

Soil Organic Carbon Mineralization and its Temperature Sensitivity Along a Vegetation Restoration Gradient in Subtropical China

Xiong Fang

Fujian Agriculture and Forestry University

Haozhao Sun

Fujian Agriculture and Forestry University

Yunpeng Huang

Fujian Academy of Forestry Science

Jundi Liu

Fujian Agriculture and Forestry University

Yulin Zhu

Fujian Agriculture and Forestry University

Xinghao Tang

Fujian Academy of Forestry Science

Yalin Hu

Fujian Agriculture and Forestry University

Zhigang Yi (✉ zgyi@fafu.edu.cn)

Fujian Agriculture and Forestry University

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Abstract

Background and aims Soil organic carbon (SOC) mineralization produces important CO₂ flux from terrestrial ecosystems which can provide feedbacks to climates. Vegetation restoration can affect SOC mineralization and its temperature sensitivity (Q_{10}), but how this effect is related to soil moisture remains uncertain.

Methods We performed a laboratory incubation using soils of different vegetation restoration stages (i.e., degraded vegetation [DS], plantation [PS], and secondary natural forest [SFS]) maintained under different moisture and temperature conditions to explore the combined effects of vegetation restoration and soil moisture on SOC mineralization and Q_{10} .

Results We found that cumulative SOC mineralization in PS and SFS were about 11.7 times higher than that in the DS, associated with higher SOC content and microbial biomass. Increased soil moisture and temperature led to higher SOC mineralization in the SFS and PS. However, in the DS, soil moisture did not affect SOC mineralization, but temperature enhancement solely increased (158.7%) SOC mineralization at the 60%MWHC treatment. Furthermore, significant interactive effect of vegetation restoration and soil moisture on Q_{10} was detected. At the 60%MWHC treatment, Q_{10} declined with vegetation restoration age. Nevertheless, at the 30%MWHC treatment, Q_{10} was lower in the DS than that in the PS. Higher soil moisture did not affect Q_{10} in the PS and SFS, but enhanced Q_{10} in the DS.

Conclusions Our results highlight that the responses of SOC mineralization and Q_{10} to vegetation restoration were highly dependent on soil moisture and substrate availability, and vegetation restoration reduced the influence of soil moisture on Q_{10} .

1. Introduction

Vegetation restoration has been expanding worldwide since the middle of the twentieth century due to environment conservation programs and policy incentives (Zhang et al. 2013; Stanturf et al. 2014; Lu et al. 2018; Pang et al. 2019). For instance, since the late 1970s, several key national ecological restoration projects have been launched to protect environment and restore degraded ecosystems in China, which substantially contributed to CO₂ mitigation (Lu et al. 2018). Soil is the largest carbon (C) pool of terrestrial ecosystems (> 1486 Pg C in the uppermost 100 cm; Crowther et al. 2019), while soil organic carbon (SOC) mineralization produces important CO₂ flux from terrestrial ecosystems which provides vitally feedbacks to climates (Heimann and Reichstein 2008; Bond-Lamberty et al. 2018). Thus, knowledge of soil C turnover in vegetation restoration processes is imperative for better understanding and managing degraded ecosystems (Stanturf et al. 2014; Morriën et al. 2017).

Previous studies reported that soil properties, such as SOC content, nutrients, C: N ratio, C quality, and soil microbes, will be changed along the vegetation restoration chronosequence (Berthrong et al. 2012; Yang et al. 2018; Lu et al. 2018; Pang et al. 2019), which will undoubtedly lead to changes in the SOC mineralization and its temperature sensitivity (Q_{10}) (Wang et al. 2019; Zhang et al. 2019; Li et al. 2021; Xu et al. 2021). In general, higher SOC and nutrient contents along the vegetation restoration gradient usually led to higher amount of the

Loading [MathJax]/jax/output/CommonHTML/fonts/TeX/fontdata.js ut, due to higher labile SOC in the forest plantation

which supported larger populations of soil microbes, Huang et al (2019) found that SOC mineralization was greater in the plantation forest than in the natural forest. The effects of soil properties on the Q_{10} of SOC mineralization are also highly inconsistent (Wang et al. 2019; Zhang et al. 2019; Li et al. 2021; Xu et al. 2021). It was shown that the ratio of actinomycetes to bacteria (Liu et al. 2017) and fungal phospholipid fatty acid (Qin et al. 2019) were positively correlated with Q_{10} , whereas the abundance of gram-negative bacteria decreased with the increasing Q_{10} (Wang et al. 2018). But, other studies have shown that changes in soil physicochemical properties rather than microbes control C mineralization (Zhang et al. 2019; Li et al. 2020). For instance, soil C: N ratio or C quality is recognized as the main factor affecting Q_{10} values (Wang et al. 2018). The large biochemical complexity of soils from a variety of ecosystems has led to great discussions about the sensitivity of SOC to temperature (Qi and Li 2017; Wang et al. 2019). However, when environmental factors were considered, the responses of SOC mineralization and Q_{10} become more confusing (Suseela et al. 2012).

Soil moisture strongly affects SOC mineralization through soil aeration, substrate supply, and microbial activity (Suseela et al. 2012; Li et al. 2018; Moyano et al. 2013). In general, the optimum soil moisture for SOC decomposition is frequently found at intermediate levels, above or below which SOC decomposition rate decreases (Craine and Gelderman 2011; Suseela et al. 2012). Studies on the effects of soil moisture on Q_{10} have produced inconsistent results. For example, Jiang et al (2013) observed a reduction in Q_{10} of soil respiration in a mixed broad-leaved forest when simulated precipitation was doubled from ambient levels. Moonis et al (2021) found an opposite result that wetting treatment (50% water-filled pore space) increased Q_{10} by 25.0%. A laboratory study found that the highest Q_{10} of R_h occurred at intermediate soil moisture levels (45%WHC), but the nature of this interaction varied between two different soils (Craine and Gelderman 2011). The inconsistency of soil moisture effects on SOC decomposition and Q_{10} is possible due to the confounded effects of different environmental factors and soil properties (Pregitzer et al. 1999; Zhou et al. 2014; Wang et al. 2019).

Among the factors affecting SOC mineralization, soil temperature has been the subject of many modeling and empirical studies of soil C dynamics under the scenario of global warming (Huang et al. 2019; Wang et al. 2019). Results from many studies have shown that rising temperature stimulated soil organic matter decomposition by increasing the activity of extracellular enzymes that degrade organic matter in soils, by increasing rates of microbial consume of soluble substrates, and by increasing microbial respiration rates (Fissore et al. 2008; Wei et al. 2014; Wang et al. 2019; Fang et al. 2020). On the contrary, some studies also have found negative soil respiration responses to warming (Liu et al. 2009; Lu et al. 2013). For example, Lavigne et al (2003) found that annual heterotrophic respiration (R_h) varied little across a natural climatic gradient. These inconsistent responses should be also due to interactions with other environmental constraints on SOC decomposition, such as soil moisture which will indirectly suppress microbial activities and respiration by soil water or oxygen deficit (Craine and Gelderman 2011; Moyano et al. 2013; Suseela et al. 2012).

