

Response of soil microbial biomass C, N, and P and microbial quotient to agriculture and agricultural abandonment in a meadow steppe of northeast China

Yuchun Yan^{a,*},¹, Chu Wang^a, Jingmin Zhang^a, Yu Sun^b, Xingliang Xu^c, Na Zhu^a, Yurong Cai^a, Dawei Xu^a, Xu Wang^a, Xiaoping Xin^a, Jinqiang Chen^a

^a Institute of Agricultural Resources and Regional Planning, Chinese Academy of Agricultural Sciences, Beijing 100081, China

^b Key Laboratory of Mollisols Agroecology, Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130102, China

^c Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy Sciences, 11A, Datun Road, Chaoyang District, Beijing 100101, China

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ABSTRACT

The carbon and nutrients in the soil microbial biomass (SMB) and their proportion in soil elements, namely soil microbial quotient (SMQ), are the key indicators of the soil quality and quickly respond to the shift in the land-use pattern. However, the degree of the land-use shift influences on the soil microbial biomass, and the soil microbial quotient in the meadow steppe is not well-understood. The soil microbial biomass carbon (MBC), nitrogen (MBN), phosphorous (MBP), and SMQ were determined separately in grassland, cropland, and abandoned cropland in four sites within 50 km at a meadow steppe in northeast China. The results showed that the soil MBC, MBN, and MBP declined significantly as soil depth increased among the three land-use patterns. Agriculture has resulted in a significant decrease in the soil MBC, MBN, MBP, and SMQ compared to their corresponding values in grassland. The soil MBC content significantly was increased at the 0–10 cm soil layer after agriculture abandonment, but the SMQ had no significant improvement in the entire profile when compared to cropland. Besides, for the three types of land-use patterns, the C, N, and P stoichiometry of the soil microbial biomass was relatively stable, except for the stoichiometry in the relatively deep soil layer. Overall, the present agricultural abandonment (~ 19 years) got a certain of restoration in soil microbial biomass. Their corresponding values, however, were significantly lower than those found in native grassland. This highlighted that the restoration of the poor soil quality caused by the long term agriculture cultivation is a slow and hard process; it is important to maintain natural grasslands for protecting and maintaining soil microbial biomass and SMQ in the meadow steppe of northeast China.

1. Introduction

The soil-mediated roles of ecosystems are usually compromised when the use of land changes from natural to agricultural type of land. A number of negative effects on productivity, nutrients, biodiversity, and habitats have been observed. (Wall et al., 2012). Grassland agriculture induces the loss of soil organic matter (Mann, 1986; Guo and Gifford, 2002; Wu et al., 2003), changes microflora (Allison et al., 2005; Zhang et al., 2020), cause nutrient depletion (Post and Kwon, 2000), and compacts the soil (Cotching et al., 2013). The conversion of cropland to

grassland by abandoning agriculture has been a widely adopted and efficient approach for reversing the reduction in the functions of the soil that occurs due to continuous agriculture (Baer et al., 2002). The extent of soil recovery, which occurs after cropland abandonment, highly depends on the soil, vegetation, and climatic conditions, and knowledge of these is needed to determine whether conservation measures can mitigate soil deterioration and recover the ecosystem functions (Dodds et al., 2008; Baer et al., 2012).

As an important component of the nutrient cycle and the food chain, soil microbial biomass (SMB) has a key function in maintaining critical

* Corresponding author.

E-mail address: yanyuchun@caas.cn (Y. Yan).

¹ No. 12, Zhonguancun South Street, Haidian District, Beijing 100081, China

soil processes like organic matter decomposition (Coleman et al., 2003). Land-use shifts can significantly influence community composition and the mass of soil microorganisms by changing the biotic and abiotic conditions (Zhang et al., 2020). For example, the significantly different litter composition and litter quantity resulting from a shift in the land-use patterns directly alter the species composition and the abundance of microorganisms that act as decomposers (Cheng, 1993). Moreover, a change in the physical and chemical conditions of the soil due to a shift in the land-use pattern also has a profound impact on the composition, function, and biomass of soil microorganisms (Graham et al., 2021). Agriculture removes a portion of soil organic matter, which intensifies carbon or nitrogen limitation on soil microbes, and the nutrient contents of microbial biomass show a significant decrease due to nutrient stress (Yan et al., 2003; Wang et al., 2009; Sun et al., 2020). Conversely, abandonment of cropland generally increases soil microbial biomass due to an increase in the availability of the substrate and an improvement in the physical and chemical environment, such as soil porosity, soil pH, etc. (Hartman and Richardson, 2013; Rosenzweig et al., 2016; Zhang et al., 2020).

Previous studies reported the negative effect of agriculture on soil and microbial biomass as well as the restoration effect of agricultural abandonment. However, up to date, there are a few studies about the influence of agriculture and agricultural abandonment on soil microbial quotient (SMQ), which represents the fraction of microbial biomass to soil organic carbon and indicates how efficiently soil organic matter is being used by microbes (Pankhurst et al., 2002; Xu et al., 2013; Liu et al., 2018). The microbial quotient can be regarded as an integrative measure of substrate quality and quantity, soil biodiversity, and edaphic properties that expresses soil microbe stress adaptation and biomass production (Manzoni et al., 2012; Lee and Schmidt, 2014; Sinsabaugh et al., 2016; Malik et al., 2018). Therefore, microbial quotient can be used as an early alert warning for microbial status during ecosystem succession caused by human disturbance or environmental stresses (Wardle and Ghani, 1995; Zhou et al., 2017; Bastida et al., 2008), including indicators for land deterioration and recovery during land use changes (Hart, 1989; Spading, 1992). Microbial quotient is influenced by biotic (e.g., plant root and microbial community) and abiotic (e.g., O₂, soil clay content, pH, and nutrient) factors (Baer et al., 2002; Fierer and Jackson, 2006; Matamala et al., 2008; Rosenzweig et al., 2016). Changes in soil aggregates and plant root distribution, for example, may influence soil physicochemical properties (e.g., substrates and pH) along with soil vertical profiles (Paul et al., 2008; Pietri and Brookes, 2008). Besides, changes in soil microbe preferential flows caused by land use changes also have an impact on SMQ (Jackson et al., 1996; Fterich et al., 2011; Malik et al., 2018; Gross and Harrison, 2019). Biotic and abiotic factors interact and thus strongly affect microbial quotient during land conversion from grassland to cropland or vice versa. Exploring change in microbial quotient is critical for understanding the impact of land use changes on carbon and nutrient cycling (Powlson et al., 1987; Martiny et al., 2006).

We chose a representative meadow steppe in northeast China as our study area to investigate the quantitative effect of land use change on soil microbial biomass and quotient. We predicted that the changes of soil microbial biomass nutrients would be similar to those of soil because substrates (in particular, the soil C and N contents) usually restrict the growth and activity of microorganisms in numerous ecosystems (Marschner et al., 2003; Teklay et al., 2006; Yoshitake et al., 2007). We also predicted that the change in the nutrients of soil microbial biomass after shifts in the land-use pattern would be even more intense than that of the soil and thus result in the difference in microbial quotient in different land use pattern. Due to soil microorganisms, as the driven factor of nutrients turnover, are more sensitive to environmental conditions (Powlson et al., 1987; Zhao et al., 2017; Soleimani et al., 2019).

2. Methods

2.1. Description of the study sites

The study was conducted in Sertala Farm (N34°49'–N34°51', E108°10'–108°12'), Inner Mongolia, China. This area has a semi-humid and temperate climate. The average annual temperature and average annual frost-free days were -0.53°C (1980–2018) and 110, respectively. The major soil type in the study area is silt loam soil, which contains about 59% silt, 28% sand, and 13% clay. The warm season ranges from June to August, with an average daily temperature of 18.98°C . Additionally, the annual precipitation is mainly from July to September (80%); the average annual precipitation from 1980 to 2018 was 352.9 mm. Temperate meadow steppe is the dominant vegetation type, mainly including *Leymus chinensis*, *Filifolium sibiricum*, and *Stipa baicalensis*. The history of agricultural management in this region dates back to the 1950 s. The croplands in our study have been converted from grasslands since the various time (1960–1989), and then a portion of the grassland-converted cropland was abandoned after 2000 for ecological recovery under the Chinese government's "Grain for Green" project.

