



Priming effect in semi-arid soils of northern Ethiopia under different land use types

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Abstract Input of organic carbon (C) to the soil stimulates soil microbial activity leading to changes in turnover of soil organic matter, a phenomenon referred to as priming effect (PE). However, contribution of various management forms in tropical drylands, the role of land use conversion and the soil depth at which such management induces altered PEs remain largely unclear. In this study, we quantified

respiration and PE in semi-arid soils of northern Ethiopia. Soils from three depths (0–30, 30–60 and 60–90 cm) in forest, croplands, enclosure and grazing land use types were sampled. The soil samples were incubated for 23 days and PE and respiration quantified after addition of ^{14}C labeled glucose corresponding to 50% of initial microbial biomass carbon (MBC). Generally, CO_2 respired was 30–63% lower in sub than in topsoil with most expressed depth gradients in croplands. The weak negative PEs in subsoil is an indication of highly stabilized C. Contrary, glucose addition induced stronger positive PEs in topsoils collected from forest, enclosure and grazing

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land. The temporal dynamics of PEs involved a strong positive peak for the first five days after glucose addition and a second smaller peak 10 days after glucose addition in natural ecosystem, corresponding to apparent and real PE, respectively. Lack of positive correlation between PEs and C/N ratio ruled out the N-mining hypothesis, but a positive correlation between PE and MBC suggests co-metabolism as possible mechanism behind the real PE. Higher priming in natural ecosystem compared to cropland is an indication that conversion of natural ecosystem to continuous cropping system leads to depletion of the “primable” C pool in dryland soils. Additionally, this land use conversion negatively affects biogeochemical C cycling by an altered response of soil microbes to C input.

Keywords Ethiopian drylands · Glucose · Land use · Mineralization · Priming effect · Soil organic matter

Highlights

- Highest priming effects was induced in forest soils with least occurring in cultivated lands
- Organic matter decomposition was more pronounced in topsoil, with lower respiration rates at depth due to labile C depletion.
- N-mining hypothesis could not explain patterns of priming effect in semi-arid soils, instead it was related to microbial biomass.

Introduction

Soils contain a large amount of carbon (C), three times as much as in the atmosphere and more than the C in vegetation and atmosphere combined (IPCC 2007). Given the size of this C pool, changes in rates of C mineralization can influence atmospheric CO₂ concentration and global climate.

Thus, priming effects (PEs), i.e. the short-term change in turnover of soil organic matter (SOM) induced by addition of organic C, and underlying mechanisms have attracted considerable research interest in recent times (Kuzyakov et al. 2000; Blagodatsky et al. 2010; Kuzyakov 2010; Blagodatskaya

et al. 2011a; Fontaine et al. 2011; Rousk et al. 2015; Mason-Jones and Kuzyakov 2017). However, most of these studies are based on temperate ecosystems' soils with little attention being paid to tropical sub-Saharan Africa. Under natural conditions, PEs are essential part of the SOM dynamics counterbalancing the C input. Yet when managed, these soils are often highly vulnerable to SOM losses which can be linked to PEs.

Land use changes can severely impact the soil C cycle (Guo and Gifford 2002; Houghton 2003a, b; Gebresamuel et al. 2020) through deforestation (Assefa et al. 2017; Berihu et al. 2017; Okolo et al. 2020a, b), reforestation (Chen et al. 2005, 2013) and other anthropogenic/management activities (Nwite and Okolo 2017; Nwite et al. 2018; Okolo et al. 2019). Conversion of natural ecosystems to managed ecosystems accounts for an estimated 12–15% of global anthropogenic CO₂ emissions (Van der Werf et al. 2009). However, effect of tropical land use systems arising from land use conversion and the soil depth up to which the altered C input induces PEs in highly weathered tropical soils is rarely investigated.

In all ecosystems, majority of aboveground litter inputs, dead fine roots at various stages of decay, and root exudates pass through microbial biomass. Accumulation of necromass in soil over time after microbial death serves as an important source of SOM (Lehmann and Kleber 2015; Liang et al. 2017). The addition of easily available organic substances to soils may strongly change the turnover of native SOM through alteration of soil microbial activity, in turn accelerating (positive PE) or retarding (negative PE) C release from soils (Paterson et al. 2009; Mason-Jones and Kuzyakov 2017). Numerous studies have revealed that native SOM decomposition is significantly triggered by the addition of external organic C, which may activate previously dormant or inactive microbial groups (Bol et al. 2003; Blagodatskaya and Kuzyakov 2008; Jia et al. 2014). Nevertheless, other studies have reported either a preferential substrate utilization leading to insignificant changes in SOM decomposition or even to negative PEs (Kuzyakov 2002; Hamer and Marschner 2005; Nottingham et al. 2009).

Even under controlled conditions, magnitude and direction of PEs vary significantly with land use, amount and quality of added C substrate and soil properties (Zhang et al. 2013; Perveen et al. 2019).

Priming effects have been studied through application of ^{14}C or ^{13}C -labeled low molecular weight organic substances (Aoyama et al. 2000; Fontaine et al. 2004; Blagodatskaya et al. 2010, 2011a, b; Fontaine et al. 2011; Mason-Jones and Kuzyakov 2017) or labeling of more complex, isotopically enriched plant material (Luna-Guido et al. 2003; Majumder and Kuzyakov 2010) to mimic the input of organic C. However, contrasting results still challenge overall interpretations and ecosystem-specific predictions, using C isotope labeling to assess the PE under particular conditions are unavoidable.

It is estimated that more than 50% of the soil carbon stock is found in the subsoil, where it is characterized by high mean residence time (MRT). Thus, subsoils comprise a major reservoir of organic C in all terrestrial ecosystems including drylands (Jobbágy and Jackson 2000; Salome et al. 2010; Lal et al. 2012). Several studies have reported decreasing microbial biomass and activity with depth (Gleixner and Kramer 2008; Hsiao et al. 2018). Moreover, their response to altered C input has received considerable attention (Sanaullah et al. 2011; Bernal et al. 2017; Heitkotter et al. 2017; Wordell-Dietrich et al. 2017; Shahzad et al. 2018, 2019). These studies indicate that litter addition induces PE in both, surface and subsurface layers at varying magnitudes. However, how deeply weathered tropical soils of semi-arid area responds to PEs remains unclear.

A positive PE is often explained by the N-Mining hypothesis (Pausch et al. 2013; Di Lonardo et al. 2019) which attributes decomposition of native SOM to the search for N bound in this SOM (Mason-Jones et al. 2018). However, knowing whether N deficiency is the driving factor for an enhanced SOM decomposition is pivotal, especially for already C-poor semi-arid tropical soil. This can be achieved by studying PEs in association with various potential indicators or regulators of PEs as the total microbial biomass C (MBC), the ratio of microbial C to N (MBC/MBN) or the soil C/N ratio. Changes in MBC/MBN ratio lead either to mineralization or to immobilization of N by microorganisms (Partey et al. 2014). High MBC/MBN ratio, which can be indicative for higher proportion of fungi in the microbial community (Partey et al. 2014) have been reported to modulate PEs (Fontaine et al. 2011). Mganga and Kuzyakov (2018) asserted that the magnitude of the PEs under different land use types could further be attributed

to differences in microbial biomass content. Consequently, PEs have been divided into two phases: real (SOM turnover) and apparent (microbial turnover). With the addition of a substrate, increase in activity of the fast-growing species (r-strategists) utilizing easily available compounds can occur leading to apparent PE (Blagodatskaya et al. 2007). With a certain delay, activation of slow-growing SOM-degrading K-strategists causes real PE (Fontaine et al. 2003).