While it is well known that soil properties, moisture and temperature are all strong controlling factors on SOC mineralization and Q_{10} (Moyano et al. 2012; Suseela et al. 2012; Min et al. 2019; Li et al. 2021; Xu et al. 2021), limited understanding of their interactive effects constrains our ability to predict ecosystem C fluxes under

restoration stages (vegetation degraded soil [DS], plantation soil [PS] and secondary natural forest soil [SFS]) maintained under different moisture (60% vs. 30% maximum water holding capacity [MWHC]) and temperature (18°C vs. 28°C). Soil physical, chemical and microbial properties were measured before the incubation. Soil microbial biomass C (MBC), dissolved organic C (DOC), microbial community composition and evolved CO₂-C were measured throughout the incubation. On the basis of our knowledge, we predicted that (1) greater SOC mineralization would be found with vegetation restoration age; (2) increased soil moisture and temperature would enhance SOC mineralization in all vegetation restoration stages; (3) lower Q_{10} would be found with vegetation restoration age, but soil moisture would have a less effect on Q_{10} in the SFS than that in the DS, due to soils with longer vegetation restoration years always have a greater biodiversity and might be more adaptive to changes in environmental conditions such as soil moisture (Yang et al. 2018; Xu et al. 2021).

2. Materials And Methods

2.1. Study site

Soil samples used for incubation were collected from a typical vegetation restoration area (116°18'-116°31'E, 25°33'-25°48'N) of Changting county, Fujian province in southeastern China. The area is characterized by a subtropical monsoon climate, with mean annual temperature of 18.3°C and mean annual rainfall of 1730 mm, of which approximately 75% occurred from March to August between 1981 and 2010. The soil of the study site is classified as red soil, equivalent to ultisol according to the USDA soil classification system (Buol et al. 2003). Due to historical reasons, forest degradation of this area was very serious in the middle of the last century. Since the 1970s, the government began to organize vegetation restoration projects which led to the vegetation coverage rate increased notably (Lu et al. 2018).

2.2. Soil sampling and preparation

Soil samples were collected from three vegetation restoration stages, namely vegetation degraded soil (DS), plantation soil (PS) and secondary natural forest soil (SFS). Currently, there are almost no serious vegetation degradation areas in Changting County. Therefore, the DS was collected from a small vegetation degradation site where was protected for science, education and visit by the local government. At the vegetation degraded site, vegetation is quite sparse, soil erosion is severe and dwarf *Pinus massoniana* Lamb. is sporadically distributed. The PS was collected from plantation forest which was restored from 1998. The dominant species of the plantation forest are *Pinus massoniana* Lamb.. We collected the SFS from a secondary natural forest (with age > 70 years) which was protected as “fengshui” site by the local peasant and monks. The dominant species in the secondary natural forest are *Schima superba* Gardn. et Champ., *Liquidambar formosana* Hance, *Syzygium grijsii* (Hance) Merr. et Perry, *Ilex pubescens* Hook. et Arn., and *Pinus massoniana* Lamb.

At each vegetation restoration site, three 10 m × 10 m plots, with a distance of 50-2000 m between each other, were randomly selected. Soils of the top 0–10 cm were collected from five subplots (1 m × 1 m) in each plot in April 2017. Before sampling, the litter layer was excluded. All soil samples from the same plot were mixed to form a composite sample and stored in a hard plastic container. And then soil samples were transported to the laboratory immediately. After roots, litter, stones and other visible plant debris in each sample were removed; soil samples were passed through a 2-mm sieve and homogenized. Three soil samples of each vegetation

restoration site were used for determining chemical and physical properties and phospholipid fatty acids (PLFAs). The remaining soil samples were stored at 4°C for weeks prior to the incubation experiment.

2.3. Soil properties and PLFA analyses

Soil pH was measured using a soil: water ratio of 1: 2.5. Soil water content was determined using the methods of oven-dried and weighted. The contents of SOC and total nitrogen (TN) measured by an elemental analyzer (EA3000, EuroVector, Italy). Total phosphorous (TP) was measured photometrically after samples were digested with perchloric acid and hydrofluoric acid.

Soil MBC was determined by the chloroform fumigation-extraction method following Brookes et al (1985). The extractable C from the unfumigated samples was considered as DOC. Particulate organic C (POC) was determined using a method that was described by Fang et al (2020). Briefly 15 g of air-dried soil was placed in a 100 mL of 5 g L⁻¹ sodium hexametaphosphate solution by handshaking the mixture for 5 min prior to being placed on a reciprocal shaker (90 r• min⁻¹) for 18 h. The dispersed soil sample was passed through a 53 µm sieve and rinsed with deionized water. The material that remained on the 53 µm sieve was considered the POC fraction. All of the samples were dried at 60°C, weighed, then finely ground for the determination of organic C. The organic C content was converted to bulk soil POC content according to the fraction mass ratios.

The measurements of PLFAs profiles were determined on 8 g of freeze-dried soil after extraction using a mixture containing chloroform, methanol and citrate buffer (Bossio and Scow 1998). And then the extracted fatty acid methyl esters were analyzed following the procedures described by Fang et al (2016). Soil microbial community was determined using specific PLFAs for the different microbial groups (Frostegård and Bååth 1996; Schindlbacher et al. 2011). Gram-positive bacteria (GP) were represented by 15:0a, 15:0i, 16:0i, 17:0a, and 17:0i; and gram-negative bacteria (GN) were identified by 17:0cy, 19:0cy, 16:1ω7c, and 18:1ω7c. Fungi were represented by 18:1ω9c, 18:2ω6, 9c, and 18:3ω6c. Total PLFAs was calculated by summing all the determined PLFAs. The abundance of PLFAs was estimated by the amount of C and then converted to mole percentage PLFA-C.

2.4. Soil incubation experiment

Soil samples were incubated under two soil moisture (60%MWHC vs. 30%MWHC) and two temperature (18°C, close to the annual mean temperature at the sampling site, and 28°C for obtaining Q_{10}) (Wang et al. 2018) regimes for 120 days. Such a design produced 12 treatment combinations with 9 replicates per combination (three vegetation stages × two moistures × two temperatures × 9 replicates). Each incubated soil sample (50 g dry) was placed in a 250 mL Erlenmeyer flasks covered by a sealing which has small holes to maintain gas exchange and is used to reduce evaporation. Soil moisture of each sample was adjusted to the designed contents by injecting distilled water slowly on the sample surface to ensure uniform moisture penetration. And soil samples were first pre-incubated at 23°C for 1 week to minimize the “plus effect” and then put into incubators set at 18 and 28°C, respectively. To maintain constant soil moisture levels, soil water was checked and adjusted every 4–5 days by weighing it. In the incubators, a certain amount of air was introduced through the air compressor to avoid anaerobic conditions (Whitaker et al. 2014).

During the incubation, three replicates of each combination were used for the determination of soil CO₂

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headspace for ca. 60 s to standardize the starting CO₂ concentration of each incubation flask (Whitaker et al. 2014) during each measurement. Gas samples were collected twice from the headspace, immediately after closing the flask and 30 min later, with a needle cylinder and stored in a gas sampling bag. The CO₂ concentration of gas samples was determined by gas chromatography (7890B, Agilent, USA) within 24 h. The standard gases used to calibrate the gas chromatograph included four different CO₂ concentrations in the N₂ makeup gas. SOC mineralization rate (R) was calculated according to Huang et al 2019 using the following equation:

$$R = 22.4 \times v / m \times \Delta c / \Delta t \times 273 / (273 + T) \times C_M \quad (1)$$

where v is head space volume of incubation flask (total volume of flask minus soil volume), m is dry soil weight, $\Delta c / \Delta t$ is the average CO₂ concentration difference per hour, T is the incubation temperature, and C_M is the molar mass of C. The ideal gas law was used to determine the molar volume of CO₂ at the incubation temperature.

