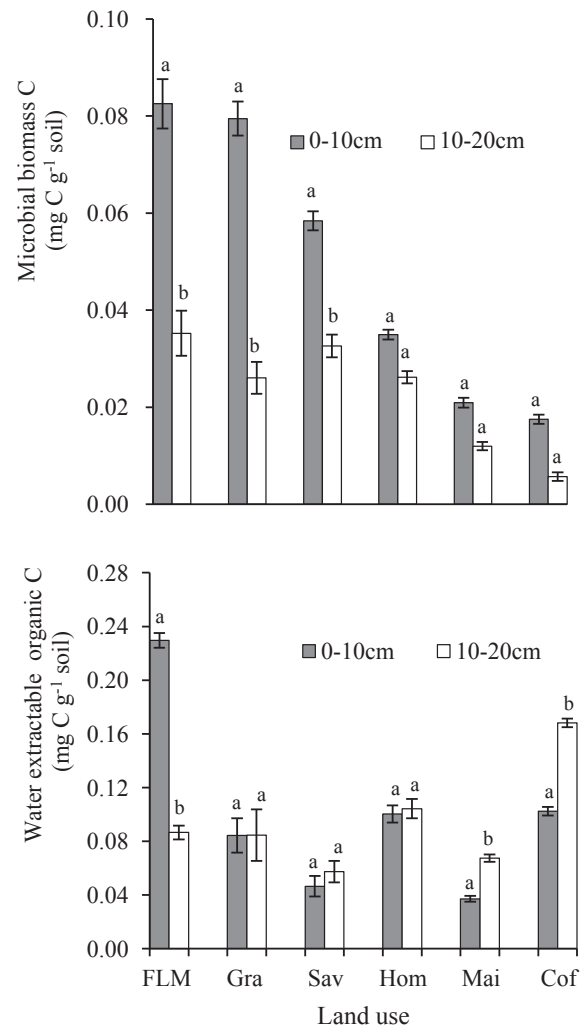

Fig. 3. Microbial biomass C (top) and water soluble organic C content (bottom) depending on soil depth and land use intensity: Natural (FLM-Lower Montane Forest, Gra-Grassland and Sav-Savannah); sustainable use/semi-natural (Hom-Homegardens) and intensive use (Mai-Maize fields and Cof-Coffee Plantation). Error bars represent the standard error of means ($n = 4$). Soil depths in an ecosystem followed by same letters are not significantly different at $P = 0.05$.

homegardens. In contrast, soils from lower elevated intensively used agroecosystems (maize fields and coffee plantation) and from savannah evolved higher $^{14}CO_2$ efflux rates from the upper 0–10 cm depth. At the end of the 65 days, 40–60% of total added ^{14}C was released as $^{14}CO_2$ (Fig. 4).

3.4. Parameters of glucose mineralization

The double exponential model fitted well to the cumulative $^{14}CO_2$ effluxes (r^2 value = 0.986). Generally, the labile C (C_{lab}) pool was increased in the lower 10–20 cm depths. Compared to natural ecosystems and semi-natural Chagga homegardens, intensively used agricultural soils had the highest decay rates of the labile C pool (Fig. 5). The half-lives in all the ecosystems varied from 0.38 ± 0.02 to 1.28 ± 0.09 days and 10.9 ± 2.9 to 22.3 ± 7.0 days for C_{lab} and C_{stab} respectively (Fig. 6).