Drylands occupy 43% of the African continent (Pravalié 2016), and plays a huge role in the global carbon cycle, regulating ecosystem services (Mondejar et al. 2021) and supporting local livelihoods (Wei et al. 2021). The Ethiopian landscapes, especially the northern semi-arid regions (drylands) have witnessed unprecedented degradation induced by land use changes and agricultural intensification for more than three millennia (Nyssen et al. 2015). Due to the need to feed the increasing population, fallowing is practically impossible and excessive pressure by continuous encroachment on the remnants of the afro-montane forests in the region is unavoidable (Assefa et al. 2017; Berihu et al. 2017). More so, enclosure establishment on previously degraded grazing land is gaining more attention in Ethiopia as a sustainable way of land restoration (Okolo et al. 2019; Gessesse et al. 2020; Yakob et al. 2022). Thus, investigating the dynamics of PEs of diverse land use conversion gradients across different depths in semi-arid area of northern Ethiopia is very pertinent. This will increase our knowledge on C sequestration potentials of these semi-arid C-limited land use systems (Bradford 2017). Thus, PE in these semi-arid C-limited land use systems could be linked to the capacity of the soils to function as source or sink of atmospheric CO_2 based on the response and activity of the soils microorganisms. Furthermore, as PEs are linked to nutrient release from SOM, they are of special importance for the low fertile and poor nutrient supplied tropical African soils (Gebresamuel et al. 2008, 2021; Mganga and Kuzyakov 2018). To our knowledge, studies on the impacts of different land use types and anticipated land use conversions on SOC dynamic and specifically the PE have not been conducted in the drylands of the semi-arid Northern Ethiopia.

Thus, we aimed at (1) determining the impact of land use on PEs, (2) assessing the extent to which such effects are controlled by microbial biomass C and N, and (3) identifying the soil depth up to which

an altered C input will have an impact on PE potentially destabilizing subsoil C stocks. We hypothesized that (i) the magnitude and direction of PEs, as directly affected by the mechanism underlying the PE, varies across sites but is always higher in natural ecosystems due to high pool of microbial biomass (ii) land use influences PEs, total CO₂ fluxes, MBC and MBN at least in the top 30 cm, with MBC playing a more active role than MBN for soil C dynamics, but (iii) PEs in subsoils are generally less expressed than in topsoils due to a reduced pool of microbial biomass with lower overall microbial activity.

Materials and methods

Site description

Soils for the study were collected from semi-arid area of Northern Ethiopia, at the locations Hugumburda (12° 40.441' N; 39° 32.053' E, 2494 m.a.s.l) and Desa'a (13° 38.879' N; 39° 46.282' E, 2433 m.a.s.l) as well as in the Geregera (13° 45.118' N; 39° 43.602' E, 2180 m.a.s.l) and Haikihelet watershed (13° 39.3853' N; 39° 51.7760' E, 2236 m.a.s.l), which can all be characterized as drylands. Such dryland sites are very important for PE studies and are characterized by two major soil types: Cambisols (Geregera, Haikihelet and Hugumburda) and Vertisols (Desa'a). The annual rainfall of the area ranges between 190 and 1063 mm year⁻¹ with an average of 503 mm year⁻¹. The peak of the single rainy season is usually in July/August and rescinds towards September and the region has an average annual temperature of 18 °C. According to the traditional agro-climate classification system of the country, the study sites were classified as mid-altitude (1800–2200 m above sea level) and high altitude (> 2200 m above sea level) classes. More information on the occurrence of soil types, land use types and characterization of the study area are presented in Supplementary Table A.1. The meteorological data, geological background information, basic soil data and the land use history are presented in Table 1.

Majority of the smallholder farmers in the region practice mixed farming (combination of crops and livestock) at subsistence level, where crop production is basically rain-fed. The land use types in Desa'a and Hugumburda are forest, grazing land,

and cropland while enclosure, grazing land and cropland are the studied land use types in Geregera and Haikihelet watersheds (See Tables 1, A.1). Enclosure basically refers to previous communal/open grazing land with activities of wood cutting and other agricultural practices undergoing natural restoration by elimination of all activities. (Tefaye et al. 2015; Mekuria et al. 2018). The enclosures were established in Haikihelet and Geregera watersheds 6 and 10 years ago, respectively. The major crops grown in the area are barley (*Hordeum vulgare*), teff (*Eragrostis tef*), wheat (*Triticum aestivum*), sorghum (*Sorghum bicolor*), maize (*Zea mays*), and bean (*Phaseolus vulgaris*). Generally, the most common crop rotation in the study area is wheat + barley + faba bean/field pea but also teff and/or maize can be included in the rotation.

Soil sampling and preparation

Soils from the four land use types (forest, enclosure, grazing and cultivated land) were sampled from 0 to 90 cm depth at intervals of 30 cm. Soils were sampled from three representative plots (50 m×50 m) of the land use treatments. Sampling was carried out simultaneously across all sites in December 2017 (in dry season) after crop harvest. The experimental plots were of the same lithology and the replicate plots were approximately 300 m apart. Three randomly located profile pits (replicates) of 1.5 m depth×1 m×1 m were established in each land use and auger samples were collected from four corners of the pit, thus giving a total of four sampling positions per soil depth and twelve samples per plot. The four soil auger samples taken from each depth were thoroughly mixed to obtain composite sample per each depth. This led to nine samples from each land use representing three composite samples from three profile pits in each land use. However, due to depth-limiting features (occurrence of bedrock at 35–40 cm depth) sampling at 90 cm depth was not achieved in some of the pits. In general, a total number of 104 samples were collected from the four locations. The soil was sieved using a 2.0 mm sieve after first removing visible roots particles and plant debris. The samples were pre-incubated for 7 days at 20 °C to reactivate the microbial cells and allow the recovery of the microbial activity.

Table 1 Site description, meteorological data, total organic carbon and total nitrogen contents of the study sites

Location (Coordinates)	Land use	Mean annual temperature (°C)	Mean annual precipitation (mm)	Geological background	Total organic carbon (mg C g ⁻¹ soil)	Total organic nitrogen (mg N g ⁻¹ soil)	pH	Year under this management	Management type/dominant vegetation
Hugumburda 12° 40.441' N 39° 32.05'	Forest	19.48	475	Tertiary basalt, alkali-alluvial basalt and tuff	14.07 ± 2.03	1.13 ± 0.17	7.87	> 100	Dry Afromontane forest with undergrowth and climbers, mainly Juniperus procera <i>Hochst. ex Endl.</i> , <i>Maytenus obscura</i> (<i>A.Rich.</i>) Cufod, <i>Olea europaea</i> ssp. <i>cuspidata</i> (<i>Wall. Ex G.Don</i>), <i>Pterobium stellatum</i> — <i>Celtis Africana</i> , and <i>Cordia urpurea</i> — <i>Opuntia ficus-indica</i> . Traces of litter removal and tree cutting and carrying (for firewood) by the local dwellers
	Grazing land				7.86 ± 2.55	0.80 ± 0.21	7.58	> 50	Native grasses with remnants of <i>Acacia</i> and <i>Tehag</i> (shrub savannah) with sparsely grown patches of trees. Lightly and periodically grazed in a communal land. No fertilizer application and no cultivation