The cumulative amount of SOC mineralized (C_m) was calculated using the following equation:

$$C_m = C_{m-1} + (R_p + R_{p-1}) / 2 * (D - D_{-1}) \quad (2)$$

Where R is daily SOC mineralization rate, p is incubation period, and D is incubation time (day). We calculated the temperature sensitivity (Q_{10}) of SOC mineralization during the incubation as follows (Conant et al. 2008; Xu et al. 2010):

$$Q_{10} = (t_c / t_w)^{10 / (T_w - T_c)}$$

3

Where t_c and t_w are the times required to respire a given amount of soil C at relatively cold (T_c , 18°C) and warm (T_w , 28°C) temperatures during incubation.

Three replicates of soil samples were collected for each treatment combination at day of 15, 45, and 120 after the start of the experiment. After soil samples were passed through a 2-mm sieve, each soil sample was divided into two parts. One part was stored at 4°C and used for determination of soil water content, MBC, and DOC content. The other part was freeze-dried and used for determination PLFAs as mentioned above. The metabolic quotient (qCO_2) and the decomposability of DOC (R_h : DOC) were estimated by dividing the cumulative mineralization by the corresponding MBC and DOC, respectively.

2.5. Statistical analysis

Data were logarithmically transformed to meet the assumptions of normality and homogeneity of variances when necessary. The differences of soil properties among three vegetation restoration stages were tested using one-way analysis of variance (ANOVA). Three-way ANOVA was used to test the effects of vegetation restoration, moisture, temperature and their interaction on cumulative SOC mineralization, MBC, DOC, qCO_2 , R_h : DOC, and microbial composition. Two-way ANOVA was used to test the effects of soil moisture, temperature

BC, DOC, qCO_2 , R_h : DOC, and microbial composition

in each vegetation restoration stage; and also used to test the effects of vegetation restoration, moisture and their interaction on Q_{10} . Individual treatment means within each moisture and temperature under the same vegetation restoration stage were compared with Duncan's Multiple Range test. Regressions were conducted to explore the relationship between SOC mineralization and MBC and DOC contents. Differences were considered to be statistically significant at $P < 0.05$. The SAS software (SAS Institute Inc., Cary, NC, USA) was used for data analysis.

3. Results

3.1. SOC mineralization

After the 120-day incubation, cumulative SOC mineralization was significantly affected by vegetation restoration, moisture, temperature and their interactions (Fig. 1, Table 1). Cumulative SOC mineralization was significantly higher in the PS (1522.7 $\mu\text{g CO}_2\text{-C g}^{-1}$ soil) and SFS (1521.3 $\mu\text{g CO}_2\text{-C g}^{-1}$ soil) than that in the DS (129.5 $\mu\text{g CO}_2\text{-C g}^{-1}$ soil). Both increased soil moisture and temperature led to significantly higher SOC mineralization in the SFS and PS (Fig. 1). However, in the DS, increased soil moisture has little effects on SOC mineralization, and increased soil temperature only increased ($P < 0.001$) SOC mineralization by 158.7% at the 60%MWHC treatment.

Table 1

Effects of vegetation restoration, soil moisture, temperature and their interaction on cumulative SOC mineralization (R_h), MBC, DOC, metabolic quotient ($q\text{CO}_2$), decomposability of DOC (R_h : DOC), the relative abundance of gram-positive bacteria (GP), gram-negative bacteria (GN), and fungi. The F values their levels of significance are shown in the table. * $P < 0.05$, ** $P < 0.01$ *** $P < 0.001$

Main effect or interactions	Dependent variable							
	R_h	MBC	DOC	$q\text{CO}_2$	R_h : DOC	GP	GN	Fungi
Vegetation restoration (R)	425.98***	126.63***	1161.2***	31.55***	145.32***	36.64***	73.39***	59.91***
Soil moisture (W)	183.54***	46.78***	76.37***	1.59	103.39***	0.28	0.51	8.70**
Soil temperature (T)	263.88***	1.48	2.54***	67.25***	160.67***	3.75	4.52*	12.18***
R×W	98.92***	1.21	23.31***	57.65***	56.95***	0.54	0.12	3.44*
R×T	40.55***	0.16	1.04	6.45**	22.27***	1.71	0.57	1.73
W×T	12.37**	0.23	1.07	0.01	11.68**	1.64	1.80	0.23
R×T×W	12.23**	0.53	0.35	2.25	8.20**	0.23	0.16	0.60

3.2 Temperature sensitivity

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Overall, vegetation restoration and soil moisture had no significant effects on Q_{10} (Fig. 2), but we detected significant interaction between the two factors ($P < 0.01$). Then, we compared the Q_{10} among different vegetation restoration stages at the same soil moisture level or between two soil moisture levels at the same vegetation restoration stage. We found that Q_{10} was significantly higher in the DS than that in the PS and SFS at the 60%MWHC treatment, but Q_{10} was significantly lower in the DS than that in the PS and SFS at the 30%MWHC treatment. Increased soil moisture did not markedly influence Q_{10} in the PS and SFS, but significantly enhanced ($P < 0.05$) Q_{10} in the DS.

3.3. Soil MBC, DOC, qCO_2 and R_h : DOC

An overall statistical analysis showed that MBC was significantly affected by vegetation restoration and soil moisture (Table 1, Fig. 3). Soil DOC content was significantly affected by vegetation restoration stage, soil moisture, temperature, and the interaction of vegetation restoration and soil moisture. Soil MBC and DOC contents were significantly higher in the SFS and PS than that in the DS (Fig. 3). Increased soil moisture significantly increased soil MBC content in the DS at two temperature levels. But, increased soil moisture only significantly increased soil MBC content at 28°C in the PS and SFS. At both of the two temperature levels, increased soil moisture significantly increased soil DOC content in the PS and SFS. Increased temperature significantly declined the DOC content in at the 60%MWHC treatment in the PS.

Vegetation restoration, temperature and their interactions significantly affected the qCO_2 and R_h : DOC (Table 1, Fig. 4). Among the three vegetation restoration stages, soil qCO_2 was the lowest in the DS and highest in the PS, especially at the 60%MWHC treatment. Soil R_h : DOC was significant lower in the DS than that in the PS and SFS. Increased soil moisture significantly increased soil qCO_2 in the PS, but decreased soil qCO_2 in the DS. Increased soil moisture significantly increased soil R_h : DOC in the PS, and increased soil R_h : DOC at the 18°C treatment in the SFS. Except for that at the 30%MWHC treatment in the DS, increased soil temperature significantly increased soil qCO_2 and R_h : DOC in all treatments.

3.4. Soil microbial composition

The relative abundance of GP and GN was solely significantly affected by vegetation restoration, and the relative abundance of fungi was significantly influenced by vegetation restoration, soil moisture, temperature and the interaction of vegetation restoration and soil moisture. (Table 1, Fig. 5). The relative abundance of GN was significantly lower in the DS than that in the PS and SFS. On the contrary, the relative abundance of GP and the ratio of GP: GN was significantly higher in the DS than that in the PS and NS. The relative abundance of fungi was significantly higher in the PS than that in the DS and SFS. The relative abundance of fungi was higher at 30%MWHC than that at the 60%MWHC in the PS. At the 60%MWHC treatment in the SFS and at the 30%MWHC treatment in the DS, increased temperature decreased the relative abundance of fungi.

