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RESEARCH ARTICLE

Ten years of warming increased plant-derived carbon accumulation in an East Asian monsoon forest

Jing Zhang · Luhui Kuang · Zhijian Mou · Toshiaki Kondo · Jun Koarashi · Mariko Atarashi-Andoh · Yue Li · Xuli Tang · Ying-Ping Wang · Josep Peñuelas · Jordi Sardans · Dafeng Hui · Hans Lambers · Wenjia Wu · Joeri Kaal · Jian Li · Naishen Liang · Zhanfeng Liu

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Abstract

Aims Soil warming significantly influences soil organic carbon (SOC) pools in terrestrial ecosystems through its impact on the processes of carbon (C) input and decomposition as well as the stabilization of SOC pools. Most studies demonstrated that soil warming reduces SOC pools, but the magnitude is highly variable, and the underlying mechanisms are poorly understood.

Methods The concentration, stability (dissolved, particulate, and mineral-associated SOC) and source (plant-derived *vs.* microbial-derived) of SOC, soil microbial community composition, and enzymatic activities were studied in a 10-year soil warming field experiment in an East Asian monsoon forest.

Results 10-year soil warming significantly enhanced SOC in the top 0–10 cm soil. The increased SOC induced by warming was mainly derived from plants, with lignin and phenol markers increasing by 60% on average, accompanied by a 27% decrease in microbial-derived SOC. However, the overall effect of warming on SOC stability was not statistically significant.

Conclusions The results suggest that the moist monsoon forest soil could sequester SOC upon long-term warming. The discrepancy between our findings and those from other regions highlights an urgent

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J. Zhang · L. Kuang · Z. Mou · Y. Li · X. Tang · W. Wu · J. Li · Z. Liu (✉)
Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems & CAS Engineering Laboratory for Vegetation Ecosystem Restoration On Islands and Coastal Zones, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
e-mail: liuzf@scbg.ac.cn

J. Zhang · Y. Li · X. Tang · W. Wu · Z. Liu
Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Guangzhou 510650, China

L. Kuang · Z. Mou
University of Chinese Academy of Sciences, Beijing 100049, China

T. Kondo
Japan International Research Center for Agricultural Sciences (JIRCAS), Tsukuba, Ibaraki 305-8686, Japan

J. Koarashi · M. Atarashi-Andoh
Nuclear Science and Engineering Center, Japan Atomic Energy Agency, Tokai-mura, Ibaraki 319-1195, Japan

Y.-P. Wang
CSIRO Oceans and Atmosphere, PMB 1, Aspendale, VIC 3195, Australia

J. Peñuelas · J. Sardans
CSIC, Global Ecology Unit CREAF-CEAB-UAB, 08193 Cerdanyola del Valles, Catalonia, Spain

need for a better understanding of how the contrasting effects of plant- and microbial-derived C mediate the response of the SOC pool to warming across biomes.

Keywords Experimental warming · Plant-derived carbon · Microbial residual carbon · Soil organic carbon stability · East Asian monsoon forest

Introduction

Global soil organic carbon (SOC) pools are estimated to be 2,476 Gt in the upper 1 m of soil (Köchy et al. 2015), which is about four times the amount of carbon (C) in the atmosphere, and six times that in vegetation biomass (IPCC 2014). Therefore, even small changes in the global SOC may have a significant influence on the climate system (Chabbi et al. 2017; Marinspiotta et al. 2010). However, the net balance between the increased C input into the soil from the CO_2 fertilization effect on plant productivity, and C release by soil respiration under warming remains uncertain (Crowther et al. 2016; García-Palacios et al. 2021). The observed warming effect on the SOC pool was highly variable among different warming studies (Wang et al. 2014; Zhou et al. 2016) and varied with the duration of the field experiments (Melillo et al. 2017; Romero-Olivares et al. 2017), and background air temperature (García-Palacios et al. 2021; Melillo et al. 2017; Yan et al. 2020), which contradicts the consistently net C release under warming by nearly all earth system models (Luo et al. 2015; Zhang et al. 2020). Thus, it is important to understand the response of SOC under long-term warming and the underlying mechanisms in diverse environments.

SOC preservation depends on the balance between the C input from both aboveground and belowground litter and root exudates on one hand and organic C decomposition on the other. In a forest ecosystem, the contribution of aboveground litter to annual litter input is similar to that of belowground litter, but aboveground litter usually decomposes faster than belowground litter (Freschet et al. 2013). Warming tends to increase the aboveground biomass of terrestrial plants, and thus above-ground litter production (Lin et al. 2010), the increased C input probably leads to the increased plant-derived SOC (Oldfield et al. 2018). The decomposition rate of plant-derived SOC is different and contributes to different SOC pools (fast-/slow-cycled pools) (Cotrufo et al., 2015). Therefore, it is worth studying the warming-affected aboveground litter input influences plant-derived SOC in controlled experiments without belowground litter response. Warming is also expected to decrease soil moisture in the long run (Cheng and Huang 2016; Cook et al. 2014). Furthermore, the soil has a strong buffer capacity to heat which implies that infrared heating above ground is likely to have a smaller drying effect on subsoil than surface soil layers.

There is increasing evidence revealing the critical roles of soil microbes in SOC formation and stability (Liang et al. 2019). Although living microbial biomass accounts for less than 5% of total SOC, soil microbial residues may contribute up to 50% of total SOC (Khan et al. 2016; Liang and Balser 2011). Microbial residues in soil often have a longer residence time than plant-derived C (Khan et al. 2016; Miltner et al. 2012). Warming may change microbial community composition and biomass (Nottingham et al. 2019; Romero-Olivares et al. 2017), and influence soil microbial residues and plant-derived SOC (Ding et al. 2020; Jing et al. 2019). Warming increased both plant-derived SOC (e.g. lignin) and microbial residues in a temperate agroecosystem (Ma et al. 2022). However, it is not clear to what extent and how microbial residues are influenced by

J. Peñuelas · J. Sardans
CREAF, 08193 Cerdanyola del Valles, Catalonia, Spain

D. Hui
Department of Biological Sciences, Tennessee State University, Nashville, TN 37209, USA

H. Lambers
School of Biological Sciences, University of Western Australia, Perth, WA 6009, Australia

J. Kaal
Pyrolyscience, Santiago de Compostela, Spain

J. Li
Key Laboratory of Urban Environment and Health, Institute of Urban Environment, Chinese Academy of Sciences, Xiamen 361021, China

N. Liang (✉)
Earth System Division, National Institute for Environmental Studies, Tsukuba, Ibaraki 305-8506, Japan
e-mail: liang@nies.go.jp

warming in comparison with plant-derived SOC in particular in forest ecosystems.

