



Original article

Microbial soil quality indicators depending on land use and soil type in a semi-arid dryland in Kenya

Kevin Z. Mganga^{a,b,c,*}, José Rolando^d, Subin Kalu^{b,c,e}, Kristiina Karhu^{b,f}^a Copernicus Institute of Sustainable Development, Utrecht University, the Netherlands^b Department of Forest Sciences, University of Helsinki, Helsinki, Finland^c Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland^d School of Biological Sciences, Georgia Institute of Technology, Atlanta, USA^e Department of Crop and Soil Sciences, North Carolina State University, Raleigh, USA^f Helsinki Institute of Life Science (HiLIFE), University of Helsinki, Finland

ARTICLE INFO

Keywords:

Cropland
Pasture
Grassland
Shrubland
Vertisol
Acrisol
Soil quality
Dryland

ABSTRACT

Soil microbial indicators help monitor soil quality. Limited studies have determined how land use in drylands affects soil microbial indices. Top soil (0–10 cm) from four land use systems in African drylands: (1) shrubland (natural), (2) grassland (natural), (3) pasture (agricultural) and (4) cropland (agricultural) occurring on two soil types: (1) Vertisol and (2) Acrisol, was used in laboratory incubations (6 days) to assess the effects of land use changes on organic carbon (C_{org}) mineralization, microbial biomass C (C_{mic}), mineralization quotient (qM), metabolic quotient (qCO_2), $C_{mic}:C_{org}$ ratio and sensitivity indices of these microbial indicators. Experimental plots were organized into a completely randomized design ($n = 3$) for every combination of land use and soil type. Cumulative CO_2 produced from native C_{org} mineralization was the highest in Acrisol ($108 \pm 2.7 \mu g CO_2-C g^{-1} soil$) and the lowest in Vertisol ($53 \pm 2.5 \mu g CO_2-C g^{-1} soil$) croplands. Vertisol shrubland ($1.34 \pm 0.09 mg C g^{-1} soil$) and Acrisol cropland ($0.28 \pm 0.07 mg C g^{-1} soil$) had the highest and the lowest C_{mic} , respectively. Acrisol cropland ($1.29 \mu g CO_2-C g^{-1} h^{-1}$) had the highest qM , approximately five times higher than the lowest qM ($0.26 \mu g CO_2-C g^{-1} h^{-1}$) in a Vertisol cropland. Highest qCO_2 was observed in an Acrisol pasture ($12.04 \mu g CO_2-C g^{-1} C_{mic} h^{-1}$), which was approximately 30 times higher compared to the lowest qCO_2 observed in a Vertisol shrubland ($0.41 \mu g CO_2-C g^{-1} C_{mic} h^{-1}$). The $C_{mic}:C_{org}$ ratio was the highest in a Vertisol shrubland (0.097), approximately five times higher than the lowest observed in an Acrisol pastureland (0.019). Our study demonstrated that the measured soil quality indicators' magnitude, direction, and sensitivity varied depending on land use and soil type. Higher N availability in Vertisols increased the biological stability of soil organic carbon (SOC) resulting to decreased SOC mineralization than Acrisols. In conclusion, the measured microbial soil quality indicators showed that Acrisols are prone to accelerated SOC mineralization after disturbance than Vertisols in the studied semi-arid dryland ecosystems. Thus, there is a need to manage natural ecosystem conversions to support sustainable crop and pasture production in African drylands.

1. Introduction

In sub-Saharan Africa, dryland ecosystems cover approximately 41 % of total landmass and are characterized by low, erratic rainfall (300–600 mm per annum) [1]. In Kenya, arid and semi-arid drylands cover almost 90 % of the country's land mass and are home to nearly 30 % of its human population and hold approximately 70 % of the national livestock herd [2]. These dryland systems are continually undergoing massive land use changes, characterized predominantly by the

conversion of natural ecosystems for crop and animal production. Global estimates demonstrate that 35–50 % of mesic (semi-arid and dry sub-humid) drylands have been converted to cropland [3]. Subsequently, there is a general global concern that continued conversion of natural ecosystems for agricultural production could irreversibly change soil quality. This is because, agricultural intensification results to losses of soil organic matter (SOM) because of reduced input of organic matter (OM), increased decomposability of organic inputs and accelerated SOM biodegradation [4]. Considering that: (1) semi-arid regions cover more

* Corresponding author. Copernicus Institute of Sustainable Development, Utrecht University, the Netherlands.

E-mail address: k.z.mganga@uu.nl (K.Z. Mganga).

<https://doi.org/10.1016/j.ejsobi.2024.103626>

Received 24 January 2024; Received in revised form 6 May 2024; Accepted 11 May 2024

Available online 17 May 2024

1164-5563/© 2024 The Authors. Published by Elsevier Masson SAS. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

than one-third of total dryland area [5], (2) most dryland soils are relatively infertile and (3) dryland ecosystems are intrinsically fragile, it is important to investigate how microbial processes respond to land use changes and influence soil biogeochemical processes.

Soil microbial indices (microbial biomass C, microbial biomass C to organic C ratio ($C_{mic}:C_{org}$), metabolic quotient (qCO_2) and mineralization quotient (qM)) have been used as biological indicators of soil quality [6–9]. This is because they can be linked to key soil ecosystem functions e.g. nutrient cycling, land structure and stability, and soil microbial and plant biodiversity, thus can be used to detect and reveal changes in land use [10]. Soil microbial biomass has been defined as the ‘eye of a needle’ through which all SOM needs to pass [11]. It is often associated to diverse soil processes e.g. SOM decomposition, nutrient cycling, soil structuring, OM storage, thus has been identified as an important component for maintaining soil quality. Soil microbial quotient (SMQ), i.e. the ratio of soil microbial biomass to total organic carbon ($C_{mic}:C_{org}$) has been used as an indicator of how efficiently SOM is being used by microbes [12]. Thus, SMQ can be used as an early warning indicator of microbial status in ecosystems undergoing land use changes or environmental stresses. Metabolic quotient for CO_2 (qCO_2), i.e. the community respiration per unit biomass, is recognized as a relative measure of efficiency in utilization of available C in soil by microorganisms [13]. Microbial qCO_2 concept has proven to be a very useful soil microbial indicator that has stood the test of time for advancing conceptual understanding of the functioning of the soil microbial community and its contribution to ecosystem functioning [14]. Thus, qCO_2 can be considered as a valuable indicator for the microbial use of C for their energy consumption and microbial soil health [12]. Mineralization quotient (qM), which expresses the fraction of total organic C mineralized over a period of time [15], indicates the efficiency of microflora in metabolizing OM, thus a valuable indicator of SOM stability. To our knowledge, there are few studies that have investigated the impacts of land use systems and conversions on microbial indicators of soil quality, especially in African drylands. Hence, our understanding of how land use and land use changes affect microbial processes and ecosystem functions in drylands is limited. Quantifying these indicators can significantly contribute to informing land use and management strategies for soil conservation which is critical for sustaining livelihoods and society.

Thus, the objective of this study was to quantify the effect of land-use conversions from natural ecosystems to crop land occurring in two different soil types (Vertisol and Acrisol) on microbial indicators of soil quality: (1) microbial biomass C (2) $C_{mic}:C_{org}$ ratio, (3) metabolic quotient (qCO_2) and (4) mineralization quotient (qM). Soils were sampled from four different land use systems common in African drylands, namely: (1) cropland (agroecosystem), (2) reseeded pasture (agroecosystem), (3) shrubland (natural) and (4) grassland (natural). The southeastern semi-arid drylands in Kenya provide a unique opportunity to investigate the effects of agricultural expansion and land use change. This is because the most common land use systems in African drylands are well represented.