In August 2019, for this study, four sites were selected simultaneously with three land-use patterns, based on land-use history, i.e., native grassland, cropland converted from grassland, and cropland-derived abandoned lands, at random. Table 1 contains additional information about each site's background data (also see Wang et al., 2021). All four sites were more than 5 km apart.

2.2. Soil sampling and analysis

In every selected site and for every land-use pattern, we demarcated three blocks (30 m \times 30 m) at random, with a mutual distance of over 100 m. There were 12 replicated blocks for every land-use pattern (4 sites \times 3 replicates). We collected soil samples at five levels of soil depth (0–10, 10–20, 20–30, 30–40, 40–50 cm) from each block at three random positions using a 6-cm stainless steel corer, then mixed the samples by separate soil depth to form a composite sample for each soil layer for each block. We used soil samples from three blocks as replicates to determine the soil characteristic indicators in each land-use pattern for each selected site. Furthermore, regardless of site differences, we considered all soil samples for each land-use pattern as replicates in order to determine the soil characteristic indicators in each land-use pattern. Every soil sample was separated into two parts, one part was subjected to air-drying under ambient temperature and filtration using the 2-mm-mesh sieve to measure soil pH, SOC, and nutrients. In contrast, the other part was taken to the laboratory and stored in the refrigerator at -18°C to determine microbial nutrients and C levels.

The dichromate oxidation method was used to measure soil organic carbon (SOC) level. The semi-micro Kjeldahl method was used to measure total nitrogen (TN) level, and molybdenum antimony resistance-colorimetry was used to determine the total phosphorus (TP) level (Bao, 2000). The pH of the soil-water suspension (deionized water-to-air-dried samples in the ratio of 2.5:1) was determined by a pH meter (Bao, 2000). The MBC, MBN, and MBP contents were determined by the chloroform fumigation-extraction method (Brookes et al., 1984, 1985; Vance et al., 1987).

2.3. Statistical analyses

We used data from each land-use type (averaged from the blocks data) of four selected sites to calculate the change ratios of the contents of microbial biomass nutrients due to land-use change at each site, then averaged the change ratios of the four sites to obtain the change ratio when site differences were ignored (Wang et al., 2021). The change ratios of the contents of microbial biomass nutrients are presented below:

Table 1

The background characteristics of different land-use types at the four sampling sites (see Wang et al., 2021).

Sites	Grassland ^a	Cropland			Abandoned land	
	Dominant species ^b	agriculture duration (years)	Crop type	Management	Dominant species ^b	Land use history ^c
Site 1 (49° 28' 44" N, 120° 21' 38" E)	<i>Potentilla tanacetifolia</i> , <i>Leymus chinensis</i> , <i>Carex pediformis</i> , <i>Koeleria cristata</i>	59	<i>Triticum aestivum</i>	<i>Triticum aestivum</i> - <i>Brassica napus</i> rotation Irrigation Fertilization ^d	<i>Leymus chinensis</i> , <i>Artemisia commutata</i>	Abandoned for 13 years (Fenced) following a 46-year agriculture
Site 2 (49° 27' 47" N, 120° 19' 01" E)	<i>Leymus chinensis</i> , <i>Festuca ovina</i> , <i>Artemisia tanacetifolia</i> , <i>Koeleria cristata</i> , <i>Iris ventricosa</i>	49	<i>Brassica napus</i>	<i>Triticum aestivum</i> - <i>Brassica napus</i> rotation Irrigation Fertilization ^d	<i>Artemisia argyi</i> , <i>Cirsium esculentum</i> , <i>Artemisia commutata</i> , <i>Vicia amoena</i>	Abandoned for 5 years (Fenced) following a 44-year agriculture
Site 3 (49° 22' 24" N, 119° 54' 40" E)	<i>Leymus chinensis</i> , <i>Artemisia tanacetifolia</i> , <i>Carex pediformis</i>	30	<i>Beta vulgaris</i>	<i>Triticum aestivum</i> - <i>Brassica napus</i> rotation Irrigation Fertilization ^e	<i>Leymus chinensis</i> , <i>Carex pediformis</i>	Abandoned for 19 years (Mowed once a year) following an 11-year agriculture
Site 4 (49° 19' 26" N, 120° 03' 01" E)	<i>Carex duriuscula</i> , <i>Koeleria cristata</i> , <i>Carex pediformis</i> , <i>Filifolium sibiricum</i> , <i>Artemisia tanacetifolia</i>	34	<i>Medicago</i>	<i>Triticum aestivum</i> - <i>Brassica napus</i> and <i>Medicago</i> rotation Irrigation Fertilization ^c	<i>Leymus chinensis</i> , <i>Potentilla bifurca</i> , <i>Carex pediformis</i>	Abandoned for 17 years (Mowed once a year) following a 17-year agriculture

^a Grassland mowing was conducted once a year, and the mowed plant matter was used as hay feed; no grazing occurred in the whole year.

^b The list of plant species was obtained from a field survey. For every land-use pattern at every position, the biomass of the dominant species comprised over 50% of the overall biomass.

^c The management during agriculture was the same as that for the corresponding cropland at a given site.

^d Fertilizers, including 50 kg ha⁻¹ year⁻¹ diammonium phosphate and 25 kg ha⁻¹ year⁻¹ urea were applied before 1980; fertilizers, including 70 kg ha⁻¹ year⁻¹ diammonium phosphate and 37 kg ha⁻¹ year⁻¹ urea were applied during 1981–2000; fertilizers, including 100 kg ha⁻¹ year⁻¹ diammonium phosphate and 50 kg ha⁻¹ year⁻¹ urea were applied after 2001.

^e Fertilizers, including 75 kg ha⁻¹ year⁻¹ diammonium phosphate and 37 kg ha⁻¹ year⁻¹ urea were applied before 2000; fertilizers, including 100 kg ha⁻¹ year⁻¹ diammonium phosphate and 50 kg ha⁻¹ year⁻¹ urea were applied after 2001.

$$R_{GC} = \frac{(X_{\text{grassland}} - X_{\text{cropland}})}{X_{\text{grassland}}} \times 100\%$$

$$R_{CA} = \frac{(X_{\text{abandoned land}} - X_{\text{cropland}})}{X_{\text{cropland}}} \times 100\%$$

R_{GC} and R_{CA} indicate the cropland-to-grassland and cropland-to-abandoned land content change ratio (%), respectively. $X_{\text{grassland}}$, X_{cropland} , and $X_{\text{abandoned land}}$ indicate the levels of soil carbon nutrients in grassland, cropland, and abandoned land, respectively. The soil microbial quotients were calculated as follows:

$$SMQ_x = SMB_x / S_x$$

where SMQ stands for soil microbial quotient, SMB stands for soil microbial biomass nutrients, and S stands for soil nutrients. X is an abbreviation for organic carbon, total nitrogen, or total phosphorous.

The SPSS software (V. 17.0) was used for statistical analysis, and $\alpha = 0.05$ was set as the significance level. Differences in soil parameters across the three land-use patterns as well as five levels of soil depth were tested by constructing general linear models and performing univariate analysis. The land-use pattern or soil depth was considered as a fixed factor, while the different sites were considered random factors. Thus, an exponential growth equation was chosen to fit the relationship between MBC and SOC, MBN and STN, and MBP and STP for the three land-use types.

3. Results

3.1. Soil pH

Soil depth variation showed no consistent trend across land-use types in soil pH. In grassland and abandoned land, the pH of the soil increased significantly with depth ($p < 0.05$) but not in cropland ($p > 0.05$).

(Supplementary material, Fig. S1). There were significant differences in soil pH between land-use types (Fig. 1). Cropland had significantly higher ($p < 0.05$) soil pH than abandoned land and grassland in the 0–10 cm soil layer, but soil pH did not differ significantly between the three land-use patterns in the 10–20, 20–30, 30–40, and 40–50 cm soil layers.