The response of SOC to long-term warming depends on whether microbes adapt to increased temperatures (Allison et al. 2010; Melillo et al. 2017), and on the changes in the stability of SOC (Fang et al. 2005; Feng et al. 2008). Both the chemical recalcitrance and physical protection of SOC (e.g., association with minerals and occlusion within aggregates) are important in mediating the accessibility and assimilatory ability of microbes to SOC (Lehmann and Kleber 2015; Luo et al. 2017). Schimel and Schaeffer (2012) indicated that the stability of SOC was controlled by physical protection, rather than chemical properties. Furthermore, theoretical modeling suggests that up to 90% of the total SOC is physically (occlusion) and/or chemically (chemisorption) protected and that the dynamics of SOC depend largely on the dynamics of protected SOC (Luo et al. 2017). Short-term warming influences the concentration of SOC and readily degraded organic C (Yuan et al. 2021), and it is, therefore, vital to understand the response of the physical stability of SOC under long-term warming.

Asian monsoon forests (20–40°N, 100–145°E) have higher net ecosystem productivity (NEP) than other forests at the same latitudes in Europe, Africa, and North America, and accounted for 8% of the global NEP from 1990 to 2010 (Yu et al. 2014). Under the influence of the Tibetan Plateau and East Asian monsoon climate, this region receives high rainfall (Wu et al. 2007). Copious rainfall and favorable temperatures combined with increasing atmospheric nitrogen deposition contribute to the high productivity and strong CO_2 sink of the region (Yu et al. 2014). This strong C sink might be significantly reduced or even become a C source under global warming because warming not only increases litter input (Ito et al. 2016) but also releases more CO_2 from the soil (Liang et al. 2017).

To investigate the impact of warming-induced aboveground litter input on the soil C balance and underlying mechanisms in Asian monsoon forests, we conducted a long-term soil warming experiment (~ 10 years) in a 35-year-old evergreen oak forest in western Japan. Trenching was used to separate the influence of aboveground litter input from roots on SOC concentration and composition, which is the common method for heterotrophic respiration measurement. We hypothesized that: 1) SOC pools would remain unaltered or even increase after 10 years of warming without belowground litter input based on the results of recent studies (Crowther et al. 2016, 2018; Zhang et al. 2020); 2) a change of SOC would be caused by changes in microbial communities, plant-derived C and microbial-derived C, and the stability of SOC under warming; 3) the mineral-associated organic carbon (MAOC) would increase, whereas dissolved organic carbon (DOC) and particulate organic carbon (POC) would decrease under warming because warming would preferentially eliminate the readily degraded SOC, and the recalcitrant component would become relatively enriched (Melillo et al. 2017) during the first 10 years of warming.

Materials and methods

Study area

The soil-warming experiment was carried out in a 35-year-old evergreen Japanese oak forest near the summit of Kagamiyama, Higashi-Hiroshima, Japan (N34°24′26″, E132°43′23″, 320 m above seas level). This area has a subtropical maritime monsoon climate, with warm, humid summers, and cool, dry winters. The mean annual precipitation is 1,458 mm and the annual mean air temperature is 13.7 °C with the highest monthly mean temperature in August (25.8 °C) and the lowest in January (2.3 °C) (1991–2017). The dominant tree species is *Quercus glauca* (Fagaceae) with a mean height of 12.9 m and leaf area index of 6.1 m^2 m^{-2} in 2018. The soil in this area originates from the volcanic substratum, is moderately brown when moist, and is classified as Cambisol according to the WRB classification system (ISSS Working Group RB, 1998). Soil texture is dominated by sand (74%), and the pH is 4.3 in the top 5 cm soil layer (Ishizuka et al. 2006).

Soil warming experiment

The warming experiment was set up in September 2007. Because of the difficulties in raising the temperature of the entire forest ecosystem (both aboveground and belowground) (Liang et al. 2017; Rich et al. 2015), we designed the experiment with a

focus on soil warming. The trenching plots subjected to warming were used to study the warming effects on SOC without belowground (root) litter input. Specifically, we set up ten 1 m × 1 m root-exclusion plots by trenching the soil to 40 cm deep and then inserted PVC sheets (4 mm thick) to prevent the ingrowth of roots. Each chamber (90 cm long × 90 cm wide × 50 cm tall) was installed in each plot. The understory vegetation inside the plots was clipped and left inside the chambers every two weeks to avoid interference. Five trenched plots were randomly assigned to warming manipulation. An 800-W carbon-filament heat lamp (0.4 m long, 5 mm wide, and 0.5 mm thick, Sakaguchi E.H. VOC. Corp., Akihabara, Tokyo, Japan) was suspended at 1.8 m above each warming chamber. The lamp was a resistive carbon filament that was enclosed in a glass vacuum tube (1 cm in diameter and 0.4 m in length), which irradiated evenly over a surface area of 1.5 m × 2.0 m. The soil was aimed to be warmed by about + 2.5 ℃ at a depth of 5 cm soil by infrared carbon-filament heat lamps in the warming plots, based on the range of warming that may occur towards the end of this century (IPCC 2013). In each chamber, soil temperature was measured by thermocouples buried at 5 cm soil depth, and soil moisture was measured at 10 cm soil depth using a sensor multiplexer every 30 min for the past 10 years. Air and soil temperature (above-ground 5 cm, litter layer, and 5, 10, 20, 30, and 50 cm below the soil surface) was also measured from December 2nd to 6th in 2021. More information about the experimental design is provided in Liang et al. (2017) and Teramoto et al. (2018).

Field sampling

On 23rd April 2018, five soil cores (1.5 cm in diameter) were randomly collected as one composite sample at 0–5 and 5–10 cm soil depths in each plot (chamber). Soil samples were thoroughly mixed and divided into two subsamples, and then transferred to different plastic zip-lock bags. One of the subsamples was stored under the ice to keep fresh during transport to the laboratory. Part of the first fresh subsample was passed through a 2-mm sieve and used for the analysis of C-, N- and P-decomposition-related enzyme activities (β-glucosidase and β-*N*-acetylglucosaminidase) within two weeks; the rest of the fresh soil was freeze-dried and used for the analysis of microbial community composition. The other subsample was air-dried directly after being transferred to the laboratory and passed through a 2-mm sieve for analyses of SOC chemical composition, SOC density fractionation, ammonium (NH_4^+-N), and nitrate-nitrogen (NO_3^--N). The rest of the air-dried soil was milled and passed through a 0.053-mm sieve to measure the concentration of total SOC, total nitrogen (TN), and soil microbial residues.

On 31st July 2019, we collected the litter inside each chamber. The litter samples were carefully divided into leaves and twigs (including acorns). Samples of the standing litter were taken to the laboratory for further measurement.

Laboratory analyses

Analysis of litter and soil properties Soil abiotic properties were measured as described by Liu et al. (1996). Specifically, soil moisture was determined by weighing after being oven-dried for 48 h at 105 °C, and litter water content was measured after being oven-dried at 80 °C. SOC was measured by titration with a $FeSO_4$ solution after dichromate oxidation. TN was measured by the micro-Kjeldahl method, NH_4^+-N was determined by the indophenol blue method followed by colorimetry, and the concentration of NO_3^--N was analyzed after cadmium reduction to nitrite, followed by the sulfanilamide-NAD reaction (Liu et al. 1996). The isotope abundance of ^{13}C ($\delta^{13}C$) and ^{15}N ($\delta^{15}N$) were measured using an Isotope Ratio Mass Spectrometer (IRMS) with a Flash 2000 HT elemental analyzer (Thermo Fisher Scientific, Waltham, MA, USA).