The selected soil types i.e. Vertisol and Acrisol, are also among the major soil types in the arid and semi-arid lands (ASALs) in Kenya [16]. Vertisols occupy 99 million hectares of Africa’s landmass located mainly in eastern Africa and around 5 % or 2.8 million hectares of Kenya’s landmass, occurring mainly in the arid and semi-arid drylands [17]. Acrisols are highly weathered and nutrient depleted and Vertisols are characterized by high clay content thus making them more resilient to soil degradation. Furthermore, land-use systems in the semi-arid ecosystems in Kenya have changed over time by expanding the area designated to agroecosystems at expense of native ecosystems [18]. Native vegetation has been converted not only to cropland but also to managed pasture agroecosystems. We hypothesize that: (1) conversion of natural systems to croplands and pastures will decrease microbial biomass C content, $C_{mic}:C_{org}$ ratio and accelerate SOM mineralization, because microbial growth depends on substrates and nutrients that

generally decrease with agricultural intensification and (2) the measured microbial indicators of soil quality will be more likely regulated by land use types than soil types, because plant roots, a main source of substrates for soil microbial growth vary with land use types.

2. Materials and methods

2.1. Study area, sampling and study site description

Soils were obtained from Kitui County (1.421017°S, 38.024145°E), a typical semi-arid environment in southeastern Kenya [19]. Rainfall pattern in the area is bimodal (March to May ‘long rains’ and October to December ‘short rains’) with annual average rainfall of 500–1000 mm per annum [20] and average annual temperature of 21 °C [21]. Characteristic high temperatures and close proximity to the equator result to high annual potential evaporation of 1500–1600 mm [22]. Well-drained, dark reddish brown to yellowish brown soils with sandy clay to clay textures support the various vegetation and land use classes [21]. Croplands are characterized by a high diversity of drought-tolerant varieties of cereals, legumes and root tubers e.g. maize, sorghum, millet, pigeon peas, cowpeas, mung beans, common beans, velvet beans and cassava.

Natural vegetation is a woodland savanna. Dominant native tree and shrub species include different Acacia species e.g. *Acacia tortilis* (Forsk) Hayne, *A. mellifera* (Vahl) Benth, *A. senegal* (L), *A. brevispica* Harms. Other common native species include *Commiphora africana* (A. Rich) Engl., *Adansonia digitata* Linn, *Tamarindus indica* L., *Grewia bicolor* Juss, *Croton megalocarpus* Hutch., *Balanites aegyptiaca* (L.) Del and *Zanthoxylum chalybeum* Engl. Herbaceous vegetation is dominated by perennial drought tolerant forage grasses such as *Cenchrus ciliaris* L, *Chloris roxburghiana* Schultz, *Panicum maximum* Jacq, *Eragrostis superba* Peyrs, *Digitaria milanijana* (Rendle) Stapf and *Enteropogon macrostachyus* Benth.

Soils from four land use systems: (1) cropland (2) reseeded pastures, (3) grassland and 4) shrubland, and two soil types: 1) Vertisol and 2) Acrisol (Table 1) were sampled at the upper 0–10 cm layer using a soil corer. These land use and soil types are commonly found in semi-arid African drylands. Three experimental plots of 50 m × 50 m approximately 1 km apart representing each land use and soil type were sampled. The three sites chosen per land use system and soil type were fair representations of the region. Soil was sampled from four corners and at the center of each plot, resulting to a total of five sampling positions. Four soil cores were taken per sampling position. This led to a total of 20 soil cores which were thoroughly mixed and aggregated to form a composite sample per plot. This translated to three samples (n = 3) for each land use system and soil type. A subset of soil samples obtained from a previous study [23] were used for this study.

2.2. Soil incubation and carbon-dioxide (CO_2) measurements

Freshly sampled soil (circa 20 g) was carefully transferred in 500 ml glass jars. Thereafter, the 500 ml glass jars were tightly closed with a rubber stopper and pre-incubated for 10 days. At the end of the pre-incubation period, the vessels were flushed with CO_2 -free air and incubated at 20 °C for 6 days in a darkened chamber and soil maintained at 60 % WHC. The short-term (6 days) incubation period was selected to enable us investigate treatment effects (i.e. land use changes) on SOC degradation and determine how much labile C is readily mineralizable under conditions similar to those experienced within the sampled soil depth [24,25].

During the incubation, CO_2 concentrations inside the bottles were measured using gas chromatography (Hewlett Packard 6890). Presented results are cumulative totals at the end of the 6 days incubation. After the gas sampling for CO_2 determination, soils were destructively sampled, and extracted for microbial biomass and mineral N concentration (see details below).

Table 1

Chemical properties of Vertisols and Acrisols under different land use in a typical semi-arid dryland in Kenya.

Land use	Soil type	pH	Available N ($\mu\text{g g}^{-1}$ soil)	Total organic C (mg C g^{-1} soil)	Total N (mg N g^{-1} soil)	Clay mg g^{-1} soil	Soil texture Silt mg g^{-1} soil	Sand mg g^{-1} soil
Cropland	Vertisol	6.32 \pm 0.01	6.82 \pm 0.3	14.1 \pm 2.3	0.9 \pm 0.05	172	554	274
	Acrisol	6.62 \pm 0.03	1.93 \pm 0.1	5.8 \pm 0.9	0.5 \pm 0.08	59	250	691
Pasture	Vertisol	6.81 \pm 0.01	26.06 \pm 0.9	14.5 \pm 0.8	1.4 \pm 0.09	74	243	683
	Acrisol	5.30 \pm 0.01	4.60 \pm 0.4	7.5 \pm 1.0	0.7 \pm 0.09	58	245	698
Grassland	Vertisol	7.69 \pm 0.01	6.96 \pm 0.1	15.3 \pm 0.3	1.3 \pm 0.03	79	308	613
	Acrisol	5.38 \pm 0.02	2.94 \pm 0.2	10.1 \pm 0.1	0.8 \pm 0.01	65	167	768
Shrubland	Vertisol	7.80 \pm 0.02	7.63 \pm 0.1	13.8 \pm 0.3	1.3 \pm 0.04	126	382	492
	Acrisol	6.60 \pm 0.02	7.96 \pm 1.1	7.4 \pm 0.3	0.7 \pm 0.02	47	145	808

Soil pH was determined in Milli-Q water (ratio of 1:2.5) using a pH meter (WTW InoLab pH Level 1 ba12217e). Available N (NH_4^+ and NO_3^-) were measured with an automated flow analyzer Lachat QuikChem 8000 (Zellweger Analytics, Milwaukee, Wisconsin, USA). Total organic carbon (TOC) and total nitrogen (TN) were measured using a varioMax CN Elemental Analyzer (Hanau, Germany). Particle size distribution (texture) of the soil was determined using air-dried samples (Coulter LS Series).

Displayed values represent arithmetic means of 3 replicates \pm standard error (SE). Table modified from Mganga et al. [23].

2.3. Soil physical and chemical analyses

Soil pH, total C and N analyses were determined using air dried soil (oven dried at 40 °C) samples. Soil pH was measured in Milli-Q water (ratio of 1:2.5) using a pH meter (WTW InoLab pH Level 1 ba12217e). Small portions of air-dried soil were manually grinded using a mortar and pestle and used for total C and N analyses. VarioMax CN Elemental Analyzer (Hanau, Germany) was used to measure total organic carbon (TOC) and total nitrogen (TN). For available soil N, approximately 5 g of fresh soil was extracted with 25 ml 1 M KCl, shaken for 30 min in an orbital shaker (200 oscillations min^{-1}) and filtered through SartoriusTM Grade 3-HW folded filters (diameter 150 mm) and stored frozen (-20 °C) before measuring with an automated flow analyzer Lachat QuikChem 8000 (Zellweger Analytics, Milwaukee, Wisconsin, USA).

2.4. Microbial parameters as indicators of soil quality

Microbial biomass C (MBC) was determined at the end of the 6-day incubation period using the chloroform fumigation-extraction (CFE) method [26]. Briefly, 3 g of fumigated and unfumigated field moist soil samples were extracted with 0.05 M K_2SO_4 at 1:10 ratio. Since not all the microbial C was extracted by the 0.05 M K_2SO_4 , k factor of 0.45 [27] was used to convert microbial C into MBC.