3.2. Soil microbial biomass C, N, and P contents

Soil depth and land-use type both had a significant impact on soil microbial biomass C, N, and P. For the three land-use patterns, MBC and nutrient levels decreased significantly ($p < 0.05$) as soil depth increased (Supplementary material, Fig. S1). The soil MBC (at top 40 cm soil layers), MBN (at top 30 cm soil layers), and MBP (at top 20 cm soil layers) levels were the highest ($p < 0.05$) in grassland among the three land-use types. A significantly lower ($p < 0.05$) mean value of MBC in cropland compared to that in abandoned land only appeared in the 0–10 cm soil layer. Differences in both soil MBN and MBP at whole soil layers were not significant ($p > 0.05$) between abandoned land and cropland (Fig. 1).

3.3. Soil microbial quotient

The increase in the soil microbial C, N, and P levels was related to the exponentially increased SOC, STN, and STP levels, independently, with the most pronounced rate of increase observed in grassland among the three land-use patterns (Fig. 2).

The soil microbial quotient (SMQ), including SMQC (SMBC: SOC), SMQN (SMBN: STN), and SMQP (SMBP: STP), showed a significant decrease ($p < 0.05$) with an increase in the soil depth across the three land-use patterns, except the soil SMQC in cropland (Supplementary material, Fig. S2). Grassland had the highest SMQC for all the soil layers and the highest SMQN and SMQP in the top 30 cm layer of soil among

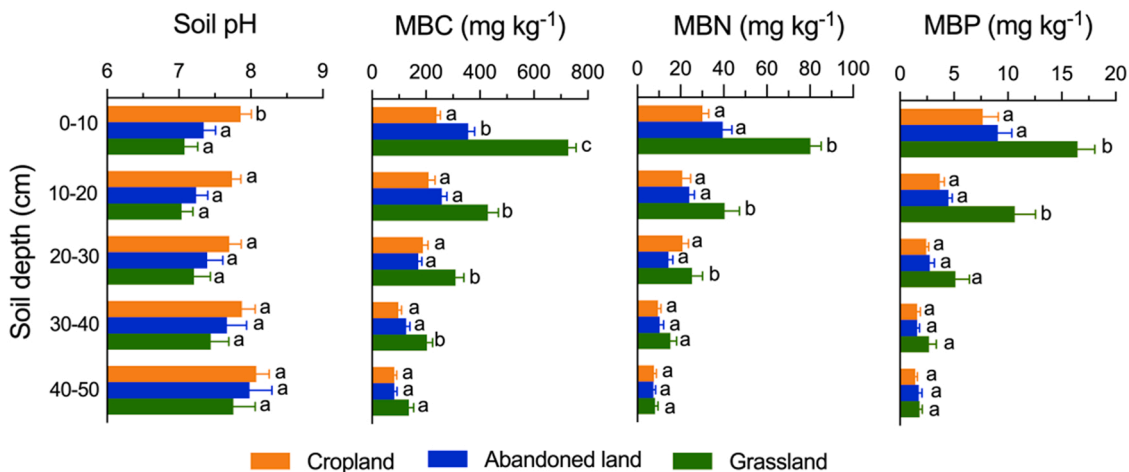


Fig. 1. The mean (\pm SE) soil pH, MBC, MBN, and MBP at different soil depths for different land-use patterns. Different letters indicate significant differences across the land-use patterns for the specific soil depth ($p < 0.05$).

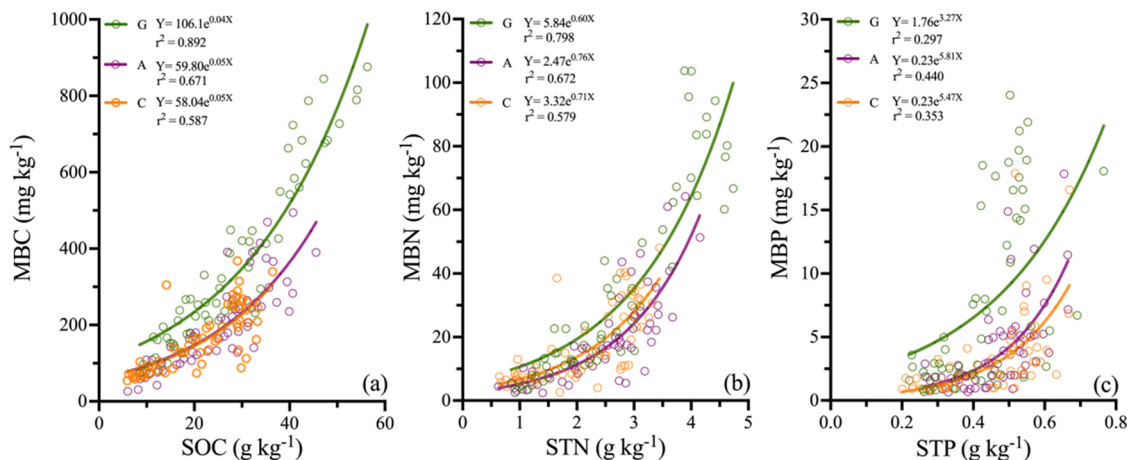


Fig. 2. The relationship between (a) MBC and SOC, (b) MBN and STN, and (c) MBP and STP for the three land-use types ($n = 180$) ($p < 0.0001$). G, grassland; A, abandoned land; C, cropland.

the three land-use types (Fig. 3). The difference in the SMQ was not significant between abandoned land and cropland for all measured soil layers ($p > 0.05$).

3.4. Stoichiometry of C, N, and P in soil and microbial biomass

Differences in the MBC to MBN ratio were not significant across the

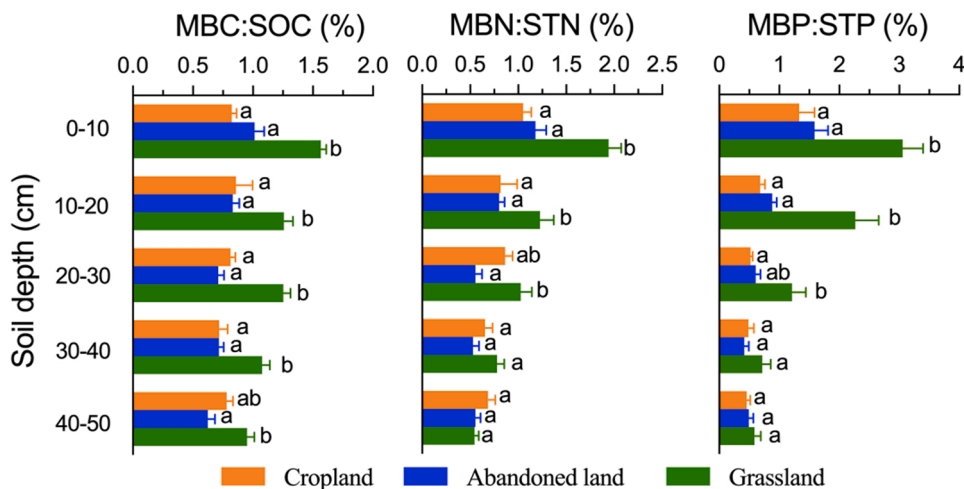


Fig. 3. The MBC to SOC (SMQC), MBN to STN (SMQN), and MBP to STP (SMQP) ratios (mean \pm SE) at different soil depths for various land-use patterns. Different letters indicate significant differences across the land-use patterns for a specific soil depth ($p < 0.05$).

three land-use patterns in the top 20 cm of the soil layer. At the same time, cropland had a significantly lower ($p < 0.05$) MBC to MBN ratio compared to that in grassland for the 20–30, 30–40, and 40–50 cm soil layers, and there was no difference in the MBC to MBN ratio between abandoned land ($p > 0.05$) and cropland, except for that in the 30–40 cm soil layer. Differences in the MBC to MBP ratio were not significant across the three land-use patterns in each soil layer, the 30–40 cm soil layer being the only exception, where grassland had the highest mean value ($p < 0.05$). Differences in the MBN to MBP ratio were not significant across the three land-use patterns in each soil layer, the 20–30 cm soil layer being the only exception, where cropland showed the highest mean value ($p < 0.05$) (Fig. 4).

The MBC to MBN ratio in cropland did not change ($p > 0.05$) with an increase in soil depth. Still, the ratio in grassland increased significantly ($p < 0.05$) with an increase in the soil depth, and the ratio in abandoned land at a soil depth of 30–40 cm was significantly greater than that at the 0–10 cm depth. Additionally, the MBC to MBP ratios increased significantly ($p < 0.05$) across the three land-use patterns as the soil depth increased. The MBN to MBP ratio in cropland showed a significantly increasing ($p < 0.05$) trend with soil depth, while the ratio in grassland and abandoned land did not change significantly ($p > 0.05$) with soil depth (Fig. S4).