3.5. Soil properties among vegetation restoration stages and correlations

Vegetation restoration has significant influences on the soil pH, SOC, TN, TP contents, and microbial composition (Table 2). Soil pH was higher ($P < 0.05$) in the DS than that in the PS and SFS. On the contrary, the SOC, TN, TP, MBC, DOC, and POC were showed the order: DS < PS < SFS. The total PLFAs content and the relative abundance of GN were also showed the order: DS < PS < SFS, but the relative abundance of GP was significantly higher ($P < 0.05$) in the DS than that in the PS and SFS. The relative abundance of fungi was significantly higher in the PS than that in the DS and SFS. The ratio of GP: GN and F: B followed the order: DS > PS > SFS.

Table 2
Soil properties and microbial community composition of degraded vegetation (DS), plantation (PS) and secondary natural forest (SFS) before the incubation

Parameters	Vegetation restoration stages		
	DS	PS	SFS
pH	4.56 ± 0.05a	4.21 ± 0.15b	4.00 ± 0.12b
SOC (g kg ⁻¹)	3.53 ± 0.25c	16.03 ± 3.38b	34.13 ± 4.56a
TN (g kg ⁻¹)	1.23 ± 0.11b	1.78 ± 0.30b	2.94 ± 0.37a
TP (g kg ⁻¹)	0.04 ± 0.00c	0.08 ± 0.01b	0.13 ± 0.01a
MBC (mg kg ⁻¹)	206.6 ± 52.4b	931.9 ± 190.2a	963.9 ± 45.4a
DOC (mg kg ⁻¹)	154.9 ± 24.5c	483.9 ± 160.0b	709.3 ± 40.8a
POC (g kg ⁻¹)	1.76 ± 0.06b	10.42 ± 4.14a	15.44 ± 5.02a
PLFAs (nmol g ⁻¹)	2.16 ± 0.37c	9.38 ± 7.49b	21.80 ± 0.01a
GP (%mol)	29.11 ± 4.04a	19.6 ± 2.51b	22.66 ± 0.15b
GN (%mol)	7.27 ± 3.37c	18.44 ± 4.83b	25.91 ± 0.09a
Fungi (%mol)	13.89 ± 3.12ab	17.3 ± 0.75a	11.58 ± 0.15b
GP:GN	4.69 ± 2.22a	1.13 ± 0.38b	0.87 ± 0.00b
F:B	0.27 ± 0.05a	0.28 ± 0.01a	0.17 ± 0.00b
SOC is soil organic carbon, TN is total nitrogen, TP is total phosphorus, MBC is microbial biomass carbon, DOC is dissolved organic carbon, POC is particulate organic carbon, GP is gram-positive bacteria, and GN is gram-negative bacteria.			

At the end of the incubation, soil cumulative SOC mineralization was positively correlated ($P < 0.001$) with the content of MBC, and increased exponentially with the increase ($P < 0.0001$) of DOC content (Fig. 6).

4. Discussion

4.1. Responses of SOC mineralization to vegetation restoration, moisture and temperature

Similar to earlier studies (Parsapour et al. 2018; Yang et al. 2018; Pang et al. 2019; Wu et al. 2019), we found that land use changes from vegetation degraded land to forest substantially increased SOC, TN, TP, MBC, DOC, POC, and total PLFAs contents (Table 2). These changes in soil properties among restoration stages, such as SOC content, nutrients, and microbes significantly affect SOC mineralization (Cates et al. 2019; Wang et al. 2019; Zhang et al. 2019; Li et al. 2021; Xu et al. 2021). As we expected, significantly lower SOC mineralization in the DS than that in the PS and SFS (Fig. 1, Table 1) was found. Lower SOC mineralization in the DS would be attributed to lower total SOC or lower labile SOC, mainly POC, DOC and MBC contents (Table 2), which supported lower populations of soil microbes and through which thus led to lower SOC mineralization (Sheng et al. 2010; Chen et al. 2014; Yang et al. 2017; Huang et al. 2019). An alternative explanation is that extremely lower ($P < 0.001$) soil microbial biomass in the DS than that in the PS and SFS (Table 2). Previous studies which presented a positive microbial biomass effect on SOC decomposition (Fig. 6) also indicating that less soil microorganisms were involved in the decomposition in the DS (Wei et al. 2014; Fang et al. 2015).

Despite very different soil properties between the PS and SFS, the Cumulative SOC mineralization did not differ. The possible reason is that, although total SOC was significantly lower in the PS than that in the SFS, the amount of POC and MBC was slightly smaller (Table 2, $P > 0.05$) in the PS than in the SFS, which likely resulted in similar amount of SOC mineralization in the PS and SFS. Likewise, Huang et al (2019) showed that although total SOC was higher in the natural forest soil, the amount of labile SOC was 27–28% greater in the plantation soil leading to greater SOC mineralization in the forest plantation soil than that in the natural forest soil. There are also some incubation experiments revealed that the fluxes of CO_2 were positively correlated with DOC during the several months of incubation suggested that soil CO_2 emission was mainly from DOC (Conant et al. 2008; Gershenson et al. 2009). The DOC content did not differ between the PS and SFS which could partly explain the similar amount of SOC mineralization in the PS and SFS (Fig. 3, 6).

The property differences among the soils of three vegetation restoration stages did not result in logical responses of SOC mineralization to the rising temperature. In detail, increased temperature significantly increased (63.4%-102.6%) the SOC mineralization in the PS and SFS under both of the two soil moisture levels, but solely significantly increased SOC mineralization under 60%MWHC level in the DS. This is partial in line with most previous observations. For instance, many studies showed that increased temperature would stimulate SOC decomposition (Fissore et al. 2008; Huang et al. 2019; Wang et al. 2019; Fang et al. 2020), due to increased temperature would decrease SOC use efficiency by changing the physiological processes of microorganisms (Schindlbacher et al. 2011; Streit et al. 2013). Consistent with the observed responses of SOC mineralization to rising temperature, increased temperature significantly increased $q\text{CO}_2$ in the PS and SFS under both of the two soil moisture levels, but solely significantly increased SOC mineralization under 60%MWHC level in the DS (Fig. 4). Such changes in $q\text{CO}_2$ suggesting that increased temperature stimulated microbial respiration in the in the PS, SFS, and 60%MWHC level in the DS in our study. Although microbial biomass and the abundance of major microbial groups were not remarkably altered by temperature (Fig. 3, 5), Schindlbacher et al (2011) also reported that five years of soil warming did not affect microbial biomass or the

abundance of major microbial groups, but significantly increased $q\text{CO}_2$, thus leading to an increase in soil respiration.