Soil metabolic quotient $q\text{CO}_2$ which is the specific soil respiration of the microbial biomass, was calculated from basal respiration values with the formula: $q\text{CO}_2 = [(\text{mg CO}_2\text{-C}/\text{mg C}_{\text{mic}} \text{ h}^{-1})]$ [28]. The mineralization quotient, $q\text{M}$, which represents the fraction of total organic C mineralized throughout the incubation period was calculated for each soil type from the measurements of the total C_{org} and the cumulative values (144 h) of CO_2 evolution, using the formula: $q\text{M} = [(\text{mg C-CO}_2/\text{mg C}_{\text{org}} \text{ h}^{-1})]$ [29]. Microbial quotient $\text{C}_{\text{mic}}:\text{C}_{\text{org}} = \text{mg of biomass C per mg total organic C ratio}$ has been used as a useful measure to monitor SOM and provide a more sensitive index than C_{org} measured alone [30].

Sensitivity index (SI) related to land use conversions (short-term, 8 years) i.e. grassland or shrubland to either cropland or pastures for the soil microbial parameters was calculated using Eq. (1) below modified from Liang et al. [31]:

$$\text{Sensitivity Index (SI)} = \frac{(\text{MI Disturbed} - \text{MI Natural})}{\text{MI Natural}} \times 100 \quad (1)$$

where MI Disturbed = Microbiological indicator for disturbed ecosystem (cropland land and pastures); MI Natural = Microbiological indicator for natural ecosystems (grassland and shrubland).

2.5. Statistical analysis

Residuals of the ANOVA model were tested for normality by

visualization and Shapiro-Wilk test, and for variance homogeneity with a Levene's test. Thereafter, the estimated microbial indicators of soil quality i.e. MBC, metabolic quotient ($q\text{CO}_2$), mineralization quotient ($q\text{M}$), $\text{C}_{\text{mic}}:\text{C}_{\text{org}}$ ratio, microbial soil respiration were analyzed using factorial ANOVA analysis (4 land use types and 2 soil types) to test for significant differences. Tukey's HSD post hoc test was used to separate significant differences between land uses and soil types at $P < 0.05$ significance level. The presented results are arithmetic means of 3 replicates \pm standard error (SE).

3. Results

3.1. Mineralization of soil organic matter

Differences in SOM mineralization rates depending on soil type were observed only in disturbed cropland and reseeded pastures, with Acrisols showing higher rates ($P < 0.05$, $F = 13.82$) compared to Vertisols. In both soil types under natural ecosystems, SOM mineralization was higher in grassland compared to shrubland. Cumulative CO_2 produced from native SOM mineralization at the end of the 6-day incubation period was highest and lowest in an Acrisol ($108 \pm 2.7 \mu\text{g CO}_2\text{-C g}^{-1}$ soil) and Vertisol ($53 \pm 2.5 \mu\text{g CO}_2\text{-C g}^{-1}$ soil) both under crop production systems, respectively (Fig. 1).

3.2. Microbial soil quality indicators

Natural ecosystems had higher ($P < 0.05$, $F = 17.64$) MBC compared to cultivated cropland and perennial pastures. Differences in MBC in the studied soils were only observed in the shrubland. Microbial biomass C in Vertisols from shrublands ($1.34 \pm 0.09 \text{ mg C g}^{-1}$ soil) was two-times higher than in shrubland Acrisols ($0.65 \pm 0.07 \text{ mg C g}^{-1}$). After the 6-days incubation period, the Vertisol shrubland ($1.34 \pm 0.09 \text{ mg C g}^{-1}$ soil) and Acrisol cropland ($0.26 \pm 0.07 \text{ mg C g}^{-1}$ soil), had the highest and lowest MBC, respectively (Fig. 2).

Mineralization quotient ($q\text{M}$) varied between soil type ($P < 0.05$, $F = 51.59$). In Vertisols, $q\text{M}$ was much higher in natural ecosystems (grassland and shrubland) compared to the disturbed cropland and established pastures. Conversely, in Acrisols, higher $q\text{M}$ were observed in cropland and established pastures compared to natural ecosystems. Mineralization quotients, $q\text{Ms}$, were consistently and higher in Acrisols compared to Vertisols across all the land use systems. Overall, the highest $q\text{M}$ was observed in a Acrisol cropland ($1.29 \mu\text{g CO}_2\text{-C g}^{-1} \text{ h}^{-1}$), which was approximately five times higher compared to the lowest $q\text{M}$ observed in a Vertisol cropland ($0.26 \mu\text{g CO}_2\text{-C g}^{-1} \text{ h}^{-1}$) (Fig. 2).

Similar to $q\text{M}$, the metabolic quotient ($q\text{CO}_2$) varied between land use and soil type ($P < 0.05$, $F = 8.44$). In both soil types, the $q\text{CO}_2$ was higher in agroecosystems (i.e. cropland and pastures), compared to the less disturbed natural ecosystems (grassland and shrubland). Similar to

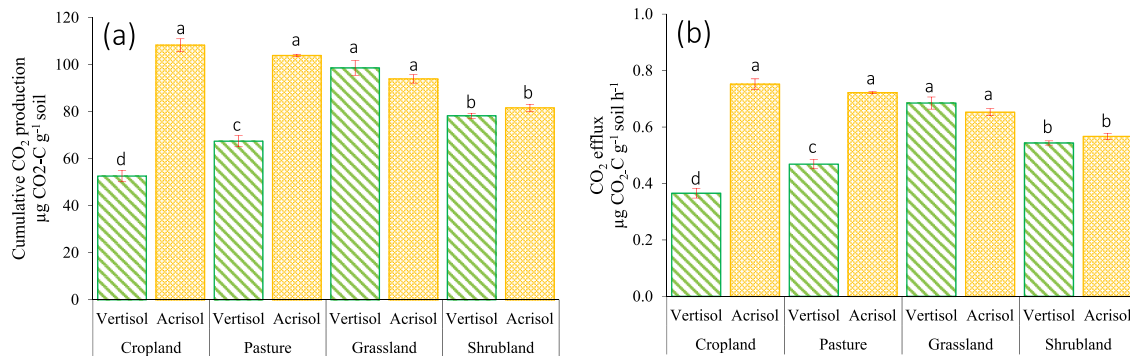


Fig. 1. (a) Cumulative CO₂ production and (b) CO₂ efflux depending on land use and soil types occurring in a typical African semi-arid environment. Values are given means \pm SE ($n = 3$). Error bars with different letters are significantly different ($P < 0.05$).