Table 1 (continued)

Location (Coordinates)	Land use	Mean annual temperature (°C)	Mean annual precipitation (mm)	Geological background	Total organic carbon (mg C g ⁻¹ soil)	Total organic nitrogen (mg N g ⁻¹ soil)	pH	Year under this management	Management type/dominant vegetation
	Crop land				6.72 ± 0.99	0.70 ± 0.09	7.90	> 50	Rainfed cultivation of sorghum (<i>Sorghum bicolor</i>), barley (<i>Hordeum vulgare</i>), teff (<i>Eragrostis tef</i>), wheat (<i>Triticum aestivum</i>), and Maize (<i>Zea mays</i>). NPK/manure application
Haikhelet 13° 39.3853' N 39° 51.7760' E	Exclosure	21.51	498	Limestone	49.29 ± 10.34	1.41 ± 0.16	7.96	6	Undisturbed trees and shrubs, mainly <i>Acacia abyssinica</i> Hochst. ex Benth ('Chea') and <i>Dodonia</i> . Grazing, cultivation, and any form of human interference/activity is strictly prohibited. No cultivation/fertilization
	Grazing land				51.93 ± 8.15	2.78 ± 0.61	7.55	> 50	Native grasses of 'Rgihe', 'Gasa', 'Saeri' and 'Geza' with <i>Acacia</i> and <i>Cynodon dactylon</i> ('Tabay'). Intensively grazed in a communal land. Never cultivated. No fertilizer application. Seasonal floodplain

Table 1 (continued)

Location (Coordinates)	Land use	Mean annual temperature (°C)	Mean annual precipitation (mm)	Geological background	Total organic carbon (mg C g ⁻¹ soil)	Total organic nitrogen (mg N g ⁻¹ soil)	pH	Year under this management	Management type/dominant vegetation
	Cropland				59.12 ± 5.80	0.18 ± 0.11	8.00	> 50	Rainfed cultivation of barley (<i>Hordeum vulgare</i>), wheat (<i>Triticum aestivum</i>), and teff (<i>Eragrostis tef</i>). Bundling, ploughing and NPK application/manure. Seasonal floodplain
Desa'a 13° 38.879' N 39° 46.282' E	Forest	14.62	532	Enticho sandstone and Crystalline Precambrian Basement	40.42 ± 10.16	0.18 ± 0.11	7.60	> 100	Dry Afromontane forest, mainly Juniperus procera Hochst. ex Endl., Maytenus obscura (A.Rich.) Cufod, Olea europaea ssp. cuspidata (Wall. Ex G.Don) Cif., Cadia purpurea Ait., and Carissa edulis Vahl., Cadia purpurea (G. Piccoli) Aiton and Tarcho-nanthus camphoratus L. Traces of litter removal and tree cutting and carrying (for fire-wood) by the local dwellers

Table 1 (continued)

Location (Coordinates)	Land use	Mean annual temperature (°C)	Mean annual precipitation (mm)	Geological background	Total organic carbon (mg C g ⁻¹ soil)	Total organic nitrogen (mg N g ⁻¹ soil)	pH	Year under this management	Management type/dominant vegetation
	Grazing land				29.43 ± 3.21	1.67 ± 0.12	7.25	> 50	Native grasses with remnants of Juniperus and Olei Africana. Lightly and periodically grazed in a communal land. No cultivation and no fertilizer application
	Crop land				20.93 ± 2.68	1.34 ± 0.14	7.58	> 50	Rainfed cultivation of barley (<i>Hordeum vulgare</i>), wheat (<i>Triticum aestivum</i>) and teff (<i>Eragrostis tef</i>)
Geregera 13° 45.118' N 39° 43.602' E	Exclosure	22.02	507	Adigrat and Enticho sandstones, with inclusion of Palaeozoic sedimentary rocks and alluvial sediments	11.14 ± 1.66	1.14 ± 0.14	7.52	10	Juniperus procera Hochst. ex Endl. ('Tsihidi'), Acacia abyssinica Hochst. ex Benth ('Chea'), Olea European subsp. cuspidata ('Auli'e'), Dodonaea angustifolia L. and Eucalyptus globulus Labill. ('TsaedaBahrzaf'). Euclea racemose Murr. subsp. schimperii (A.DC.) F. Whit ('Keleaw') and Becciumgrandiflorum ('Tebeb'). No cultivation/fertilization

Table 1 (continued)

Location (Coordinates)	Land use	Mean annual temperature (°C)	Mean annual precipitation (mm)	Geological background	Total organic carbon (mg C g ⁻¹ soil)	Total organic nitrogen (mg N g ⁻¹ soil)	pH	Year under this management	Management type/dominant vegetation
	Grazing land				13.47 ± 5.40	1.28 ± .50	7.43	> 50	Different species of <i>Sesbania</i> and diverse vegetation, including <i>Cynodon dactylon</i> ('Tahay') and <i>Hyperthemia hirta</i> ('Goiti ebab'). Lightly and periodically grazed in a communal land. No cultivation/fertilization
	Crop land				6.49 ± 2.02	0.63 ± 0.10	7.82	> 50	Rainfed cultivation of cereals: <i>teff</i> (<i>Eragrostis tef</i>), barley (<i>Hordeum vulgare</i>), wheat (<i>Triticum aestivum</i>), Sorghum bicolor (sorghum) and maize (<i>Zea mays</i>); Urea/DAP and animal manure application

The last crops at the point of sampling are the first two crops in each cropland and appears in bold (Modified from Okolo et al. 2020a)

Microbial biomass carbon and nitrogen

Before pre-incubation, MBC and MBN were determined by the chloroform fumigation-extraction method (Vance et al. 1987) based on the difference between C or N extracted from 24 h chloroform-fumigated and non-fumigated soil samples using 0.05 M K_2SO_4 . 0.05 M K_2SO_4 is preferred because the salt does not clog the machine tubes in the long run and there isn't much differences between 0.5 M and 0.05 (Makarov et al. 2015). Extract efficiency (kEC) factor 0.45 and 0.54 were used to convert microbial C and N into MBC (Joergensen 1996) and MBN (Joergensen and Mueller 1996), respectively.

Total carbon and total nitrogen

Total C and N contents in soil were determined by dry combustion with Elementar Vario EL analyzer (Elementar Analysensysteme GmbH, Germany). Considering the negligible carbonate contents (based on acid test) of the soils, the total C content was considered as soil organic C.

Soil pH

The soil pH measurement was done in soil–water (1:2.5) suspensions (McLean 1982).

