Different effects of warming and cooling on the decomposition of soil organic matter in warm–temperate oak forests: a reciprocal translocation experiment

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Abstract A reciprocal soil monolith-transfer experiment was conducted along an altitude gradient to investigate the effect of climate change on soil carbon (C) processes in two warm–temperate oak forests in Baotianman Nature Reserve, Henan Province, China. Microclimate conditions, soil surface CO_2 flux, and labile organic C were measured for in-situ and transferred soils at both high and low-elevation sites. The soil temperature at 5 cm depth was, on average, 3.27 °C warmer at the low-elevation site than at the high-elevation site. Net CO_2 flux (911 g C m^{-2} 13 months^{-1}, 4.7 % of total C) of soil monoliths transferred from the high to the low-elevation site (simulating warming) was substantially (44 %) greater than for high-elevation soil monoliths incubated in situ (633 g C m^{-2} 13 months^{-1}, 3.3 % of total C) during 13 months of incubation. Increased extractable organic C (K_2SO_4-C) supply with warming partly explained the increase of soil CO_2 flux. Simulated warming also significantly increased the temperature sensitivity (Q_{10} values) of soil organic matter decomposition. The positive linear relationship between microbial metabolic quotient (qCO_2) and Q_{10} suggests a connection between microbial population

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and Q_{10} under warming conditions. Transfer of soil monoliths from the low to the high-elevation site (simulating cooling) substantially (30 %) reduced soil CO_2 flux (383 g C m^{-2} 13 months^{-1}, 2.5 % of total C) compared with those incubated in situ (550 g C m^{-2} 13 months^{-1}, 3.5 % of total C). However, this was not accompanied by consistently opposite changes, to a similar extent, in labile organic C (microbial biomass carbon and K_2SO_4-C) and decomposition results (i.e., Q_{10} and R_{10}, soil respiration at 10 °C), indicating that the soil organic matter decomposition process may not respond equally to cooling and warming. Different soil organic matter decomposition responses to cooling and warming should be considered for paleoecological modeling when both warming and cooling are involved in the changes in regional and global climates, particularly during the Holocene.

Introduction

The decomposition of organic matter (OM) is a fundamental global biogeochemical process, because it is important in the recycling of nutrients between soil and plant communities. Changes in the rates of OM decomposition can have profound effects on ecosystem function and productivity (Salinas et al. 2011). Because the soil carbon (C) pool is much larger than the atmospheric C pool, even a small change in the rate of decomposition of the large soil organic C pool could have a significant effect on atmospheric CO_2 concentrations (Bottner et al. 2000). However, soil OM decomposition (Davidson and Janssens 2006) and microbial population size and functional group composition (Zhang et al. 2005; Zogg et al. 1997) are strongly temperature dependent. Therefore, an increase in the global mean annual temperature of 1.5–4.5 °C over the next 50–100 years is likely to have a substantial effect on the terrestrial ecosystem C cycle (IPCC 2007). Understanding the response of soil OM decomposition to climate change is a critical aspect of ecosystem responses to global changes (Conant et al. 2011).

A large number of warming experiments have been conducted to elucidate the effects of global warming on soil OM decomposition (Hopkins et al. 2012; Knorr et al. 2005; Luo et al. 2001; Melillo et al. 2002). However, the possibility of a cooler and wetter future climate is rarely considered in global climate change research, although rapid cooling events have occurred during the Holocene (Mayle and Cwynar 1995) and seasonal cooling is also frequently a part of the inter-annual variability of the climate (Brando et al. 2010; Le Barbé et al. 2002; Liang et al. 2011). It is still not clear whether or not this opposite process (i.e., cooling) will have an effect on soil OM decomposition opposite to that of warming.

