Science of the Total Environment 767 (2021) 145298

Contents lists available at ScienceDirect

Science of the Total Environment

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

Soil carbon accumulation with increasing temperature under both managed and natural vegetation restoration in calcareous soils

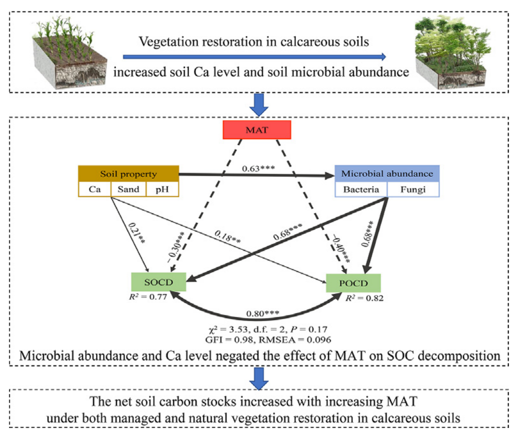
Peilei Hu [a,b], Wei Zhang [a,b,*], Hongsong Chen [a,b], Dejun Li [a,b], Yuan Zhao [a,b,d], Jie Zhao [a,b], Jun Xiao [a,b], Fangji Wu [a,b], Xunyang He [a,b], Yiqi Luo [c], Kelin Wang [a,b,*]

[a] Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, China
[b] Huanjiang Observation and Research Station for Karst Ecosystems, Huanjiang 547100, China
[c] Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86011, USA
[d] University of Chinese Academy of Science, Beijing 100049, China

HIGHLIGHTS

- Managed and natural vegetation restoration were compared along a climatic gradient.
- Both vegetation restoration strategies increased soil carbon stocks in warmer regions.
- Higher temperature shifted soil microbial community structure.
- Restored vegetation had higher microbial abundance and calcium than cropland.
- Microbial abundance and calcium negated effect of temperature on SOC decomposition.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 17 October 2020
Received in revised form 14 January 2021
Accepted 15 January 2021
Available online 22 January 2021

Editor: Jay Gan

Keywords:
Soil organic carbon fraction
Soil microbial community
Calcium
Climatic gradient
Karst ecosystem

ABSTRACT

Vegetation restoration has been proposed as an effective strategy for increasing soil organic carbon (SOC) sequestration. However, the responses of SOC to managed and natural vegetation restoration strategies at a large scale are poorly understood due to the varying SOC components and changing climatic conditions. Here, we measured bulk SOC, particulate organic carbon (POC), and mineral-associated organic carbon (MOC) after 15 years of vegetation restoration along an elevation gradient with a corresponding temperature gradient in the calcareous soils of karst region, Southwest China. We compared managed plantation forest and naturally recovered shrubland vegetation restoration strategies, using cropland and mature forest as references. Overall, we found that the SOC and POC densities in both plantation forest and shrubland were significantly higher than in the cropland but lower than in the mature forest. There were no significant differences in the SOC pool between the plantation forest and shrubland. Furthermore, the relative changes in the SOC and POC densities increased with increasing mean annual temperature in the plantation forest and shrubland. Our results showed that both vegetation restoration strategies, characterized by higher soil microbial abundance and exchangeable Ca concentration, were beneficial to POC but not MOC accumulation, and sufficiently compensated SOC decomposition at lower elevation with higher MAT. Our results highlight the potential of both vegetation restoration strategies for promoting SOC accumulation in warmer karst regions and emphasize the necessity to understand soil carbon stabilization mechanisms in calcareous soils.

* Corresponding authors at: Key Laboratory of Agro-ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, China.
E-mail addresses: zhangw@isa.ac.cn (W. Zhang), kelin@isa.ac.cn (K. Wang).

https://doi.org/10.1016/j.scitotenv.2021.145298
0048-9697/

1. Introduction

Soil is estimated to contain approximately three times more carbon than the atmosphere (Stockmann et al., 2013), and thus soil respiration and the accumulation of soil organic carbon (SOC) are, respectively, a major source and sink of atmospheric carbon dioxide (Davidson and Janssens, 2006). Vegetation restoration has garnered attention mainly because of its ability to sequester carbon, and thus offset anthropogenic carbon emissions and mitigate climate change (Bastin et al., 2019; Wang and Huang, 2020). The restoration of degraded ecosystems at the global scale is one of the main measures to limit the increase in global mean air temperature to below 1.5 °C by 2050 (IPCC, 2018). A recent study showed that one third of Earth's vegetated lands are greening and that ecological restoration is an important driver of the greening earth (Chen et al., 2019a). However, soil carbon accumulation often lags behind plant production and greatly varies in response to different vegetation restoration strategies (Li et al., 2012). Whether the restoration goals are achievable has been questioned because little is known about the responses of SOC to different vegetation restoration strategies under current and future climate conditions.

Managed and natural vegetation restoration are two important strategies to remediate degraded ecosystems. Owing to the differences in management, microclimate, species composition, and plant litter quantity and quality (Laganiere et al., 2010; Shi et al., 2013; Solly et al., 2014), the two restoration strategies may induce distinct profiles of soil microbial growth and activity (Yang et al., 2020a, b), which are likely to cause inconsistent SOC accumulation rates. Additionally, other soil properties, such as soil mineral characteristics and aggregate formation, can also be affected by vegetation restoration strategies (Dou et al., 2020; Zhang et al., 2019), further influencing the capacity of soil to stabilize SOC (Li et al., 2017). However, the effects of both vegetation restoration strategies on SOC accumulation and the regulating factors have been mainly conducted at ecosystem or catchment scales (Hu et al., 2018a, Jin et al., 2014; Wang et al., 2015), and we lack a comprehensive understanding of the responses of SOC to different vegetation restoration strategies at large scales. Given the variation in temperature and precipitation at the regional scale, the capacity of SOC sequestration and its determinants following vegetation restoration may differ from that at the local scale. Specifically, changes in temperature and precipitation affect soil microbial community composition and/or structure (Chen et al., 2016) and thus result in diverse responses of SOC to climatic gradients under different vegetation restoration strategies. However, it is not clear whether the observed patterns of SOC accumulation between managed and natural vegetation restoration at the local scale are also applicable at the regional scale, which contains different climatic gradients.

Furthermore, the fate of SOC following different vegetation restoration strategies under future climate change is difficult to predict due to the varying SOC components (Luo et al., 2020). Specifically, SOC is composed of various functional pools that are characterized by different turnover rates and stabilized by different mechanisms such as the active and stable SOC fractions (Luo et al., 2015). Conceptualizing SOC into particulate organic carbon (POC) and mineral-associated organic carbon (MOC) is considered a suitable way to predict large scale SOC dynamics (Lavallee et al., 2020). A previous study conducted at the local scale found that afforested soils mainly sequestered POC, whereas soils restored with natural vegetation preferentially sequestrated MOC (DeGryze et al., 2004). Additionally, large-scale studies have shown that climatic factors differently influence POC and MOC (Luo et al., 2020). Consequently, POC and MOC may respond differently to changes in temperature or precipitation under managed and natural vegetation restoration strategies, and thus may represent a critical carbon–climate feedback in the long term. However, due to the scarcity of direct SOC measurements from large-scale field sampling, the response of SOC fractions to different vegetation restoration strategies along a climatic gradient at the regional scale remains uncertain, and the main influencing factors remain unknown. This hinders our ability to improve carbon models and to predict the capacity of soils to sequester carbon under future climate change scenarios.

The karst region in Southwest China is important for the exploration of the magnitude and direction of changes in SOC fractions to climatic gradients following vegetation restoration because this region is highly sensitive and vulnerable to changes in climate, has become a hotspot of vegetation restoration (Chen et al., 2019a; Tong et al., 2020), and has substantial temperature differences due to considerable variation in elevation (Wang et al., 2019). The karst ecosystem of Southwest China (>0.54 million km^2) is one of the largest continuous exposed carbonate rock areas globally (Tong et al., 2018). In the context of the "Grain for Green" project, most seriously degraded croplands have undergone vegetation restoration through natural vegetation recovery and active tree planting (Wang et al., 2019). A previous study reported that, in a relatively short period, natural vegetation restoration was more beneficial to SOC sequestration than managed vegetation restoration at the catchment scale (Hu et al., 2018a). However, the regulatory factors that drive the accumulation of SOC following vegetation restoration remain unclear. Furthermore, long-term continuous data indicate the increasing risk and severity of extreme climate events in Southwest China (Liu et al., 2014). However, it remains unclear how the SOC fractions will respond to the climatic gradient under managed and natural vegetation restoration strategies, which increases the difficulty in managing the trade-offs between soil carbon accumulation and adjusting vegetation restoration strategies under future climate change.

To address the abovementioned uncertainties, we compared bulk SOC, POC, and MOC in soils subjected to restoration strategies with managed plantation forest and naturally recovered shrubland vegetation along an elevation gradient with a corresponding climatic gradient typical of the subtropical karst region of Southwest China to those in cropland. We also selected nearby mature forests as references to test the capacity of SOC sequestration and the correlation with the climatic gradient in undisturbed soils. Our aim was to address the following questions: (1) do bulk, active, and stable SOC increase following vegetation restoration, and do they differ between managed and natural vegetation restoration strategies; (2) how do the SOC fractions respond to the climatic gradient after vegetation restoration; and (3) what are the regulatory factors that significantly drive the accumulation of SOC?

2. Materials and methods

2.1. Study region

The study region was located in Guizhou and Guangxi Provinces, Southwest China (22°42′N to 27°53′N; 104°82′E to 108°37′E), and the sampling sites were selected in a karst area typical of the study region (Fig. 1). The elevation of the karst region ranges from 142 m a.s.l. in the south to 2264 m a.s.l. in the northwest. Climate data for 2000–2015 were collected from the National Meteorological Information Center of China (http://data.cma.cn/). The MAT and mean annual precipitation (MAP) in the study region ranges from 12.6 °C to 21.8 °C and 1013 to 1607 mm yr^{-1}, respectively (Table A.1). Along the transect, MAT is considerably negatively correlated with elevation ($r = -0.91$), i.e., MAT increases from the northwest to the south. The lithology in the karst regions is dolomite, limestone, and their mixtures. The soil is calcareous lithosols (limestone soil) according to the FAO/UNESCO classification system or entisols in the U.S. Soil Taxonomy.