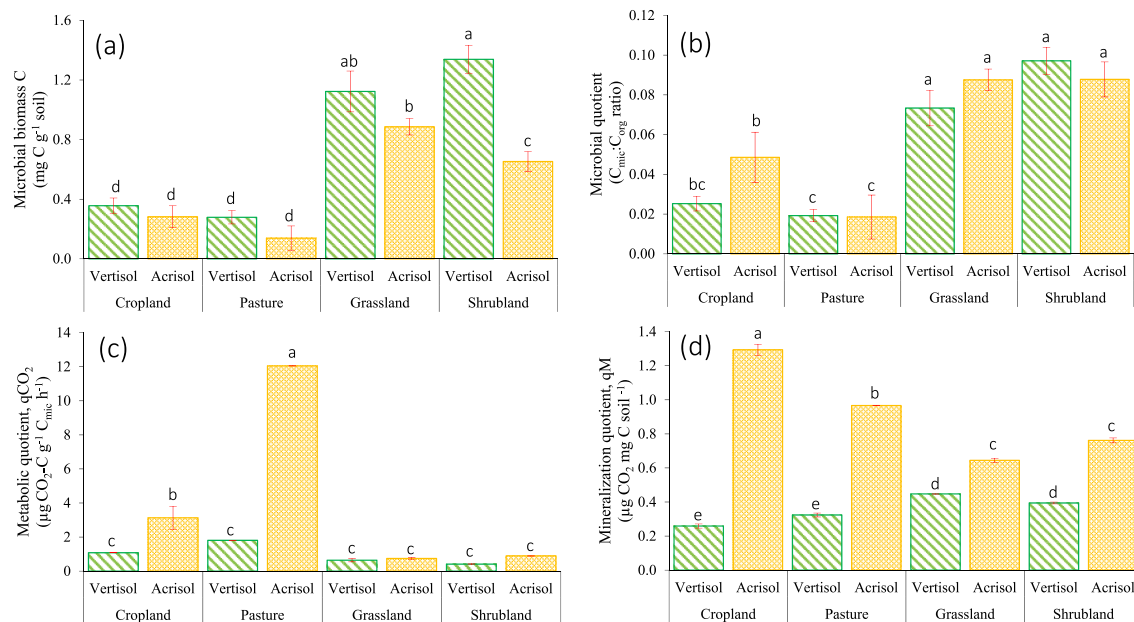


Fig. 2. Microbial indicators of soil quality: (a) microbial biomass C, (b) microbial quotient ($C_{\text{mic}}:C_{\text{org}}$ ratio), (c) metabolic quotient ($q\text{CO}_2$) and (d) mineralization quotient ($q\text{M}$) depending on land use and soil types occurring in a typical African semi-arid environment. Values are given means \pm SE ($n = 3$). Error bars with different letters are significantly different ($P < 0.05$).

the observed trend in $q\text{M}$, the $q\text{CO}_2$ values, were also consistently higher in Acrisols compared to Vertisols across all the land use systems. The highest $q\text{CO}_2$ was observed in a pasture established on an Acrisol ($12.04 \mu\text{g CO}_2\text{-C g}^{-1}\text{ C}_{\text{mic}}\text{ h}^{-1}$), which was approximately 30-times higher compared to the lowest $q\text{CO}_2$ observed in a Vertisol shrubland ($0.41 \mu\text{g CO}_2\text{-C g}^{-1}\text{ C}_{\text{mic}}\text{ h}^{-1}$) (Fig. 2).

Ratio of MBC and total organic C ($C_{\text{mic}}:C_{\text{org}}$) was higher ($P < 0.05$, $F = 26.33$) in natural ecosystems compared to agroecosystems in both soil types. Large difference in $C_{\text{mic}}:C_{\text{org}}$ between the soil types was only observed in cropland, where Acrisol had a ratio of 0.05 compared to 0.03 observed in a Vertisol. All the other land use systems had comparable $C_{\text{mic}}:C_{\text{org}}$ ratios. Overall, the highest $C_{\text{mic}}:C_{\text{org}}$ ratio was observed in a Vertisol shrubland (0.097), which was approximately five times higher compared to the lowest $C_{\text{mic}}:C_{\text{org}}$ ratio observed in a Acrisol pastureland (0.019) (Fig. 2).

3.3. Sensitivity of soil microbial indicators

Calculated SI parameters demonstrated that $q\text{CO}_2$ was the most sensitive microbial indicator of conversion from natural to disturbed

ecosystems in both soil types (Fig. 3). Additionally, its sensitivity to change was more pronounced when the natural ecosystems (grassland and bushland) were converted to pastures than cropland (Fig. 3). Sensitivity to land conversions were also influenced by soil type. Our SI of $q\text{CO}_2$ results (Fig. 3) strongly suggest that Acrisols were generally more sensitive to similar land use changes and conversions compared to Vertisols. On average, sensitivity to change of the estimated microbial indices was more pronounced in natural ecosystems conversions to established pastures compared to cropland (Fig. 3).

4. Discussion

4.1. Mineralization of soil organic matter

Higher CO₂ effluxes from native SOM mineralization in natural compared to agricultural systems under Vertisols can be attributed to MBC content. Soil organic matter mineralization is a microbial-mediated process, thus its rate is partly regulated by microbial abundance [32,33]. Carbon introduced in soil as microbial biomass is distributed in three pathways: 1) incorporation into other microorganisms, 2) stabilization

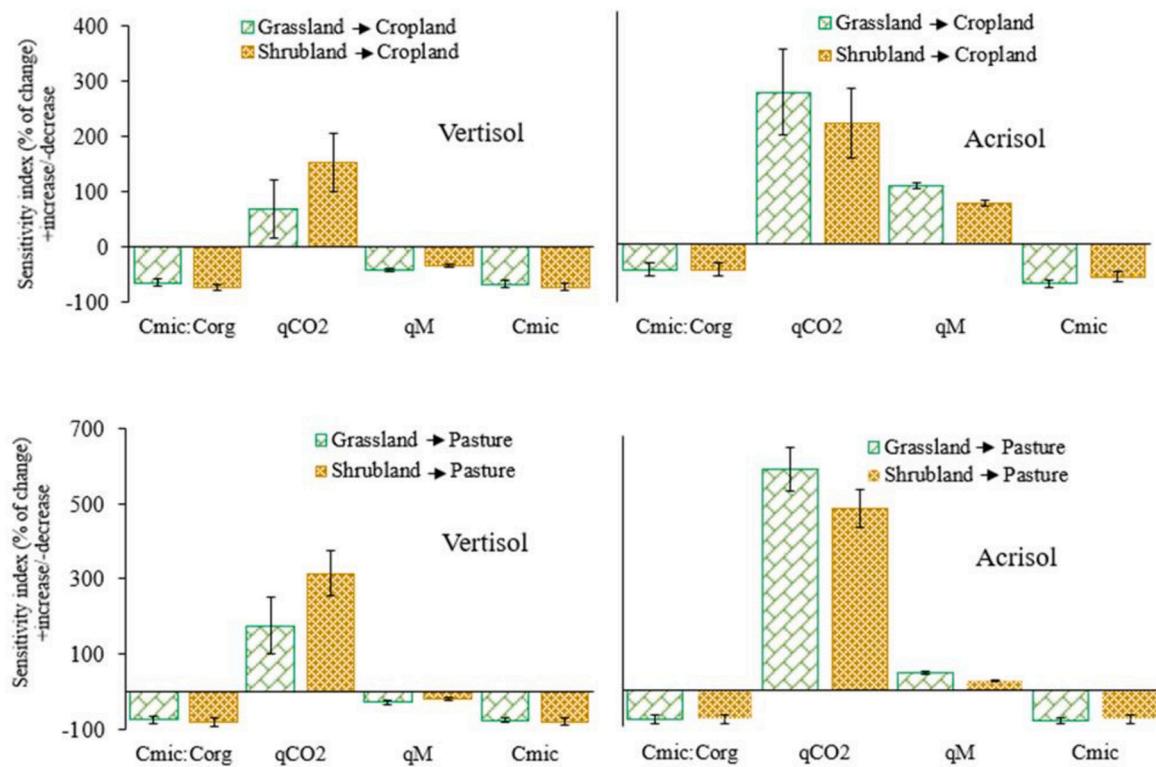


Fig. 3. Sensitivity indices of bioindicators of soil quality: Microbial quotient (Cmic:Corg ratio), metabolic quotient (qCO_2), mineralization quotient (qM) and microbial biomass C (Cmic) depending on land use change from natural (grassland and shrubland) to agroecosystems (agricultural cropland and pasture). Error bars represent the standard error (SE) of means.

in non-living SOM and 3) degradation [34]. Consequently, higher CO_2 production in natural compared to agricultural systems in Vertisols suggests a higher turnover of microbial biomass. Considering that microbial biomass turnover is much faster than plant residues, microbe-derived C input to SOM mineralization could have been significant in Vertisols. In some soils, more than 50 % of the extractable humic substance fraction originates from intact and degraded microbial biomass [35]. Conversely, low CO_2 production in agroecosystems under Vertisols strongly suggest that residual C is more stabilized by minerals and less prone to microbial degradation.