3.5. Change ratio of C, N, and P in soil and microbial biomass

The average grassland-to-cropland (R_{GC}) change ratios in soil microbial C, N, and P decreased significantly ($p < 0.05$) as soil depth increased and were positive except for the R_{GC} of N at 40–50 cm soil layer (Supplementary material, Table S1). Microbial biomass had significantly higher R_{GC-C} (R_{GC} of C level) and R_{GC-P} (R_{GC} of P level) ($p < 0.05$) compared to those at a depth of 0–40 cm of soil, while the difference in the R_{GC} of N was not significant ($p > 0.05$) between microbial biomass and soil (Fig. 5a). Additionally, the average R_{CA-N} (R_{CA} of N level) and R_{CA-P} (R_{CA} of P level) in SMB were significantly higher ($p < 0.05$) than that at a soil depth of 10–20 cm, while the R_{CA} of N was significantly lower ($p < 0.05$) than that at a soil depth of 20–30 cm. The difference in the R_{CA} of C was not significant ($p > 0.05$) in the soil compared to that in the microbial biomass (Fig. 5b).

The grassland-to-cropland (R_{GC}) change ratios of MBC, MBN, and MBP showed varying degrees of fluctuation with time since agriculture, and the R_{GC} of MBC and MBP were generally positive values. The R_{GC} of MBN appeared to be a single valley trend and had the lowest value in all the soil layers at the site, which was cultivated for 49 years, except at the

30–40 cm depth (Fig. 6a). On the contrary, the cropland-to-abandoned land (R_{CA}) change ratios of MBC, MBN, and MBP in the different soil layers fluctuated inconsistently with time since abandonment. However, most of them had positive mean values (Fig. 6b).

4. Discussion

4.1. The relationship between soil pH and land-use shift

Soil pH increased significantly after grassland agriculture (Fig. 1), mainly attributed to a decrease in the organic matter in cropland compared to grassland, which further reduced the release of organic acid produced by the decomposition of soil organic matter (Zhang et al., 2012; Deng et al., 2016). In contrast, agricultural abandonment had the opposite effect on soil pH due to increased soil organic matter (Wang et al., 2021). In our study, soil pH was negatively correlated with soil organic matter, which supported the above explanation (Fig. S3). However, the variation in soil pH with soil depth in grassland disappeared after agriculture, probably due to the mixing of soil from different depths through stirring and plowing (Six et al., 1998).

4.2. The relationship of soil microbial C, N, and P with land-use shift

Based on our results, prolonged agriculture dramatically decreased SMC, SMN, and SMP levels in the surface soil layers compared to the levels in grassland (Fig. 1). This could be the result of each land-use type's integrative response to human management practices. The composition of vegetation and the amount of organic matter vary by land-use type change, influencing soil microbial biomass (Lepcha and Devi, 2020). On a global scale, Xu et al. (2013) discovered that soil microbial C, N, and P were significantly lower in cropland than in grassland. These reductions were mainly due to the lower availability of organic matter in cropland than in grassland (Lepcha and Devi, 2020; Wang et al., 2021). This is because soil organic matter, as a substrate, directly influences soil microbial biomass (Chen et al., 2006). This was shown by the significantly positive correlation of soil microbial biomass nutrients and soil nutrients in our study (Fig. 2), as well as shown in other studies (Chen et al., 2017; Padalia et al., 2018). The change ratio of microbial biomass in the various soil layers from grassland to cropland was relatively stable (e.g., SMBC) or showed a certain degree of fluctuation (e.g., SMBN, SMBP) with time (30–59 years) since land-use shift (Fig. 6a). This indicated that the effect of agriculture for 30 years (the shortest duration of agriculture in this study) on soil microbial biomass

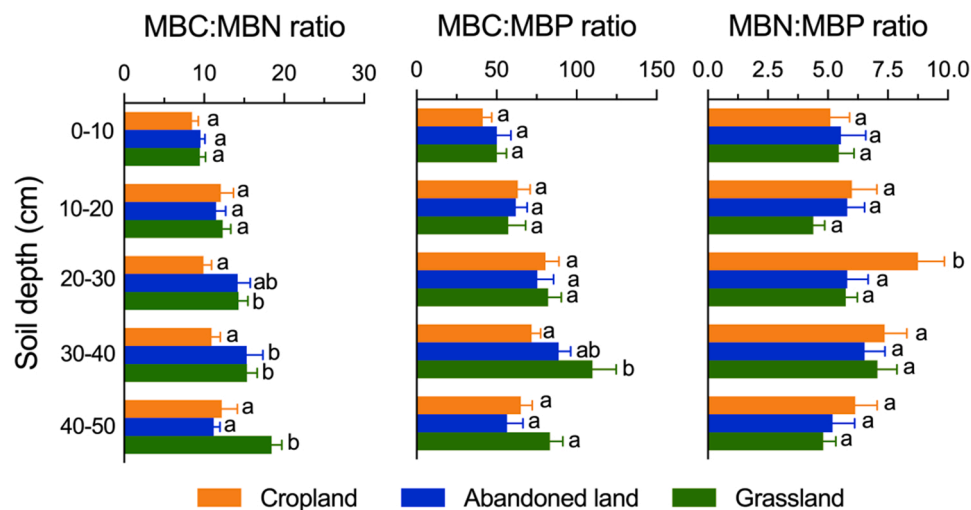


Fig. 4. The MBC to MBN ratio, MBC to MBP ratio, and MBN to MBP ratio (mean \pm SE) at different soil depths for the three land-use patterns. Different letters indicate significant differences across the land-use patterns for a specific soil depth ($p < 0.05$).

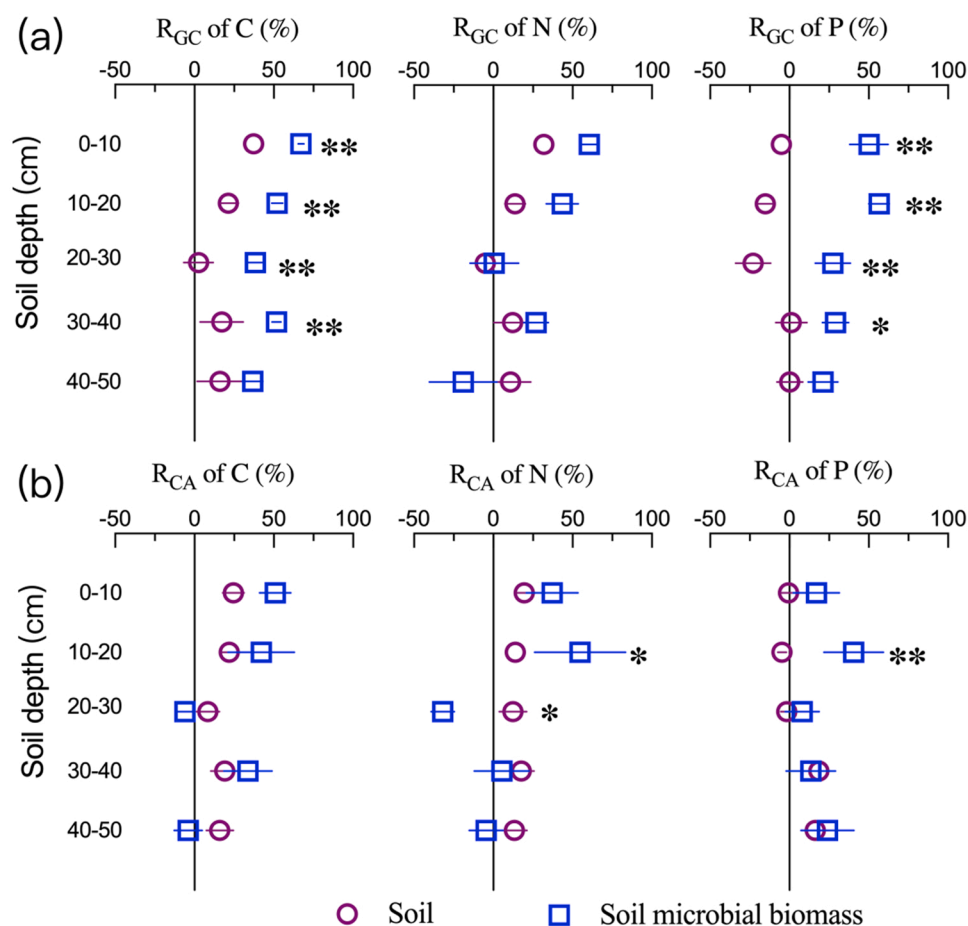


Fig. 5. The mean (\pm SE) change ratios of C, N, and P levels in soil microbial biomass at different soil depths due to the alteration of land use. (a) R_{GC} indicates grassland-to-cropland change ratio, and (b) R_{CA} indicates cropland-to-abandoned land change ratio; Asterisks on the side of each pair of points indicate significant differences between soil microbial biomass and soil for change ratios of C, N, and P. One asterisk indicates significant at $p < 0.05$, double asterisks indicate significant at $p < 0.01$.

had reached a relatively stable state.