Phospholipid fatty acid (PLFA) analysis Four-gram freeze-dried soil was analyzed for microbial community composition according to Bossio and Scow (1998), with minor modifications. The abundance of individual fatty acids was calculated by the inner standard fatty acid (19:0) and expressed as nmol per gram of dry soil. The i15:0, 15:0. i16:0, 16:1ω9, 16:1ω7t, i17:0, a17:0, 17:0, cy17:0, 18:1ω7, and cy19:0 represent bacteria (Frostegård and Bååth 1996). The sum of i15:0, a15:0, i16:0, i17:0, a17:0 and the sum of 16:1ω9c, 16:1ω7c, 18:1ω7c, cy17:0, cy19:0 are indicators of Gram-positive and Gram-negative bacteria, respectively (Zelles 1999). The sum of 16:0 10-methyl, 17:0 10-methyl, and 17:0

10-methyl represents actinomycetes PLFAs (Frostegård and Bååth 1996). The fungal biomass was identified by the specific PLFA 18:2ω6,9 (Frostegård and Bååth 1996), and the biomarker of 16:1ω5 was used to represent arbuscular mycorrhizal fungi (AMF) PLFA (Olsson 1999). The ratio of fungi to bacteria (F:B) was estimated by the ratio of 18:2ω6,9 to total bacterial PLFAs in the soil (Frostegård and Bååth 1996).

Soil enzyme activities The β-glucosidase activity (βG) was measured by the method of Eivazi and Tabatabai (1988), with 25 mM *p*-nitrophenyl-β-D-glucopyranoside as substrate. The activity of β-1,4-*N*-acetylglucosaminidase (NAG) was analyzed by the procedure of Pazferreiro et al. (2014), with *p*-nitrophenyl-*N*-acetyl-β-D-glucosaminidine as substrate. Acid phosphomonoesterase (AP) activity was measured following Schneider et al. (2000), using *p*-nitrophenyl phosphate tetrahydrate as substrate.

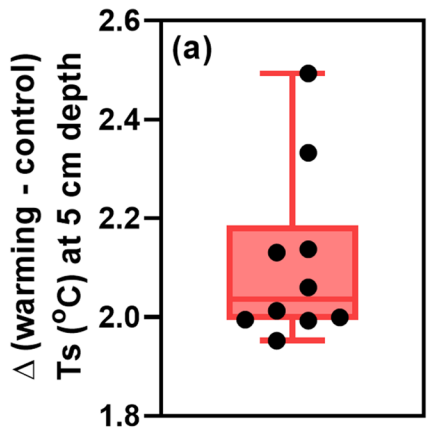
The molecular composition of SOC Soil was analyzed by pyrolysis-GC–MS (Py-GC–MS) to obtain a semi-quantitative estimate of the balance between the different microbial and plant-derived macromolecules. The soil was pretreated in dilute HF to eliminate reactive minerals (Miltner and Zech 1997). Briefly, 1.0 g of ground soil was treated with 40 mL of 2% (v/v) HF solution, and the suspension was allowed to react overnight in an orbital shaker. After centrifugation at 800 × *g* for 10 min, the supernatant was discarded, and the HF treatment was repeated three times. Conventional Py-GC–MS was performed with a Pyroprobe 5000 (CDS Analytical, Oxford, PA, USA) coupled with a 6890 N GC and 5975B MSD (Agilent Technologies, Santa Clara, USA). Aliquots of 1 mg samples were pyrolyzed at 650 °C for 20 s (heating rate 10 °C ms^{-1}) in glass wool-containing fire-polished quartz tubes. The pyrolysis-GC interface, GC inlet, and GC–MS interface were set at 325 °C. The GC was equipped with an HP-5MS (nonpolar) column. Relative proportions of the pyrolysis products were calculated as the percentage of the total quantified peak area (TQPA), using the main fragment ions (*m*/*z*) of each product. The relative proportion of lignin compounds was used to indicate the C derived from plants (Mendu et al. 2011; van Erven et al. 2017).

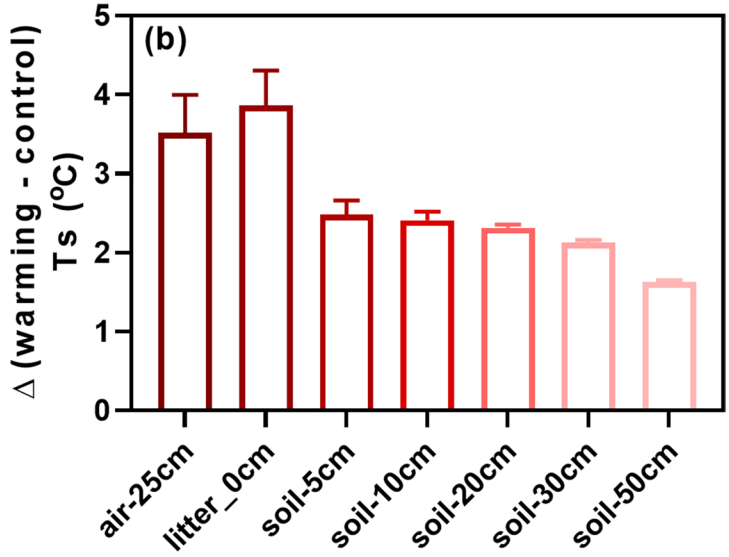
Soil organic carbon density fractionation To isolate the bioavailable SOC pool, SOC was treated with a low-C and -N sodium polytungstate (SPT, 1.65×10^{-3} g mm^{-3}), creating a light fraction comprising primarily particulate organic material (POM), and a heavy fraction consisting of mineral-associated organic material (MAOM). We followed the procedures of Keiluweit et al. (2017). Briefly, 15 mL SPT solution (> 1.8 g cm^{-3}) was added to 4 g air-dried soil, and centrifuged at 1,446 × g for 30 min after shaking for 1 h. Then POM was collected using a 0.45-μm filter. For the residue, we added 15 mL SPT solution again; and repeated the step until the supernatant was devoid of floating particles. Both fractions were dried at 50ºC, weighed, milled, and then analyzed for the C concentration to obtain the POC and MAOC percentages (%, Eq. (1)). Dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were measured by Elementar Vario TOC analyzer (Langenselbold, Germany) after immersion in potassium sulfate (K_2SO_4) for 24 h and then filtered using 0.45-μm polysulfone membrane filters (Xu et al. 2010).