Conversely, in Acrisols, agroecosystems characterized by lower MBC produced higher CO_2 effluxes. These results show that higher microbial biomass does not necessarily lead to higher SOM degradation. Low SOM mineralization in natural ecosystems in Acrisols could be indicative of: 1) microorganisms that are metabolically less active, 2) decline in microbial turnover rates and 3) a microbial community dominated by microorganisms with higher C use efficiency or 4) a low C accessibility. Although we did not measure the microbial community structure, it is plausible that less disturbance in natural ecosystems under Acrisols might have contributed to the build-up and dominance of fungal biomass, leading to lower SOM mineralization [36]. Previous studies have demonstrated that agricultural tillage practices, favors bacterial growth with lower C use efficiency and transformation of organic C into microbial biomass, while less disturbance favors fungal growth with higher C use efficiency and less C loss [37,38]. Our results compare well with other studies that have also reported higher SOM mineralization in cropland soils compared to less disturbed natural ecosystems (e.g. Ref. [39]).

High CO_2 effluxes from SOM mineralization observed in more sandy Acrisols under crop production is linked to several factors and mechanisms. Litter quality in croplands is usually more labile and less stabilized. This makes it easily decomposable by microbes resulting to higher CO_2 efflux per soil C content compared to natural ecosystems dominated

by recalcitrant litter. Moreover, low N availability stimulated microbes to mine SOM in search of nutrients for growth [40]. Also, high CO_2 produced could also be a result of mineralization of microbial necromass [41] especially in African drylands where croplands are left bare after harvest. During periods of severe and prolonged droughts, the microbial population dies and is readily mineralized when soil is rewetted at the onset of the rains. Consequently, comparable outcomes are expected during short soil incubations after rewetting. Lastly, is the nutrient bank mechanism [33]. It stipulates that microbial mining is stimulated when N availability is limited, inducing soil nutrients release [23,40]. Our results compare well with other studies that have also demonstrated higher SOM mineralization in soils with low N availability [42,43]. Higher SOM mineralization in soils with low N availability strongly suggest that microbial dependence on native SOM as a C source can be reduced when N availability is increased, because additional N is needed to satisfy the microorganisms demand for N.

Conversely, Vertisols, especially in cropland, displayed the least CO_2 production. This can be attributed to the higher proportion of fine textured soil fraction compared to the other soils. Soil organic matter molecules can be adsorbed by clay minerals via cation exchange for positively charged organic compounds, hydrophobic bonding (neutral molecules) to pre-existing organic coatings of the minerals and polyvalent cation bridges (organic anions) [41]. Strong adsorption of SOM to minerals protects OM from biodegradation by soil microorganisms. This could have improved soil aggregation and physical structure leading to reduced mineralization. Furthermore, SOM can also be enclosed in micropores that are inaccessible to microorganisms. Extracellular enzymes are sorbed by clays and cannot reach substrates in the micropores. Consequently, clay minerals with high porosities and proportions of finer pores are very effective stabilizers and SOM decomposition determined as CO_2 losses are reduced. Our results conform to previous studies demonstrating that protection of SOM by clays results to low CO_2 production [8,39,44].

4.2. Microbial soil quality indicators

Higher MBC content in natural ecosystems compared to agricultural systems is attributed to differences in intensity of use (soil disturbance) and organic C inputs (roots inputs and litter accumulation). Our results align well with previous studies that have investigated effect of land use on MBC in similar African environments [7,45]. We attribute the lower MBC content in agricultural soils to traditional ox-plough tillage practice and dryland cropping system characterized by repeated clean-till and less residues incorporation in the soil. Consequently, low soil MBC observed due to ox-driven ploughing and barren fallow periods demonstrate that this cropping system might not be sustainable in African drylands.

Minimal soil disturbance, plant litter accumulation and continuous organic C inputs from roots in biodiversity rich natural ecosystems provides a set of substrates of different quality for microbial metabolism. This induces higher soil microbial biomass content. Moreover, accumulation of plant litter increases microbial abundance because of suitable micro-climatic conditions (higher soil moisture and lower temperatures) for growth and reproduction [46]. Continuous plant litter addition from perennial natural vegetation ensures a constant supply of fresh, non-humified fractions from residue accumulation than more humified C from older crop residues buried belowground from previous growing season. Rate of organic C input (root exudates and rhizodeposits) is considered a dominant factor controlling microbial biomass content in soil. Consequently, as total organic C pool expands or contracts due to changes in C inputs, soil microbial pool also expands or contracts. Continuous supply of C from largely perennial vegetation inputs in natural ecosystems serve as an energy source for microbes, stimulating higher MBC. It is plausible also that higher MBC in natural ecosystems is due to the abundance of dormant microbial cells.

Land use had a larger impact on MBC content than soil type in this study. However, Vertisols consistently displayed higher MBC compared to Acrisols, but was only much higher in shrubland. Clay rich soils have higher MBC and microbial activities, compared to coarser texture soils. This is due to reduced fluctuation in soil water content or protection of microorganisms from faunal grazing [47]. Fine-textured soils similar to Vertisols hold more C, N and water. These conditions increase plant growth and microbial biomass and activity than coarse-textured soils. Higher proportion of sand compared to clay and silt in Acrisols means that the SOM is degraded more rapidly leaving the microbial biomass 'starved'. Other studies have also found higher proportions of soil C in the microbial biomass in fine-textured than coarse-textured grassland soils and dry tropical agroecosystems [8,48]. Furthermore, the highest microbial biomass content in this study corresponded with soil pH values greater than 7 (Fig. S1). These results strongly suggest that soil pH near 7.0 is most suitable for microbial biomass accumulation. In their study, Pietri and Brookes [49], also found the highest MBC concentrations in agricultural soils with pH greater than 7. The weak alkaline conditions provide favorable conditions to support plant growth that contributes to increased inputs of plant-derived organic substrates (e.g. roots, root exudates) to support a large microbial population. Consequently, our findings conform to previous work that have demonstrated that differences in soil pH within a single soil type and between soil types can have marked effects upon MBC. Likewise, this current study supports the hypothesis that organic C, texture, pH are key soil properties that affect soil MBC concentration.

Higher $C_{mic}:C_{org}$ ratios observed in natural compared to agricultural systems demonstrate that intensive cultivation in croplands decimated the microbial community. Furthermore, this result show that natural ecosystems are more stable and microbes use available organic substrates for growth. This can be attributed to higher litter diversity and substrate availability in soils under natural vegetation. Similarly, higher crop and litter diversity in the croplands under cereal and legume crops mixtures than pasture monocultures led to higher $C_{mic}:C_{org}$ ratios in cropland than established pastures. Decrease in $C_{mic}:C_{org}$ ratio due to

land use changes from natural to intensive agricultural systems has been observed in other studies [6,45,50]. This can be attributed to a decline in available substrate due to enhanced land-use intensity. Comparable $C_{mic}:C_{org}$ ratios in the studied soils under the same land use system demonstrate the limited effect of soil type in a typical African semi-arid dryland. Microbial quotients ($C_{mic}:C_{org}$ ratio) of the studied soils were comparable under similar land use type. This shows that microbial quotient can be used as an indicator for the intensity of management in dryland systems in Africa irrespective of the soil type.

Unlike $C_{mic}:C_{org}$ ratios, qM varied between soil types and was much higher in Acrisols compared to Vertisols in all land use systems. This can be attributed to differences in clay content. Higher qM has also been observed in soils from semi-arid drylands with higher proportion of sand (loamy sand) compared to clay (clay loam) particles [51]. Higher qM indicates soil microbes efficiency in metabolizing SOM. In Vertisols, natural ecosystems displayed higher qM compared to disturbed cropping systems. In their study, Francaviglia et al. [52] also observed much higher qM in natural than agricultural systems. Conversely, in Acrisols, disturbed soils under crop production had higher qM values than natural ecosystems. Higher qM values have also been observed in agroecosystems (maize fields and *Chagga* homegardens) compared to natural (savannah grassland and lower montane forest) soils in Africa [7]. These findings strongly suggest that in the studied semi-arid dryland, Acrisols are more fragile and prone to produce more CO_2 after disturbance compared to Vertisols. Our results show that qM depicted opposite trends in the studied soil types. This could be indicative that qM might not be a good universal soil quality indicator in different soils where litter quality and strength of mineral stabilization are affecting the results in different directions.