3.5. ^{14}C glucose in microbial biomass and water extractable organic carbon

At the end of the incubation period, incorporation of ^{14}C labelled glucose into soil microorganisms ranged between 1 and 7% of the ^{14}C input and differed both, between land use types and depths. For both soil layers, the incorporation of glucose C into microbial biomass (MB) was highest in savannah soils with 5.80 and 6.72% at
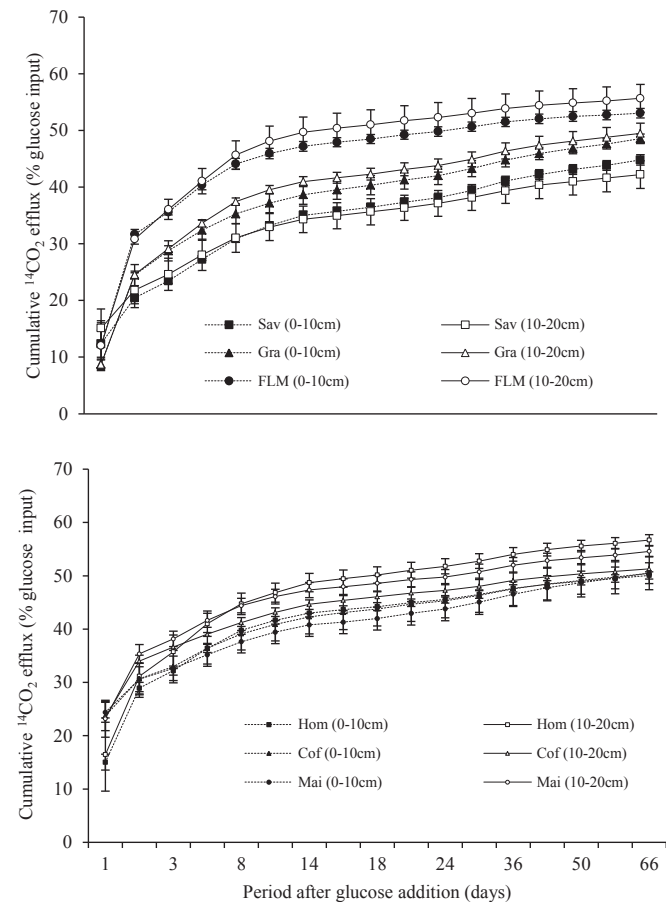
0–10 cm and 10–20 cm depths, respectively. Lowest ^{14}C incorporation in MB was observed in lowest in lower montane forest soils at 0–10 cm and in coffee plantation soils at 10–20 cm (Fig. 7). Because nearly all glucose was taken up by microorganisms from the solution, we found no ^{14}C from glucose in WOC.

4. Discussion

4.1. Effects of land use on soil C and N content

High productivity of African tropical forests as a result of high precipitation, provide important ecosystem services, such as storing C in plant biomass and soil, thus reducing levels of CO_2 in the atmosphere [42]. Ecosystems dominated by grass species, e.g. grasslands and savannah also store high amounts of SOC because of high residue input by roots [14,35,43] through the progressive root biomass senescence and reduced turnover particularly during dry
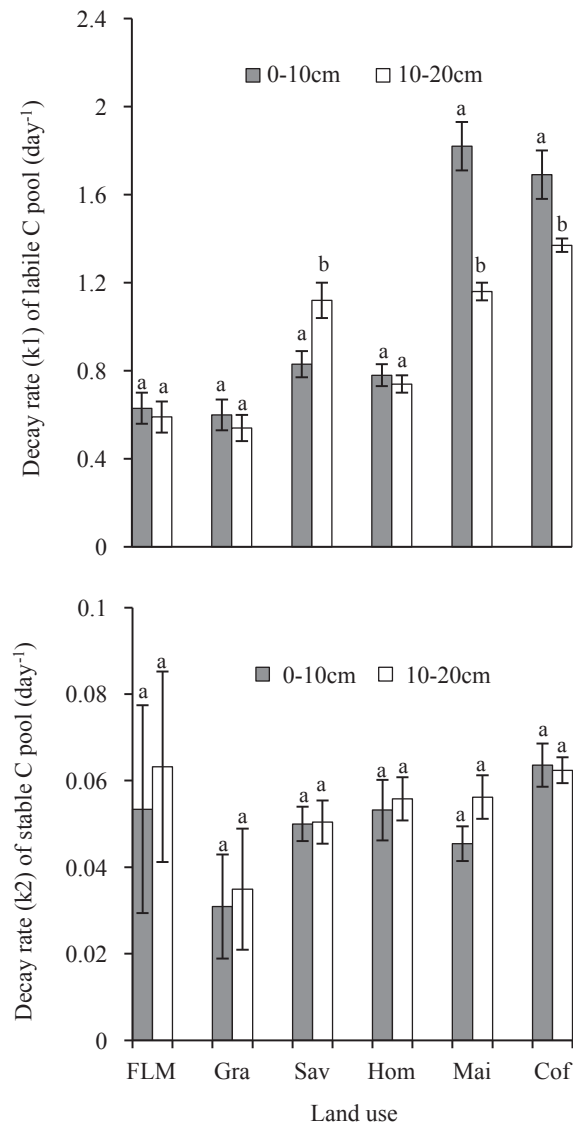