Several field experimental approaches have been used to investigate potential effects of global warming on the ecosystem, for example field warming using external heat inputs (Luo et al. 2001; Melillo et al. 2002), observing differences in ecosystems along natural climatic gradients (Conant et al. 2000; Rodeghiero and Cescatti 2005), or transferring ecosystem components to a new site with different climatic conditions (Breeuwer et al. 2010; Hart 2006; Link et al. 2003; Rey et al. 2007). Especially, reciprocal treatment (simulating climate cooling) to that of warming can strengthen the conclusions drawn from warming treatment in which temperature has a dominant effect on soil–plant processes (Hart and Perry 1999). Reciprocal soil translocation experiments have been widely used to understand the potential effects of climate change on C and nitrogen (N) cycles (Hart 2006; Hart and Perry 1999; Link et al. 2003; Rey et al. 2007; Zimmermann et al. 2009) and soil microbial communities (Budge et al. 2011).

The Baotianman Nature Reserve in Henan Province, China, is located in the transitional region between the northern subtropics and the warm-temperate zone. Previous research in this region revealed that the seasonality of soil temperature was the main condition affecting seasonal variation of soil CO_2 flux (Luan et al. 2011a); its effect was even larger than that of soil moisture availability (Luan et al. 2012). This is a region in which the effects of climate change are expected to be substantial but the effect of warming on soil OM decomposition is poorly understood. The reserve has elevation range in excess of 1,400 meters with a 3–5 °C difference in soil temperature between low and high-elevation sites. We used the altitude gradient along the slopes of the

Baotianman Nature Reserve to conduct a reciprocal soil monolith translocation experiment to simulate temperature changes (i.e., warming and cooling). We hypothesized that both warming and cooling (with the same extent of temperature change) will affect soil CO_2 flux, labile organic C, and decomposition behavior, and that changes in labile organic C could explain the effect of soil CO_2 flux caused by simulated climate change. Our specific objectives were to: (1) investigate the response of soil CO_2 flux to reciprocal soil monolith transfer treatments; and (2) assess how labile organic C and decomposition parameters (i.e., soil respiration at 10 °C, R_{10}; temperature sensitivity of soil OM decomposition, Q_{10}; microbial metabolic quotient, qCO_2) respond to simulated cooling as compared with simulated warming treatments.

Materials and methods

Study sites

Two sites (a high-elevation site and a low-elevation site) located in the Baotianman Natural Reserve in Henan Province, China, were selected to conduct the reciprocal transfer experiment. The high-elevation site (33°29′51″N, 111°55′58″E) was located approximately 1,400 m.a.s.l., with a slope <8 %. The site was occupied by secondary forest regenerated from a clear-cut harvest approximately 50 years ago, with *Quercus aliena* var. *acuteserrata* as the dominant species. In addition to the dominant species, other abundant tree species include *Carpinus cordata*, *Cornus controversa* Hemsl, and *Tilia americana*. Annual average precipitation and air temperature measured at a nearby weather station were 900 mm and 15.1 °C, respectively. Precipitation mainly falls from June to August. Soils were dominated by a Ferric Luvisols, on the basis of the FAO system of soil classification (FAO 1990). The low-elevation site (33°28′55″N, 111°52′52.8″E) was located at approximately 620 m.a.s.l., with a slope <10 %. The forest at this site was regenerated from a clear-cut harvest approximately 30 years ago. The dominant species at this site was *Quercus variabilis* B. Other abundant tree species include *C. controversa* Hemsl., *Toxicodendron verniciﬂuum* (Stokes) F. A. Barkl., and *Quercus serrata* var. *brevipetiolata* (A. DC.) Nakai. Annual average precipitation and air temperature were ca. 800 mm and 19.8 °C, respectively. Precipitation mainly occurs from

June to August. Soils were dominated by a Chromic Luvisol, on the basis of the FAO system of soil classification (FAO 1990). The basic stand attributes of the two sites are summarized in Table 1.