Before the 1990s, a large portion of the karst ecosystems was severely degraded by increased intensive agricultural activities. Since 2002, under the "Grain for Green" project, most croplands in the degraded karst regions have undergone ecological restoration through either managed tree plantations or natural vegetation regeneration.

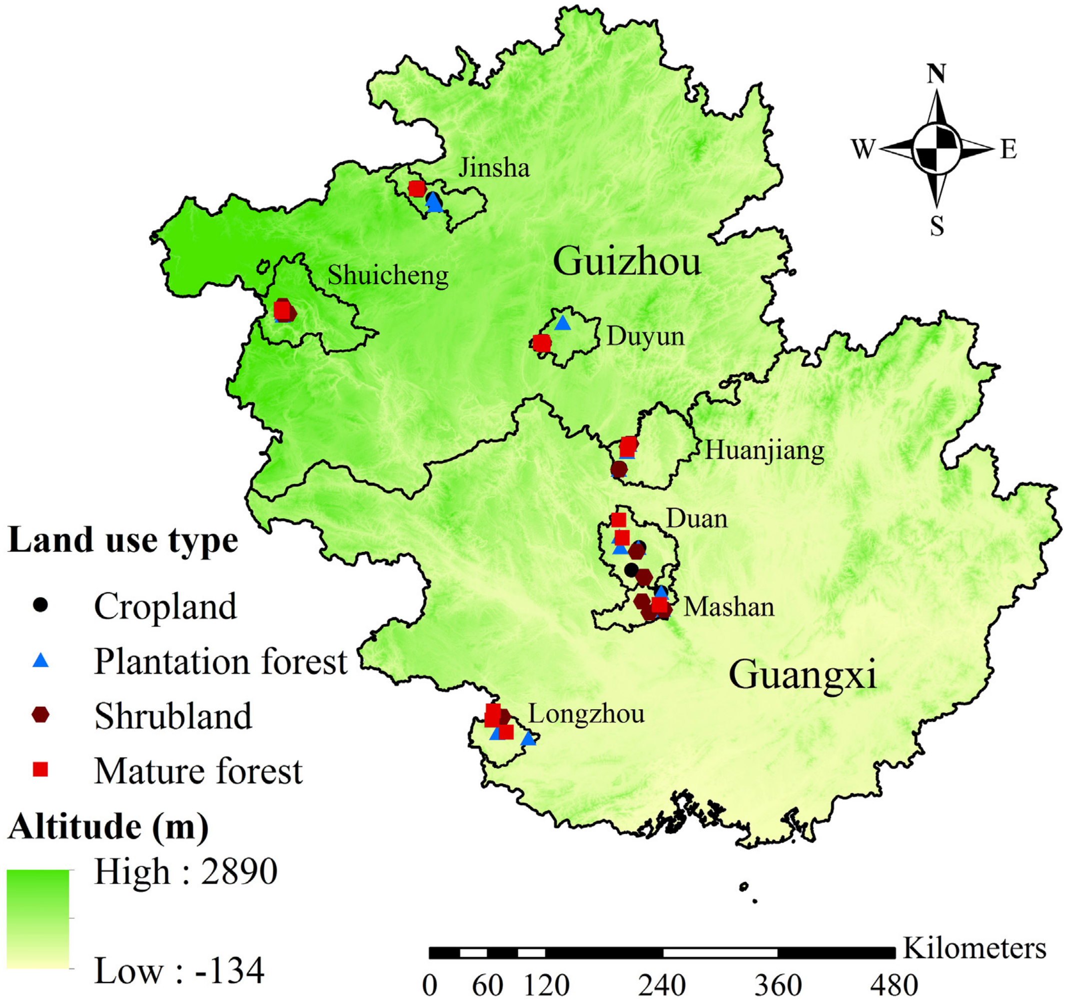


Fig. 1. Spatial distribution of field sampling sites in the karst region in Guizhou and Guangxi Provinces, Southwest China.

2.2. Experimental design

The field investigation and soil sampling were conducted from August to October 2018. Soil samples were collected from Shuicheng, Jinsha, and Duyun in Guizhou Province and Huanjiang, Duan, Mashan, and Longzhou in Guangxi Province (Fig. 1). Four land-use types, namely cropland, plantation forest, shrubland, and mature forest, were selected in each county with three replicates (84 sampling sites in total: 7 counties, 4 land-use types, and 3 replicates of each land-use type in each county). The land-use types were selected based on the following criteria. (1) The sites had to have the same history and duration of land-use type along the climatic gradient, which was determined using data from the local forestry administration. The cropland must have been under maize cultivation for at least 100 years. The plantation forest and shrubland sites were previously cropland and restored by tree plantation and natural vegetation regeneration since 2002–2003, respectively, with about 15 years of restoration before sampling. The mature forest represented subclimax vegetation that had been preserved for approximately 60 years. (2) The sites must have had the same geochemical background and soil types as other selected sites. (3) The sites must have been located in the foot slope because this is where ecological engineering mainly occurred. (4) The slope gradient was typically 15°–20° with a south or southeast aspect. The distance between any two sampling locations within the same county was normally <10 km, except in some cases where the distance was approximately 50 km (Fig. 1). The MAT, MAP, altitude, and dominant species of the selected land-use types are presented in Table A.1. Soil physicochemical and microbial properties of the land-use types are presented in Table 1.

In each sampling site, a plot of 30 m × 30 m was established. An apparent organic layer was absent in most sampling sites; thus this layer was not sampled. As only the shallow soil layer could be found in most sampling sites, mineral soils were collected from the 0–15 cm layer after removing the organic layer where present. In each plot, 20 soil cores (38 mm in diameter) were collected randomly and pooled. Stones and roots were removed from the soil samples by using a pair of tweezers, and then soils were sieved through a 2-mm mesh. Each soil sample was divided into three subsamples: one stored at −20 °C before soil microbial community analysis, and the soil samples stored in the freezer were immediately transported to the laboratory for analysis after the soil was sampled in each county to guarantee that the storage time was <1 week; one air-dried and used to separate different SOC fractions and measure the organic carbon concentration; and one air-dried and used to measure bulk SOC and other soil physicochemical properties.

2.3. Soil physicochemical analyses

Soil bulk density (BD) for each sampling site (10 replications) was determined by collecting soil in a steel ring (volume: 100 cm^3) and weighing it after oven drying at 105 °C to a constant weight. Bulk SOC concentration was measured by wet oxidation using the dichromate redox colorimetric method (Nelson et al., 1996). The carbon isotope ratio of SOC (δ^{13}C-SOC, ‰) was analyzed using a MAT 253 isotope-

Table 1
Soil physical and chemical properties under different land-use types along a climatic gradient in a subtropical karst region in Southwest China.

	CR	PF	SH	MF
pH (H_2O)	6.51 (0.20)	6.63 (0.16)	6.42 (0.15)	6.47 (0.17)
BD (g cm^{-3})	1.21 (0.04) ab	1.28 (0.03) a	1.15 (0.03) b	0.99 (0.04) c
Clay (%)	30.9 (5.9)	26.5 (4.9)	22.7 (4.3)	20.9 (4.2)
Silt (%)	48.0 (4.2)	49.0 (2.7)	46.5 (3.1)	48.1 (2.8)
Sand (%)	21.0 (4.3) b	24.5 (3.0) ab	30.8 (4.1) a	31.0 (4.0) a
SOC (g kg^{-1})	20.13 (1.72) c	29.9 (2.76) b	32.85 (2.64) b	50.96 (4.60) a
TN (g kg^{-1})	2.14 (0.19) c	2.85 (0.22) b	3.04 (0.25) b	4.65 (0.39) a
C:N	9.6 (0.3) b	10.5 (0.4) ab	10.8 (0.4) a	11.0 (0.3) a
Ca (cmol kg^{-1})	19.95 (2.84) b	26.46 (2.57) b	23.28 (2.58) b	35.65 (3.05) a
Mg (cmol kg^{-1})	4.48 (0.73) b	6.74 (1.26) ab	6.34 (1.19) ab	9.37 (1.78) a
Bacteria (nmol g^{-1})	25.44 (1.83) c	48.71 (4.54) b	55.39 (5.26) b	85.08 (7.99) a
Fungi (nmol g^{-1})	3.58 (0.27) c	7.08 (0.54) b	7.61 (0.46) b	10.88 (0.97) a
F:B	0.14 (0.01)	0.15 (0.01)	0.15 (0.01)	0.13 (0.01)
GP:GN	1.49 (0.11) a	1.29 (0.06) b	1.21 (0.05) b	1.20 (0.05) b

Note: CR, cropland; PF, plantation forest (managed vegetation restoration); SH, shrubland (natural vegetation restoration); MF, mature forest; pH, soil pH value; BD, soil bulk density; SOC, soil organic carbon; TN, soil total nitrogen; C:N, ratio of SOC to soil TN; Ca, soil exchangeable Ca^{2+}; Mg, soil exchangeable Mg^{2+}; Bactria, the abundance of bacterial PLFAs; Fungi, the abundance of fungal PLFAs; F:B, ratio of fungal to bacterial PLFAs; GP:GN, ratio of Gram-positive to Gram-negative bacterial PLFAs. The values are presented as means with standard errors in parentheses. Different letters represent significant differences among the land-use types at $P < 0.05$. There were no significant differences in pH, clay, silt, and F:B among the four land-use types.

ratio mass spectrometer (Thermo Finnigan MAT, Bremen, Germany) after the removal of carbonate carbon using H_3PO_4 (Bernard et al., 1995). Size fractionation was performed to isolate SOC into POC (>53 μm) and MOC (<53 μm) as described by Franzluebbers and Arshad (1997). Briefly, 10 g of soil was dispersed in 30 mL of sodium hexametaphosphate solution (5 g L^{-1}) for 4 h by shaking in a reciprocating shaker. The dispersed soil suspension was passed through a 53-μm mesh after rinsing several times with distilled water. All materials remaining on the mesh were considered the particulate organic fraction, whereas the other materials were considered the mineral-associated organic fraction. The particulate and mineral-associated materials were dried at 55 °C to a constant weight. Organic carbon in both fractions was then analyzed using the same method as that used to determine bulk SOC. Bulk soil total nitrogen concentration was measured using an elemental analyzer (vario MAX; Elementar, Hanau, Germany). Soil exchangeable Ca and Mg were displaced via compulsive exchange in 1 M ammonium acetate of pH 7.0, and then analyzed by ICP-OES (Agilent, Santa Clara, CA, USA). Soil pH (10 g of soil in 25 mL of water) was measured using a pH meter (FE20K; Mettler-Toledo, Greifensee, Switzerland). Soil texture (clay, silt, and sand) was measured using a laser diffraction particle size analyzer (Mastersizer 2000; Malvern Instruments Ltd., Malvern, UK) after the removal of soil organic matter (SOM) and carbonates by hydrogen peroxide and hydrochloric acid, respectively (Chen et al., 2019a, b).