Incubation and CO_2 analyses after ^{14}C labeling

The influence of land use on C dynamics were studied in an incubation experiment after amending the soils with ^{14}C labeled glucose. Topsoil (0–30 cm) and subsoil (30–60 and 60–90 cm) from the four land use types across all locations were incubated in closed vessels for 23 days in a dark room at room temperature (~ 20 °C) and total respired CO_2 and PE were determined. The incubation period was informed by previous similar studies (Schneckenberger et al. 2008; Hoang et al. 2020). For each land use, site and depth, 40 g soil were weighed into 450 ml glass jar. The soil moisture was maintained at 60% of water holding capacity (WHC) and the CO_2 traps were changed periodically throughout the incubation period. The total quantity of CO_2 trapped in NaOH of soil was measured by TC analysis (TOC-L Shimadzu Total Organic Carbon Analyzer, Shimadzu Scientific Instruments Inc. Columbia, Maryland,

USA). Glucose was used because it is the most abundant monomer entering soils and a preferred energy and C source for microbes (Fischer et al. 2007; Perveen et al. 2014; Mganga and Kuzyakov 2018). After pre-incubation, an amount corresponding to about 50% of initial MBC was added uniformly to the soil surface as 1 ml aqueous solution to stimulate microbial activity (Blagodatskaya and Kuzyakov 2008). Correspondingly, control soil (without glucose addition) was treated with equivalent amount of deionized water and used to observe basal respiration. Small vials with 5 ml of 1.0 M NaOH solution were placed in the vessels to trap CO_2 and were changed periodically (after 1, 2, 3, 5, 7, 10, 15, 21 and 23 days). One milliliter aliquots of the CO_2 traps were mixed with 3 ml of the scintillation cocktail Rotiszint Eco Plus (Carl Roth Company, Karlsruhe, Germany) and ^{14}C activities measured using a Beckman LS 6500 Liquid Scintillation Counter (Beckman Coulter Inc., Atlanta, Georgia, USA). Four empty bottles were used as blanks during the incubation to account for atmospheric CO_2 .

Calculations and statistical analysis

Priming effect was calculated as the difference between total soil respiration following substrate addition less the amount of C respired from the added substrate and respiration from the control soil (Blagodatskaya et al. 2007)

$$PE = (\text{Total } CO_2 - \text{substrate derived } CO_2)_{AS} - (\text{Total } CO_2)_{CS} \quad (1)$$

where the subscripts AS and CS indicate amended soil with substrate and control soil, respectively.

The curves of the cumulative respired CO_2 were fitted with the nonlinear single exponential model (Kuzyakov 2011)

$$CO_2(t) = a(1 - \exp(-k \times t)) \quad (2)$$

where: $CO_2(t)$ = amount of cumulative CO_2 depending on time, a = potentially mineralizable pool of soil C, k = mineralization rate, and t = time.

Cumulative respired C in CO_2 , priming rate (PR), PE (cumulative) and MBC/MBN ratio were analyzed using one-way ANOVA to test for significant differences between land uses within site and same depth (Software STATISTICA Version 12.0, StatSoft

GmbH, Hamburg, Germany). A general linear model was applied on C/N, MBC/MBN, SOC, MBC, glucose respiration and $q\text{CO}_2$ to identify their impact on PE. The Levene and Kolmogorov–Smirnov tests were used to check for homogeneity of variances and normality, respectively. Duncan's post hoc test was used to separate the means at $P < 0.05$ significance level. All reported results represent means of three replicates \pm standard error (SE).

Results

CO₂ efflux from soils

Irrespective of the land use, total CO₂ efflux from soil decreased with increasing depth across the locations (Fig. 1). Total respired CO₂ was highest in soils collected from forest and grazing lands (Fig. 1). Croplands always showed lowest soil CO₂ respiration with the 30–60 cm soil depth of Geregera having the overall lowest cumulative CO₂ (0.08 ± 0.01 mg C

g^{-1} ; Fig. 1). The cumulative CO₂ emitted from exclosures—the restored landforms—never exceeded total respiration from grazing lands, with the maximum of observed cumulative CO₂ in topsoil (0–30 cm) of Haikihelet grazing land (0.28 ± 0.02 mg C g^{-1}).

Priming effects

Soil depth was the major factor defining whether positive and negative PEs occurred (Figs. 2 and 3). Strong positive PEs (increase in SOC mineralization with the addition organic or mineral substance) dominated the first days in topsoils of Haikihelet and Desa'a. Negative PEs i.e., decrease in SOC mineralization with the addition organic or mineral substance, occurred mainly in subsoils and were quantitatively lower than the positive topsoil PEs at these sites. On the contrary, the magnitude of positive PEs in topsoils of Geregera and Hugumburda (except for the croplands) was in the same range as negative PE in subsoils, potentially canceling each other over the entire

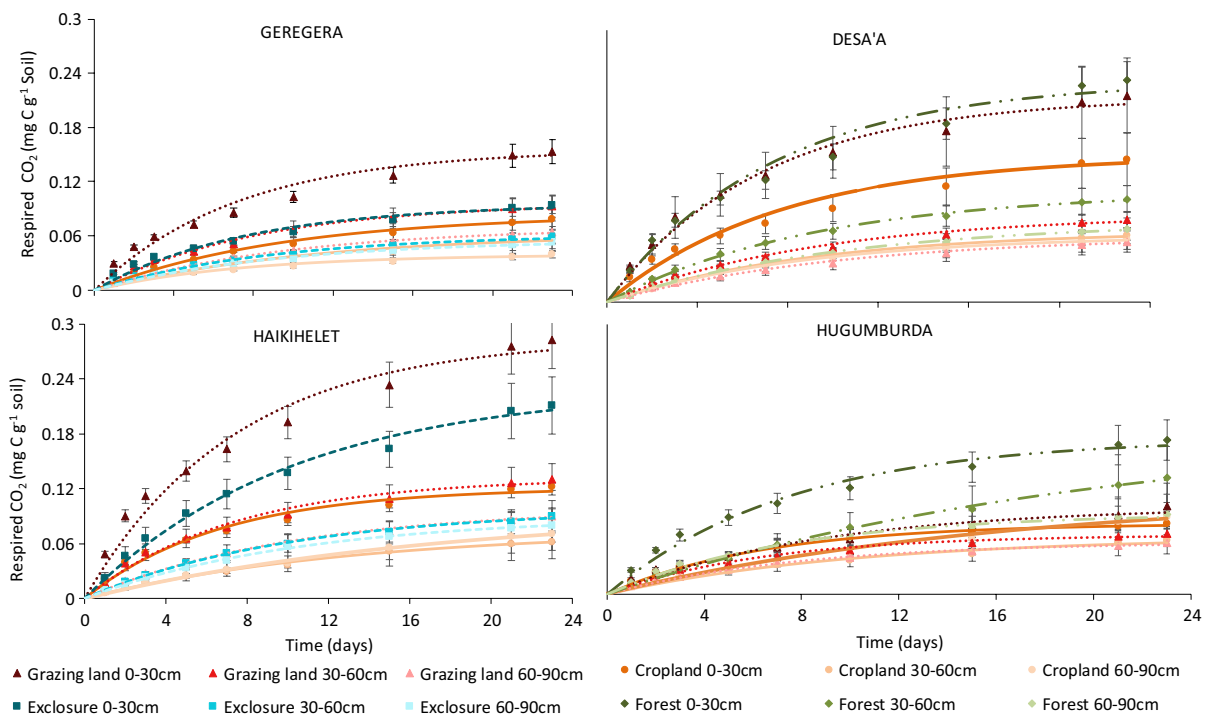


Fig. 1 Cumulative respired CO₂ depending on land use and depth at Geregera, Haikihelet, Desa'a and Hugumburda. Error bars indicate standard error of the mean. The curves were fit-

ted with nonlinear least-square regressions according to single exponential Eq. (2) and parameter estimates are presented in Supplementary Table A.2, A.3, A.4, and A.5. $n = 104$