Experimental design

In July 2008, eight 3 × 3 m plots were established randomly at both the high and low-elevation sites. Three intact soil monoliths (30 cm diameter, 40 cm deep from the surface of the O horizon) were collected from adjacent locations within each plot, with the least possible disturbance, by use of PVC cylinders. The first monolith collected was returned to the laboratory for processing, the second monolith was returned to its original location within the site (in-situ soil monolith, IS_{HE}: high-elevation soil monoliths incubated in situ; IS_{LE}: low-elevation soil monoliths incubated in situ), and the third monolith was transferred to the other forest site for incubation (transferred soil monolith, TR_{H-L}: a soil monolith transferred from the high to the low-elevation site; TR_{L-H}: a soil monolith transferred from the low to the high-elevation site). At each site, four 1 × 1 m plots trenched to 0.6 m depth on the perimeter were established to check on the soil coring effect (trenched). One PVC collar (19.6 cm in diameter) was installed permanently in each soil monolith (centric avoiding edge effect) or trenched plot. Because one of the soil monoliths to be transferred from the low to the high-elevation site was lost during the translocation process, this experimental design had eight replicates for the high-elevation site and seven replicates for the low-elevation site, per treatment (incubated in situ or transferred) and four replicates for the trenching treatment. Vegetation (grasses and saplings) which occasionally grew in the monolith at the beginning of and during the experiment was manually removed. The soil water content of the monoliths incubated in the high-elevation site was much higher than that of those incubated in the low-elevation site. Therefore, we conducted a precipitation exclusion experiment at the high-elevation site for both the IS_{HE} ($n = 4$) and TR_{L-H} ($n = 3$) treatments to further investigate the effect of soil water content on soil CO_2 emission, starting from August 15, 2009. Translucent roofs, each 3 × 3 m, were constructed and placed 1.6 m above the soil monoliths to exclude the rainfall.

Table 1 Stand characteristics and basic soil properties of the high and low-elevation sites used for the reciprocal soil monolith transfer experiment in Baotianman National Nature Reserve

Site	DBH (cm)	Density (trees ha^{-1})	LAI (cm^3 cm^{-3})	BD (g cm^{-3})	SOC (g C kg^{-1} soil)	TN (g N kg^{-1} soil)	C:N (g g^{-1})	pH
High-elevation	13.72[a] (1.09)	1833[a] (89)	2.81[a] (0.08)	0.76[a] (0.02)	63.47[a] (3.59)	4.36[a] (0.23)	14.56[a] (0.18)	5.03[a] (0.11)
Low-elevation	5.46[b] (0.26)	3900[b] (141)	4.25[b] (0.11)	1.17[b] (0.05)	33.11[b] (4.36)	2.16[b] (0.25)	15.55[a] (0.76)	5.43[a] (0.16)

Values in parentheses are SE. Different lowercase letters in each column indicate a significant difference at $P = 0.05$ level

DBH diameter at breast height, *LAI* leaf area index, *BD* bulk density, *SOC* soil organic carbon, *TN* total nitrogen, *C:N* carbon to nitrogen ratio, *pH* pH value

Soil respiration, temperature, and moisture content

Soil respiration was measured from September 2008 to November 2009, by use of an Li-8100 soil CO_2 flux system (Li-Cor, Lincoln, NE, USA) for each soil monolith. Soil temperature at 5 cm depth from the soil surface (T_5) was measured adjacent to each respiration collar with a portable temperature probe provided with the Li-8100. Soil volumetric water content at 0–5 cm depth (SWC) was measured by use of an MPKit-B portable time domain reflectometer soil moisture meter (NTZT, Nantong, China) at three points close to each collar. Measurements were made twice a month, but no measurements were made in December 2008 and January and February 2009 because the ground was covered with snow.

Soil and forest stand characteristics

Soil bulk density, organic C, total N, and pH were determined for the initial samples collected in July 2008 ($n = 8$). Soil bulk density every 20 cm for the 40-cm-long monoliths was determined by use of 100 mL (50.46 mm diameter, 50 mm high, $n = 3$) sampling corers and placing intact samples in an oven at 105 °C for 24 h to determine soil water content. Organic C content was determined by the wet oxidation method with 133 mmol L^{-1} $K_2Cr_2O_7$ and digestion at 170–180 °C. Soil N concentration was determined by a micro-Kjeldahl method (DK-152 Kjeltec Auto Analyzer; VELP, Italy) (Lu 2000).