Similar to qM , qCO_2 values were higher in Acrisols than Vertisols in the studied land use systems. High qCO_2 in Acrisol is an indication of the inefficiency in C use. When the microflora is less efficient, a larger proportion of metabolized C is lost as CO_2 through respiration as opposed to support growth. Moreover, higher clay content in Vertisols compared to Acrisols also resulted to a reduction in qCO_2 . Physical protection is known as a primary mechanism for C sequestration. Labile C is less accessible to microorganisms in clayey soils than in more sandy or loam soils. This could partly explain the comparable qCO_2 in the studied land use types in Vertisols. However, in Acrisols, agroecosystems displayed higher qCO_2 values than natural ecosystems, demonstrating their higher sensitivity to land use change than Vertisols. These findings are coherent with previous studies reporting higher qCO_2 in intensively cultivated agricultural systems compared to natural systems [6,7,53]. Our results show that the ratio of CO_2 efflux to C_{mic} is a sensitive indicator of land use changes and disturbance. However, the magnitude and direction of land use changes that soil microorganisms are exposed to are regulated by inherent soil properties.

4.3. Sensitivity of soil microbial indicators

Higher magnitude of change (i.e. sensitivity indices) of qCO_2 demonstrates its greatest sensitivity to alternative land use systems compared to the other soil microbial indicators ($C_{mic}:C_{org}$ ratio, qM and C_{mic}). Our results concur with previous studies demonstrating high sensitivity of qCO_2 to alternative land use systems (e.g. Ref. [9,54]). The magnitude of sensitivity of microbial indicators to alternative land uses is also closely associated with the prevailing environmental and soil factors [55]. This hypothesis can be supported by the fact that Acrisols demonstrated higher sensitivity to alternative land use systems compared to Vertisols. Higher sensitivity of land use changes observed in Acrisols compared to Vertisol can mainly be attributed to the differences in clay content. Higher clay content in Vertisols compared to Acrisols increased its resilience and resistance to disturbance exemplified by much lower sensitivity indices. Our results are comparable to previous studies in drylands that have demonstrated different land use systems (e.g. crop production, livestock grazing) have less impact on soil

quality indices of Vertisols characterized by a combination of high resistance and/or resilience [56–58].

Conversion of natural systems for native pasture production resulted to a higher magnitude of positive increase in qCO_2 than intensive crop production. These results seem to contradict those obtained from other studies demonstrating that pasture cultivation is a more sustainable land use in tropical agroecosystems (e.g. Ref. [59,60]). This is because established deep-rooted tropical pastures tend to enhance microbial soil quality by improving the size and stability of soil aggregates and ensuring a continuous vegetation cover compared to soils under continuous crop production, which are often left bare during the fallow period [7]. Our results suggest that even though perennial grasses can play a major role in long-term C-sequestration, converting natural systems for pasture establishment can actually increase CO_2 emissions in the short-term compared to cropland. This underscores the significance of managing recently established native pastures to minimize accelerated CO_2 emissions to enhance their potential for C-sequestration.

5. Conclusions

Conversion of natural ecosystems for agricultural production decreased MBC and microbial quotient in both soils but accelerated qM only in Acrisols. This partially aligns to our hypothesis and suggests that the measured microbial indicators of soil quality were regulated by both land use and soil type. Higher sensitivity of microbial indices due to land use changes, in Acrisols compared to Vertisols, demonstrate that Vertisols are more resilient to alternative land use systems. Metabolic quotient was the most sensitive microbial indicator of land use changes in both soils. Furthermore, conversion of natural African drylands ecosystems for native pasture production, accelerated soil degradation compared to cropland. Thus, integrating deep-rooted perennial grasses in cropland i.e. pasture-cropping system could be a viable option to ensure sustainable use of these dryland soils for crop and pasture production. Microbial soil quality indicators are robust and reliable measurements to quantify and evaluate the effect of land use changes in African drylands. Considering that soil type also regulate the magnitude and direction of changes in soil quality, there is need to align specific land use conversions to inherent site characteristics to ensure sustainable use and management of African dryland systems.

CRedit authorship contribution statement

Kevin Z. Mganga: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **José Rolando:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Subin Kalu:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis. **Kristiina Karhu:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition.

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.

Acknowledgements and funding

This research was supported by funds from the Academy of Finland (AKA) (Grant number 316401) and Helsinki Institute of Life Science (HiLIFE) Fellow funding for K.K. The authors sincerely thank Marjut Wallner for help with C and N analysis.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ejsobi.2024.103626>.