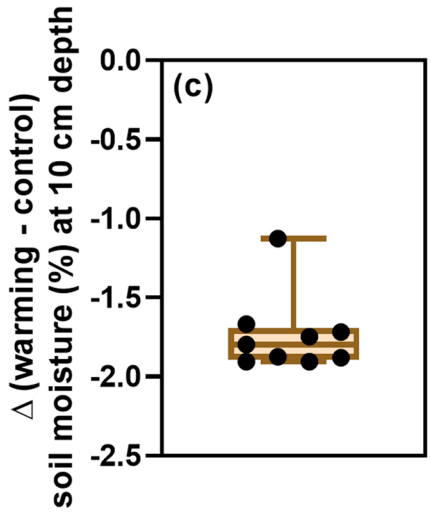
$$\mathrm{POC\ (or\ MAOC)} = \mathrm{a} \times \mathrm{b}\ /\mathrm{SOC} \times 100\% \quad (1)$$

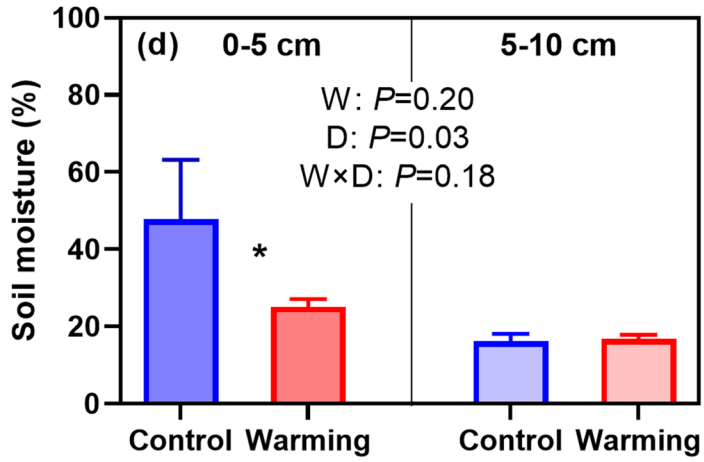
(a, C concentration in POM (or MAOM)(g kg^{-1}); b, POM (or MAOM) weight ratio per gram soil; SOC, soil organic carbon (g kg^{-1}))

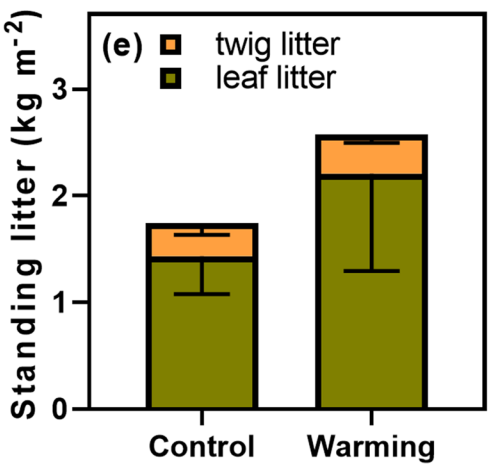
Soil microbial residues Soil amino sugars, biomarkers of soil microbial residues, which include glucosamine (GluN), muramic (MurN), and galactosamine (GalN), were measured according to Indorf et al. (2011). GluN and MurN were assumed to be biomarkers of fungal and bacterial residues, respectively (Engelking et al. 2007). In brief, 0.5 g of air-dried soil (< 2 mm) was hydrolyzed in 10 mL 6 mol L^{-1} hydrochloric acid (HCl) in an oven (105ºC) for 6 h. Then, 1 mL supernatant was N_2 dried with heated water at 45ºC after vortexing and standing for 30 min. Aliquots of 1 mL Milli-Q water were added

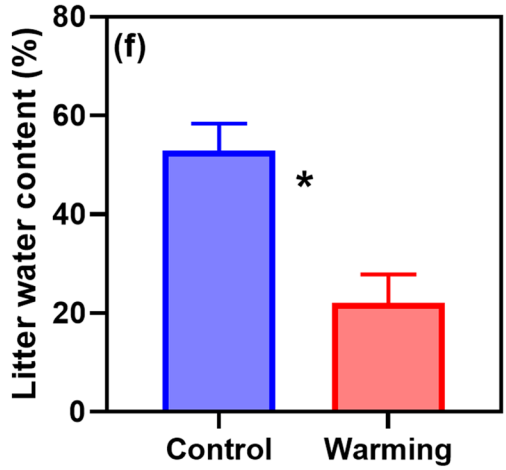

(a)
Δ (warming - control)
Ts (°C) at 5 cm depth
2.6
2.4
2.2
2.0
1.8


(b)
Δ (warming - control)
Ts (°C)
5
4
3
2
1
0
air-25cm
litter_0cm
soil-5cm
soil-10cm
soil-20cm
soil-30cm
soil-50cm


(c)
Δ (warming - control)
soil moisture (%) at 10 cm depth
0.0
-0.5
-1.0
-1.5
-2.0
-2.5


(d)
0-5 cm
5-10 cm
W: P=0.20
D: P=0.03
W×D: P=0.18
Soil moisture (%)
100
80
60
40
20
0
*
Control
Warming
Control
Warming


(e)
twig litter
leaf litter
Standing litter (kg m-2)
3
2
1
0
Control
Warming


(f)
Litter water content (%)
80
60
40
20
0
*
Control
Warming

◂**Fig. 1** The effect of warming on soil temperature (**a**) at 5 cm depth, and soil moisture content (**c**) at 10 cm depth compared with the control (△(Warming-Control)) at the end of the experiment (2007–2017). Panel **b** shows the warming effect on temperature from 25 cm aboveground to 50 cm belowground every 30 min over two days during the sampling period. The data showed in Panels **a**, **b**, **c** was measured by sensor multiplexer in situ, whereas the data presented in panels **d**, **f** and **e** were measured in the lab after we collected the samples. Panels **d**, **f**, and **e** present the warming effect on soil moisture content (0–5 and 5–10 cm), standing litter, and litter moisture content, respectively, for once measurement. The dots in panels **a**, and **c** represent the mean value of each parameter for each year. * represents a significant difference between the control and warming treatment at $P < 0.05$. W, warming effect; D, depth; W × D: the interaction between warming effect and depth. The same below

and dried with N_2 again, and this was repeated twice. Amino sugars were determined using high-performance liquid chromatography (Dionex Ultimate3000, Thermo Fisher Scientific, Waltham, MA, USA) after filtration using syringe filters.

Data analyses

All statistical analyses were performed using R software version 4.1.0 (R Core Team, 2021), and figures were drawn using GraphPad Prism version 8.0 for Windows (GraphPad Software, San Diego, CA, USA). A two-factor ANOVA by the 'dplyr' package in R was used to analyze the effect of warming and soil depth on soil factors with $P < 0.05$ as the significance level, and $P < 0.10$ as the marginal significant level (Treseder and Allen 2002; Zhou et al. 2012).