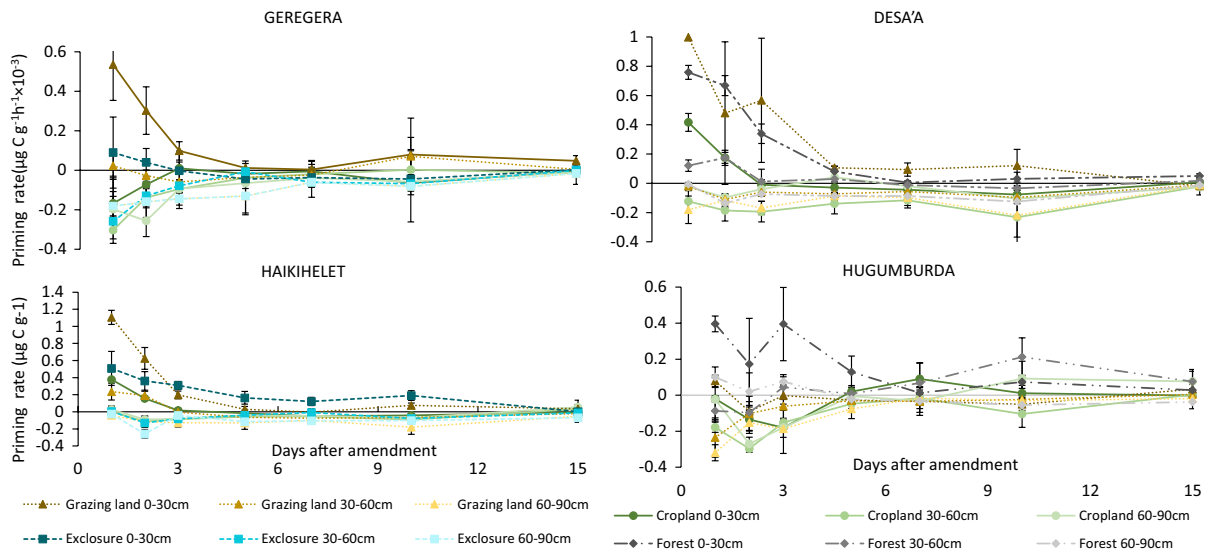


Fig. 2 Priming rate depending on land use and depth at Geregera, Haikihelet, Desa'a and Hugumburda. Error bars indicate standard error of the mean. Note different Y scales for the four locations. $n = 104$

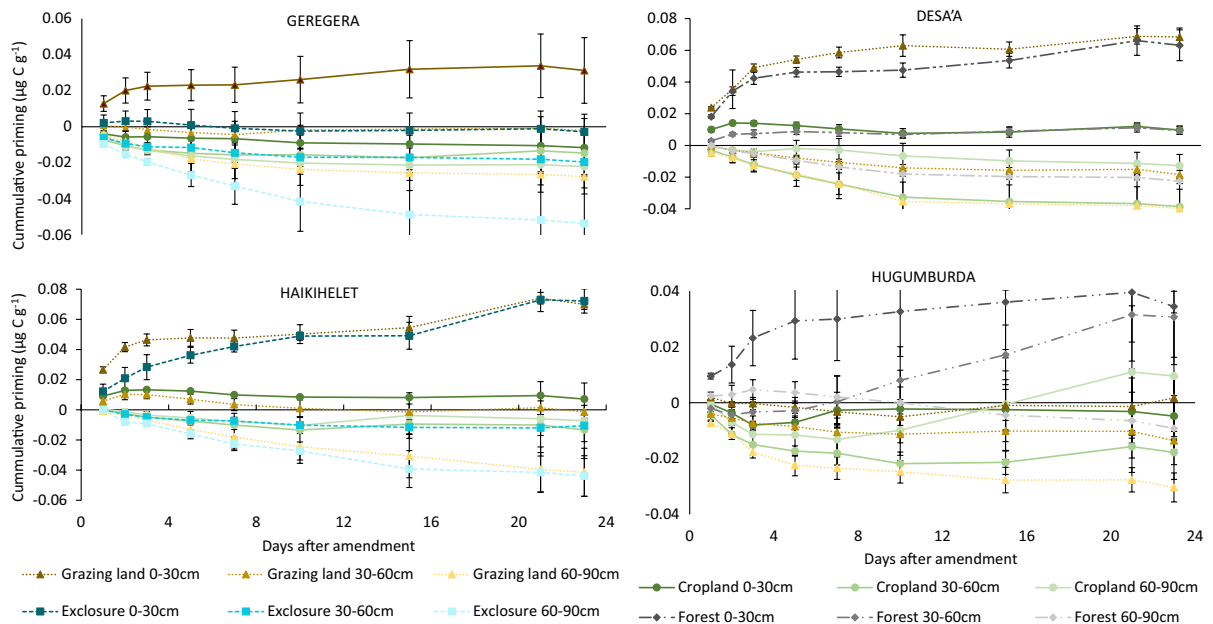


Fig. 3 Priming effect depending on land use and depth at Geregera, Haikihelet, Desa'a, and Hugumburda. Error bars indicate standard error of the mean and the letters above the error

bars indicate significant differences ($P < 0.05$) between land uses at 0–30 cm (a), 30–60 cm (a') and 60–90 cm (a''). Note different Y scales for the four locations and both ratios. $n = 104$

soil profile in case relative C input occurs equally in all depths.

Except for Haikihelet enclosure topsoil, the strong positive PE peak immediately after glucose addition

rapidly decayed to values close to zero between day 3 and 5. The temporal dynamic of this first priming peak tended to be very similar at all land use types and soil depth (Fig. 2). After the decay, a second

weak positive priming peak re-emerged across all the locations around the 10th day (Fig. 2). In general, positive priming occurred mainly in the topsoils while negative priming was observed in subsoils for both priming peaks (Fig. 3).

In terms of land use types, much higher positive PEs were recorded in soils from forests, exclosures and grazing lands than in croplands, where the PEs did not deviate significantly from zero (Table 2). Strong negative priming occurred at 60–90 cm depth, especially in soils from exclosure and grazing land. The most surprising priming pattern was shown in

Hugumburda forest soils at depth 30–60 cm, where positive PE increased strongly at very late time point of 7 days, representing the only soil with such a late, very pronounced priming response.