References

- [1] K. Vohland, B. Barry, A review of *in situ* rainwater harvesting (RWH) practices modifying landscape functions in African drylands, *Agric. Ecosyst. Environ.* 131 (2009) 119–127, <https://doi.org/10.1016/j.agee.2009.01.010>.
- [2] D.A. Amwata, D.M. Nyariki, N.K.R. Musimba, Factors influencing pastoral and agropastoral household vulnerability to food insecurity in the drylands of Kenya: a case study of Kajiado and Makueni counties, *J. Int. Dev.* 28 (2016) 771–787, <https://doi.org/10.1002/jid.3123>.
- [3] B.T. Bestelmeyer, G.S. Okin, M.C. Duniway, S.R. Archer, N.F. Sayre, J. C. Williamson, J.E. Herrick, *Front. Ecol. Environ.* 13 (2015) 28–36, <https://doi.org/10.1890/140162>.
- [4] A. Lagomarsino, A. Benedetti, S. Marinari, L. Pompili, M.C. Moscatelli, P. Roggero, R. Lai, L. Ledda, S. Grego, Soil organic C variability and microbial functions in a Mediterranean agro-forest ecosystem, *Biol. Fertil. Soils* 47 (2011) 283–291, <https://doi.org/10.1007/s00374-010-0530-4>.
- [5] J. Huang, H. Yu, X. Guan, G. Wang, R. Guo, Accelerated dryland expansion under climate change, *Nat. Clim. Change* 6 (2016) 166–171, <https://doi.org/10.1038/nclimate2837>.
- [6] H. Pabst, F. Gerschlaue, R. Kiese, Y. Kuzyakov, Land use and precipitation affect organic and microbial carbon stocks and the specific metabolic quotient in soils of eleven ecosystems of Mt. Kilimanjaro, Tanzania, *Land Degrad. Dev.* 27 (2016) 592–602, <https://doi.org/10.1002/ldr.2406>.
- [7] K.Z. Mganga, B.S. Razavi, Y. Kuzyakov, Land use affects soil biochemical properties in Mt. Kilimanjaro region, *Catena* 141 (2016) 22–29, <https://doi.org/10.1016/j.catena.2016.02.013>.
- [8] S. Sugihara, S. Funakawa, M. Kilasara, T. Kosaki, Effect of land management and soil texture on seasonal variations in soil microbial biomass in dry tropical agroecosystems in Tanzania, *Appl. Soil Ecol.* 44 (2010) 80–88, <https://doi.org/10.1016/j.apsoil.2009.10.003>.
- [9] T. Yan, L. Yang, C.D. Campbell, Microbial biomass and metabolic quotient of soils under different land use in the Three Gorges Reservoir area, *Geoderma* 115 (2003) 129–138, [https://doi.org/10.1016/S0016-7061\(03\)00082-X](https://doi.org/10.1016/S0016-7061(03)00082-X).
- [10] M. Muñoz-Rojas, Soil quality indicators: critical tools in ecosystem restoration, *Curr. Opin. Environ. Sci. Health* 5 (2018) 47–52, <https://doi.org/10.1016/j.coesh.2018.04.007>.
- [11] R. Lal, Carbon farming by recarbonization of agroecosystems, *Pedosphere* 33 (2023) 676–679, <https://doi.org/10.1016/j.pedsph.2023.07.024>.
- [12] M.N. Ashraf, M.A. Waqas, S. Rahman, Microbial metabolic quotient is a dynamic indicator of soil health: trends, implications and perspectives, *Eurasian Soil Sci.* 55 (2022) 1794–1803, <https://doi.org/10.1134/S1064229322700119> (Review).
- [13] E. Blagodatskaya, Y. Kuzyakov, Active microorganisms in soil: critical review of estimation criteria and approaches, *Soil Biol. Biochem.* 67 (2013) 192–211, <https://doi.org/10.1016/j.soilbio.2013.08.024>.
- [14] D.A. Wardle, A. Ghani, A tale of two theories, a chronosequence and a bioindicator of soil quality, *Soil Biol. Biochem.* 121 (2018) A3–A7, <https://doi.org/10.1016/j.soilbio.2018.01.005>.
- [15] R. Saikia, S. Sharma, H.S. Thind, Y. Singh, Tillage and residue management practices affect soil biological indicators in a rice–wheat cropping system in north-western India, *Soil Use Manag.* 36 (2020) 157–172, <https://doi.org/10.1111/sum.12544>.
- [16] J.K. Itabari, K. Kweni, A.O. Esilaba, A.N. Kathuku, L. Muhammad, N. Mangale, P. Kathuli, Land and water management research and development in arid and semi-arid lands of Kenya, in: A. Bationo, B. Waswa, J. Okeyo, F. Maina, J. Kihara (Eds.), *Innovations as Key to the Green Revolution in Africa*, Springer, Dordrecht, 2011, https://doi.org/10.1007/978-90-481-2543-2_44.
- [17] E. Ikito, J. Okalebo, C. Othieno, Towards sustainable land use in Vertisols in Kenya: challenges and opportunities, in: A. Bationo, B. Waswa, J. Okeyo, F. Maina, J. Kihara (Eds.), *Innovations as Key to the Green Revolution in Africa*, Springer, Dordrecht, 2011, https://doi.org/10.1007/978-90-481-2543-2_67.
- [18] K.Z. Mganga, B.S. Razavi, Y. Kuzyakov, Microbial and enzymes response to nutrient additions in soils of Mt. Kilimanjaro region depending on land use, *Eur. J. Soil Biol.* 69 (2015) 33–40, <https://doi.org/10.1016/j.ejsobi.2015.05.001>.
- [19] C.B. Schmitt, D. Kisangau, K.W. Matheka, Tree diversity in a human modified riparian forest landscape in semi-arid Kenya, *For. Ecol. Manage.* 433 (2019) 645–655, <https://doi.org/10.1016/j.foreco.2018.11.030>.
- [20] E.W. Mugi-Ngenga, M.N. Kiboi, M.W. Mucheru-Muna, J.N. Mugwe, F.S. Mairura, D.N. Mugendi, F.K. Ngetich, Indigenous and conventional climate-knowledge for enhanced farmers' adaptation to climate variability in the semi-arid agro-ecologies of Kenya, *Environ. Chall.* 5 (2021) 100355, <https://doi.org/10.1016/j.envc.2021.100355>.
- [21] I. Hayashi, Five years experiment on vegetation recovery of drought deciduous woodland in Kitui, Kenya, *J. Arid Environ.* 34 (1996) 351–361, <https://doi.org/10.1006/jare.1996.0115>.
- [22] R. Lasage, J. Aerts, G.C.M. Mutiso, A. de Vries, Potential for community based adaptation to droughts: sand dams in Kitui, Kenya, *Phys. Chem. Earth* 33 (2008) 67–73, <https://doi.org/10.1016/j.pce.2007.04.009>.