2.4. Soil microbial community abundance and composition analyses

The phospholipid fatty acid (PLFA) approach was used to assess soil microbial community abundance and composition (Qin et al., 2019). Soil water content was determined by weighing the soil sample before and after oven drying at 105 °C to a constant weight. Soils were not overly wet when sampled from each site, so the PLFAs were extracted from 8 g of fresh soil and analyzed as described by Bossio and Scow (1998). The abundance of bacterial PLFAs was calculated as the total abundance of i14:0, a15:0, i15:0, i16:0, 16:1ω7c, 17:0, a17:0, i17:0, cy17:0, 18:0, 18:1ω7c, and cy19:0 (Li et al., 2018a). The abundance of gram-positive bacterial PLFAs was represented as the sum of i14:0, a15:0, i15:0, i16:0, a17:0, and i17:0, whereas that of gram-negative bacterial PLFAs was represented by the sum of 16:1ω7c, cy17:0, 18:1ω7c, and cy19:0 (Li et al., 2018a). The abundance of fungal PLFAs was calculated as the sum abundance of 18:1ω9c and 18:2ω6,9c (Chung et al., 2007). In addition, the ratio of gram-positive to gram-negative bacterial PLFAs (GP:GN) and fungal to bacterial PLFAs (F:B) was calculated and used to assess the soil microbial community structure.

2.5. Calculations and statistical analysis

Soil organic carbon density (SOCD, kg m^{-2}) in the topsoil (0–15 cm) was calculated as follows:

$$SOCD = \frac{SOC \times BD \times D \times (1-C)}{100}$$

where, SOC is the SOC concentration (g kg^{-1}), BD is the soil bulk density (g cm^{-3}), D is the soil depth (D = 15 cm), and C is the coarse particle concentration (>2 mm, %).

To determine the rate of change in SOC along the climatic gradient following vegetation restoration, the relative stock change in SOC (%) following vegetation restoration was calculated using the following equation:

$$\text{Relative stock change of SOC} = \frac{SOCD_{VR} - SOCD_{CR}}{SOCD_{CR}} \times 100$$

where, $SOCD_{VR}$ and $SOCD_{CR}$ are the SOCD (kg m^{-2}) of vegetation restoration sites and cropland, respectively. Similarly, POC density (POCD) and MOC density (MOCD), and the relative changes in POC and MOC stocks following vegetation restoration were calculated using the above equations.

The data were checked for normal distribution and homogeneity of variance before analysis. A one-way analysis of variance with the least significant difference in multiple comparisons was used to test the effects of land-use type on soil physicochemical and microbial properties and SOC fractions. Regression models were used to determine the relationships of relative stock change in the SOC fractions, δ^{13}C-SOC, and soil microbial community structure (GP:GN ratio) with MAT. The statistical analyses were carried out using SPSS 18.0 (SPSS Inc., Chicago, IL, USA) and OriginPro 2020 (OriginLab, Hampton, MA, USA).

Variance partitioning was conducted to analyze the influence of explanatory variables on the SOC accumulation. A few explanatory variables were significantly correlated with MOCD, and MOCD was regarded as a stable SOC pool with a slow turnover rate. Thus, only SOCD and POCD were considered in the variance partitioning. The statistical analysis was carried out using Canoco 5.0 (Centre for Biometry, Wageningen, the Netherlands) and was determined using the Monte Carlo permutation method based on 999 runs with randomized data.

Soil texture (clay, silt, and sand), physicochemical properties (pH and exchangeable Ca and Mg), and microbial community abundance (bacteria and fungi) and structure (F:B and GP:GN) were analyzed to determine if they were correlated with the SOC fractions (Fig. A.1). The results showed that the soil property group and microbe group were the main factors significantly correlated with SOC (Fig. A.1). To determine the role of the above listed soil and microbial properties on SOC accumulation along the climatic gradient, a partial correlation analysis was conducted to evaluate the relationship between the SOC fractions and MAT after controlling the soil and microbial properties separately and in combination. Pearson's correlation analysis was conducted using the packages corrplot and psych, and partial correlation analysis was conducted using ggm, psych, and ComplexHeatmap in R v.3.5.2.

The direct and indirect relationships among the SOC fractions, MAT, soil properties, and soil microbial abundance were evaluated using structural equation modeling (SEM). Owing to the strong correlations among variables in the soil property group (i.e., soil exchangeable Ca, sand, and pH) and between variables in the soil microbe group (i.e., fungal and bacterial abundance), we developed a multivariate functional index through principal component analysis before SEM

(Chen et al., 2019b). The first principle component (PC1), which explained 42.7% and 97.5% of the total variance in soil property and soil microbe groups, respectively, was introduced in the subsequent analysis as a new variable to represent the combined group properties. To simplify the model, only SOCD and POCD were used because they were found to be the major response variables to soil properties according to the Pearson's correlations. Based on prior knowledge, an initial meta-model was constructed for evaluation (Fig. A.2). The SEM fit was evaluated using *P*-values, chi-squared values, goodness-of-fit index, and root mean square error of approximation. The SEM was conducted using the Amos 18.0 software package (Amos Development Corporation, Chicago, IL, USA). Unless otherwise specified, the results were considered to be significant at $P < 0.05$.

3. Results

3.1. Overall effects of vegetation restoration on SOC accumulation

Both vegetation restoration strategies significantly increased SOCD. Specifically, SOCD in the plantation forest and shrubland was significantly higher by 53% and 54% on average, respectively, relative to the SOCD in the cropland, but was significantly lower than the SOCD in the mature forest (Fig. 2a). Conversely, the δ^{13}C-SOC was the highest in the cropland, intermediate in the plantation forest and shrubland, and lowest in the mature forest (Fig. 2b). Furthermore, SOCD and δ^{13}C-SOC in the shrubland were not significantly different from those in the plantation forest (Fig. 2a and b).

POCD exhibited a similar pattern as SOCD, in that POCD significantly increased by 97% and 123% on average in the plantation forest and shrubland, respectively, relative to POCD in the cropland (Fig. 2c). There was no significant difference in POCD between the plantation forest and shrubland. The difference in MOCD among the four land-use types was not significant (Fig. 2d). The POC:SOC ratio significantly increased from cropland to plantation forest to shrubland and mature forest, whereas the MOC:SOC ratio decreased (Fig. 2e and f).

3.2. Changes in the SOC fractions along the climatic gradients

The correlations between the SOC fractions and climatic factors (MAP and MAT) were inconsistent among the land-use types (Table 2). The δ^{13}C-SOC in the cropland, plantation forest, and shrubland significantly increased with increasing MAT, but this was not observed in the mature forest. For the SOC pool density, SOCD and POCD in the cropland significantly decreased with MAT and MAP, whereas no significant correlation was observed in the plantation forest, shrubland, and mature forest. In contrast, the MOCD in the plantation forest, shrubland, and mature forest significantly increased with MAT (Table 2). With respect to the proportion of SOC fractions, generally, the POC:SOC and POC:MOC ratios decreased with MAT, whereas the MOC:SOC ratio increased.