MBC/MBN and C/N ratio as explanatory variables for priming

The MBC content was lowest in croplands and highest in forest and grazing land – covering a range from 0.03 to 0.83 $\mu\text{g g}^{-1}$ (Supplementary Fig. 1). The MBC/MBN ratio ranged from

Table 2 Results of the analysis of variance (ANOVA) for the entire 23 days of sampling for the effects of glucose respiration, C:N, MBC:MBN, SOC, MBC and $q\text{CO}_2$ on PE (Data on MBC and $q\text{CO}_2$ taken from our earlier study: Okolo et al. 2020a)

Location	Effects	Degrees of Freedom	Sum of squares	Mean square	F-ratio	P-value
Geregera	Intercept	1	0.000846	0.000846	1.029	0.323
	Glucose resp	1	0.000020	0.000020	0.024	0.877
	C:N	1	0.000182	0.000182	0.221	0.643
	MBC:MBN	1	0.000033	0.000033	0.040	0.843
	SOC	1	0.001525	0.001525	1.854	0.188
	MBC	1	0.004733	0.004733	5.754	0.026*
	$q\text{CO}_2$	1	0.001545	0.001545	1.879	0.186
	Error	20	0.016450	0.000822		
Desa'a	Intercept	1	0.000650	0.000650	1.076	0.312
	Glucose resp	1	0.000141	0.000141	0.233	0.634
	C:N	1	0.000513	0.000513	0.849	0.368
	MBC:MBN	1	0.001136	0.001136	1.882	0.185
	SOC	1	0.000636	0.000636	1.052	0.317
	MBC	1	0.004913	0.004913	8.133	0.009*
	$q\text{CO}_2$	1	0.000035	0.000035	0.058	0.811
	Error	20	0.012079	0.000604		
Haikihelet	Intercept	1	0.001244	0.001244	1.377	0.254
	Glucose resp	1	0.000146	0.000146	0.161	0.692
	C:N	1	0.001378	0.001378	1.526	0.231
	MBC:MBN	1	0.000031	0.000031	0.034	0.854
	SOC	1	0.003382	0.003382	3.745	0.067
	MBC	1	0.00709	0.00709	7.783	0.011*
	$q\text{CO}_2$	1	0.001553	0.001553	1.719	0.204
	Error	20	0.018063	0.000903		
Hugumburda	Intercept	1	0.000172	0.000172	1.029	0.515
	Glucose resp	1	0.001809	0.001809	4.624	0.044
	C:N	1	0.000300	0.000300	0.767	0.392
	MBC:MBN	1	0.000184	0.000184	0.469	0.501
	SOC	1	0.000085	0.000085	0.218	0.645
	MBC	1	0.001441	0.001441	3.682	0.069
	$q\text{CO}_2$	1	0.008140	0.008140	20.799	0.000
	Error	20	0.007827	0.000391		

C:N carbon to nitrogen ratio, *Glucose resp* glucose respiration, *MBC:MBN* microbial biomass carbon to microbial biomass nitrogen ratio, *MBC* microbial biomass carbon, *SOC* soil organic carbon, *PE* priming effect, *qCO₂* metabolic quotient

*Significant difference ($P < 0.05$)

approximately 4 in Hugumburda (60–90 cm) to 20 in Desa'a (30–60 cm) cropland soils (Fig. 4). Generally, soils from 30 to 60 cm displayed highest MBC/MBN ratios across the locations except for Hugumburda, which had successively decreasing ratios from top- to subsoils. A land use trend for MBC/MBN can only be found for topsoils with decreasing ratios in order forest/exclosure > cropland > grazing land, suggesting highest N demand in the natural ecosystems and lowest under grazing. This trend was not visible at Hugumburda where MBC/MBN ratios among land uses were comparable. The soil C/N ratio ranged between 9.2 and 102.4 with varying patterns depending on the locations. In Desa'a and Haikihelet, a general trend of increasing C/N ratios with depth was recorded with Haikihelet subsoil C/N ratios being extraordinarily high (exception: Haikihelet grazing land, where soil C/N ratios remained constant across depth). Constant C/N ratios with soil depth were displayed in

all the land use forms in Geregera and Hugumburda soils. Hugumburda was also the only site displaying a clear land use effect on soil C/N ratios with higher values in forests compared to grazing and cropland.

A general linear model containing C/N, MBC/MBN, SOC, MBC, glucose respiration and qCO_2 (microbial metabolic quotient) [last three data taken from our earlier study (Okolo et al. 2020a)] as factors displayed total MBC as the only factor significantly affecting the PE in Geregera, Desa'a and Haikihelet ($P < 0.05$) by a positive interaction. The qCO_2 was calculated by dividing the average C released as CO_2 in mg (per day/g soil) with MBC. A direct regression displays that PEs increase with increasing MBC (see Fig. 5; Table 2). Only Hugumburda showed a deviating behavior with significant influence of glucose respiration and qCO_2 on the priming effect—suggesting mechanistic differences underlying the observed PE in Hugumburda compared to all other sites.

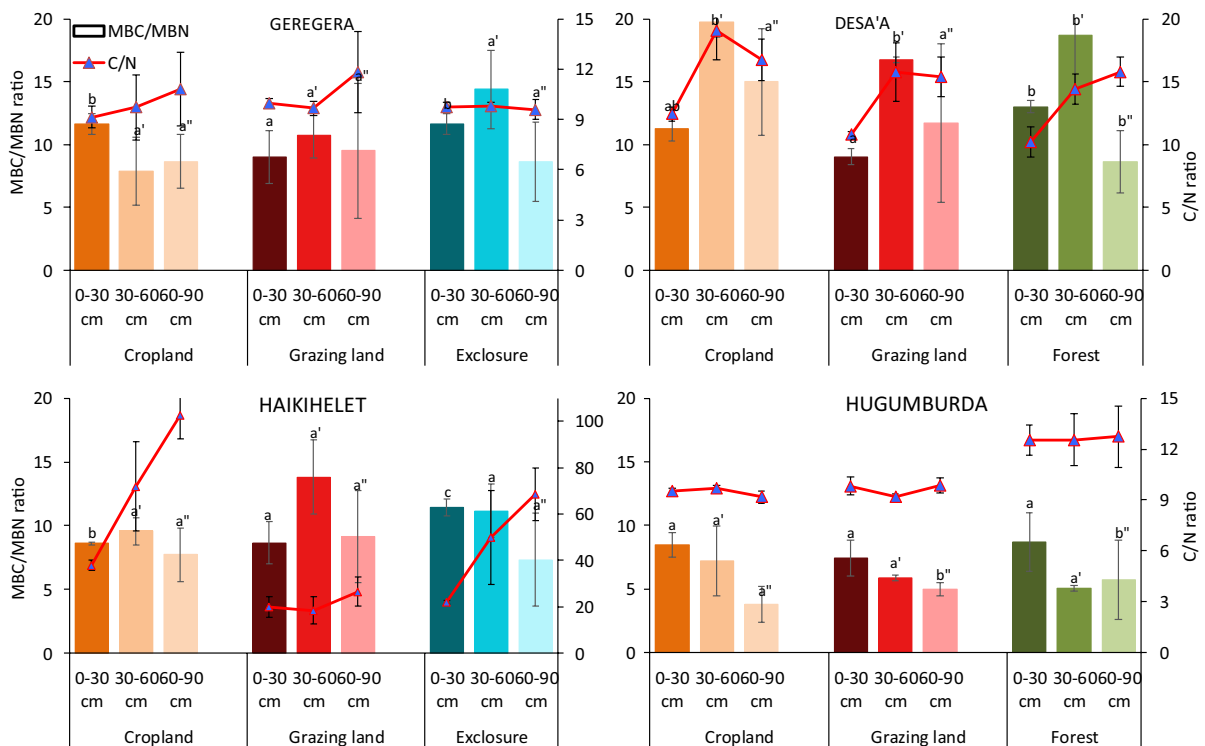


Fig. 4 MBC/MBN (bars) and C/N ratio (symbols) depending on land use and depth at Geregera, Haikihelet, Desa'a, and Hugumburda. MBC/MBN refers to left and C/N refers to right y-axis. Note different Y scales for the four locations and

both ratios. Error bars indicate standard error of the mean and the letters above the error bars indicate significant differences ($P < 0.05$) between land uses at 0–30 cm (a), 30–60 cm (a') and 60–90 cm (a''). $n = 104$