However, increased temperature did not enhance SOC mineralization under 30%MWHC level in the DS which may be relate to the interactive effect of soil water deficit and substrate limitation (Suseela et al. 2012; Moyano et al. 2013). Most studies have demonstrated that the optimum for soil respiration is frequently found at intermediate soil water content, with decreases in rate both above and below the optimum soil water content (Craine et al. 2011; Suseela et al. 2012; Zhang et al. 2015). At intermediate soil moisture, which not only facilitates the diffusion of soluble C substrates, extracellular enzymes, and microbes in water film (Davidson et al. 2006), but also may help to improve microbial substrate availability through increasing labile C and nutrients pools (Balogh et al. 2011). Therefore, under the 30%MWHC treatment in the DS, the extremely lower labile SOC (i.e. POC and DOC) content (Table 4) combined with lower soil water content may hinder the diffusion of limited soluble C substrates, resulting in insensitive responses of SOC mineralization to rising temperature. Although we cannot provide conclusive evidence, the lowest MBC concentrations under the 30%MWHC treatment in the DS observed in this study (Fig. 3) does support this postulated mechanisms. Without substrate limitation, even at 20% MWHC, Zhou et al (2014) also revealed that SOC mineralization could still increase with temperature. The results meant that effects of temperature on SOC mineralization at different soil moisture levels would be affected by soil properties.

In the PS and SFS, we found that SOC mineralization was significant higher at 60%MWHC level (almost at an optimum soil water content for microbial respiration) than that at 30%MWHC level. As mentioned above, suitable soil moisture can facilitate the diffusion of soluble C substrates (Davidson et al. 2006) and improve microbial substrate availability (Balogh et al. 2011), which can stimulate the microbial decomposition of SOC. Compared to 30%MWHC, significantly increased MBC and DOC content at 60%MWHC level in the PS and SFS (Fig. 3, 6) could support this point. But increased soil moisture did not stimulate SOC mineralization in the DS, which may due to the limited soluble C substrates in the DS (Moyano et al. 2012). In the DS, 60%MWHC treatment did not increase DOC content under both two incubation temperatures also indicated the substrate limitation (Fig. 3). In addition, the inherent lower labile SOC content (Table 1) in the DS also should be responsible for the substrate limitation for microbes. These findings suggested that, to some extent, rising moisture and temperature would stimulate SOC decomposition, but these responses are highly dependent on soil properties or the quantity and quality of the substrates.

4.2. Responses of Q_{10} to vegetation restoration and soil moisture

Generally, soils with longer vegetation restoration years always have greater biodiversity and stability of biogeochemical processes (Yang et al. 2018; Zhang et al. 2019), we expected which may lead to lower Q_{10} values with the extension of vegetation restoration years (Deng et al. 2012; Xu et al. 2021). However, we found that the response of Q_{10} to vegetation restoration was highly dependent on soil moisture. In detail, at the 60%MWHC treatment, Q_{10} was decreased with vegetation restoration age (Fig. 2), this partly supports our expectation. Inversely, at the 30%MWHC treatment, Q_{10} was significantly lower in the DS than in the PS and SFS (Fig. 2). Likewise, previous studies presented soil property may interact with numerous climatic variables, eng et al. 2012; Davidson and Janssens 2006).

The optimum SWC was usually somewhere at 60% water-filled pore space, where the macropore spaces were mostly air filled, thus facilitating O_2 diffusion; the micropore spaces were mostly water filled, thus facilitating diffusion of soluble substrates (Suseela et al. 2012; Zhou et al. 2014; Zhang et al. 2015). Under the 60%MWHC condition, microbes should be no longer constrained by various substrates, thus the inherent properties of the soils converted to the predominant factor associated with the variations in soil respiration and Q_{10} (Craine et al. 2011; Suseela et al. 2012). Firstly, although water limitation was removed, quite limited labile substrate in the DS would be rapidly depleted (Table 2), which may lead to the longer the incubation time, the more time microbes had to consume the recalcitrant C, thus resulting in higher Q_{10} in the DS than that in the PS and SFS (Davidson and Janssens 2006; Wang et al. 2019). Secondly, soils with longer vegetation restoration years always have greater biodiversity (Yang et al. 2018), and Xu et al (2020) reported that high microbial diversity can stabilize the responses of SOC decomposition to warming. Thirdly, some studies showed that soils with more fungi or GP: GN ratio would have larger Q_{10} (Wang et al. 2018; Huang et al. 2019; Fang et al. 2020). This hypothesis is supported, to a certain extent, by our observations of the inherent higher abundance of fungi and GP: GN ratio in the DS (Table 2), and the incubation experiment done little to reverse this trend (Fig. 5).

We found Q_{10} was significantly lower in the DS than in the PS and SFS at the 30%MWHC treatment (Fig. 2). Under a water deficit condition, substrate availability of the soils may convert to the predominant factor associated with the variations in soil respiration and Q_{10} (Craine et al. 2011; Suseela et al. 2012). Although water deficit also existed in the PS and SFS, to some extent, the inherent higher labile SOC content could support microbial consumption in the PS and SFS (Table 2). On the contrary, at the 30%MWHC treatment in the DS, limited diffusion of soluble substrates combined with lower inherent higher labile SOC ultimately may inhibit the growth of microbes (Craine et al. 2011). The significantly lower MBC content at 30%MWHC level in the DS (Fig. 3) could support this point.

The absence of consensus on the responses of Q_{10} to soil moisture may be caused by the differences in soil properties across a variety of ecosystem types (Craine et al. 2011; Deng et al. 2012; Zhang et al. 2015). The result that increased soil moisture did not affect Q_{10} in the PS and SFS, but enhanced Q_{10} in the DS, which is consistent with our expectations that soil moisture had a less effect on Q_{10} in the SFS than in the DS. The potential mechanism could also be explained by the substrate availability. In our study, water deficit limited microbial biomass at the 30%MWHC in the DS which could lead to a lower Q_{10} (Fig. 3, 6). Previous studies also have shown that drying can decrease Q_{10} of soil respiration, and which was attributed to substrate limitation caused by the limited diffusion of solutes in thin soil water films (Davidson and Janssens 2006; Suseela et al. 2012; Moonis et al. 2021). At the 60%MWHC in the DS, water condition facilitated but substrates limited the microbial growth (Table 2, Fig. 3), leading to a disproportionately increase in microbial respiration and qCO_2 in the 28°C, which may also lead to a higher Q_{10} (Schindlbacher et al. 2011). In a modeling study, Moyano et al (2012) showed that the decomposition of SOC response to moisture depends on soil properties. Thus, these results also partly support the positive biodiversity-ecosystem stability hypothesis (Xu et al. 2021).

5. Conclusion

In this study, we found that cumulative SOC mineralization in PS and SFS was about 11.7 times higher than

Loading [MathJax]/jax/output/CommonHTML/fonts/TeX/fontdata.js t and microbial biomass in the DS. Increased soil

moisture and temperature led to significantly higher SOC mineralization in the SFS and PS. However, increased soil moisture did not affect SOC mineralization in the DS, and increased temperature solely increased SOC mineralization at the 60%MWHC treatment in the DS. The discrepancy responses of SOC mineralization to moisture and temperature indicated that, to some extent, rising temperature and moisture would stimulate SOC decomposition, but these responses are highly influenced by soil inherent substrate availability. Higher soil moisture did not affect Q_{10} in the PS and SFS, but enhanced Q_{10} in the DS. The Q_{10} value declined ($P < 0.05$) with vegetation restoration age at the 60%MWHC treatment, but it was significantly lower in DS than that in the PS at the 30%MWHC treatment. Our results suggested that the response of Q_{10} to vegetation restoration was highly dependent on soil moisture and substrate availability.