- [23] K.Z. Mganga, J.L. Rolando, S. Kalu, C. Biasi, K. Karhu, Priming effect depending on land use and soil types in a typical semi-arid landscape in Kenya, *Biogeochemistry* 163 (2023) 49–63, <https://doi.org/10.1007/s10533-023-01016-z>.
- [24] X. Guan, J. Jiang, X. Jing, W. Feng, Z. Luo, Y. Wang, X. Xu, Y. Luo, Optimizing duration of incubation experiments for understanding soil carbon decomposition, *Geoderma* 428 (2022) 116225, <https://doi.org/10.1016/j.geoderma.2022.116225>.
- [25] C. Schädel, J. Beem-Miller, M. Aziz Rad, S.E. Crow, C.E. Hicks Pries, J. Ernakovich, A.M. Hoyt, A. Plante, S. Stoner, C.C. Treat, C.A. Sierra, Decomposability of soil organic matter over time: the Soil Incubation Database (SIDb, version 1.0) and guidance for incubation procedures, *Earth Syst. Sci. Data* 12 (2020) 1511–1524, <https://doi.org/10.5194/essd-12-1511-2020>.
- [26] E.D. Vance, P.C. Brookes, D.S. Jenkinson, An extraction method for measuring soil microbial biomass C, *Soil Biol. Biochem.* 19 (1987) 703–707, [https://doi.org/10.1016/0038-0717\(87\)90052-6](https://doi.org/10.1016/0038-0717(87)90052-6).
- [27] R.G. Jørgensen, The fumigation-extraction method to estimate soil microbial biomass: calibration of the kEC value, *Soil Biol. Biochem.* 28 (1996) 25–31, [https://doi.org/10.1016/0038-0717\(95\)00102-6](https://doi.org/10.1016/0038-0717(95)00102-6).
- [28] T.H. Anderson, K.H. Domsch, Carbon assimilation and microbial activity in soil, *J. Plant Nutr. Soil Sci.* 149 (1986) 457–468, <https://doi.org/10.1002/jpln.19861490409>.
- [29] F. Pinzari, A. Trinchera, A. Benedetti, P. Sequi, Use of biochemical indices in the Mediterranean environment: comparison among soils under different forest vegetation, *J. Microbiol. Methods* 36 (1999) 21–28, [https://doi.org/10.1016/S0167-7012\(99\)00007-X](https://doi.org/10.1016/S0167-7012(99)00007-X).
- [30] T.H. Anderson, K.H. Domsch, Ratios of microbial biomass carbon to total organic carbon in arable soils, *Soil Biol. Biochem.* 21 (1989) 471–479, [https://doi.org/10.1016/0038-0717\(89\)90117-X](https://doi.org/10.1016/0038-0717(89)90117-X).
- [31] Q. Liang, H. Chen, Y. Gong, M. Fan, H. Yang, R. Lal, Y. Kuzyakov, Effects of 15 years of manure and inorganic fertilizers on soil organic carbon fractions in a wheat-maize system in the North China plain, *Nutrient Cycl. Agroecosyst.* 92 (2012) 21–33, <https://doi.org/10.1007/s10705-011-9469-6>.
- [32] K. Ekschmitt, M. Liu, S. Vetter, O. Fox, V. Wolter, Strategies used by soil biota to overcome soil organic matter stability – why is dead organic matter left over in the soil? *Geoderma* 128 (2005) 167–176, <https://doi.org/10.1016/j.geoderma.2004.12.024>.
- [33] S. Fontaine, S. Barot, Size and functional diversity of microbe populations control plant persistence and long-term soil carbon accumulation, *Ecol. Lett.* 8 (2005) 1075–1087, <https://doi.org/10.1111/j.1461-0248.2005.00813.x>.
- [34] A. Miltner, P. Bombach, B. Schmidt-Brücken, M. Kästner, SOM genesis: microbial biomass as a significant source, *Biogeochemistry* 111 (2012) 41–55, <https://doi.org/10.1007/s10533-011-9658-z>.
- [35] A.J. Simpson, M.J. Simpson, E. Smith, B.P. Kelleher, Microbially derived inputs to soil organic matter: are current estimates too low? *Environ. Sci. Technol.* 41 (2007) 8070–8076, <https://doi.org/10.1021/es071217x>.
- [36] J. Rousk, S.D. Frey, Revisiting the hypothesis that fungal-to-bacterial dominance characterizes turnover of soil organic matter and nutrients, *Ecol. Monogr.* 85 (2015) 457–472, <https://doi.org/10.1890/14-1796.1>.
- [37] V. Kabiri, F. Raiesi, M.A. Ghazavi, Tillage effects on soil microbial biomass, SOM mineralization and enzyme activity in a semi-arid Calceixerepts, *Agric. Ecosyst. Environ.* 232 (2016) 73–84, <https://doi.org/10.1016/j.agee.2016.07.022>.
- [38] B. Zhang, H. He, X. Ding, X. Zhang, X. Zhang, X. Yang, T.R. Filley, Soil microbial community dynamics over a maize (*Zea mays* L.) growing season under conventional and no-tillage practices in a rainfed agroecosystem, *Soil Tillage Res.* 124 (2012) 153–160, <https://doi.org/10.1016/j.still.2012.05.011>.
- [39] J. Six, R.T. Conant, E.A. Paul, K. Paustian, Stabilization mechanisms of soil organic matter: implications for C-saturation of soils, *Plant Soil* 241 (2002) 155–176, <https://doi.org/10.1023/A:1016125726789>.
- [40] B. Dimassi, B. Mary, S. Fontaine, N. Perveen, S. Revaillot, J.-P. Cohan, Effect of nutrients availability and long-term tillage on priming effect and soil C mineralization, *Soil Biol. Biochem.* 78 (2014) 332–339, <https://doi.org/10.1016/j.soilbio.2014.07.016>.
- [41] W. Zech, N. Senesi, G. Guggenberger, K. Kaiser, J. Lehmann, T.M. Miano, A. Miltner, G. Schroth, Factors controlling humification and mineralization of soil organic matter in the tropics, *Geoderma* 79 (1997) 117–161, [https://doi.org/10.1016/S0016-7061\(97\)00040-2](https://doi.org/10.1016/S0016-7061(97)00040-2).
- [42] L.-J. Li, X. Zhu-Barker, R. Ye, T.A. Doane, W.R. Horwath, Soil microbial biomass and soil carbon influence the priming effect from carbon inputs depending on nitrogen availability, *Soil Biol. Biochem.* 119 (2018) 41–49, <https://doi.org/10.1016/j.soilbio.2018.01.003>.
- [43] J.M. Craine, C. Morrow, N. Fierer, Microbial nitrogen limitation increases decomposition, *Ecology* 88 (2007) 2105–2113, <https://doi.org/10.1890/06-1847.1>.
- [44] J.M. Cable, K. Ogle, D.G. Williams, J.F. Weltzin, T.E. Huxman, Soil texture drives responses of soil respiration to precipitation pulses in the Sonoran desert: implications for climate change, *Ecosystems* 11 (2008) 961–979, <https://doi.org/10.1007/s10021-008-9172-x>.
- [45] H. Pabst, A. Kühnel, Y. Kuzyakov, Effect of land use and elevation on microbial biomass and water extractable carbon in soils of Mt. Kilimanjaro ecosystems, *Appl. Soil Ecol.* 67 (2013) 10–19, <https://doi.org/10.1016/j.apsoil.2013.02.006>.
- [46] B. Govaerts, M. Mezzalama, Y. Unno, K.D. Sayre, M. Luna-Guido, K. Vanherck, L. Dendooven, J. Deckers, Influence of tillage, residue management and crop rotation on soil microbial biomass and catabolic diversity, *Appl. Soil Ecol.* 37 (2007) 18–30, <https://doi.org/10.1016/j.apsoil.2007.03.006>.
- [47] M. von Lütow, J. Leifeld, M. Kainz, I. Kögel-Knabner, J.C. Munch, Indications for soil organic matter quality in soils under different management, *Geoderma* 105 (2002) 243–258, [https://doi.org/10.1016/S0016-7061\(01\)00106-9](https://doi.org/10.1016/S0016-7061(01)00106-9).
- [48] J. Hassink, Effect of soil texture on the size of the microbial biomass and on the amount of C and N mineralized per unit of microbial biomass in Dutch grassland soils, *Soil Biol. Biochem.* 26 (1994) 1573–1581, [https://doi.org/10.1016/0038-0717\(94\)90100-7](https://doi.org/10.1016/0038-0717(94)90100-7).
- [49] J.C.A. Pietri, P.C. Brookes, Relationships between soil pH and microbial properties in a UK arable soil, *Soil Biol. Biochem.* 40 (2008) 1856–1861, <https://doi.org/10.1016/j.soilbio.2008.03.020>.
- [50] S.A. Blagodatskii, I.N. Bogomolova, E.V. Blagodatskaya, Microbial biomass and growth kinetics of microorganisms in Chernozem soils under different land use modes, *Microbiology* 77 (2008) 99–106, <https://doi.org/10.1134/S0026261708010141>.
- [51] N. Yazdanpanah, M. Mahmoodabadi, A. Cerdà, The impact of organic amendments on soil hydrology, structure and microbial respiration in semiarid lands, *Geoderma* 266 (2017) 58–65, <https://doi.org/10.1016/j.geoderma.2015.11.032>.
- [52] R. Francaviglia, G. Renzi, L. Ledda, A. Benedetti, Organic carbon pools and soil biological fertility are affected by land use intensity in Mediterranean ecosystems of Sardinia, Italy, *Sci. Total Environ.* 599–600 (2017) 789–796, <https://doi.org/10.1016/j.scitotenv.2017.05.021>.
- [53] A. Eleftheriadis, M.-B. Turrión, Soil microbiological properties affected by land use, management, and time since deforestations and crop establishment, *Eur. J. Soil Biol.* 62 (2014) 138–144, <https://doi.org/10.1016/j.ejsobi.2014.03.001>.
- [54] S.J. Chapman, C.D. Campbell, G. Puri, Native woodland expansion: soil chemical and microbiological indicators of change, *Soil Biol. Biochem.* 35 (2003) 753–764, [https://doi.org/10.1016/S0038-0717\(03\)00091-9](https://doi.org/10.1016/S0038-0717(03)00091-9).
- [55] W. Xu, J.P. Schimel, I.A. Janssens, X. Song, C. Song, G. Yu, R.L. Sinsabaugh, D. Tang, X. Zhang, P.E. Thornton, Global pattern and controls of soil microbial metabolic quotient, *Ecol. Monogr.* 87 (2017) 429–441, <https://doi.org/10.1002/ecm.1258>.
- [56] V.A. Rincon-Florez, Y.P. Dang, M.H. Crawford, P.M. Schenk, L.C. Carvalhais, Occasional tillage has no effect on soil microbial biomass, activity and composition in Vertisols under long-term no-till, *Biol. Fertil. Soils* 52 (2016) 191–202, <https://doi.org/10.1007/s00374-015-1066-4>.
- [57] J. Ryan, S. Kapur, H. Ibrici, M. Singh, Cultivation intensity in relation to organic matter and related properties in a Vertisol in southern Turkey, *J. Sustain. Agric.* 35 (2011) 613–623, <https://doi.org/10.1080/10440046.2011.586577>.
- [58] A.T. Ayoub, Extent, severity and causative factors of land degradation in the Sudan, *J. Arid Environ.* 38 (1998) 397–409, <https://doi.org/10.1006/jare.1997.0346>.
- [59] J.L. Rolando, Jr., J.C.B. Dubeux, D.A. Ramirez, M. Ruiz-Moreno, C. Turin, V. Mares, L.E. Sollenberger, R. Quiroz, Land use effects on soil fertility and nutrient cycling in the Peruvian high-andean puna grasslands, *SSA (Soil Sci. Soc. Am.) J.* 82 (2018) 463–474, <https://doi.org/10.2136/sssaj2017.09.0309>.
- [60] E. Amézquita, R.J. Thomas, I.M. Rao, D.L. Molina, P. Hoyos, Use of deep-rooted tropical pastures to build-up an arable layer through improved soil properties of an Oxisol in the Eastern Plains (Llanos Orientales) of Colombia, *Agric. Ecosyst. Environ.* 103 (2004) 269–277, <https://doi.org/10.1016/j.agee.2003.12.017>.