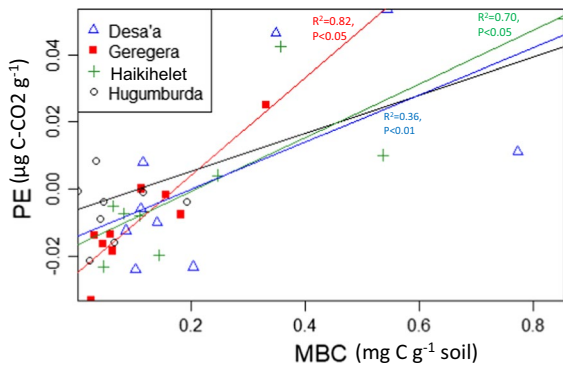


Fig. 5 Correlation between priming effect (PE) and microbial biomass carbon (MBC) across locations. $n = 104$

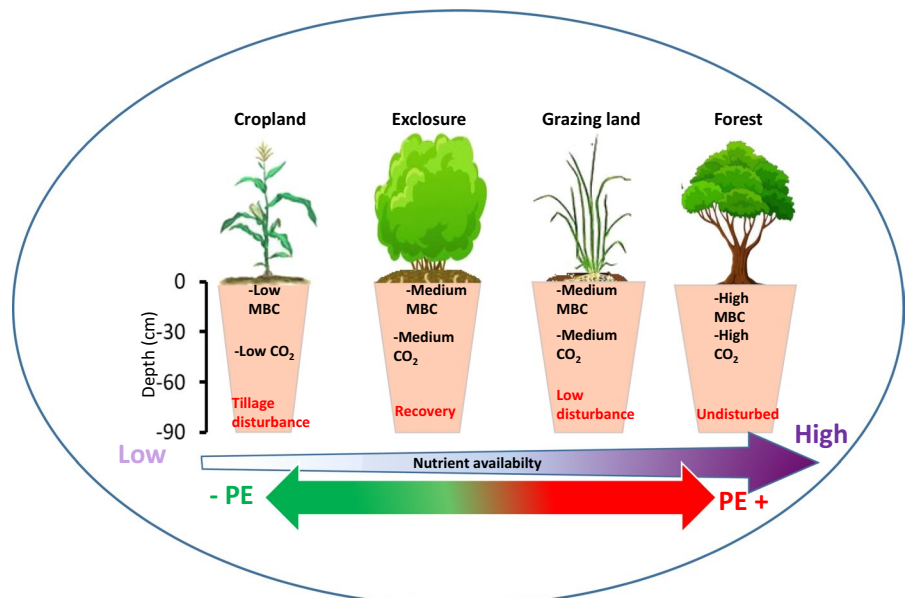
Discussion

Land use impacts on PE-generating processes

Land use alters soil properties and microbial communities with potential consequences for PEs (Mganga and Kuzyakov 2018). We found strong total CO₂ release in soils collected from forest, exclosure and grazing lands compared to cropland soils. A similar finding of higher CO₂ emission from soils under natural vegetation compared to cultivated croplands was reported by Mganga et al. (2016). The influence of land use on CO₂ release corresponded to the

observed trends in PEs. Strong positive PEs occurred in natural and partially restored ecosystems, which contrasted with PEs in croplands that did not significantly deviate from zero. Because PEs are an ultimate consequence of microbial activity, strong positive PEs (increase in decomposition of native SOM) in the natural ecosystems are an indication of high microbial activity (Bastida et al. 2019). The high microbial biomass contents found in these ecosystems is one of the prerequisites for this high activity. Large quantities of decaying litter and rhizodeposits entering these soils regularly most likely provide a valuable C and energy sources for microbes promoting their proliferation and very likely counterbalances or even outcompetes high C losses by priming in natural soils (Mganga and Kuzyakov 2018). Additionally, low disturbances due to plant litter cover that prevents disruptive effects in the natural and semi-natural ecosystems ensures an environment conducive for microbial growth (Mganga et al. 2016; Fig. 6). The SOC sequestration potential of exclosures were comparable to those of forest ecosystems, thus a good reflection of C sink. Under such conditions, an accelerated decomposition of native SOM (positive priming) to provide substrates for the rapidly growing microbial population will be inevitable whenever microbial activity and growth is stimulated in response to altered amounts of available C (Blagodatskaya and Kuzyakov 2008).

Fig. 6 Conceptual diagram summarizing priming effect under different land use types in semi-arid area of northern Ethiopia. The nutrient availability arrow illustrates the concentration pathway and distribution of SOC and TN contents across the land use types. The double-headed priming arrow indicates the direction of priming effect. The sizes of the pots simply refers to the “amount” of the SOC pools across land use types



In croplands, soil disturbances such as tillage destabilizes the soil structure (Borie et al. 2006; Okebalama et al. 2017) with the consequence of exposing protected SOM to microbial mineralization. This results in a reduction in soil C and microbial biomass content (Banfield et al. 2018; Okolo et al. 2020a) and retardation of SOM decomposition (negative priming). This implies preferential switching from soil organic C decomposition to glucose mineralization by microbial communities in cropland soils. Siles et al (2022) reported a less negative PE in croplands in comparison with semi-natural ecosystems, showing that PE intensity is dependent on land use. Furthermore, the fungal hyphal network is destroyed by tillage leading to a reduction of fungal biomass and diversity (Alguacil et al. 2008). However, further non-reported management effects as consequence of, e.g. fertilization or pesticide application may be involved in this process too. Such land use induced shifts in PEs cannot be generalized for the tropics and also contrasting results were detected. Perveen et al (2019) reported a positive PE in cropland soils across the globe, cutting across Europe, Africa, Asia, America and Australia while negative PE in cropland and semi-natural soils taken from 22 European countries was reported by Siles et al (2022). This calls for more detailed mechanistic evaluation weighting the individual influencing management factors as potential explanation for the magnitude and direction of PEs.

To summarize, higher PEs in natural ecosystems than croplands indicate that land use change towards intensive agriculture leads not only to a depletion of soil C sources but also a reduction in the activity of these soils' microbial communities and soil nutrient turnover (Fig. 6). However, to be able to estimate the impact of land use induced changes in PEs on soil C storage capacity, it is important to know up to which depth altered C inputs affect the soil C dynamics.

PEs in topsoil versus subsoil

Positive PEs were more pronounced in topsoils (0–30 cm) of forests, grazing land and exclosure compared to subsoil PEs. Accumulation of organic matter in topsoils of natural ecosystems promotes microbial growth and activity by increasing the content of easily available C. The rather active microbial communities in topsoils induce the positive PEs initiated by glucose addition (Mganga and Kuzyakov 2018).

Microbial hotspots are the main locations for PE and SOM turnover by priming (Blagodatsky et al. 2010; Kuzyakov 2010). Such hotspots are highly abundant in intensively rooted topsoils as well as in or directly below the litter layer. Both, can be found in the topsoils of natural ecosystems. Conversely, homogenized topsoils, depleted C amounts and low microbial biomass content in croplands accounted for a lack of PEs in these soils, even in topsoils (Fig. 6).