Fig. 4. Cumulative $^{14}CO_2$ emission after addition of ^{14}C glucose from soils depending on land use types and depth (0–10 cm, 10–20 cm). Natural ecosystems (FLM-Lower Montane Forest, Gra-Grassland, Sav-Savannah) (top); sustainable use/semi natural (Hom-Homegarden) and intensive use (Mai-Maize fields and Cof-Coffee Plantation) (bottom). Error bars represent the standard error of means ($n = 4$).

Fig. 5. Decay rates of glucose labile C pool (k1) and stable C pool (k2) using a double exponential model: $C_t = C_{lab} \cdot (1 - exp(-ka \cdot t)) + C_{re} \cdot (1 - exp(-kb \cdot t))$ depending on soil depth and land use intensity: Natural(FLM-Lower Montane Forest, Gra-Grassland and Sav-Savannah); sustainable use/semi natural(Hom-Homegardens) and intensive use(Mai-Maize fields and Cof-Coffee Plantation), Error bars represent the standard error of means ($n = 4$).
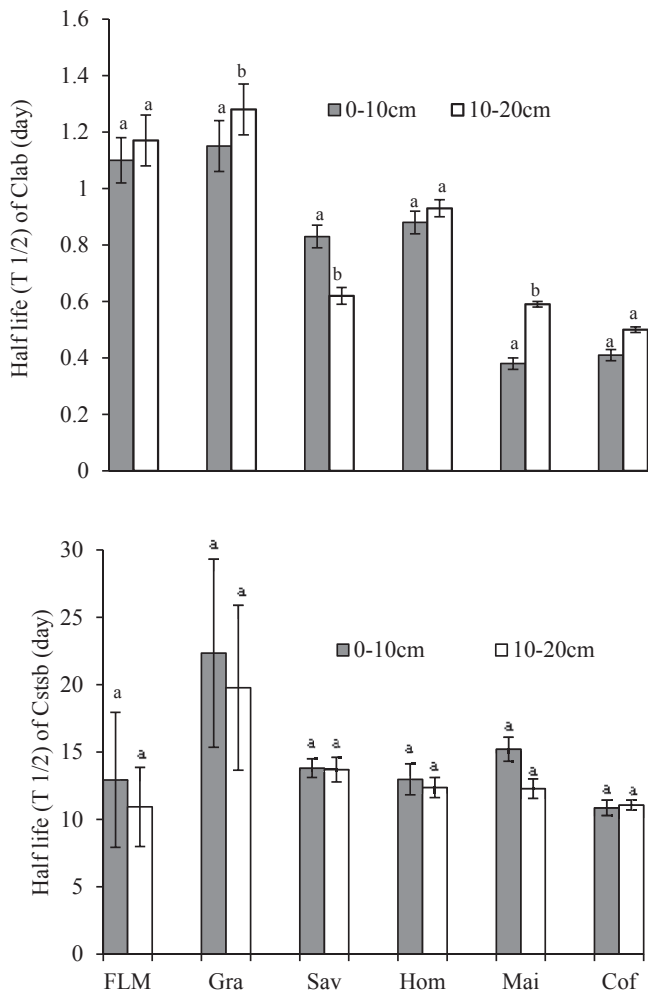
Fig. 6. Half-live (T ½) of glucose labile C pool (k1) and stable C pool (k2) depending on soil depth and land use intensity: Natural(FLM-Lower Montane Forest, Gra-Grassland and Sav-Savannah); sustainable use/semi natural(Hom-Homegardens) and intensive use(Mai-Maize fields and Cof-Coffee Plantation), Error bars represent the standard error of means ($n = 4$).