Results

Soil abiotic properties, microbial communities, and enzymes activities

As compared with the soil in the control, the mean soil temperature was increased by 2.1 ± 0.05 °C at 5 cm depth (Fig. 1a) and soil moisture was slightly decreased by 1.6 ± 0.18% at 10 cm soil depth (Fig. 1c) in the warmed plots after 10 years of the warming treatment. The warming intensity declined gradually from ambient air, and litter to soil profiles with temperature increased by 4 °C in the litter layer and by 1.5 °C in deep soil (50 cm) (Fig. 1b). Compared to the control, the surface litter layer and topsoil (0–5 cm) in the warmed plots were drier, and the warming effect on subsoil (5–10 cm) was significantly less than that on topsoil (Fig. 1d, f). Moreover, the biomass of standing litter was marginally significantly increased by 48% ($P = 0.10$) in warmed plots after 10 years of warming (Fig. 1e).

Warming did not significantly influence most of the measured soil properties at both sampling depths, except for an increased soil TN concentration in the 5–10 cm soil layer ($P < 0.05$), and a decreased $\delta^{13}C$ at both sampling depths ($P < 0.01$, Table 1). Compared to the topsoil, concentrations of TN, NH_4^+-N, and DON were significantly decreased whereas the abundances of $\delta^{13}C$ and $\delta^{15}N$ were increased in the 5–10 cm soil layer (Table 1).

Warming significantly changed soil microbial biomass (total PLFA) and community composition in the top 10 cm of soil (Fig. 2). Specifically, total microbial biomass increased by 138% under warming in the 5–10 cm soil ($P < 0.05$, Fig. 2a). Warming significantly decreased the concentration of bacterial PLFA (Fig. 2e), especially Gram-positive bacteria (Fig. 2g) in the top 5 cm soil, whereas it significantly increased the concentration of actinomycete PLFA, fungal PLFA, and Gram-negative bacterial PLFA in the 5–10 cm layer ($P < 0.05$, Fig. 2c, d, h). However, the ratios of fungi to bacteria (F: B) and Gram-positive to Gram-negative bacteria (GP: GN) were not affected by warming at either 0–5 cm or 5–10 cm (Fig. 2f, i). The activities of NAG in the topsoil and βG in the subsoil significantly increased under warming (Fig. 2j, k). Neither the warming nor the soil depth significantly affected the activity of AP (Fig. 2l).

SOC concentration, molecular composition, and stability

The concentration of SOC was significantly greater in the topsoil (0–5 cm) than in the subsoil (5–10 cm). SOC concentration insignificantly changed in the topsoil ($P > 0.05$), whereas increased by 131% in the subsoil ($P = 0.03$, Fig. 3a) under warming. Pyrolysis-GC–MS and amino sugar analysis showed that the increased SOC by warming was mainly derived from plants (Fig. 3b), rather than microbes (Fig. 3c). Warming increased plant-derived

Table 1 The responses of soil abiotic properties to warming in the 0–5 cm and 5–10 cm soil layers (mean ± SE, $n = 5$)

Soil layer (cm)	Condition	TN (mg g^{-1})	NO_3^--N (mg kg^{-1})	NH_4^+-N (mg kg^{-1})	Soil $\delta^{13}C$	Soil $\delta^{15}N$	DON (mg kg^{-1})	DON:TN (%)
0–5	Control	5.3 ± 1.0	3.1 ± 2.7	47 ± 21	-28.3 ± 0.3	0.3 ± 0.6	246 ± 82	1.4 ± 0.4
	Warming	7.9 ± 1.2	11 ± 5	59 ± 20	-28.8 ± 0.1	-0.3 ± 0.3	392 ± 180	2.4 ± 1.2
5–10	Control	**1.8 ± 0.2**	1.3 ± 0.5	9 ± 2.3	**-27.6 ± 0.2**	2.0 ± 0.6	99 ± 19	1.3 ± 0.2
	Warming	**3.7 ± 0.5***	4.4 ± 1.9	21 ± 7	**-28.5 ± 0.2***	0.5 ± 0.4	159 ± 29	0.8 ± 0.1
Soil layer t test (*P* value)		**< 0.01**	> 0.05	**< 0.01**	**0.03**	**0.02**	**< 0.01**	0.07
Soil depth * warming (*P* value)		0.89	0.63	0.76	0.54	0.26	0.54	0.58

Asterisks (*) represent significant differences between the control and warming treatment ($P < 0.05$). The last row shows the *P-value* of the significance test (independent *t-test*) for the difference between sampling depths. All significant values are shown in **bold**. TN, total nitrogen; NO_3^--N, nitrate-nitrogen; NH_4^+-N, ammonium nitrogen; DON, dissolved organic nitrogen; DON: TN, the ratio of DON to TN