Our study indicated that the C and nutrients in microbial biomass generally had greater change ratios than that in the soil during grassland-cropland conversion (Fig. 5a). These results implied that microbial biomass is more sensitive to environmental changes than soil organic matter (Follett and Schimel, 1989; Shao et al., 2019); therefore, agriculture might damage the microbial community and reduce microbial biomass in the process of consumption of soil organic matter (Graham et al., 2021). In addition, it is worth noting that we found a diametrically opposite change in P content in soil microbial biomass and in the soil during grassland-cropland conversion (Fig. 5a). Specifically, the soil P increased significantly due to long-term agriculture. This increase was mainly due to fertilizer inputs in cropland; moreover, phosphorus is easier to be preserved in soil because soil particles have a higher adsorption potential for P, and there are lesser ways to lose P than lose N (Newman, 1997; McLauchlan, 2006; Wang et al., 2021). However, contrary to the STP, the soil MBP showed a significant decrease when grassland was converted to cropland (Fig. 1), which indicated that P was not a limiting element for microbial growth in the study area. Thus, the increase in the P element in the environment did not result in an increase in microbial biomass P. This was also supported by our observations of a relatively stable C, N, and P stoichiometry of microbial biomass across the three land-use patterns in most soil layers examined in this study (Fig. 4).

Contrary to agriculture, agricultural abandonment elevated the levels of SMB in this study (Fig. 1); there was a 50.9%, 37.1%, and 17.1% increase in SMBC, SMBN, and SMBP, respectively, in the surface soil (0–10 cm) in the abandoned land compared to that in the cropland (Fig. 5b). This increase could be due to more suitable conditions, e.g., greater substrate availability for soil organic matter, plant litter, and

lower compaction of the abandoned soil, relative to that in cropland (Rosenzweig et al., 2016). The change ratio of microbial C and nutrients for the entire soil profile from cropland to abandoned land did not show an expected increase with time since abandonment except for the 10–20 cm soil layer. Still, they showed an inconsistent fluctuation (Fig. 6b). There could be two plausible but not exclusive explanations for this result. First, the restoration of soil microbial biomass is a relatively slow process, where the number of years of abandonment (5–19 years) was not sufficient to yield a noticeable difference (Wang et al., 2011). Second, the difference in planting history and management after abandonment, for example, mowing once a year, might have slowed down the SOC and microbial biomass accumulation in the two treatments with longer abandonment years (17 and 19 years) (Table. S1).

4.3. Relationship between the soil microbial quotient and land-use shift

Soil microorganisms play a critical role in mediating soil organic matter by regulating the formation and decomposition of soil organic matter (Sun et al., 2020). The soil microbial quotient, i.e., the proportion of soil elements in the SMB, is extensively used to reflect soil quality and could be a latent regulator of the dynamics of soil organic carbon and nutrients (Carter et al., 1991; Sparling, 1992; Joergensen, 1999). Our results showed that agriculture significantly reduced soil microbial quotient compared to the microbial quotient in the natural grassland (Fig. 3). The exponential increase in SMB was associated with increased soil nutrients, and grassland had the highest rate of increase among the three land-use types (Fig. 2). This implied that the soil microbial biomass was lower for the same soil C and nutrients levels in cropland compared to grassland.

Many previous studies have found disproportionate levels of

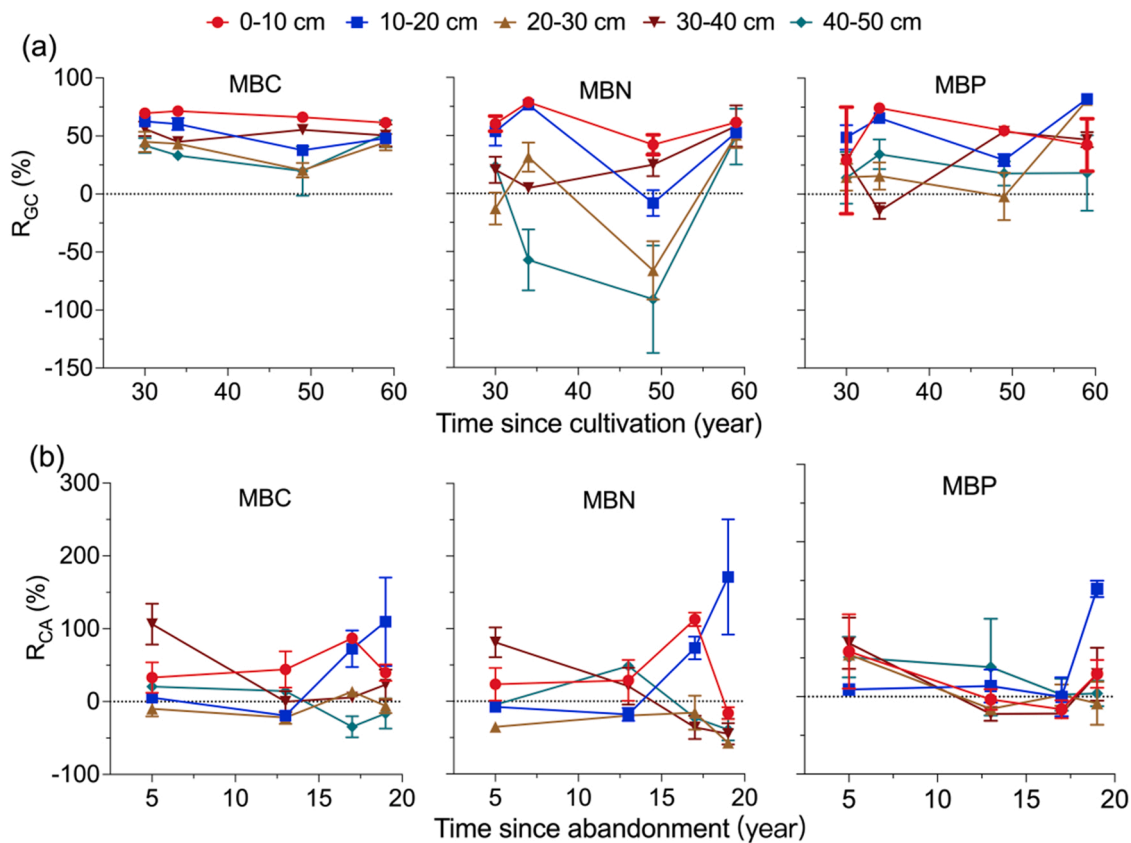


Fig. 6. The associations of the change ratios of the MBC, MBN, and MBP levels with the duration of land-use alteration. (a) R_{GC} indicates the grassland-to-cropland change ratio, and (b) R_{CA} indicates the cropland-to-abandoned land change ratio.

nutrients and C content in soil and the SMB (Franchini et al., 2007; Zhou et al., 2017; Yan et al., 2003; Raiesi, 2012). It is most likely because the living conditions (e.g., soil porosity, soil pH, root vertical distribution) as microbial growth control factors are more favorable in grassland than in cropland. First, soil compaction, associated with inappropriate tillage affects the physical properties of the soil due to a decrease in porosity and an anoxic environment, which suppresses microbial activities and biochemical processes and reduces microbial biomass (Li et al., 2002; Jiao et al., 2018). Second, alkalization after agriculture might result in the microbial community shifting toward copiotrophic life strategies to alleviate alkalinity-related stress. The microbial carbon use efficiency generally decreases and leads to wasteful metabolism, causing microbial biomass to decrease. Therefore, a lower proportion of substrate allocated to biosynthesis in cropland causes a decrease in the soil microbial quotient (Malik et al., 2018). Additionally, the negative effects of these changes in soil conditions on plant growth also suppress microbial growth by weakening the mutually beneficial relationship between plants and soil microorganisms. For example, a decrease in the supply of root exudates directly reduces the availability of C, which is used for microbial growth (Li et al., 2002; Zak et al., 2000).