Fig. 7. ^{14}C from labelled glucose in microbial biomass after 65 incubation days depending on soil depth and land use intensity: Natural (FLM-Lower Montane Forest, Gra-Grassland and Sav-Savannah); sustainable use/semi-natural (Hom-Homegardens) and intensive use (Mai-Maize fields and Cof-Coffee Plantation). Error bars represent the s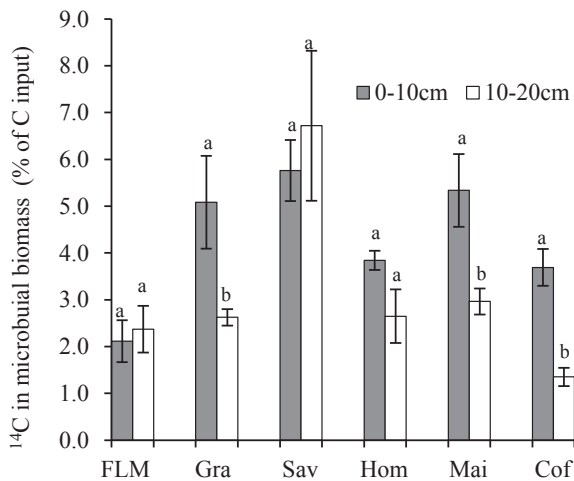tandard error of means ($n = 4$). Soil depths in an ecosystem followed by same letters are not significantly different at $P = 0.05$.

periods [54,55]. Additionally, the more favourable soil conditions for soil biota in grasslands also enhance aggregate structure and its stability, thus provides a physical protection for SOM [3,8].

In this study, natural ecosystems had significantly higher C content compared to agriculturally modified ecosystems (Fig. 1). These results clearly demonstrate that agricultural practices significantly reduce the amount of C and N stored in soils. Differences between the land use types were particularly pronounced for total C rather than N because N is usually added as fertilizer in agricultural ecosystems.

Intensive cultivation results in significant reduction in C additions in soil, rapid decomposition of SOM and erosion. Soil tillage increases the aeration and often accelerates SOM decomposition [4,10]. Previous studies have shown a decrease in soil C content after land use change from natural and semi-natural to agricultural use [50]. SOM losses after land use change are most rapid in temperate regions during the first 25 years of cultivation with losses of 50% of original C reported. In contrast, such C losses in tropics may occur within 5 years after land use change from natural to agricultural ecosystems [45]. In the US, land use change from grassland to agriculture resulted in a significant decrease of total soil C of up to 26% [67]. This was attributed mainly to the combined effects of rapid decomposition of SOM by intensive ploughing and significant reduction of C input by roots and aboveground biomass under cultivation.

Cultivating virgin soils has been reported to cause a massive drop in SOM, whereas average losses of native C have been reported to range from 10 to 55% in cultivated virgin grassland and tropical forest soils. The variation between the studies is explained mainly by climate and soil texture with the maximum losses occurring during the wettest periods and in coarse textured soils. Moreover, changes in C input and soil erosion also contributed to the drop in C content after conversion. Crop production also modifies the soil parameters, C sources, nutrients availability to microorganisms as well as microbial and fauna diversity [4]. Macroaggregates present in undisturbed soils of natural ecosystems provide an important protection mechanism against SOM decomposition that would otherwise be mineralized under intensive ploughing because of aggregate destruction [15]. The relative inaccessibility and protection of organic matter from microbial and enzymatic attacks resulted in higher C content in natural ecosystems.