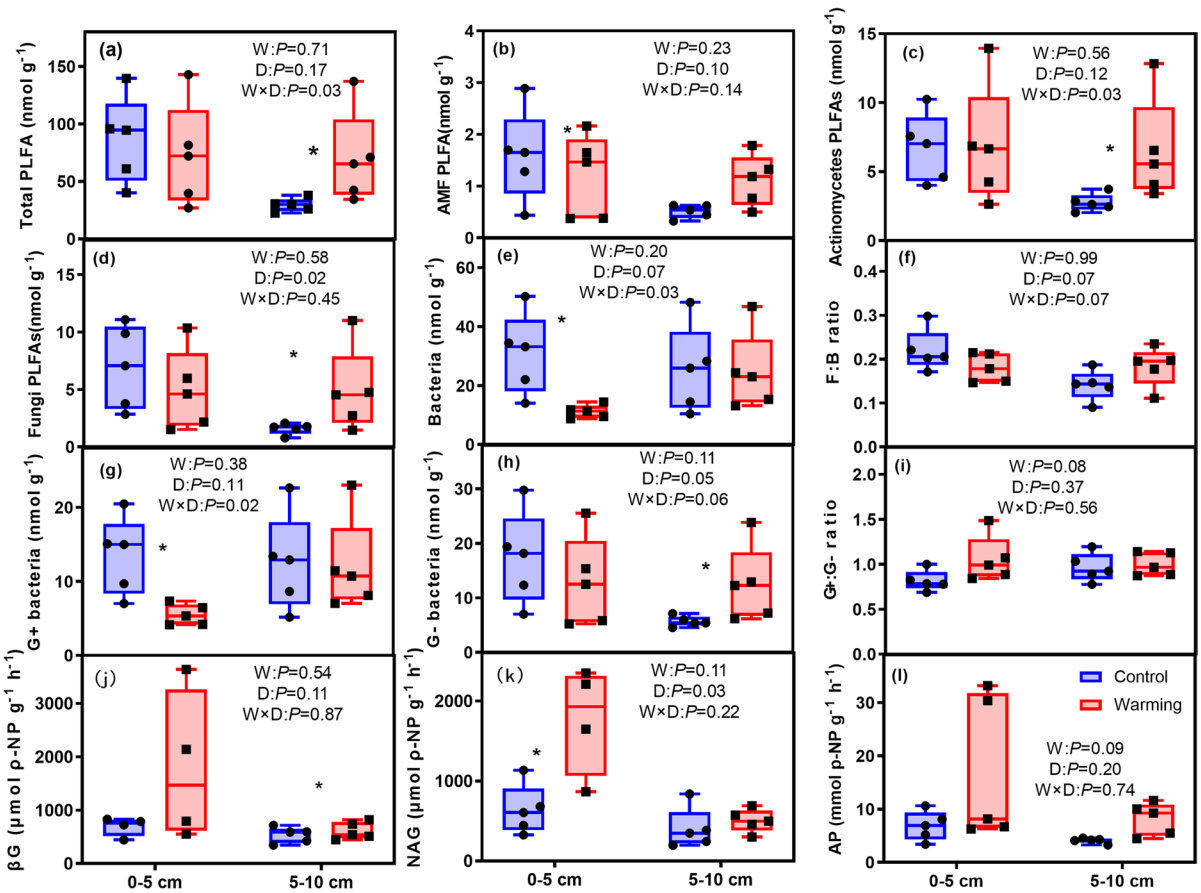


Fig. 2 Effect of warming on soil microbial communities based on phospholipid fatty acid (PLFA) analysis. Data are means ± SE ($n = 5$). Total PLFA (**a**); AMF PLFA (**b**), arbuscular mycorrhizal fungi PLFA; Actinomycetes PLFAs (**c**); Fungal PLFAs (**d**); Bacteria (**e**); F: B ratio (**f**), fungal to bacterial PLFA ratio; G+ bacteria (**g**), Gram-positive bacteria; G-bacteria (**h**), Gram-negative bacteria; G+: G-ratio (**i**), Gram-positive to Gram-negative bacterial PLFA ratio; βG (**j**), β-glucosidase activity; NAG (**k**), β-1,4-*N*-acetylglucosaminidase; AP (**l**), acid phosphomonoesterase. *, $P < 0.05$

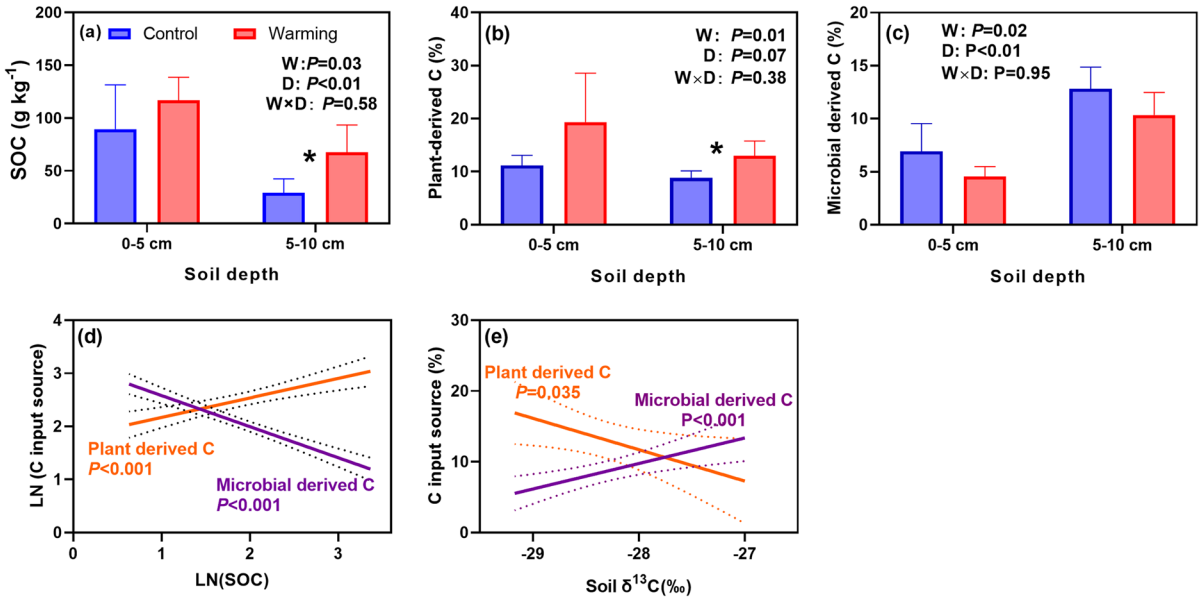


Fig. 3 Effect of warming on soil organic carbon (SOC, panel **a**), SOC pool component and their correlation with soil $\delta^{13}C$ abundance after 10 years of experimental warming. (**b**) Plant-derived C as a percentage of lignin and phenolics in SOC is determined by pyrolysis gas chromatography-mass spectrometry (Py-GC–MS). (**c**) Percentage of microbial residual C in SOC. Error bars denote SE ($n = 5$). Two-way ANOVAs were performed to test the effect size of warming, sampling depth and their interactions; P values are denoted only when the effect size was significant at $P < 0.05$. Linear regression analysis was performed to test the correlation of plant-derived C and microbial-derived C with SOC (panel **d**) and $\delta^{13}C$ (panel **e**). Dashed lines around each fitted curve represent 95% confidence intervals and $R.^2$ and P values ($n = 20$) are denoted in the figures accordingly. *, $P < 0.05$

C (in particular lignin products such as guaiacol and syringol, but also levoglucosan from plant polysaccharides) by 74% in the topsoil and by 47% in the subsoil, while it decreased microbial-derived C (amino sugars) by 34% in the topsoil and 19% in the subsoil, respectively (Fig. 3c). Regression analysis indicated that the relative proportion of plant-derived C increased linearly with increasing SOC concentration, whereas the percentage of microbial-derived C was negatively correlated with SOC concentration (Fig. 3d). Furthermore, plant-derived C was significantly positively correlated with soil $\delta^{13}C$, whereas microbial-derived C was significantly negatively correlated with soil $\delta^{13}C$ (Fig. 3e).

SOC density fractionation analysis showed that the stability of SOC was marginally changed by warming ($P < 0.10$, Fig. 4). Warming increased POC by 13% in the topsoil and by 17% in the subsoil ($P < 0.10$, Fig. 4b), and tended to decrease the percentages of MAOC and DOC at both sampling depths ($P > 0.05$, Fig. 4a, c).