Declarations

Acknowledgement

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Figures

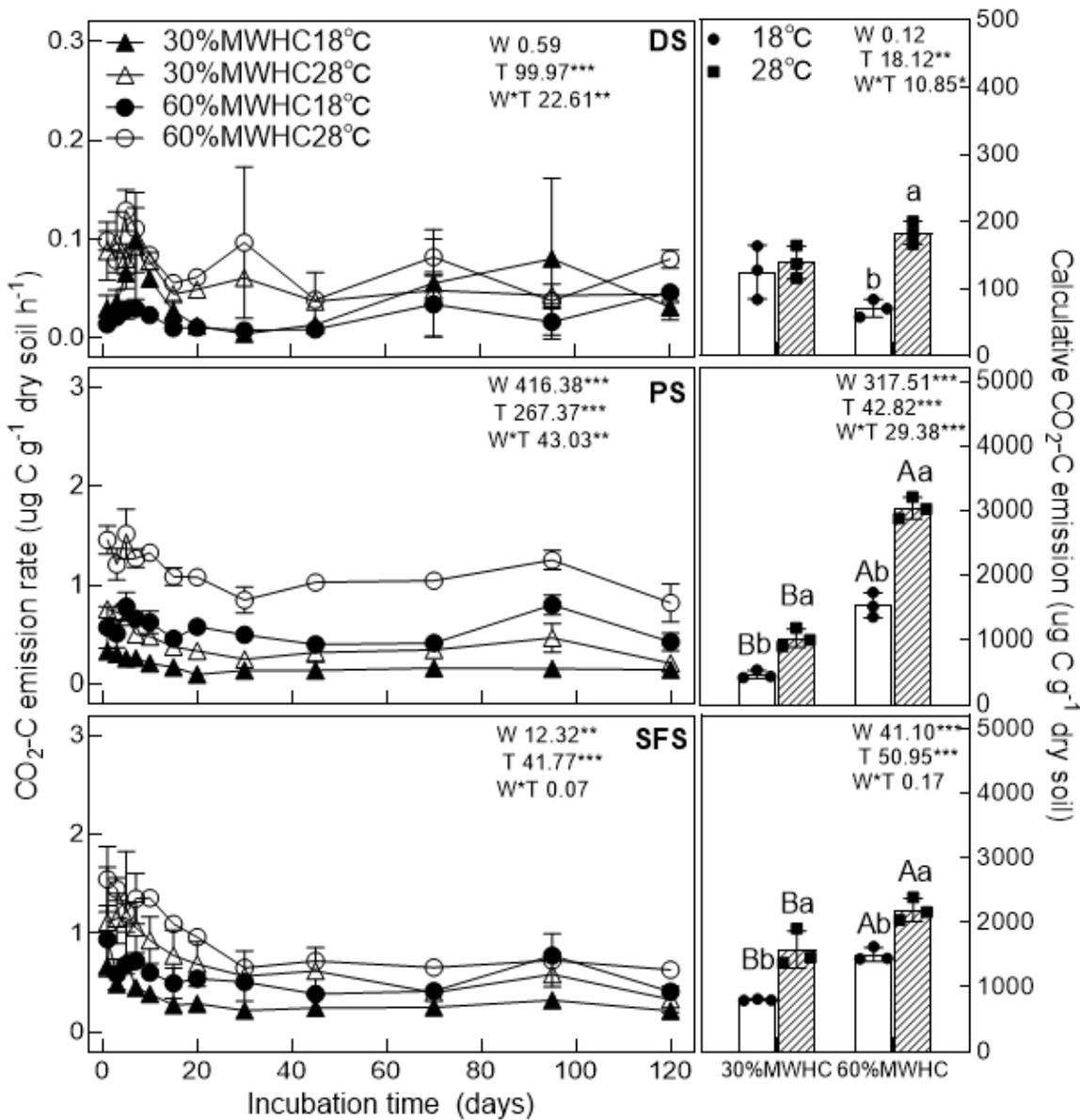


Figure 1

The CO₂-C emission rate (left) and cumulative CO₂-C emission (right) in soils of degraded vegetation (DS), plantation (PS) and secondary natural forest (SFS) incubated under different soil moistures and temperatures. The individual values of cumulative CO₂-C emissions are shown as circles or squares on the bar charts. Bars are standard deviation. Different superscript letters indicate significant differences between temperature treatments under the same soil moisture treatment (lowercase letters) and soil moisture treatments under the same temperature treatment (uppercase letters). F-values of the two-way ANOVA of soil moisture (W), temperature (T), and their interactions (W*T) are indicated in each vegetation restoration state. * P<0.05, ** P<0.01 *** P<0.001

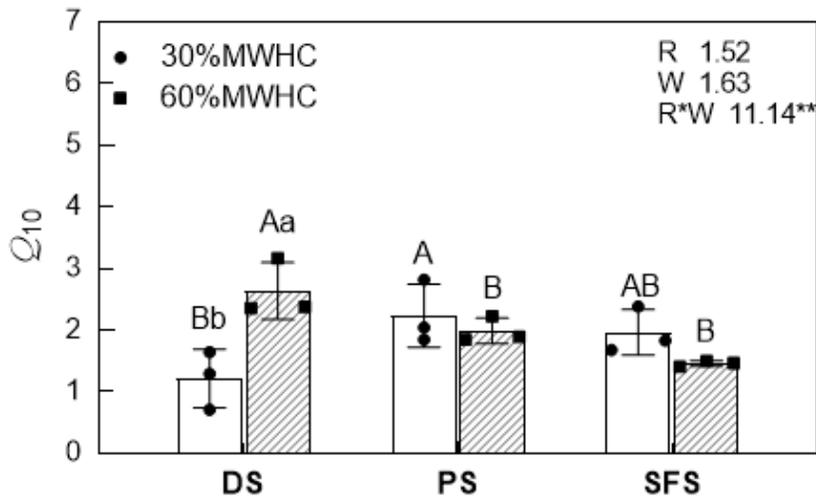


Figure 2

The Q10 of SOC mineralization in soils of degraded vegetation (DS), plantation (PS) and secondary natural forest (SFS) incubated under different soil moisture (W) treatments. R is re-vegetation. The values of individual observations are shown as circles or squares on the bar charts. Bars are standard deviation. Different superscript letters indicate significant differences among vegetation restoration stages under the same soil moisture treatment (lowercase letters) and soil moisture treatments under the same vegetation restoration stages (uppercase letters). F-values of the two-way ANOVA of vegetation restoration (R), soil moisture (W), and their interactions (R*W) are indicated. * P<0.05, ** P<0.01 *** P<0.001