Higher amounts of C in homegardens compared to intensively cultivated coffee plantations not only show the potential of incorporating tree species in crop production systems to slow down depletion of C after conversion but also to sequester C in soil. Although the potential of C storage in traditional agroforestry systems such as the Chagga homegardens is lower compared to natural forests, it is still much higher compared to intensively cultivated land. Furthermore, the woody component in such agroforestry systems also serves as a source of fuel, reducing pressure on remaining natural forests [62].

Crop removal in crop production systems accounts for a majority of the N that leaves the soil and as a consequence only reduced root biomass contributes to litter input. After harvest, dead roots cannot trap the nutrients released by decomposition and consequently the nutrients, especially N will be leached and lost from the system [32,33,36]. In intensive agriculture systems in the temperate regions, the litter input by maize including rhizodeposition accounts only 35% of the aboveground biomass (Pausch et al., 2013). In contrast, natural ecosystems have much higher amounts of litter and that of better quality (e.g. with high N content). This results in faster decomposition and release of nutrients into the soil. These nutrients, including N, will be trapped by shallow roots and mycorrhiza penetrating the litter (O) horizon. The complete and continued removal of aboveground biomass, as well as soil

erosion, runoff and leaching is reflected in the very low amounts of N in agroecosystems, despite fertilization. We can therefore conclude that the higher N content in undistured natural ecosystems compared to disturbed agroecosystems is the result of nearly closed N cycle and very small annual N losses and also to quality and quantity of litter input.

Soil C:N ratio reflects partly the stability of SOM and is a good indicator of degree of decomposition and quality of OM in the soil [6]. Generally, natural ecosystems have higher C:N ratios and thus contain a higher amount of stable SOM compared to disturbed agricultural soils. In summary, natural ecosystems are characterised by higher soil C sequestration and experience minimal N leaching compared to agricultural soils. Consequently, due to the conversion of natural ecosystems, agricultural soils in the tropics are sources of comparably high amounts of CO_2 [45]. Higher C:N ratio observed in savannah soils reflect the annual drought periods during which the decomposition of litter stops and strongly suggests a higher stability of SOM compared to coffee plantation soil with the least C:N ratios.

4.2. Effect of land use on microbial biomass carbon and water extractable organic carbon

Ecosystems located at higher elevation favour microorganisms because of higher amounts of precipitation, which result in higher plant biomass. Litter accumulation from plant the biomass provides a favourable micro-climate for soil microbial populations by lowering soil temperature, increasing soil aggregation and provision of substrates [5]. Previous studies in tropical climate have reported higher MBC content in ecosystems at a higher elevation [50,53]. Higher amounts of MBC content in undistured tropical forest soils than savannah and grassland soils have been reported in India [60]. The high MBC content observed in lower montane forest soils in this study is attributed to higher productivity of the forest ecosystem, litter accumulation and its higher elevation. Additionally, ecosystems with higher amounts of easily available OM compounds (e.g. rhizodeposits released by grass roots) tend to have higher MBC contents because organic substrates are the preferred energy source for microorganisms [7,15]. The dense root system characteristic of grassland and savannah ecosystems contributed to a higher MBC content compared to agroecosystems at located at the same elevation.