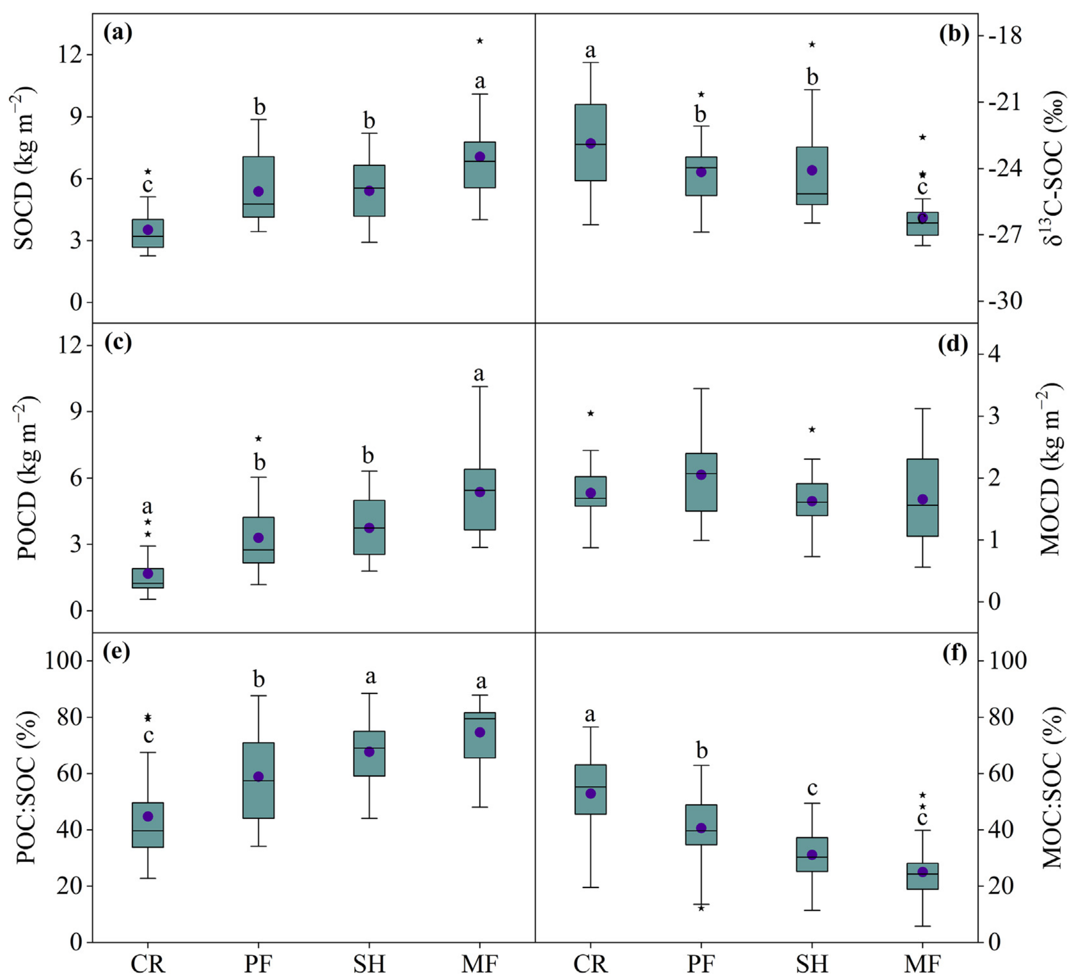


Fig. 2. Effect of land-use type on (a) soil organic carbon density (SOCD), (b) carbon isotope ratio of SOC (δ^{13}C-SOC), (c) particulate organic carbon density (POCD), (d) mineral-associated organic carbon density (MOCD), (e) proportion of POC in SOC (POC:SOC), and (f) proportion of MOC in SOC (MOC:SOC). The ends of the boxes represent the 25th and 75th percentiles, and the central lines and purple dots represent the medians and means, respectively. The maximum whisker length is 1.5 times the interquartile range, and outliers are marked with a pentagram. Different letters represent significant differences among the land-use types at $P < 0.05$. CR, cropland; PF, plantation forest (managed vegetation restoration); SH, shrubland (natural vegetation restoration); MF, mature forest.

Table 2
Pearson's correlation between SOC fractions and climatic factors (MAP and MAT) based on land-use type.

Land-use type	Climatic factor	δ13C-SOC	SOCD	POCD	MOCD	POC:SOC	MOC:SOC	POC:MOC
CR	MAP	0.46*	−0.55*	−0.51*	−0.07	−0.42	0.47*	−0.30
	MAT	0.85**	−0.63**	−0.76**	0.23	−0.70**	0.73**	−0.66**
PF	MAP	0.32	−0.30	−0.30	0.08	−0.29	0.36	−0.23
	MAT	0.45*	−0.15	−0.35	0.51*	−0.48*	0.52*	−0.52*
SH	MAP	0.65**	−0.11	−0.11	0.06	−0.11	0.30	−0.20
	MAT	0.44*	0.00	−0.16	0.47*	−0.40	0.53*	−0.49*
MF	MAP	0.25	0.29	0.12	0.59**	−0.35	0.34	−0.30
	MAT	0.25	−0.15	−0.29	0.59*	−0.45*	0.52*	−0.62**

Note: CR, cropland; PF, plantation forest (managed vegetation restoration); SH, shrubland (natural vegetation restoration); MF, mature forest; MAP, mean annual precipitation; MAT, mean annual temperature; SOC, soil organic carbon; SOCD, soil organic carbon density; POCD, particulate organic carbon density; MOCD, mineral organic carbon density; POC:SOC, percentage of POC relative to total SOC; MOC:SOC, percentage of MOC relative to total SOC; POC:MOC, ratio of POC to MOC.
* Indicates significant difference at $P < 0.05$.
** Indicates significant difference at $P < 0.01$.

The relative changes in the SOC and POC stocks after the implementation of the two vegetation restoration strategies increased as MAT increased. Generally, the changes were significantly higher than zero in the regions where MAT was higher than 16 °C (Fig. 3). Moreover, the relative changes in the SOC or POC stock in each MAT region showed no significant differences between managed and natural vegetation restoration.

3.3. Determinants of SOC accumulation following vegetation restoration

Generally, soil microbial abundance, Ca, and sand were the main factors positively correlated with SOCD and POCD (Fig. A.1). Variance partitioning further indicated that these variables together explained most of the variation in SOCD and POCD (Fig. 5). Among them, soil bacterial abundance and fungal abundance were the primary variables. Consequently, significantly higher bacterial and fungal abundance, Ca concentration, and sand proportion (Table 1) could be responsible for the higher SOCD and POCD in plantation forest, shrubland, and mature forest.

3.4. Determinants of SOC accumulation along the climatic gradient

The partial correlation analysis results further supported the importance of soil microbial abundance and Ca concentration (Fig. 6). Specifically, slight changes were observed in the strength of the correlations between the SOC fractions and MAT in cropland without (zero-order correlation) or with controlling the soil microbial abundance or Ca concentration (Fig. 6a). No significant correlations between SOCD and POCD and MAT were observed in the plantation forest, shrubland, and mature forest without controlling any variables. However, the MAT was negatively correlated with SOCD and POCD after controlling the effect of soil microbial abundance or Ca concentration, especially after controlling soil microbial abundance (Fig. 6b–d). Our findings highlight that high soil microbial abundance and Ca concentration in vegetation restoration sites could negate the effect of MAT on SOC decomposition in restored vegetation types.

The SEM analyses comprehensively revealed the determinants of SOC dynamics along the climatic gradient in the karst region (Fig. 7). Higher MAT decreased SOCD and POCD, whereas higher soil microbial abundance and soil Ca concentration increased SOCD and POCD (Fig. 7). Of the factors evaluated in the study, soil microbial abundance had the largest direct effect, whereas soil properties had the largest indirect effects through their associations with soil microbial abundance. Additionally, the soil properties also exerted direct effects on SOC accumulation.

Our statistical analyses showed that under both vegetation restoration strategies, higher soil microbial abundance and exchangeable Ca concentration increased the accumulation of SOC, which exceeded the decomposition of SOC caused by increased MAT. Consequently, the relative changes in SOC and POC stocks increased as MAT increased.

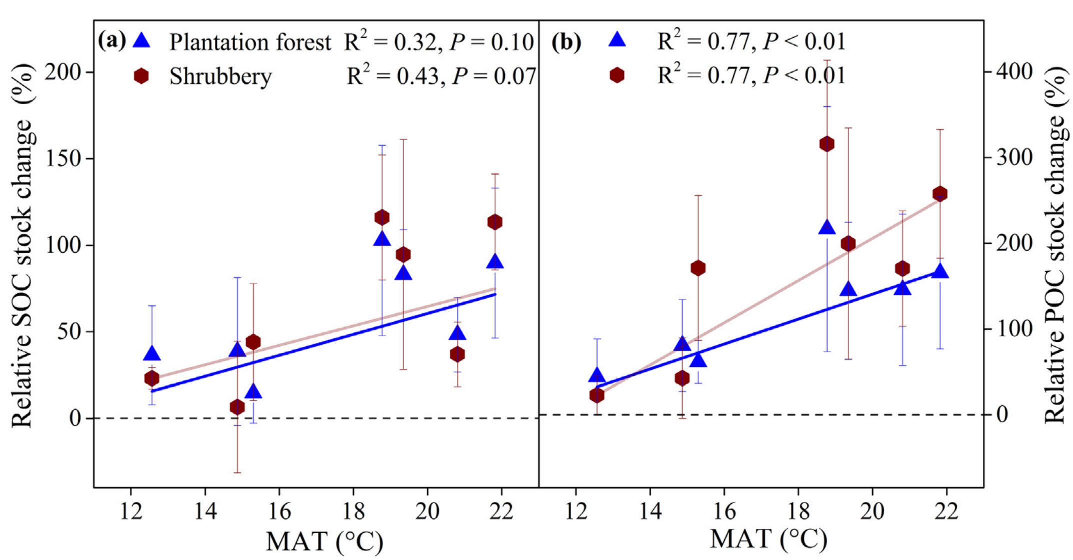


Fig. 3. Regression analysis of relative stock change in (a) soil organic carbon (SOC) and (b) particular organic carbon (POC) following managed (plantation forest) and natural vegetation restoration (shrubland) in comparison with the cropland with increasing mean annual temperature (MAT). The error bars represent the 95% confidence intervals (CI) of the means (95% CI). The observed effect sizes were considered statistically different from zero when the 95% CI did not include zero, and the effects of plantation forest and shrubland on relative SOC or POC stock change were considered significantly different when the 95% CI did not overlap.

4. Discussion

4.1. Effect of vegetation restoration on SOC accumulation

Relative to the cropland, SOCD and POCD significantly increased under both managed and natural vegetation restoration after approximately 15 years of cropland abandonment (Fig. 2a). The average accumulation rate of SOC following vegetation restoration in our study was relatively higher than the average value in China (Deng and Shangguan, 2017) or the world (Li et al., 2012). This result is consistent with that reported previously at the catchment scale (Hu et al., 2018b). In contrast, MOCD showed no significant differences among the four land-use types. Here, MOC (<53 μm, silt and clay associated carbon) was regarded as a stable SOC pool, which could persist for decades to centuries due to physical, chemical, and biological constraints, and is less sensitive to land-use changes (Six et al., 2002). POC (>53 μm, including free and occluded carbon in aggregates) is determined mainly based on the balance between carbon input (e.g., plant residues and root exudates) and carbon output (e.g., decomposition, leaching, and erosion) (Luo et al., 2020). Tillage in the karst region mainly disrupts large macroaggregates, resulting in a decline in the physical protection of SOC (Ye et al., 2020), which accelerates the decomposition and loss of the active SOC pool. Additionally, less active carbon fractions in soil usually leads to higher microbial carbon limitation, and a large portion of stable carbon remains undecomposed (Blagodatskaya and Kuzyakov, 2013; Fontaine et al., 2007). Consequently, compared with restored vegetation types and mature forest, POCD was lower but MOCD remain unchanged in cropland.