The soil microbial quotient decreased significantly with soil depth, except for the SMQC in cropland (Fig. S2). There could be several explanations for this. First, the decrease in the microbial quotient could be associated with a decrease in the distribution of roots with soil depth (Jackson et al., 1996; Xu et al., 2013). It is because the reduced roots directly caused a decrease in root exudates and rhizosphere conduits, limiting the energy source and oxygen supply required for microbial growth (Helal and Sauerbeck, 1986; Chapin et al., 2002). Additionally, other changes in soil conditions, such as compaction and alkalization with changes in soil depth, could also contribute to the decrease in soil microbial quotient (Li et al., 2002; Malik et al., 2018).

4.4. Relationship of the stoichiometry of C, N, and P in soil microbial biomass with land-use shift

Except for the deeper soil layer, the C, N, and P stoichiometry of the SMB was relatively stable across the three land-use types (Fig. 4). This result support to the idea of regional stoichiometric homeostasis of the soil microbial community (Hartman and Richardson, 2013; Mooshammer et al., 2014a, 2014b). This homeostasis can be explained by nutrient co-limitation (e.g., soil phosphorus availability) to all microbial species in mixed communities, which is caused by niche partitioning, resulting in the coexistence of microorganisms with different nutrient use strategies (Hartman and Richardson, 2013). When distinguishing microbial species, element ratios vary greatly among different microorganisms (e.g., fungi versus bacteria) (Mouginot et al., 2014). Therefore, differences in the responses of the deeper soil layers could be attributed to relatively simpler communities that were not stable enough to withstand environmental disturbances and were more sensitive when confronted with land-use changes (Jiao et al., 2021).

Additionally, according to our results, there was, generally, an increasing trend in the MBC to MBN and the MBC to MBP ratios as the soil depth increased across the three land-use patterns, the MBC to MBN ratio of cropland being the only exception (Fig. 5). This increase could be ascribed to environmental stress, such as drier soils and higher degrees of compaction in the deeper soil layers. Environmental stress might cause a shift in the life strategies of soil microorganisms from fast-growing copiotrophs (R-strategists) to slow-growing oligotrophs (K-strategists). Since the K-strategists have slower growth and demand lesser nutrients (N, P), the microorganisms can invest greater nutrients to produce extracellular enzymes to acquire elemental nutrients. This accounts for higher microbial C to P and C to N ratios compared to those in the surface microorganisms (Fierer et al., 2007; Liu et al., 2020).

5. Conclusions

Given the importance of soil microorganisms in regulating both soil organic matter decomposition and formation, understanding the response of soil microbial biomass and microbial quotient to land-use changes can help us better understand soil carbon and nutrient dynamics in terrestrial ecosystems. Our research yielded three major findings. 1) Agriculture dramatically decreased the SMC, SMN, and SMP contents. The present abandonment (5–19 years) showed an increase (17.1%–50.9%) in the levels of MBC, MBN, and MBP at the soil surface compared to the levels in cropland. Still, considerably lower levels of MBC, MBN, and MBP were observed in the abandoned land than that in the native grassland. 2) Overall, our results supported the notion of a large degree of stoichiometric homeostasis of soil microbial communities. However, the homeostasis was affected by environmental stress, such as drier soils and greater degrees of compaction in deeper soil layers. 3) Agriculture significantly reduced the soil microbial quotient, the decrease ratio of C and nutrients in the microbial biomass was significantly greater than in the soil during grassland-cropland conversion. However, the microbial quotient did not significantly increase after cropland abandonment, indicating that the restoration effect of cropland abandonment on soil microbial biomass is a slow process, similar to soil nutrient restoration. These findings highlighted the significant negative impact of the grassland-cropland conversion on soil microbial biomass and quotient. As a result, more appropriate management practices, such as increasing organic matter return, should be implemented to promote the reversal of the negative effect on soil quality caused by agricultural activities.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.still.2022.105475](https://doi.org/10.1016/j.still.2022.105475).

References

Allison, V.J., Miller, R.M., Jastrow, J.D., Matamala, R., Zak, D.R., 2005. Changes in soil microbial community structure in a tallgrass prairie chronosequence. *Soil Sci. Soc. Am. J.* 69, 1412–1421. <https://doi.org/10.2136/sssaj2004.0252>.

Baer, S.G., Heneghan, L., Eviner, V.T., 2012. Applying soil ecological knowledge to restore ecosystem services. In: Wall, D.H., Bardgett, R.D. (Eds.), *Soil ecology and ecosystem services*. Oxford University Press, Oxford, UK, Oxford, pp. 377–393.

Baer, S., Kitchen, D., Blair, J., Rice, C., 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. *Ecol. Appl.* 12, 1688–1701. <https://doi.org/10.2307/3099932>.

Bao, S.D., 2000. *Soil Agrochemical Analysis*. China Agricultural Press, Beijing.

Bastida, F., Zsolnay, A., Hernández, T., García, C., 2008. Past, present and future of soil quality indices: a biological perspective. *Geoderma* 147 (3), 159–171.

Brookes, P., Landman, A., Pruden, G., Jenkinson, D., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biol. Biochem.* 17, 837–842. [https://doi.org/10.1016/0038-0717\(85\)90144-0](https://doi.org/10.1016/0038-0717(85)90144-0).

Brookes, P.C., Powlson, D., Jenkinson, D., 1984. Phosphorus in the soil microbial biomass. *Soil Biol. Biochem.* 16, 169–175. [https://doi.org/10.1016/0038-0717\(84\)90108-1](https://doi.org/10.1016/0038-0717(84)90108-1).

Carter, M., 1991. The influence of tillage on the proportion of organic carbon and nitrogen in the microbial biomass of medium-textured soils in a humid climate. *Biol. Fertil. Soils* 11, 135–139. <https://doi.org/10.1007/BF00336378>.

Chapin, F.S., Matson, P.A., Mooney, H.A., Vitousek, P.M., 2002. *Global biogeochemical cycles*. In: Chapin, F.S., Matson, P.A., Mooney, H.A. (Eds.), *Principles of terrestrial ecosystem ecology*. Springer, New York, pp. 35–55.

Cheng, D.S., 1993. *Forest Microorganisms Ecology*. Northeast Forestry University Press, Harbin.

Chen, C., Liu, W., Jiang, X., Wu, J., 2017. Effects of rubber-based agroforestry systems on soil aggregation and associated soil organic carbon: implications for land use. *Geoderma* 299, 13–24. <https://doi.org/10.1016/j.geoderma.2017.03.021>.

Chen, F., Zeng, D., Zhou, B., Singh, A., Fan, Z., 2006. Seasonal variation in soil nitrogen availability under Mongolian pine plantations at the Keerqin Sand Lands, China. *J. Arid. Environ.* 67, 226–239. <https://doi.org/10.1016/j.jaridenv.2006.02.017>.

Coleman, D.C., Crossley Jr., D., Hendrix, P.F., 2003. *Fundamentals of Soil Ecology*. Academic press, San Diego.

Cotching, W., Oliver, G., Downie, M., Corkrey, R., Doyle, R., 2013. Land use and management influences on surface soil organic carbon in Tasmania. *Soil Res* 51, 615–630. <https://doi.org/10.1071/sr12251>.

Deng, Y.S., Dong, X., Cai, C.F., Ding, S.W., 2016. Effects of land uses on soil physico-chemical properties and erodibility in collapsing-gully alluvial fan of Anxi County, China. *J. Integr. Agric.* 15, 1863–1873. [https://doi.org/10.1016/S20953119\(15\)61223-0](https://doi.org/10.1016/S20953119(15)61223-0).