Subsoils have the capacity to store large amounts of C with high MRT, which make them attractive as long-term C sinks (Dignac et al. 2017). Leaching and accumulation of leachates, rhizodeposition and transport of dissolved organic C to subsoil by soil fauna e.g. earthworms (Banfield et al. 2018) can induce priming of stabilized SOM, causing C losses (Fontaine et al. 2007; Kuzyakov 2010). Accordingly, many studies in both temperate (Jia et al. 2014; Hoang et al. 2017) and tropical regions (Shahzad et al. 2019) have reported relatively higher positive PE in sub- than the respective topsoils. In contrast, the addition of glucose, as a representative component of the dissolved organic C reaching subsoils, retarded SOM decomposition (negative PEs) in our subsoils (30–90 cm) irrespective of the land use type (Fig. 2). This result highlights that priming response of tropical soils may substantially deviate from those observed in temperate soils representing the majority of existing studies. This decrease in PEs correlates with MBC contents (Fig. 5). Low contents of MBC in subsoils are mostly explained by a decreased availability of labile C (Banfield 2018) and thus imply rather 'starved' microorganisms. Consequently, the added glucose was preferentially used for direct demand for anabolism or energy production but was not sufficient to stimulate microbial activities up to a degree inducing the decomposition of native SOM. Besides, high stability of subsoil C possibly due to its physical protection and thus the higher energy demand accessing this C accounts for the negative PE (Rumpel and Kögel-Knabner 2011). This makes tropical drylands' subsoil C pools highly resistant to degradation and, thus, would explain why land use change had little impact on subsoil C. This demonstrates that the highest proportion of C losses following conversion of natural ecosystems to intensively used cropland occurs in topsoils, which confirms our second hypothesis. It also suggests that tropical subsoils have great potential to sequester C or act as sink.

Nonetheless, exceptions to this general phenomenon were observed. Hugumburda forest subsoils (30–60 cm) with lower MBC/MBN than its topsoil, for example, (Fig. 4) exhibited stronger positive PEs than their topsoils (Fig. 3). Similar findings were reported by Shahbaz et al. (2018) and Shahzad et al. (2019) in an Aridisol in Pakistan. Since up to 75% of forest root biomass is in subsoils (Rumpel et al. 2002), rhizodeposition supplies easily assimilable compounds to the subsoil that sustains a considerable active microbial population. The strong positive PEs displayed towards the end of incubation in the subsoil of this site can most likely be attributed to K-strategist in these subsoils, e.g. fungi (Fontaine et al. 2003). K-strategists grow slowly and are less competitive for easily available C but invest intensively in the production of exoenzymes that depolymerize SOM when energy rich-compounds are available (Fontaine et al. 2003). This result supports our first hypothesis that the magnitude, direction and drivers of PE as directly affected by the priming mechanism vary from site to site.

Kinetics and mechanisms of priming effects

Primed soil respiration is in many cases not just a short-term response but can persist for several weeks or months after exhaustion of the added substrate (Fontaine et al. 2004). In our study, a strong positive PE occurred immediately after glucose application which rapidly peaked and disappeared within 3–5 days (Fig. 2). This immediate PE can be explained by chemosensory inducing a triggering effect that accelerates microbial internal metabolism in anticipation of the ‘food event’ (De Nobili et al. 2001; Mason-Jones and Kuzyakov 2017). Triggering effects last only for a few minutes to several hours after substrate addition (Blagodatskaya and Kuzyakov 2008) and cannot solely account for the up to 5 days priming effect observed after glucose addition. This duration indicates that pool substitution followed the triggering effect after glucose uptake and subsequently apparent priming took place (Blagodatskaya and Kuzyakov 2008). Such responses are normally associated to r-strategists such as Gram negative bacteria which are known to be highly competitive for low molecular weight compounds (Fontaine et al. 2003; Apostel et al. 2015). However, high MBC/MBN ratio (8–11) in topsoils with exception

of Hugumburda grazing land (Fig. 4) means that a contribution of a fungal response cannot be ruled out (Partey et al. 2014). Similar responses in fallow Chernozems amended with glucose were shown to be initiated by fungal growth (Panikov 1995).

Ten days after glucose addition, a second weak positive PE occurred in the topsoils of the natural ecosystems. This suggests the presence of a second, different priming mechanisms. After exhaustion of the added glucose, activities of r-strategists diminish, and slow-growing K-strategists start to dominate the PEs (Fontaine et al. 2003; Blagodatskaya and Kuzyakov 2008). Given the huge pool of plant-derived organic matter and high MBC/MBN ratios in the natural ecosystems of our study sites, fungi especially saprotrophic fungi are likely the dominant group within the K-strategists. Fungal investment of C and energy from the assimilated glucose in the synthesis of exoenzymes that hydrolyzes SOM could explain the second peak in PE observed after 10 days. Negative PEs even in the extremely N deficient Haikihelet subsoils (Fig. 4) and a lack of correlation between PE and C/N ratio (Table 2) rules out the N-mining hypothesis and leaves the co-metabolism as most probable mechanism causing PEs after 10 days. Temporal dynamics and the linkage to the presence of a high SOM stock suggest this second peak in PE to be related to the decomposition of native SOM and thus can be regarded as real PE.

Conclusion

Addition of glucose to Ethiopian dryland soils from four ecological zones resulted in greater positive PEs in topsoils compared to weak negative PEs in lower soil depths irrespective of the land use. These results indicate that topsoil C losses due to land use change from natural ecosystem to intensive agriculture induce a sequence of changes in biogeochemistry and microbiology that result in strong implications for PEs. Higher positive PEs were observed in forest, enclosure and grazing land relative to cropland and were strongly correlated to the MBC content. Thus, soil microbial biomass plays an active governing role in SOM turnover, acting as a driver of PEs. Magnitude and direction of PEs appear to be driven by soil microbial biomass content and further influencing soil properties across depth such as the physical

stabilization of SOM rather than by the soil C/N ratio. Thus, differences in PEs within our dataset could not be explained by the N-mining hypothesis but rather by a change in total microbial biomass as the active drivers of PEs and potentially by a shift in microbial community structure which is expected to leave an imprint on the MBC/MBN ratio. Low PEs in croplands are an indication for an already degraded status of these soils with low C and nutrient contents and low activity of its microbial communities. However, this negative land use impact was solely detected in topsoils suggesting subsoil C stocks are rather stable in these tropical dryland soils even if under intensive agricultural use. This suggests that conversion of natural ecosystems to cropland could be a considerable source of atmospheric CO₂ based on the topsoil C losses. Such losses might not be trivial to mitigate and regenerate, as the biogeochemical cycling in these soils is strongly changed and the altered microbial communities may respond very differently to the input of fresh, available C sources. Sustainable farming practises protecting large proportions of the natural soil organic C stocks and establishment of exclosures (protected areas with zero grazing and prohibited human activities) might be the preferred compromise between local food security and the maintenance of the topsoils' ecosystem services to future generations. In addition to being a unique mechanism for restoration of degraded ecosystems, exclosure establishment enhanced carbon stocks and acted as carbon sink accounting for appreciable increase in soil biomass. From a sustainability point of view anchoring on our findings, exclosure establishment should be adopted across African dryland areas due to its potential in stabilizing the topsoil C and its functionality.

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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