Discussion

Experimental soil warming increased soil organic carbon concentration

After 10 years of warming, SOC concentration was increased indicating that warming stimulated C accumulation in soil. Furthermore, the responses of SOC to warming were highly depth-dependent with more C accumulated in the subsoil (5–10 cm) than in the topsoil (0–5 cm). The insignificantly increased SOC induced by warming in the topsoil probably can be explained by the counterbalance between the increased litter input and the dried litter layer and soil layer (Fig. 1d and f). Specifically, on the one hand, warming increased plant biomass and thus increased the litter derived from leaves (Peng and Liu 2002; Lin et al. 2010). The dry and fragile litter was probably easily fragmented by animals and then transformed to SOC by soil microbes which might facilitate SOC accumulation in the topsoil. On the other hand, the dried topsoil was not conducive to decomposition

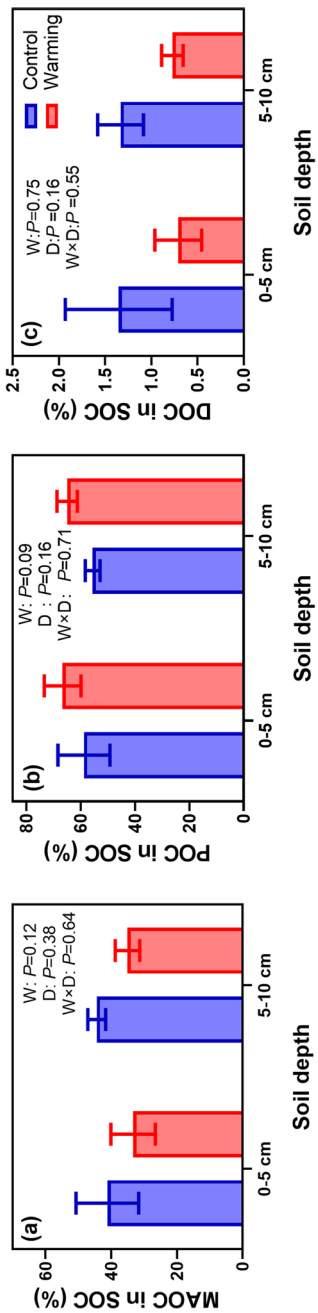


Fig. 4 Percentage of mineral-associated organic carbon (MAOC, **a**), particulate organic carbon (POC, **b**), and dissolved organic carbon (DOC, **c**) in soil organic carbon (SOC) based on density fraction analysis in a sodium polytungstate (SPT) solution (Keiluweit et al. 2017)

(Christiansen et al. 2017). The significant increase of SOC in the 5–10 cm soil was derived from the rapid transformation of litter into SOC because the plant-derived C increased with warming and significantly positively correlated with SOC (Fig. 3). Soil water content in the subsoil (5–10 cm) was less affected by warming (Fig. 1d) and favored fast litter decomposition (Berbeco et al. 2012), which was in line with the observed increase and significantly positively correlated with total PLFAs, fungal PLFAs, and βG under warming in the subsoil in our study (Fig. 2, Fig. S1), and therefore facilitate for the transforming of litter to SOC. However, whether the increased plant-derived C in this layer derived from the vertical translocation by soil fauna, more semi-decomposed litter particles transferring with soil water from the soil surface to subsoil due to dried litter and topsoil, and/or the remaining buried coarse roots after 10 years trenching will be worth studying in the future. Moreover, the influence of warming on SOC was greater in 5–10 cm than in 0–5 cm soil, which probably indicated that the warming effect is deeper in soil than we expected because soil temperature still increased more than 1 °C at 50 cm depth in our study site (Fig. 1b).

We found marginally greater standing litter (Fig. 1e) and more dry litter (Fig. 1f) in warmed plots, suggesting that the response of aboveground litter to warming played a vital role in mediating SOC response to warming. Partial warming (experimental branch warming) may increase tall tree acorn production (Nakamura et al. 2010), bud and flower production, stem length (Nakamura et al. 2016), and open-top chamber warming also enhanced leaves and shoot growth (Xu et al. 2012). IR lamps warmed the understory vegetation (height < 1.8 m) in our study which possibly also warmed the aboveground branches and leaves (around 1.8 m) and hence increasing the aboveground biomass. Therefore, the increased litter input may have offset the warming-induced increase in CO_2 efflux with SOC concentration overall unchanged (Giardina et al. 2014). A national-scale modeling study also showed that the increased NPP by warming generally led to a net SOC increase (Gao et al. 2013). The significantly increased litter decomposition was accompanied by increased soil nutrient concentrations such as plant-available soil P, and available N (Table 1). The increased available nutrients would move down with soil water and enhance plant growth and increase biomass and standing litter in the

long run. A study conducted in a New England forest also showed that soil warming significantly increased soil plant-available N and resulted in enhanced tree growth (Butler et al. 2012). The increased soil nutrients probably weakened the microbial mining effect on SOC, which facilitated the SOC accumulation in return (Craine et al. 2007; DeForest 2019). Therefore, warming parts of the ecosystem (e.g., soil) might change the whole ecosystem C, N, and P cycling, and ecosystem functioning in the long term.

The increased SOC by warming was mainly derived from plant residues

The increased accumulation of lignin and phenol biomarkers in SOC indicated that the increased C under warming was mainly derived from plants. Partial warming (branch warming, soil warming) in the forest ecosystem alters leaf phenology and increases the total phenolics of leaves in tall trees (Nakamura et al. 2010, 2015). This probably explains why the proportion of lignin increased under warming in our study, because the increased standing litter in the warming chamber was mainly caused by marginally increased leaf litter production (Fig. 1e). Feng et al. (2008) showed that warming increases litter decomposition on the soil surface, and hence increases the input of plant-derived C into the soil. However, a long-term soil warming experiment in a Norway spruce forest found no significant influence of warming on plant-derived C (lignin + phenolics) concentrations, owing to their divergent responses to litter decomposition and input (Schnecker et al. 2016). Therefore, plant-derived C exhibits a dynamic balance under warming among study sites.

There was an opposite effect of plant-derived and microbial-derived C in response to experimental warming. In contrast to plant-derived C, the contribution of microbial-derived C to the SOC pool decreased by warming at both sampling depths. The changes in microbial residues can be explained by a shift in soil microbial community composition under warming. For example, warming reduced the abundance of Gram-positive bacteria in topsoil (Fig. 2g), but increased the abundance of Gram-negative bacteria in subsoil (Fig. 2h). Since Gram-negative bacteria prefer plant-derived C and Gram-positive bacteria use more SOM-derived C (Kramer and Gleixner 2008), such changes in abundance probably affect SOC decomposition and synthesis under warming. In addition, warming can cause disproportional losses of humified SOM by enhancing microbial mineralization with more microbial-derived C being degraded than plant-derived C (Li et al. 2012). Hence, microbial-derived C became relatively depleted because of the greater incorporation of lignocellulose into SOC (particularly in the POC fraction). Similar results were also observed in a nine-year warming experiment in California grasslands which showed that warming reduced the contribution of microbial-derived C to the SOC pool (Liang and Balser 2012; Liang et al. 2015).

The response of microbial residues to warming also depends on the annual mean temperature (MAT) of the study site and the contribution of microbial residues to SOC, following a parabolic relationship with a maximum reached when the temperature was 10ºC (Amelung et al. 1999). At our study site, the MAT is 15ºC, which supports the observed decreased contribution of microbial residue in a warmer environment in this study based on the prediction of Amelung et al. (1999). Since microbial residues are enriched in ^{13}C relative to plant biomass (Ehleringer et al. 2000), the decreased $\delta^{13}C$ abundance (Table 1) in warmed plots and the negative correlation between $\delta^{13}C$ and plant-derived C / microbial-derived C (Fig. 3e) are probably further indicated that warming-enhanced SOC mainly resulted from plant-derived C, rather than microbial residues at our study site.