Dodds, W.K., Wilson, K.C., Rehmeier, R.L., Knight, G.L., Wiggam, S., Falke, J.A., Dalgleish, H.J., Bertrand, K.N., 2008. Comparing ecosystem goods and services provided by restored and native lands. *BioScience* 58, 837–845. <https://doi.org/10.1641/B580909>.

Fierer, N., Bradford, M.A., Jackson, R.B., 2007. Toward an ecological classification of soil bacteria. *Ecology* 88, 1354–1364. <https://doi.org/10.1890/05-1839>.

Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. *Proc. Nat. Acad. Sci.* 103, 626–631.

Follett, R., Schimel, D., 1989. Effect of tillage practices on microbial biomass dynamics. *Soil Sci. Soc. Am. J.* 53, 1091–1096.

Franchini, J., Crispino, C., Souza, R.A., Torres, E., Hungria, M., 2007. Microbiological parameters as indicators of soil quality under various soil management and crop rotation systems in southern Brazil. *Soil Tillage Res* 92, 18–29. <https://doi.org/10.1016/j.still.2005.12.010>.

Fterich, A., Mahdhi, M., Mars, M., 2011. The effects of *Acacia Tortilis* subsp. *Raddiana*, soil texture and soil depth on soil microbial and biochemical characteristics in arid zones of Tunisia. *Land Degrad. Dev.* 25, 143–152. <https://doi.org/10.1002/ldr.1154>.

Graham, C., Ramos-Pezzotti, M., Lehman, M., 2021. Short-term impacts to the soil microbial population during grassland conversion to cropland. *Soil Tillage Res* 206, 104839. <https://doi.org/10.1016/j.still.2020.104839>.

Gross, C.D., Harrison, R.B., 2019. The case for digging deeper: soil organic carbon storage, dynamics, and controls in our changing world. *Soil Syst.* 3, 28. <https://doi.org/10.3390/soilsystems3020028>.

Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. *Glob. Change Biol.* 8, 345–360. <https://doi.org/10.1046/j.1354-1013.2002.00486.x>.

Hartman, W.H., Richardson, C.J., 2013. Differential nutrient limitation of soil microbial biomass and metabolic quotients (q CO₂): is there a biological stoichiometry of soil microbes? *PLoS One* 8, e57127. <https://doi.org/10.1371/journal.pone.0057127>.

Helal, H., Sauerbeck, D., 1986. Effect of plant roots on carbon metabolism of soil microbial biomass. *J. Plant Nutr. Soil Sci.* 149, 181–188. <https://doi.org/10.1002/jpln.19861490205>.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H., Sala, O., Schulze, E.-D., 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108, 389–411. <https://doi.org/10.1007/BF00333714>.

Jiao, S., Chen, W.M., Wang, J.L., Du, N.N., Li, Q.P., Wei, G.H., 2018. Soil microbiomes with distinct assemblies through vertical soil profiles drive the cycling of multiple nutrients in reforested ecosystems. *Microbiome* 6, 146. <https://doi.org/10.1186/s40168-018-0526-0>.

Jiao, K., Zhang, X., Xu, M., Liu, X.J., Q.D, A., C.Y, Z., 2021. Depth-related characteristics of soil microbial community along the soil profile of typical dark coniferous forest in southeast Tibet. *Sheng Tai Xue Bao* 41, 4864–4875. <https://doi.org/10.5846/stxb202004291047>.

Joergensen, R.G., 1999. Depth gradients of microbial and chemical properties in moder soils under beech and spruce. *Pedobiologia* 43, 34–44.

Lee, Z.M., Schmidt, T.M., 2014. Bacterial growth efficiency varies in soils under different land management practices. *Soil Biol. Biochem.* 69, 282–290.

Lepcha, N.T., Devi, N.B., 2020. Effect of land use, season, and soil depth on soil microbial biomass carbon of Eastern Himalayas. *Ecol. Process.* 9, 1–14. <https://doi.org/10.1186/s13717-020-00269-y>.

Liu, Y., Ma, W., Kou, D., Niu, X., Wang, T., Chen, Y., Chen, D., Zhu, X., Zhao, M., Hao, B., 2020. A comparison of patterns of microbial C: N: P stoichiometry between topsoil and subsoil along an aridity gradient. *Biogeosciences* 17, 2009–2019. <https://doi.org/10.5194/bg-17-2009-2020>.

Li, C., Ma, B., Zhang, T., 2002. Soil bulk density effects on soil microbial populations and enzyme activities during the growth of maize (*Zea mays* L.) planted in large pots under field exposure. *Can. J. Soil Sci.* 82, 147–154. <https://doi.org/10.4141/S01-026>.