Soil organic matter (SOM) and the structure of the soil are strongly related soil attributes, which determine the microenvironmental conditions in which microorganisms develop [28]. Regular tillage practices causes changes in the soil physicochemical environment, which affects microbial populations. Additionally, the use of Cu-based fungicides for pest control in agroecosystems has been reported to reduce MBC content in soil [16,46]. This attributed to the high affinity of Cu to SOM [19]. Application of 75% copper-based, broad spectrum fungicides has been used by coffee farmers to control major coffee pests for many years [49]. Cu accumulation and conventional tillage practices are likely to have contributed to lower MBC content in coffee plantation soils. Previous studies also found reduction in soil MBC and microbial activity after long-term application of Cu-containing fungicides in citrus grove and avocado orchard soils [16,46]. Low amount of MBC content in agricultural soils of Mt. Kilimanjaro ecosystems strongly implies decreased C_{lab} concentrations and thus microorganisms are more or less 'starved'. Higher MBC content in the upper layers compared to the lower layers in this study are in accordance with several other studies [53,68] that observed a pronounced decrease in MBC down the soil profile. The decline in MBC down the soil profile is attributed to the decrease in substrate input by plant residues.

The dynamics and movement of WOC in soils are important mechanisms influencing soil formation, activity of microorganisms and loss of C from ecosystems through leaching. WOC is often considered the most labile portion of OM is soil, thus negligible with respect to C sequestration [31]. According to [31] the top soil layers are the main sources of DOM in soils. Fungi are thought to play an important role in the production of DOM [11,59]. Therefore, the mechanical breakdown of the organic rich top layer and high fungal biomass present in the tropical montane forest floor in Mt. Kilimanjaro [59] compared to disturbed agricultural soils could partially explain higher WOC in lower montane forest. Increased tillage intensity in agroecosystems enhances oxidative microbial activity, thus resulting in lower WOC content, which corresponds with our measurements from soils under maize production. For Mt. Kilimanjaro ecosystems, this effect was also described by Ref. [50].

4.3. Mineralization of ^{14}C-labelled glucose depending on land use

Cu forms strong complexes with soil OM and as a result, Cu based fungicides accumulate and remain in soil for very long periods. The strong complexes formed with OM decrease its turnover rate, presumably because of inhibitory effects on microorganisms [63]. High doses of pesticide application and accumulation of more resistant chemicals may have negative effects on soil microbial populations and their functions in the soil environment [39]. This may include a slower decomposition of the available and easily decomposable substrates leading to lower CO_2 emissions. Low $^{14}CO_2$ emissions in the 0–10 cm layer of coffee plantation soils is attributed to a low soil microbial population as a result of the intensive use of Cu based fungicides to control coffee berry disease and coffee leaf rust and continuous tillage practices.

Intensive cultivation destroys the aggregate structure of soil and disrupts fungal networks and their re-establishment. A previous study showed that populations of extracellular enzymes and their activities are higher in macro-aggregates compared to micro-aggregates [15]. Alguacil et al. [2] found a significantly lower diversity of mycorrhizal fungi in agricultural systems which included tilled as well as non-tilled reference sites. Soil microbial populations at 10–20 cm depth are usually less affected by tillage practices compared to top soil layer [72] and this could explain the general higher cumulative $^{14}CO_2$ emissions from the 10–20 cm soil layers compared to the 0–10 cm layer except in savannah. This suggests that microorganisms in savannah soils utilized the available organic substrate more for biomass synthesis rather than a source of energy. Therefore, savannah ecosystems have a high potential of reducing CO_2 emissions by to increasing SOC storage in soils.

4.4. Parameters of glucose mineralization in soils depending on land use

The double exponential model (Eq. (1)) was used to describe the decomposition of two pools, labile pool (C_{lab}) and stable pool (C_{stab}). C_{lab} has a higher decomposition rate (ka) whereas C_{stab} is more resistant and consequently has a low decomposition rate (kb). These decomposition rates enabled us to estimate the half-lives of mineralization (Fig. 6).

Labile C pool (carbohydrates and microbial biomass) is important as it fuels the soil food web and therefore, affects nutrient cycling and enhances soil quality and ecosystem productivity. Labile C pools of SOM are especially important because they are affected by altered temperature and soil moisture regimes as a result of climate change [29]. Additionally, oxidation of the labile C pool drives the CO_2 flux from soils to the atmosphere [44]. Pure agricultural practices reduce ecosystem C stocks due to loss of soil C

as CO_2 [47]. However, previous studies have found that the inclusion of trees in the agricultural landscapes often provide opportunities to create C sinks [1] and decrease N leaching [57].