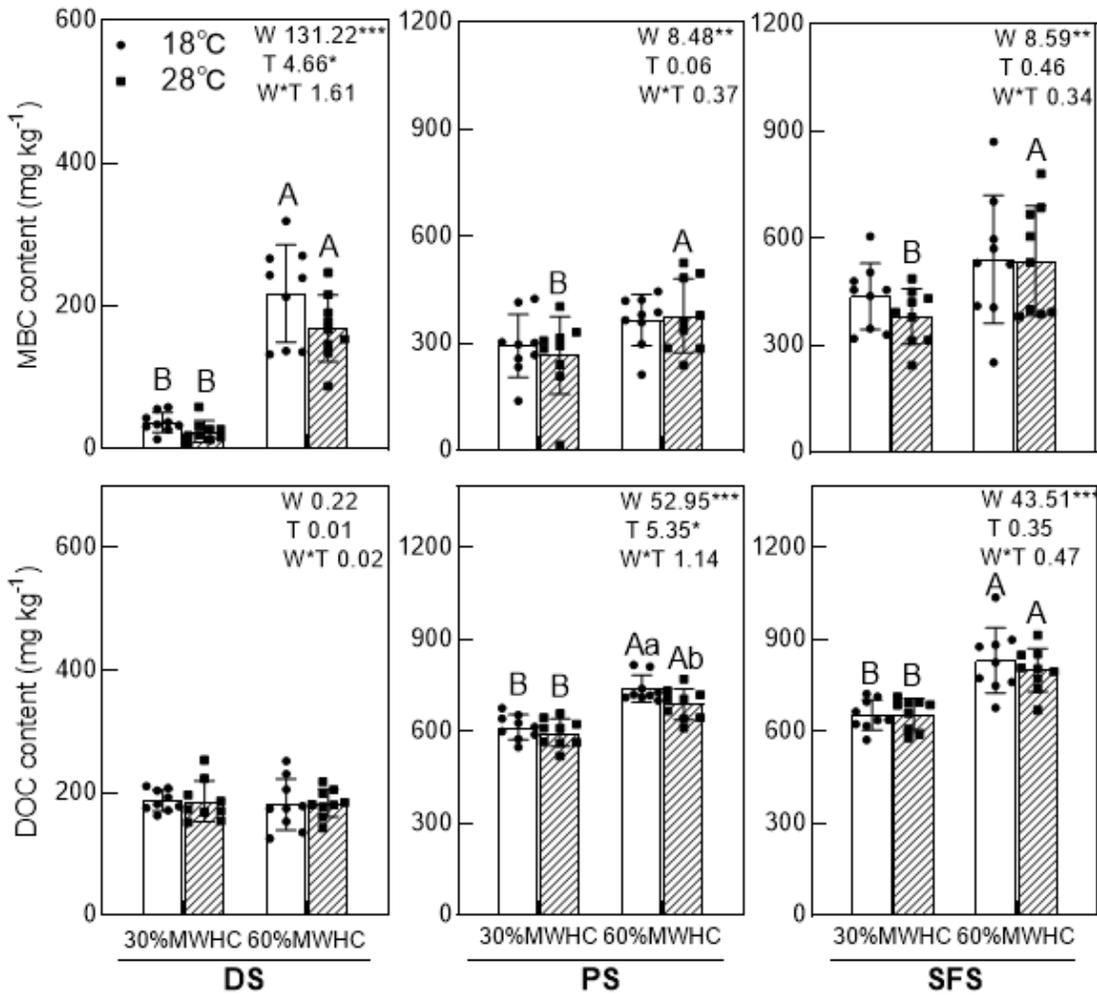


Figure 3

Soil microbial carbon (MBC) and dissolved organic carbon (DOC) contents of degraded vegetation (DS), plantation (PS) and secondary natural forest (SFS) under different moisture (W) and temperature (T) levels. The values of individual observations during the incubation process are shown as circles or squares on the bar charts. Bars are standard deviation. Different superscript letters indicate significant differences between temperature treatments under the same soil moisture treatment (lowercase letters) and soil moisture treatments under the same temperature treatment (uppercase letters). F-values of the two-way ANOVA of soil moisture (W), temperature (T), and their interactions (W*T) are indicated in each vegetation restoration state. * P<0.05, ** P<0.01 *** P<0.001

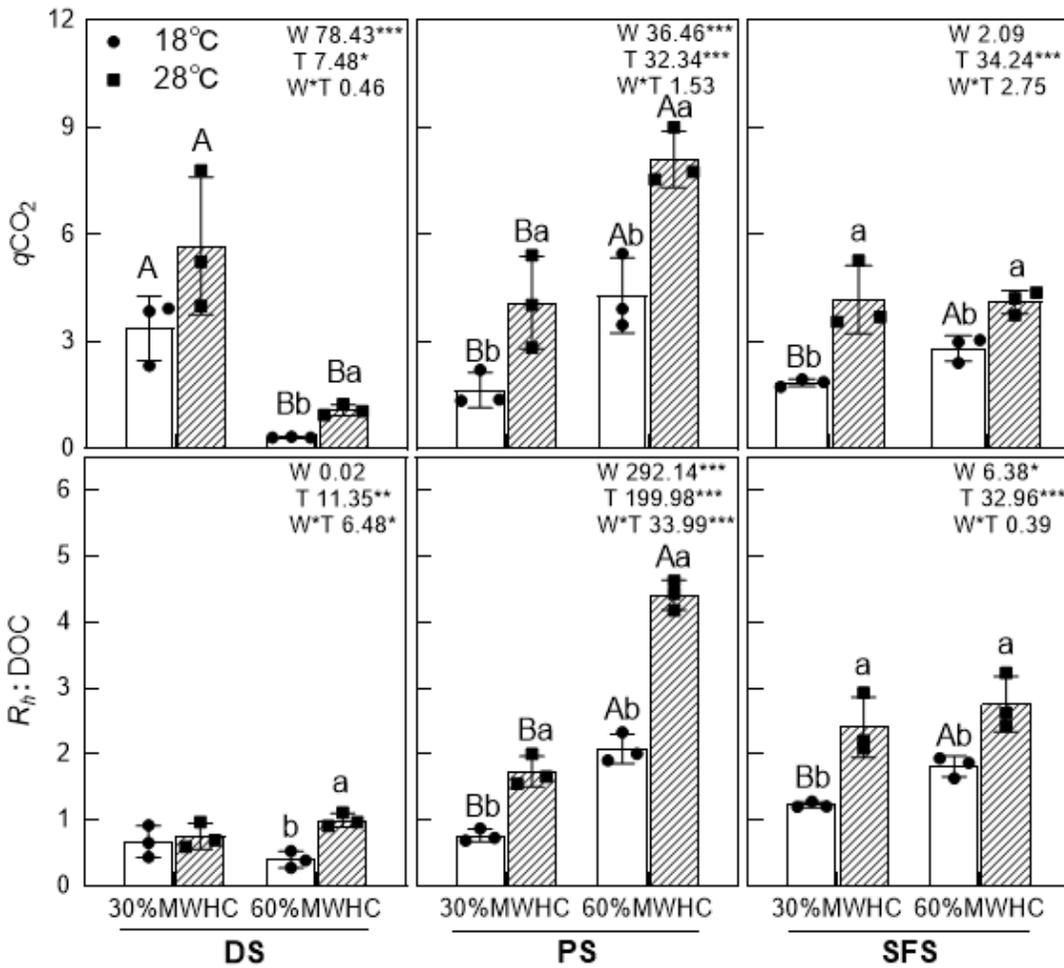


Figure 4

The metabolic quotient (qCO_2), decomposability of DOC ($R_h: DOC$) in soils of degraded vegetation (DS), plantation (PS) and secondary natural forest (SFS) under different moisture (W) and temperature (T) levels. The values of individual observations are shown as circles or squares on the bar charts. Bars are standard deviation. Different superscript letters indicate significant differences between temperature treatments under the same soil moisture treatment (lowercase letters) and soil moisture treatments under the same temperature treatment (uppercase letters). F-values of the two-way ANOVA of soil moisture (W), temperature (T), and their interactions (W*T) are indicated in each vegetation restoration state. * $P < 0.05$, ** $P < 0.01$ *** $P < 0.001$