Our results demonstrated that SOC accumulation following vegetation restoration was primarily influenced by soil microbial abundance. Although soil microorganisms can decompose SOM and promote soil carbon release into the atmosphere, they can also promote SOC formation by ex vivo modification and in vivo turnover (Liang et al., 2017; Schimel and Schaeffer, 2012). For ex vivo modification, plant materials and residues can be deposited as SOM through microbial extracellular enzymes. Through the in vivo turnover pathway, microbial-derived carbon can accumulate in soil through microbial uptake, assimilation, growth, and death, and microbial necromass can account for more than half of the total SOC pool (Liang et al., 2019). A previous study reported that soil microbial necromass in karst soils is usually determined by living microbial biomass (Huang et al., 2019). As a result, significantly higher bacterial and fungal abundance in the restored vegetation sites increases the contribution of microbial necromass to SOC. However, the contribution of soil microbial abundance to MOC accumulation was negligible, which was mainly because soil aggregate formation functions differently between calcareous soils and other soil types. Specifically, because of the dissolution and re-precipitation phenomena in calcareous soils, carbonate precipitation accumulates secondary carbonate crystals that fill the pores of macroaggregates or the surface of SOC (Fernández-Ugalde et al., 2014) and prevents the disruption of soil macroaggregates to microaggregates and mineral-associated fractions (Rowley et al., 2018). For example, compared with non-calcareous soil, the transfer of SOC from macroaggregates to microaggregates and the destabilization of macroaggregates upon SOC degradation were negligible in calcareous soil (Fernández-Ugalde et al., 2011). Therefore, significantly higher bacterial and fungal abundance is primarily responsible for the higher POCD and has negligible contribution to MOCD in the restored vegetation types in the karst region.

Our results also demonstrated that soil exchangeable Ca concentration and sand proportion could contribute to SOC and POC accumulation. Soil exchangeable Ca has a positive effect on the formation and stability of aggregates, and thereby indirectly promotes the occlusion and accumulation of SOC (Wiesmeier et al., 2019). Although soil exchangeable Ca may also stabilize and constrain SOC decomposition by forming inner- and outer-sphere cation bridges, the stabilization of SOC by cation bridging is expected to be weak when the soil pH is near neutral (Rowley et al., 2018). This weak stabilization may explain the negligible effect of soil exchangeable Ca on MOC in the restored vegetation types. Soil sand was another factor affecting SOC accumulation. Soil carbon sequestration of fresh organic matter begins in the large particle fraction (Liu et al., 2018), and the sand fraction helps sequester the active carbon pool (von Luetzow et al., 2007). Thus, we conclude that the higher soil exchangeable Ca concentration and sand proportion in restored vegetation types than in the cropland could also be beneficial for soil aggregate-associated carbon, but not for mineral-associated carbon.

The differences in the capacity of soil for carbon sequestration under managed and natural vegetation restoration strategies have been extensively studied (Reid et al., 2018). However, controversies stem from the contribution of the many factors that affect soil carbon sequestration, such as climate, study site characteristics, and plant species (Reid et al., 2018). No significant differences in the SOC pool between the two vegetation restoration strategies might be related to the marginal differences in soil physicochemical properties and the soil microbial community abundance and structure between the strategies (Table 1). However, our previous study revealed that after nine years of restoration, natural vegetation restoration resulted in a significantly higher SOC accumulation rate than what was observed under managed vegetation restoration (Hu et al., 2018a). The inconsistencies between these results were mainly due to the differences in the duration of vegetation restoration. During the initial stages of restoration, the majority of carbon in the plantation forest was likely retained as standing biomass rather than being sequestered in soil (Eclesia et al., 2016). In the later stages, SOC in the plantation forest will likely increase when the carbon input from vegetation is sufficient to compensate for the decomposition of soil carbon (Laganiere et al., 2010; Wang and Huang, 2020). Thus, as vegetation restoration progresses, soil microbial communities and carbon pools in the plantation forest are expected to approximate those in naturally restored vegetation in the karst region. Our findings highlight the importance of the duration of vegetation restoration when comparing managed and natural vegetation restoration strategies in the karst region.

4.2. Influence of climatic factors on SOC accumulation following vegetation restoration

We found that SOC was more sensitive to temperature than precipitation in the karst region in Southwest China. Whether the variability in SOC was more closely related to MAT or MAP remains unclear given the differences in the results of previous studies (Chen et al., 2015; Xin et al., 2020), and it depends on the climatic zones (Wang and Huang, 2020). Precipitation may not have limited plant growth or soil microbial activity in our study because all the study sites received a substantial amount of precipitation (MAP > 1000 mm). In contrast, temperature among the study sites substantially differed due to the wide range in elevation (Table A.1). Therefore, we infer that temperature is a more important driver of soil carbon than precipitation via its effects on plant growth and soil microbial activity in the subtropical karst region.

Our results also indicated that both vegetation restoration strategies could increase the net soil carbon stocks at lower elevation with higher MAT in the subtropical karst region. This increase can be attributed to the different responses of SOC to MAT in the cropland and restored vegetation sites. Usually, higher temperature promotes soil microbial activity and stimulates the net loss of soil carbon to the atmosphere (Crowther et al., 2016; Zhao et al., 2019). We found that MAT can significantly shift the soil microbial community structure, i.e., positively affect the GP:GN ratio in all four land-use types (Fig. A.3). A previous field-warming experiment also revealed that soil warming significantly increased the GP:GN ratio (Jing et al., 2019). Compared with Gram-negative bacteria, Gram-positive bacteria have thicker walls and better

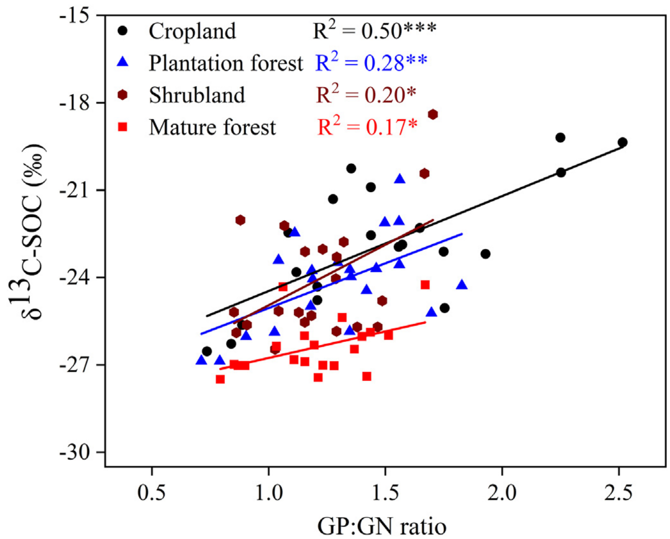


Fig. 4. Regression analysis of the ratio of gram-positive to gram-negative bacterial phospholipid fatty acids (PLFAs) (GP:GN ratio) and carbon isotope ratio of soil organic carbon (δ^{13}C-SOC) for different land-use types. *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$.

osmoregulatory ability and thus, have better adaptability in higher-temperature regions (Drenovsky et al., 2010; Yu et al., 2018). Therefore, the GP:GN ratio would theoretically increase with increasing MAT. Gram-positive bacteria use more SOM-derived carbon sources, whereas Gram-negative bacteria use more plant-derived carbon sources, suggesting that the two groups play different functional roles in the decomposition of SOM (Fanin et al., 2019). Thus, a higher GP:GN ratio means that Gram-positive bacteria dominate the bacterial community in higher MAT regions, and would probably accelerate the turnover of active SOC. This conclusion was further supported by the positive correlation between the GP:GN ratio and δ^{13}C-SOC in each land-use type in our study (Fig. 4). The less negative value of δ^{13}C-SOC in the same land-use type indicated that SOC was more intensively decomposed by microorganisms (Guillaume et al., 2015). Furthermore, the GP:GN ratios among the four land-use types were similar at the lowest MAT (12.6 °C); however, the slope of the regression between the GP:GN ratio and MAT was higher in the cropland than in the other three land-use types (Fig. A.3). Consequently, higher GP:GN in warmer cropland may accelerate soil carbon decomposition such that less active carbon is retained in soils.

Increased SOC accumulation driven by higher soil microbial abundance and exchangeable Ca concentration following vegetation restoration could negate the effect of increasing MAT on SOC decomposition. For example, higher MAT would probably promote the turnover of soil microbes, and then lead to higher microbial residues accumulated in soils following vegetation restoration at lower elevation with higher MAT (Yang et al., 2020a, b). Carbonate precipitation in calcareous soils could prevent the formation and association of SOC with the mineral fraction and lead to the contribution of soil microbial abundance and Ca concentration to POC but not to MOC accumulation. However, the stability of SOC in aggregates could also be high in calcareous soils without disturbance. The high stability could be because inorganic binding agents (carbonates) and carbonate precipitation in calcareous soils make the pore space in soil aggregates less habitable and reduce the accessibility of SOC to microorganisms (Fernández-Ugalde et al., 2014; Ye et al., 2020). Both vegetation restoration strategies help stabilize SOC in soil aggregates, as indicated by the linear relationship between δ^{13}C-SOC and the log-transformed SOC concentration (Fig. A.4). Specifically, the slope of the regression between the δ^{13}C value and log-transformed SOC concentration, termed β, was regarded as a proxy for SOC turnover rates, and more negative β values (i.e., steeper slopes) were usually associated with higher SOC turnover rates (Guillaume et al., 2015; Li et al., 2020). The β value in the cropland was more negative than that in the plantation forest and shrubland (Fig. A.4), which indicated that the turnover and decomposition rates decreased following vegetation restoration. In addition to the above mechanisms, plant litter and root carbon might also partially compensate the positive effect of MAT on SOC decomposition. For example, higher temperature has been reported to increase the input of plant carbon to soil (Zhou et al., 2012). Future studies should incorporate plant, soil, and microbial properties to fully understand these mechanisms. Overall, the observed responses of SOC to temperature change following vegetation restoration could result from the balance between increased carbon input and decreased carbon decomposition.