The response of SOC stability to warming

POC is mainly derived from plant litter and is considered the relatively easily-decomposable component of SOC. It usually consists of holocellulose (von Luetzow et al. 2007) with fewer relatively recalcitrant components from tannin, cutin, etc. (Schnecker et al. 2016). The small increase of POC in warmed plots (Fig. 3b) was likely caused by the significantly increased plant-derived SOC (Fig. 3b). On the contrary, MAOC usually has a slower turnover than POC and is considered a recalcitrant component of SOC (Schulze et al. 2009). Previous studies found that the temperature sensitivity of labile SOC does not differ significantly from that of recalcitrant SOC (Fang et al. 2005; Poeplau et al. 2017; Schnecker et al. 2016). Therefore, the response of POC and MAOC to warming probably can be explained by their similar

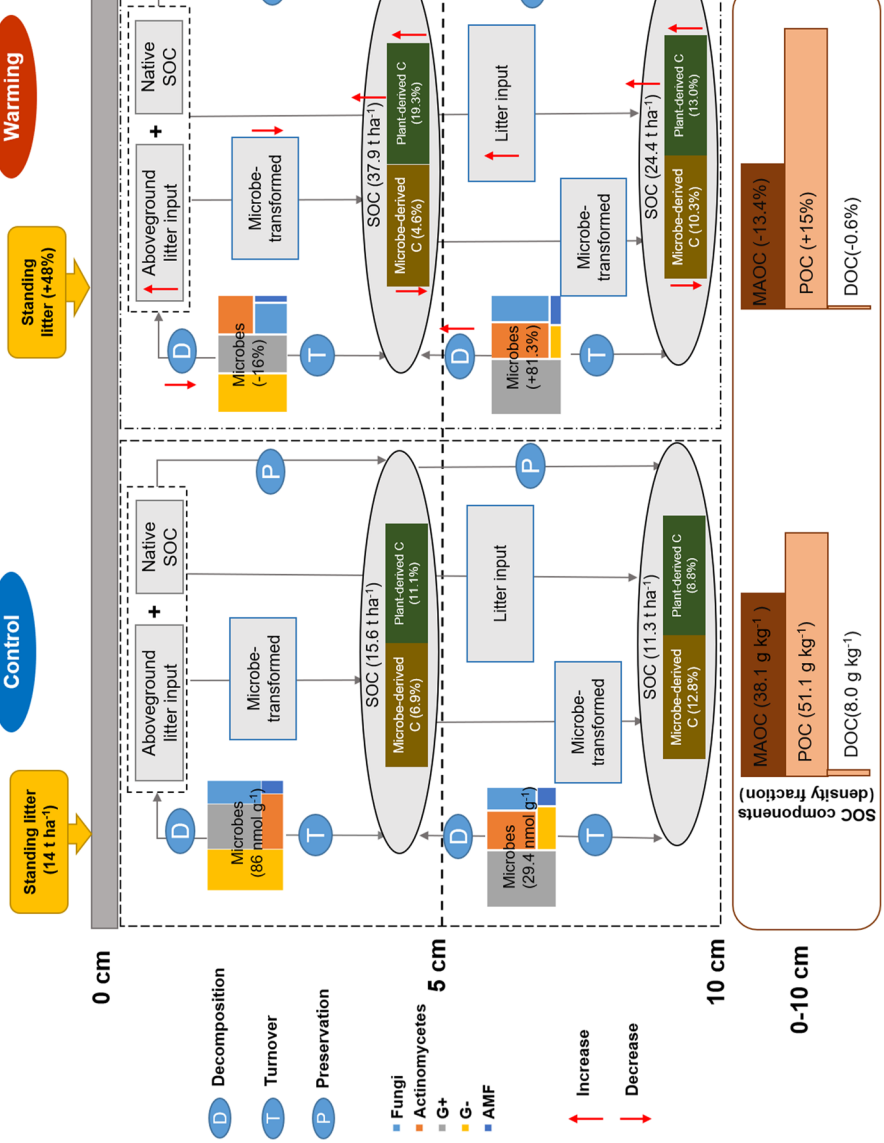


Fig. 5 Conceptual diagram of warming effects on soil organic carbon (SOC) concentrations and components through microbial decomposition and mineral protection pathways in 0–5 and 5–10 cm soil layers. AMF, arbuscular mycorrhizal fungi; G-, Gram-negative bacteria; G+, Gram-positive bacteria; MAOC, mineral-associated organic carbon; POC, particulate organic carbon; DOC, dissolved organic carbon. ↑, increase; ↓, decrease

temperature sensitivity. However, other studies also showed that warming had a significant influence on POC and MAOC because these two pools were controlled by the different formation and decomposition processes (Rocci et al. 2021).

The methods, magnitude, and duration of experimental warming might contribute to divergent responses of SOC to warming (Lu et al. 2013; Wu et al. 2020). For example, a study conducted in Iceland showed that geothermal warming by 0.6ºC significantly increased SOC concentrations, whereas warming beyond 0.6ºC led to an exponential depletion in SOC pools (Poeplau et al. 2017). Warming methods may have different influences on different ecosystem processes. But due to technical difficulties, most warming studies in mature forests only consider soil warming or partial warming using heaters, as in the present study. Furthermore, we only focused on the aboveground litter input effect and excluded the belowground litter input and living roots as well as the potential rhizosphere priming effects associated with the trenching method in our study which might also lead to the different SOC responses compared with those in other experimental warming studies. For example, warming significantly enhanced SOC concentration by regulating the priming effect in temperate forest soil (Feng et al. 2021). It is worth noting that while warming using IR heaters was adequate to study different soil respiration and SOC dynamics, whole-ecosystem warming could provide more accurate estimates of other ecosystem processes such as photosynthesis and productivity.

Conclusions

Our study shows that the East Asian monsoon forests functioned as a strong SOC sink after 10 years of soil warming. The increased SOC was mainly derived from plants, rather than microbes (Fig. 5). Our study revealed the important role of plant-derived C in the SOC pool and in particular the newly sequestered SOC. Such information is invaluable for modeling the warming effects on soil C cycling under future climate change. Long-term field warming studies combined with deep soil sampling are needed in future studies.

Author contributions ZL and JZ conceived and designed the study, and led the writing of the manuscript. NL designed and established the warming experiments and provided the heterotrophic respiration data. TK, JK, and MA collected the litter sample and provided the data. ZL, XT, and JZ collected the soil samples. JZ, LK, ZM, YL, and WW performed the experiment and analyzed the data. XT, YW, JP, JS, DH, HL, JK and JL contributed substantially to manuscript revisions. All authors reviewed and edited the manuscript.

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Data availability All data that support this finding of this study are available in Zenodo (http://doi.org/10.5281/zenodo.5905432).

Declarations

Competing interests The authors declare to have no conflict of interest.

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