- Malik, A.A., Puissant, J., Buckeridge, K.M., Goodall, T., Jehmlich, N., Chowdhury, S., Gweon, H.S., Peyton, J.M., Mason, K.E., van Agtmaal, M., 2018. Land use driven change in soil pH affects microbial carbon cycling processes. *Nat. Commun.* 9, 1–10. <https://doi.org/10.1038/s41467-018-05980-1>.
- Mann, L., 1986. Changes in soil carbon storage after cultivation. *Soil Sci.* 142, 279–288. <https://doi.org/10.1097/00010694-198611000-00006>.
- Manzoni, S., Taylor, P., Richter, A., Porporato, A., Agren, G.L., 2012. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *N. Phytol.* 196, 79–91.
- Marschner, P., Kandeler, E., Marschner, B., 2003. Structure and function of the soil microbial community in a long-term fertilizer experiment. *Soil Biol. Biochem.* 35, 453–461. [https://doi.org/10.1016/S0038-0717\(02\)00297-3](https://doi.org/10.1016/S0038-0717(02)00297-3).
- Martiny, J.B.H., Bohannan, B.J.M., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J. L., Horner-Devine, M.C., Kane, M., Krumins, J.A., Kuske, C.R., Morin, P.J., Naeem, S., Ovreas, L., Reysenbach, A.L., Smith, V.H., Staley, J.T., 2006. Microbial biogeography: putting microorganisms on the map. *Nat. Rev. Microbiol.* 4, 102–112. <https://doi.org/10.1038/nrmicro1341>.
- Matamala, R., Jastrow, J.D., Miller, R.M., Garten, C.T., 2008. Temporal changes in C and N stocks of restored prairie: implications for C sequestration strategies. *Ecol. Appl.* 18, 1470–1488.
- McLaughlan, K., 2006. The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. *Ecosystems* 9, 1364–1382. <https://doi.org/10.1007/s10021-005-0135-1>.
- Mooshammer, M., Wanek, W., Hämmerle, I., Fuchslueger, L., Hofhansl, F., Knoltsch, A., Schneckler, J., Takriti, M., Watzka, M., Wild, B., 2014a. Adjustment of microbial nitrogen use efficiency to carbon: nitrogen imbalances regulates soil nitrogen cycling. *Nat. Commun.* 5, 1–7. <https://doi.org/10.1038/ncomms4694>.
- Mooshammer, M., Wanek, W., Zechmeister-Boltenstern, S., Richter, A.A., 2014b. Stoichiometric imbalances between terrestrial decomposer communities and their resources: mechanisms and implications of microbial adaptations to their resources. *Front. Microbiol.* 5, 22. <https://doi.org/10.3389/fmicb.2014.00022>.
- Mouginot, C., Kawamura, R., Matulich, K.L., Berlemont, R., Allison, S.D., Amend, A.S., Martiny, A.C., 2014. Elemental stoichiometry of Fungi and Bacteria strains from grassland leaf litter. *Soil Biol. Biochem.* 76, 278–285. <https://doi.org/10.1016/j.soilbio.2014.05.011>.
- Newman, E., 1997. Phosphorus balance of contrasting farming systems, past and present. *Can. Food Prod. be Sustain. ? J. Appl. Ecol.* 1334–1347.
- Padalia, K., Bargali, S., Bargali, K., Khulbe, K., 2018. Microbial biomass carbon and nitrogen in relation to cropping systems in Central Himalaya, India. *Curr. Sci.* 115, 1741–1750. <https://doi.org/10.18520/cs/v115/i9/1741-1750>.
- Paul, S., Flessa, H., Veldkamp, E., Lopez-Ulloa, M., 2008. Stabilization of recent soil carbon in the humid tropics following ecosystem type changes: evidence from aggregate fractionation and stable isotope analyses. *Biogeochemistry* 87, 247–263. <https://doi.org/10.1007/s10533-008-9182-y>.
- Pietri, J.C.A., Brookes, P.C., 2008. Relationships between soil pH and microbial properties in a UK arable soil. *Soil Biol. Biochem.* 40, 1856–1861. <https://doi.org/10.1016/j.soilbio.2008.03.020>.
- Post, W.M., Kwon, K.C., 2000. Soil carbon sequestration and land-use change: processes and potential. *Glob. Change Biol.* 6, 317–327. <https://doi.org/10.1046/j.1365-2486.2000.00308.x>.
- Powlson, D.S., Prookes, P., Christensen, B.T., 1987. Measurement of soil microbial biomass provides an early indication of changes in total soil organic matter due to straw incorporation. *Soil Biol. Biochem.* 19, 159–164.
- Raiesi, F., 2012. Land abandonment effect on N mineralization and microbial biomass N in a semi-arid calcareous soil from Iran. *J. Arid Environ.* 76, 80–87. <https://doi.org/10.1016/j.jaridenv.2011.08.008>.
- Rosenzweig, S.T., Carson, M.A., Baer, S.G., Blair, J.M., 2016. Changes in soil properties, microbial biomass, and fluxes of C and N in soil following post-agricultural grassland restoration. *Appl. Soil Ecol.* 100, 186–194. <https://doi.org/10.1016/j.apsoil.2016.01.001>.
- Shao, P., Liang, C., Lynch, L., Xie, H., Bao, X., 2019. Reforestation accelerates soil organic carbon accumulation: evidence from microbial biomarkers. *Soil Biol. Biochem.* 131, 182–190. <https://doi.org/10.1016/j.soilbio.2019.01.012>.
- Sinsabaugh, R.L., Turner, B., Talbot, J., Waring, B., Powers, J., Kuske, C., Moorhead, D., Follstad, S.J., 2016. Stoichiometry of microbial carbon use efficiency in soils. *Ecol. Monogr.* 86, 172–189.
- Six, J., Elliott, E., Paustian, K., Doran, J., 1998. Aggregation and soil organic matter accumulation in cultivated and native grassland soils. *Soil Sci. Soc. Am. J.* 62 (5), 1367–1377. <https://doi.org/10.2136/sssaj1998.03615995006200050032x>.
- Soleimani, A., Hosseini, S.M., Bavani, A.R.M., Jafari, M., Francaviglia, R., 2019. Influence of land use and land cover change on soil organic carbon and microbial activity in the forests of northern Iran. *Catena* 177, 227–237. <https://doi.org/10.1016/j.catena.2019.02.018>.
- Spading, G.P., 1992. Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. *Soil Res* 30, 195–207.
- Sparling, G.P., 1992. Ratio of microbial biomass carbon to soil organic carbon as a sensitive indicator of changes in soil organic matter. *Soil Res* 30, 195–207. <https://doi.org/10.1071/sr9920195>.
- Sun, T., Wang, Y., Hui, D., Jing, X., Feng, W., 2020. Soil properties rather than climate and ecosystem type control the vertical variations of soil organic carbon, microbial carbon, and microbial quotient. *Soil Biol. Biochem.* 148, 107905. <https://doi.org/10.1016/j.soilbio.2020.107905>.
- Teklay, T., Nordgren, A., Malmer, A., 2006. Soil respiration characteristics of tropical soils from agricultural and forestry land-uses at Wondo Genet (Ethiopia) in response to C, N and P amendments. *Soil Biol. Biochem.* 38, 125–133. <https://doi.org/10.1016/j.soilbio.2005.04.024>.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. *Soil Biol. Biochem.* 19, 703–707. [https://doi.org/10.1016/0038-0717\(87\)90052-6](https://doi.org/10.1016/0038-0717(87)90052-6).
- Wall, D.H., Behan-Pelletier, V., Jones, T.H., Ritz, K., Six, J., Strong, D.R., van der Putten, W.H., 2012. Soil Ecology and Ecosystem Services. Oxford University Press, Oxford.
- Wang, C., Li, L., Yan, Y., Cai, Y., Xu, D., Wang, X., Chen, J., Xin, X., 2021. Effects of cultivation and agricultural abandonment on soil carbon, nitrogen and phosphorus in a meadow steppe in eastern Inner Mongolia. *Agric. Ecosyst. Environ.* 309, 107284. <https://doi.org/10.1016/j.agee.2020.107284>.
- Wang, Y., Tu, C., Cheng, L., Li, C., Gentry, L., Hoyt, G., Zhang, X.C., Hu, S.J., 2011. Long-term impact of farming practices on soil organic carbon and nitrogen pools and microbial biomass and activity. *Soil Tillage Res* 117, 8–16. <https://doi.org/10.1016/j.still.2011.08.002>.
- Wang, Q., Yin, F., Hao, S., Li, C., 2009. Effects of subsoil bulk density on rhizospheric soil microbial population, microbial biomass carbon and nitrogen of corn (*Zea mays* L.) field. *Sheng Tai Xue Bao* 29, 3096–3104. [https://doi.org/10.1016/S1003-6326\(09\)60084-4](https://doi.org/10.1016/S1003-6326(09)60084-4).
- Wardle, D.A., Ghani, A., 1995. A critique of the microbial metabolic quotient (qCO₂) as a bioindicator of disturbance and ecosystem development. *Soil Biol. Biochem.* 27 (12), 1601–1610.
- Wu, H., Guo, Z., Peng, C., 2003. Land use induced changes of organic carbon storage in soils of China. *Glob. Change Biol.* 9, 305–315. <https://doi.org/10.1046/j.1365-2486.2003.00590.x>.
- Xu, X.F., Thornton, P.E., Post, W.M., 2013. A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems. *Glob. Ecol. Biogeogr.* 22, 737–749. <https://doi.org/10.1111/geb.12029>.
- Yan, T., Yang, L., Campbell, C., 2003. Microbial biomass and metabolic quotient of soils under different land use in the Three Gorges Reservoir area. *Geoderma* 115, 129–138. [https://doi.org/10.1016/S0016-7061\(03\)00082-X](https://doi.org/10.1016/S0016-7061(03)00082-X).
- Yoshitake, S., Uchida, M., Koizumi, H., Nakatsubo, T., 2007. Carbon and nitrogen limitation of soil microbial respiration in a High Arctic successional glacier foreland near Ny-Ålesund, Svalbard. *Polar Res.* 26, 22–30. <https://doi.org/10.1111/j.1751-8369.2007.00001.x>.
- Zak, D.R., Pregitzer, K.S., KING, J.S., Holmes, W.E., 2000. Elevated atmospheric CO₂, fine roots and the response of soil microorganisms: a review and hypothesis. *N. Phytol.* 147, 201–222.
- Zhang, X., Li, W., Zhong, Z., Zhang, Q., Wang, X., Han, X., Ren, C., Yang, G., 2020. Response of soil microbial community to C: N: P stoichiometry along a caragana korshinskii restoration gradient on the Loess Plateau, China. *Forests* 11, 823. <https://doi.org/10.3390/f11080823>.
- Zhang, D., Zhou, Z., Zhang, B., Du, S., Liu, G., 2012. The effects of agricultural management on selected soil properties of the arable soils in Tibet. *China Catena* 93, 1–8. <https://doi.org/10.1016/j.catena.2012.01.004>.
- Zhao, H., Sun, J., Xu, X., Qin, X., 2017. Stoichiometry of soil microbial biomass carbon and microbial biomass nitrogen in China's temperate and alpine grasslands. *Eur. J. Soil Biol.* 83, 1–8. <https://doi.org/10.1016/j.ejsobi.2017.09.007>.
- Zhou, H.M., Zhang, D.X., Wang, P., Liu, X.Y., Cheng, K., Li, L.Q., Zheng, J.W., Zhang, X. H., Zheng, J.F., Crowley, D., Zwieten, L.V., Pan, G.X., 2017. Changes in microbial biomass and the metabolic quotient with biochar addition to agricultural soils: a Meta-analysis. *Agric. Ecosyst. Environ.* 239, 80–89. <https://doi.org/10.1016/j.agee.2017.01.006>.