4.3. Implications for future vegetation restoration

To the best of our knowledge, our study is the first to explore the effects of both managed and natural vegetation restoration strategies on

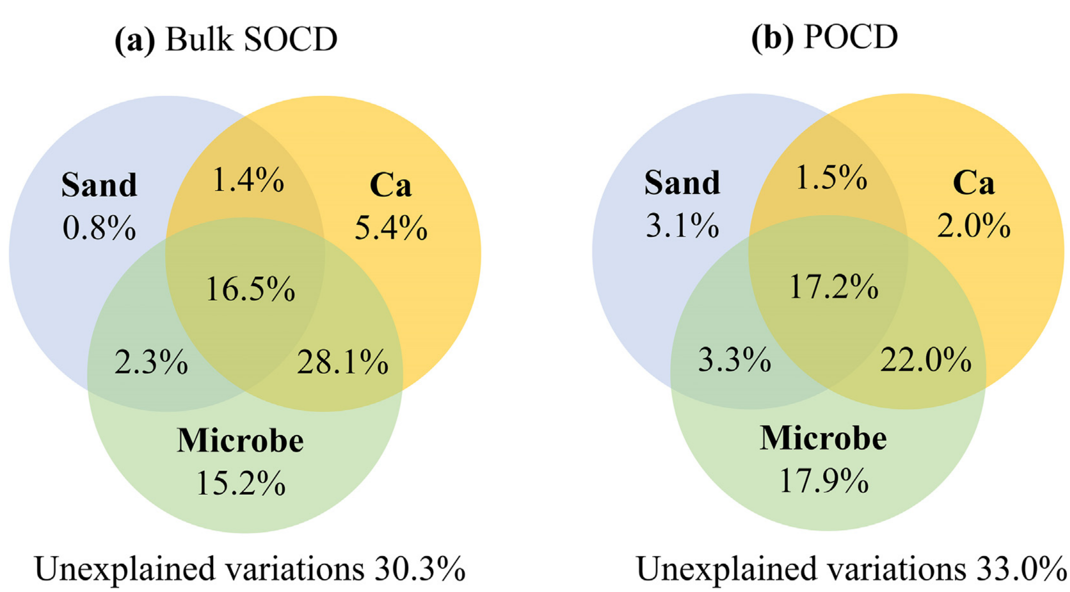


Fig. 5. Variance partitioning for (a) bulk soil organic carbon density (SOCD) and (b) particulate organic carbon density (POCD). Variation was partitioned into the following fractions: pure and joint effect of sand, Ca, and soil microbes and unexplained variations. Soil microbes include two variables, i.e., the bacterial and fungal abundance. Ca, soil exchangeable Ca^{2+} concentration; sand, soil sand proportion.

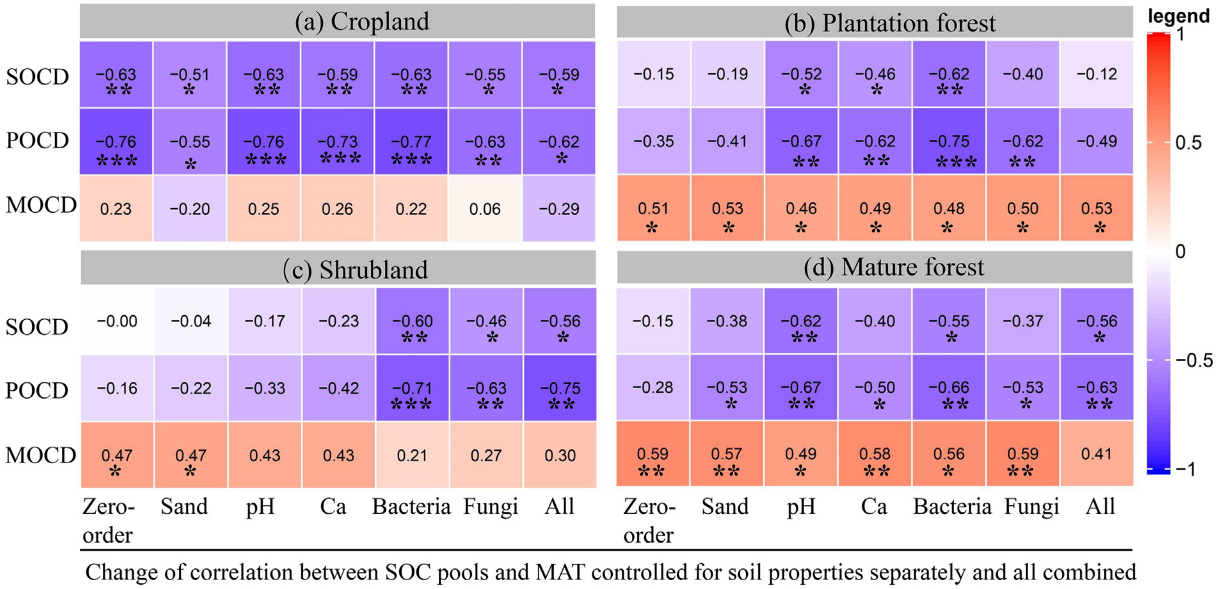


Fig. 6. Partial correlations between the SOC fractions and mean annual temperature (MAT) after controlling the related soil properties in (a) cropland, (b) plantation forest, (c) shrubland, and (d) mature forest. The x-axis shows the zero-order (without controlling any factors) and factors being controlled separately and all combined (column "all"). The y-axis shows the variables (SOCD: soil organic carbon density, POCD: particulate organic carbon, MOCD: mineral-associated organic carbon density) that correlated with MAT. The color and numbers shown indicate the strength and sign of correlation. *$P < 0.05$; **$P < 0.01$; *$P < 0.001$.

the SOC fractions along a climatic gradient in karst regions. We observed that, at the regional scale, both vegetation restoration strategies followed the "Field of Dreams" expectation (Strickland et al., 2017), which is that aboveground vegetation restoration was accompanied by the restoration of belowground soil properties. Additionally, after approximately 15 years of vegetation restoration, SOC and soil microbial community abundance were still considerably lower than those in the mature forest, which suggested that both vegetation restoration

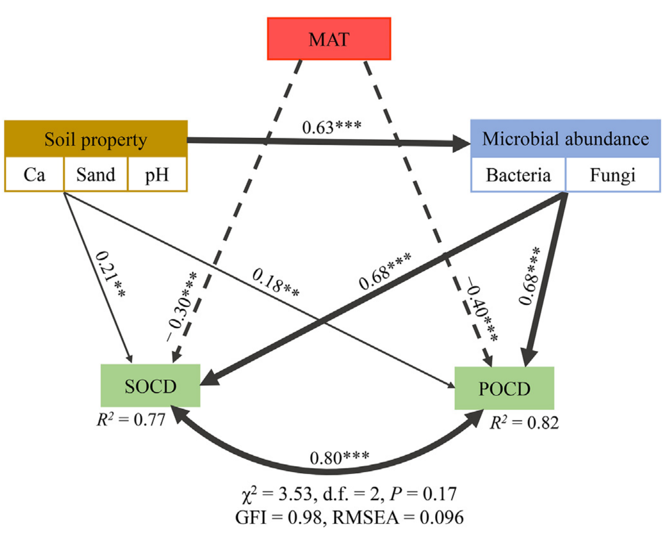


Fig. 7. Structural equation model showing the effects of mean annual temperature (MAT), soil properties, and soil microbial abundance on bulk soil organic carbon density (SOCD) and particulate organic carbon density (POCD). Solid and dotted arrows indicate positive and negative relationships, respectively. The numbers adjacent to the arrows are the standardized path coefficients, and the arrow width indicates the strength of the standardized path coefficient. Multi-layer rectangles represent the first component from the principal component analysis of soil properties and microbial abundance. Soil properties included exchangeable Ca^{2+} (Ca) concentration, sand proportion, and soil pH. Soil microbial abundance included bacterial and fungal abundance. R^2 values represent the proportion of variance in SOCD and POCD explained by the selected variables. χ^2, chi-square values; d.f., degree of freedom; GFI, goodness-of-fit index; RMSEA, the root mean square error of approximation.

strategies may require at least decades to reach the carbon storage potential of the mature forest. Furthermore, our results indicated that net soil carbon stocks increased with increasing MAT after vegetation restoration. Together, these findings imply that vegetation restoration in the warmer karst region increased the carbon sequestration potential of soils, and thus may contribute to long-term negative feedback under global climate change.

Our results further emphasize the pivotal role of including SOC components in models of soil carbon dynamics following vegetation restoration, especially under the condition of global warming, because the responses of SOC to climatic gradients are fraction-dependent. Additionally, the different control factors and stabilization mechanisms of SOC fractions should be considered for maximizing vegetation restoration carbon sequestration. Furthermore, our results indicate that the effects of the soil microbial community and Ca on SOC fractions in karst soils differed from those in non-karst soils, highlighting the necessity to understand the unique stabilization mechanisms of soil carbon in calcareous soils.