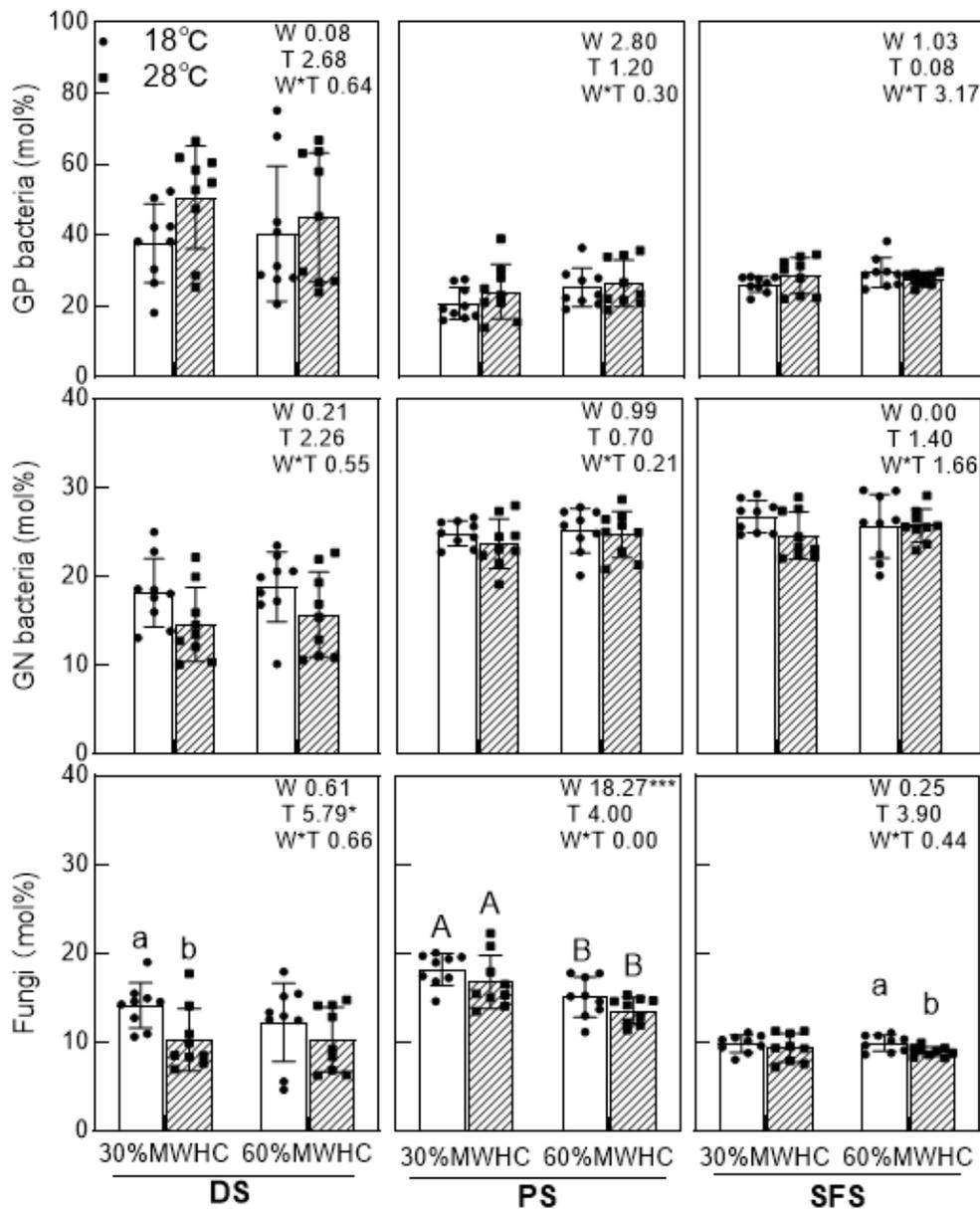


Figure 5

The relative abundance of GP, GN and fungi in soils of degraded vegetation (DS), plantation (PS) and secondary natural forest (SFS) under different moisture (W) and temperature (T) levels. The values of individual observations during the incubation process are shown as circles or squares on the bar charts. Bars are standard deviation. Different superscript letters indicate significant differences between temperature treatments under the same soil moisture treatment (lowercase letters) and soil moisture treatments under the same temperature treatment (uppercase letters). F-values of the two-way ANOVA of soil moisture (W), temperature (T), and their interactions (W*T) are indicated in each vegetation restoration state. * P<0.05, ** P<0.01, *** P<0.001

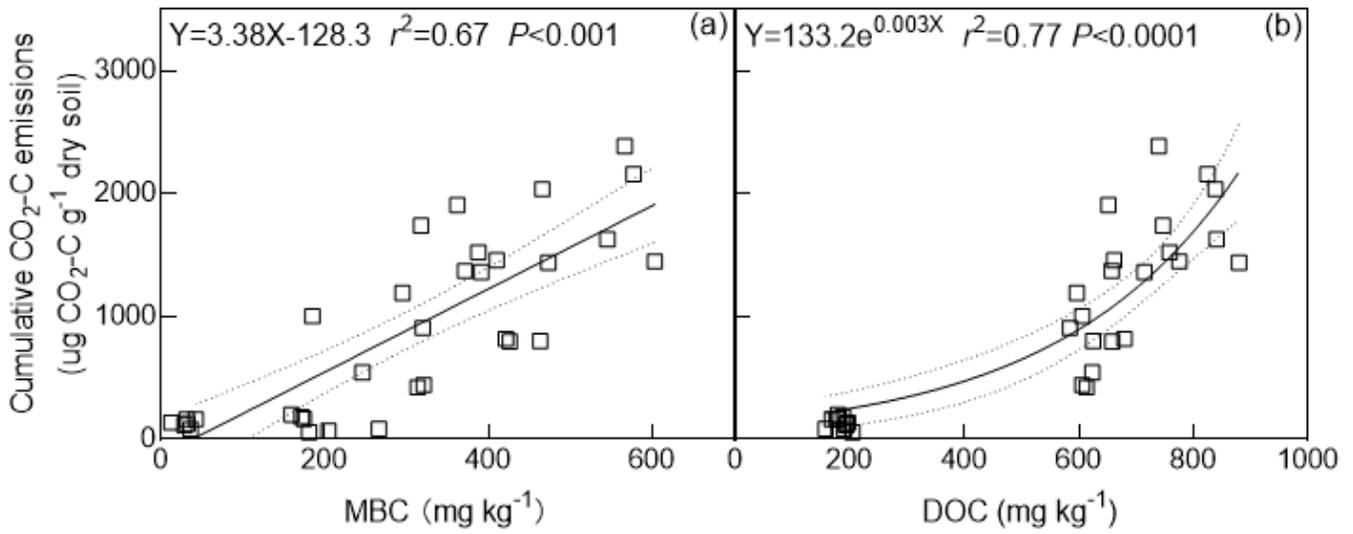


Figure 6

Regression plots linking cumulative CO₂-C emission to soil microbial carbon (MBC) and dissolved organic carbon (DOC) content. The dotted lines represent 95% confidence intervals.