Higher decomposition rates of C_{lab} in agricultural soils compared to soils under natural ecosystems in this study show that conversion of natural ecosystems to agricultural land is a major factor leading to losses in C stocks and increased efflux of greenhouse gases [1,47]. The lower decomposition rate of C_{lab} in homegardens soils suggest that homegardens can decelerate the C cycle and improve C sequestration in soil compared to intensive use agricultural practices.

The size of the more resistant C_{stab} reflects the ^{14}C of glucose incorporated in microbial biomass. Most of the dry and hot savannah zone in Mt. Kilimanjaro has been converted to intensive maize cropping and C_{stab} in soils under maize cultivation was less compared to savannah soils. This reflects a higher turnover and less storage of C in microbial biomass. This reduction in C storage after the conversion from savannahs has also been reported by Ref. [22]. Savannah soils had the largest stable pool compared to all the other ecosystems and this supports the potential of savannah landscapes to store C in soils.

4.5. Incorporation of ^{14}C into microbial biomass carbon

Incorporation of ^{14}C labelled glucose into microbial biomass reflects substrate use efficiency of microorganisms. The amount of ^{14}C incorporated into microbial biomass shows which portion of the substrate is being used by microorganisms at the time of sampling and indirectly reflects microbial availability of the substrate [38]. In presence of heavy metals [9] reported a considerable reduction of C incorporated into microbial biomass. Cu accumulation in soil inhibits the incorporation of ^{14}C glucose in microbial biomass making such soils less efficient in utilizing available substrates for microbial synthesis.

However, ^{14}C from glucose incorporated into MB decreased with soil depth in most of the land use types in Mt. Kilimanjaro (Fig. 7). ^{14}C glucose incorporated into C_{stab} fraction in soils from coffee plantations had a very high turnover rate.

Organic C stored in soil results from the net balance between the rate of SOC inputs and rate of mineralization of in the various organic C pools [52]. A large portion of the microbial population in savannah soils was able to utilize the added glucose for its biomass synthesis compared to the other ecosystems investigated and was incorporated into C_{stab}. It is therefore rational to conclude that microorganisms in savannah are more efficient in the utilization of organics for biomass synthesis and thus favours C stabilization and its accumulation in soils. Low incorporation of ^{14}C labelled glucose suggests a faster turnover of the ^{14}C glucose through the microbial biomass, released as CO_2 and are less readily used by microbial population.

5. Conclusions

Increased land use intensity through the conversion of natural ecosystems for agricultural use, in Mt. Kilimanjaro ecosystems contributes to losses of soil C, increased flux of greenhouse gases and further reduces the fertility of the soils that are generally poor in nutrients.

The mean residence time of glucose added to soils was higher in agroforestry system compared to purely agroecosystems. This shows that agroforestry systems in the tropics may decelerate the C cycle by sequestering C in the soil and that intensive cultivation is not a sustainable land use system in Mt. Kilimanjaro ecosystem.

Higher MBC content in the natural and semi-natural ecosystems compared to agricultural lands shows that intensive cultivation

depletes soil of its nutrients leading to soil degradation because soil MBC content is an important indicator of soil quality and source of plant nutrients.

Savannah soils incorporated the highest amount of glucose into microbial biomass. This strongly suggests that savannah ecosystems are more efficient in utilizing available organic substrates for biomass synthesis and are an available land-use option for C sequestration in soils in the tropics.

Although the lack of full site identity and advanced site history information as well as controlled conditions might suggest that the drawn conclusions may be quite ambitious, our study contributes to the general understanding of land use effects on microbial processes and C sequestration in tropical soils of various land use.

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