It should be noted that, although the net soil carbon accumulation in plantation forests approximated that in naturally restored vegetation along the climatic gradient, caution must be exerted when planning future forest plantation projects in the subtropical karst region. A previous study indicated that planting trees in water-limited regions may lead to a significant reduction in water yield (Yu et al., 2019). As karst soil has a relatively low water-retention capacity owing to its geological conditions (Wang et al., 2020), large-scale plantation programs may accelerate negative effects on the regional water balance. Similarly, another study indicated that further afforestation could increase the risk of enhancing soil moisture deficit in Southwest China (Li et al., 2018b). We suggest that future research on the large-scale assessment of the effectiveness and efficiency of different vegetation restoration strategies must consider both carbon sequestration and hydrological processes.

5. Conclusions

Through our systematic measurement of SOC fractions, soil properties, and microbial characteristics, we observed that both managed and natural vegetation restoration strategies significantly increased SOC and POC accumulation along a climatic gradient in the subtropical karst region of Southwest China. We also found that both restoration strategies increased net carbon accumulation more in warmer regions. The higher bacterial and fungal abundance and soil exchangeable Ca concentration in the restored vegetation types than in the cropland resulted in higher soil carbon accumulation, which could negate the positive effect of MAT on SOC decomposition. These findings imply that both vegetation restoration strategies have the potential to increase soil carbon accumulation in calcareous soils, especially at lower elevations with higher temperatures.

Funding

The work was supported by the National Natural Science Foundation of China [grant numbers 41930652, 31870502, 32001231, and 42001049], China Postdoctoral Science Foundation [grant number 2020M682585], the National Natural Science Foundation of Guangxi Province [2018GXNSFBA138014], and the Guangxi Bagui Scholarship Program to Dejun Li.

CRediT authorship contribution statement

Peilei Hu: Writing – original draft, Investigation, Formal analysis. **Wei Zhang:** Conceptualization, Writing – review & editing, Funding acquisition. **Hongsong Chen:** Conceptualization, Investigation, Funding acquisition. **Dejun Li:** Conceptualization, Investigation. **Yuan Zhao:** Investigation. **Jie Zhao:** Investigation. **Jun Xiao:** Investigation. **Fangji Wu:** Investigation. **Xunyang He:** Investigation. **Yiqi Luo:** Writing – review & editing. **Kelin Wang:** Conceptualization, Writing – review & editing, 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.

Acknowledgments

We thank Dr. Kongcao Xiao, Dr. Yunpeng Nie, Dr. Zhiyong Fu, Dr. Wanxia Peng, Dr. Xingyu Ma, Dr. Jun Zhang, Mr. Chunheng Zhou, and Miss Ming Cheng for assistance with field data collection. We thank Russell Doughty of the Division of Geological and Planetary Sciences, California Institute of Technology, whose inputs have improved the quality of the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.145298.

References

Bastin, J.F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C.M., Crowther, T.W., 2019. The global tree restoration potential. Science 365 (6448), 76–79.

Bernard, B.B., Bernard, H., Brooks, J.M., 1995. Determination of Total Carbon, Total Organic Carbon and Inorganic Carbon in Sediments. TDI-Brooks International/B&B Laboratories Inc., College Station, Texas 77845.

Blagodatskaya, E., Kuzyakov, Y., 2013. Active microorganisms in soil: critical review of estimation criteria and approaches. Soil Biol. Biochem. 67, 192–211.

Bossio, D.A., Scow, K.M., 1998. Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. Microb. Ecol. 35 (3), 265–278.

Chen, C., Park, T., Wang, X., Piao, S., Xu, B., Chaturvedi, R.K., Fuchs, R., Brovkin, V., Ciais, P., Fensholt, R., Tommervik, H., Bala, G., Zhu, Z., Nemani, R.R., Myneni, R.B., 2019a. China and India lead in greening of the world through land-use management. Nat. Sustain. 2, 122–129.

Chen, D., Mi, J., Chu, P., Cheng, J., Zhang, L., Pan, Q., Xie, Y., Bai, Y., 2015. Patterns and drivers of soil microbial communities along a precipitation gradient on the Mongolian Plateau. Landsc. Ecol. 30 (9), 1669–1682.

Chen, L., Liu, L., Qin, S., Yang, G., Fang, K., Zhu, B., Kuzyakov, Y., Chen, P., Xu, Y., Yang, Y., 2019b. Regulation of priming effect by soil organic matter stability over a broad geographic scale. Nat. Commun. 10 (1), 5112.

Chen, Y.L., Ding, J.Z., Peng, Y.F., Li, F., Yang, G.B., Liu, L., Qin, S.Q., Fang, K., Yang, Y.H., 2016. Patterns and drivers of soil microbial communities in Tibetan alpine and global terrestrial ecosystems. J. Biogeogr. 43 (10), 2027–2039.

Chung, H., Zak, D.R., Reich, P.B., Ellsworth, D.S., 2007. Plant species richness, elevated CO_2, and atmospheric nitrogen deposition alter soil microbial community composition and function. Glob. Chang. Biol. 13 (5), 980–989.

Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C., Machmuller, M.B., Snoek, B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M., Bridgham, S.D., Burton, A.J., Carrillo, Y., Reich, P.B., Clark, J.S., Classen, A.T., Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D., Guo, J., Harte, J., Jiang, L., Johnson, B.R., Kroel-Dulay, G., Larsen, K.S., Laudon, H., Lavallee, J.M., Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Penuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L., Schmidt, I.K., Sistla, S., Sokol, N.W., Templer, P.H., Treseder, K.K., Welker, J.M., Bradford, M.A., 2016. Quantifying global soil carbon losses in response to warming. Nature 540 (7631). https://doi.org/10.1038/nature20150 104-+.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440 (7081), 165.

DeGryze, S., Six, J., Paustian, K., Morris, S.J., Paul, E.A., Merckx, R., 2004. Soil organic carbon pool changes following land-use conversions. Glob. Chang. Biol. 10, 1120–1132.

Deng, L., Shangguan, Z.P., 2017. Afforestation drives soil carbon and nitrogen changes in China. Land Degrad. Dev. 28 (1), 151–165.

Dou, Y.X., Yang, Y., An, S.S., Zhu, Z.L., 2020. Effects of different vegetation restoration measures on soil aggregate stability and erodibility on the Loess Plateau, China. Catena 185, 104294.

Drenovsky, R.E., Steenwerth, K.L., Jackson, L.E., Scow, K.M., 2010. Land use and climatic factors structure regional patterns in soil microbial communities. Glob. Ecol. Biogeogr. 19 (1), 27–39.

Eclesia, R.P., Jobbagy, E.G., Jackson, R.B., Rizzotto, M., Piñeiro, G., 2016. Stabilization of new carbon inputs rather than old carbon decomposition determines soil organic carbon shifts following woody or herbaceous vegetation transitions. Plant Soil 409 (1), 99–116.

Fanin, N., Kardol, P., Farrell, M., Nilsson, M.C., Gundale, M.J., Wardle, D.A., 2019. The ratio of Gram-positive to Gram-negative bacterial PLFA markers as an indicator of carbon availability in organic soils. Soil Biol. Biochem. 128, 111–114.

Fernández-Ugalde, O., Virto, I., Barré, P., Gartzia-Bengoetxea, N., Enrique, A., Imaz, M.J., Bescansa, P., 2011. Effect of carbonates on the hierarchical model of aggregation in calcareous semi-arid Mediterranean soils. Geoderma 164, 203–214.

Fernández-Ugalde, O., Virto, I., Barré, P., Apesteguía, M., Enrique, A., Imaz, M.J., Bescansa, P., 2014. Mechanisms of macroaggregate stabilisation by carbonates: implications for organic matter protection in semi-arid calcareous soils. Soil Res. 52, 180–192.

Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., Rumpel, C., 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450 (7167), 277–280.

Franzluebbers, A.J., Arshad, M.A., 1997. Particulate organic carbon content and potential mineralization as affected by tillage and texture. Soil Sci. Soc. Am. J. 61 (5), 1382–1386.

Guillaume, T., Damris, M., Kuzyakov, Y., 2015. Losses of soil carbon by converting tropical forest to plantations: erosion and decomposition estimated by $\delta^{13}C$. Glob. Chang. Biol. 21 (9), 3548–3560.

Hu, P.L., Liu, S.J., Ye, Y.Y., Zhang, W., He, X.Y., Su, Y.R., Wang, K.L., 2018b. Soil carbon and nitrogen accumulation following agricultural abandonment in a subtropical karst region. Appl. Soil Ecol. 132, 169–178.

Hu, P.L., Liu, S.J., Ye, Y.Y., Zhang, W., Wang, K.L., Su, Y.R., 2018a. Effects of environmental factors on soil organic carbon under natural or managed vegetation restoration. Land Degrad. Dev. 29 (3), 387–397.

Huang, Y., Liang, C., Duan, X., Chen, H., Li, D., 2019. Variation of microbial residue contribution to soil organic carbon sequestration following land use change in a subtropical karst region. Geoderma 353, 340–346.

IPCC, 2018. An IPCC Special Report on the Impacts of Global Warming of 1.5 °C Above Pre-industrial Levels and Related Global Greenhouse Gas Emission Pathways, in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable Development, and Efforts to Eradicate Poverty.

Jin, Z., Dong, Y., Wang, Y., Wei, X., Wang, Y., Cui, B., Zhou, W., 2014. Natural vegetation restoration is more beneficial to soil surface organic and inorganic carbon sequestration than tree plantation on the Loess Plateau of China. Sci. Total Environ. 485–486, 615–623.

Jing, Y., Wang, Y., Liu, S., Zhang, X., Wang, Q., Liu, K., Yin, Y., Deng, J., 2019. Interactive effects of soil warming, throughfall reduction, and root exclusion on soil microbial community and residues in warm-temperate oak forests. Appl. Soil Ecol. 142, 52–58.

Laganiere, J., Angers, D.A., Pare, D., 2010. Carbon accumulation in agricultural soils after afforestation: a meta-analysis. Glob. Chang. Biol. 16 (1), 439–453.

Lavallee, J.M., Soong, J.L., Cotrufo, M.F., 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Glob. Chang. Biol. 26, 261–273.

Li, D., Wen, L., Zhang, W., Yang, L., Xiao, K., Chen, H., Wang, K., 2017. Afforestation effects on soil organic carbon and nitrogen pools modulated by lithology. For. Ecol. Manag. 400, 85–92.

Li, D., Wen, L., Jiang, S., Song, T., Wang, K., 2018a. Responses of soil nutrients and microbial communities to three restoration strategies in a karst area, southwest China. J. Environ. Manag. 207, 456–464.

Li, D.J., Niu, S.L., Luo, Y.Q., 2012. Global patterns of the dynamics of soil carbon and nitrogen stocks following afforestation: a meta-analysis. New Phytol. 195 (1), 172–181.

Li, H.Z., Yan, F., Tuo, D.F., Yao, B., Chen, J.H., 2020. The effect of climatic and edaphic factors on soil organic carbon turnover in hummocks based on $\delta^{13}C$ on the Qinghai-Tibet Plateau. Sci. Total Environ. 741, 140141.

Li, Y., Piao, S., Li, L.Z.X., Chen, A., Wang, X., Ciais, P., Huang, L., Lian, X., Peng, S., Zeng, Z., Wang, K., Zhou, L., 2018b. Divergent hydrological response to large-scale afforestation and vegetation greening in China. Sci. Adv. 4 (5), eaar4182.

Liang, C., Schimel, J.P., Jastrow, J.D., 2017. The importance of anabolism in microbial control over soil carbon storage. Nat. Microbiol. 2 (8), 1–6.

Liang, C., Amelung, W., Lehmann, J., Kästner, M., 2019. Quantitative assessment of microbial necromass contribution to soil organic matter. Glob. Chang. Biol. 25 (11), 3578–3590.

Liu, M., Xu, X., Sun, A.Y., Wang, K., Liu, W., Zhang, X., 2014. Is southwestern China experiencing more frequent precipitation extremes? Environ. Res. Lett. 9 (6), 064002.

Liu, Y., Liu, W., Wu, L., Liu, C., Wang, L., Chen, F., Li, Z., 2018. Soil aggregate-associated organic carbon dynamics subjected to different types of land use: evidence from ^{13}C natural abundance. Ecol. Eng. 122, 295–302.

von Luetzow, M., Koegel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., 2007. SOM fractionation methods: relevance to functional pools and to stabilization mechanisms. Soil Biol. Biochem. 39 (9), 2183–2207.

Luo, Y., Keenan, T.F., Smith, M., 2015. Predictability of the terrestrial carbon cycle. Glob. Chang. Biol. 21 (5), 1737–1751.

Luo, Z., Viscarra Rossel, R.A., Shi, Z., 2020. Distinct controls over the temporal dynamics of soil carbon fractions after land use change. Glob. Chang. Biol. 26, 4614–4625.

Nelson, D.W., Sommers, L.E., Sparks, D.L., Page, A.L., Helmke, P.A., Loeppert, R.H., Soltanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E., 1996. Total carbon, organic carbon, and organic matter. Methods Soil Anal. 9, 961–1010.

Qin, S., Chen, L., Fang, K., Zhang, Q., Wang, J., Liu, F., Yu, J., Yang, Y., 2019. Temperature sensitivity of SOM decomposition governed by aggregate protection and microbial communities. Sci. Adv. 5 (7), eaau1218.

Reid, J.L., Fagan, M.E., Zahawi, R.A., 2018. Positive site selection bias in meta-analyses comparing natural regeneration to active forest restoration. Sci. Adv. 4 (5).

Rowley, M.C., Grand, S., Verrecchia, É.P., 2018. Calcium-mediated stabilisation of soil organic carbon. Biogeochemistry 137 (1), 27–49.

Schimel, J., Schaeffer, S., 2012. Microbial control over carbon cycling in soil. Front. Microbiol. 3 (348).

Shi, S., Zhang, W., Zhang, P., Yu, Y., Ding, F., 2013. A synthesis of change in deep soil organic carbon stores with afforestation of agricultural soils. For. Ecol. Manag. 296, 53–63.

Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241 (2), 155–176.

Solly, E.F., Schöning, I., Boch, S., Kandeler, E., Marhan, S., Michalzik, B., Müller, J., Zscheischler, J., Trumbore, S.E., Schrumpf, M., 2014. Factors controlling decomposition rates of fine root litter in temperate forests and grasslands. Plant Soil 382 (1), 203–218.

Stockmann, U., Adams, M.A., Crawford, J.W., Field, D.J., Henakaarchchi, N., Jenkins, M., Minasny, B., McBratney, A.B., Courcelles, V.D.R.D., Singh, K., Wheeler, I., Abbott, L., Angers, D.A., Baldock, J., Bird, M., Brookes, P.C., Chenu, C., Jastrow, J.D., Lal, R., Lehmann, J., O'Donnell, A.G., Parton, W.J., Whitehead, D., Zimmermann, M., 2013. The knowns, known unknowns and unknowns of sequestration of soil organic carbon. Agric. Ecosyst. Environ. 164, 80–99.

Strickland, M.S., Callaham, M.A., Gardiner, E.S., Stanturf, J.A., Leff, J.W., Fierer, N., Bradford, M.A., 2017. Response of soil microbial community composition and function to a bottomland forest restoration intensity gradient. Appl. Soil Ecol. 119, 317–326.

Tong, X., Brandt, M., Yue, Y., Horion, S., Wang, K., De Keersmaecker, W., Tian, F., Schurgers, G., Xiao, X., Luo, Y., 2018. Increased vegetation growth and carbon stock in China karst via ecological engineering. Nat. Sustain. 1 (1), 44–50.

Tong, X., Brandt, M., Yue, Y., Ciais, P., Rudbeck Jepsen, M., Penuelas, J., Wigneron, J.P., Xiao, X., Song, X.P., Horion, S., Rasmussen, K., Saatchi, S., Fan, L., Wang, K., Zhang, B., Chen, Z., Wang, Y., Li, X., Fensholt, R., 2020. Forest management in southern China generates short term extensive carbon sequestration. Nat. Commun. 11 (1), 129.

Wang, K., Zhang, C., Chen, H., Yue, Y., Zhang, W., Zhang, M., Qi, X., Fu, Z., 2019. Karst landscapes of China: patterns, ecosystem processes and services. Landsc. Ecol. 1–21.

Wang, S., Huang, Y., 2020. Determinants of soil organic carbon sequestration and its contribution to ecosystem carbon sinks of planted forests. Glob. Chang. Biol. 26 (5), 3163–3173.

Wang, S., Fu, Z., Chen, H., Nie, Y., Xu, Q., 2020. Mechanisms of surface and subsurface runoff generation in subtropical soil-epikarst systems: implications of rainfall simulation experiments on karst slope. J. Hydrol. 580, 124370.

Wang, Z., Guo, S., Sun, Q., Li, N., Jiang, J., Wang, R., Zhang, Y., Liu, Q., Wu, D., Li, R., Du, L., Zhao, M., 2015. Soil organic carbon sequestration potential of artificial and natural vegetation in the hilly regions of Loess Plateau. Ecol. Eng. 82, 547–554.

Wiesmeier, M., Urbanski, L., Hobley, E., Lang, B., von Luetzow, M., Marin-Spiotta, E., van Wesemael, B., Rabot, E., Liess, M., Garcia-Franco, N., Wollschlaeger, U., Vogel, H.J., Koegel-Knabner, I., 2019. Soil organic carbon storage as a key function of soils — a review of drivers and indicators at various scales. Geoderma 333, 149–162.

Xin, X., Jin, D., Ge, Y., Wang, J., Chen, J., Qi, J., Chu, H., Shao, C., Murray, P.J., Zhao, R., Qin, Q., Tang, H., 2020. Climate change dominated long-term soil carbon losses of Inner Mongolian grasslands. Glob. Biogeochem. Cycles 34, e2020GB006559.

Yang, L.M., Lyu, M.K., Li, X.J., Xiong, X.L., Lin, W.S., Yang, Y.S., Xie, J.S., 2020b. Decline in the contribution of microbial residues to soil organic carbon along a subtropical elevation gradient. Sci. Total Environ. 749, 141583.

Yang, Y., Cheng, H., Liu, L., Dou, Y., An, S., 2020a. Comparison of soil microbial community between planted woodland and natural grass vegetation on the Loess Plateau. For. Ecol. Manag. 460, 117817.

Ye, Y., Xiao, S., Liu, S., Zhang, W., Zhao, J., Chen, H., Guggenberger, G., Wang, K., 2020. Tillage induces rapid loss of organic carbon in large macroaggregates of calcareous soils. Soil Tillage Res. 199, 104549.

Yu, H., Ma, Q., Liu, X., Xu, Z., Zhou, G., Shi, Y., 2018. Short- and long-term warming alters soil microbial community and relates to soil traits. Appl. Soil Ecol. 131, 22–28.

Yu, Z., Liu, S., Wang, J., Wei, X., Schuler, J., Sun, P., Harper, R., Zegre, N., 2019. Natural forests exhibit higher carbon sequestration and lower water consumption than planted forests in China. Glob. Chang. Biol. 25 (1), 68–77.

Zhang, Y., Xu, X., Li, Z., Liu, M., Xu, C., Zhang, R., Luo, W., 2019. Effects of vegetation restoration on soil quality in degraded karst landscapes of southwest China. Sci. Total Environ. 650, 2657–2665.

Zhao, Z., Wei, X., Wang, X., Ma, T., Huang, L., Gao, H., Fan, J., Li, X., Jia, X., 2019. Concentration and mineralization of organic carbon in forest soils along a climatic gradient. For. Ecol. Manag. 432, 246–255.

Zhou, J., Xue, K., Xie, J., Deng, Y., Wu, L., Cheng, X., Fei, S., Deng, S., He, Z., Van Nostrand, J.D., Luo, Y., 2012. Microbial mediation of carbon-cycle feedbacks to climate warming. Nat. Clim. Chang. 2 (2), 106–110.