At the end of the study period (August 29, 2010), soil samples were collected from the 0–15 cm layer of all monoliths, by use of a 2.54 cm diameter corer, to determine soil microbial biomass C (MBC) and K_2SO_4-extractable C (K_2SO_4-C) after 13 months of treatment. Three cores were taken from each monolith and mixed to form a composite sample. The samples were kept in a cooler and delivered immediately to the laboratory for analysis. The samples were kept at 4 °C in a refrigerator before determination of MBC by use of the chloroform fumigation–extraction method; MBC was calculated by dividing the fumigation C-flush by a K_{EC} factor of 0.45 (Sparling et al. 1990). Each sample was extracted with 0.5 mol L^{-1} potassium sulfate (K_2SO_4) to determine K_2SO_4-C, as described by Weintraub et al. (2007).

Tree diameter at breast height (DBH) was measured 1.3 m from the ground for each tree in both sites. Leaf

area index (LAI) was measured in August 2009 along a 25 m transect in each stand, by use of WinSCAN-OPY (Regent Instruments, Quebec, Canada).

Data analysis

Numerous equations have been developed to express the temperature sensitivity of respiration (Kirschbaum 2000; Janssens and Pilegaard 2003). We first used the most common expression (Davidson et al. 2006), the van't Hoff equation (Eq. 1), to describe the relationship between soil respiration (R_S) and soil temperature at 5 cm depth (T_5):

$$R_S = ae^{bT_5}, \tag{1}$$

where R_S is soil respiration rate, T_5 is the soil temperature at 5 cm depth, a and b are fitted variables, and R_{10} is defined as the respiration rate at 10 °C. The temperature-sensitivity variable, Q_{10}, was calculated by use of the equation:

$$Q_{10} = e^{10b}. \tag{2}$$

We then used the Lloyd and Taylor (1994) function:

$$R_S = a \times e^{-E_0/(T_5-T_0)}, \tag{3}$$

where a, E_0, and T_0 are fitted variables, and T_5 is the soil temperature at 5 cm depth.

It has been suggested that this function is a better and unbiased expression of the relationship between respiration and soil temperature than the standard Arrhenius function (Fang and Moncrieff 2001) for fitting measured soil respiration rates and soil temperature data. Temperature sensitivity, as expressed by Q_{10} values, was then calculated by comparing respiration rates at 5 °C above and below the site specific mean annual temperature (T_5), as described in Zimmermann et al. (2010):

$$Q_{10} = R_{T_5+5} / R_{T_5-5}. \tag{4}$$

Soil microbial respiration (the total soil respiration reported in this study, because vegetation was excluded so there was no autotrophic respiration in our monoliths) and soil microbial biomass was used to calculate the microbial metabolic quotient (qCO_2), which is the amount of CO_2–C produced per unit of microbial biomass carbon (Anderson and Domsch 1993; Wardle and Ghani 1995).

Comparisons of soil monoliths collected from the high-elevation site and incubated in situ with those transferred and incubated at the low-elevation site were made to assess the potential effects of global warming on soil pools and processes. The soil monoliths collected from the low-elevation site and incubated in situ was compared with those transferred to the high-elevation site to evaluate the simulated cooling effect on these pools and processes. Comparison of measurements made on soil monoliths incubated in situ with those made on ambient trenched soil was used to test the potential effect of soil containment on soil microclimate and on CO_2 flux at each site.

A repeated-measures general linear model (GLM) was used to evaluate the effects of the treatments (ambient trenched, in situ, and transferred) on R_S, SWC, and T_5. One-way analysis of variance (ANOVA) was used to evaluate the effects of the treatments (in situ, transferred) on MBC and K_2SO_4-C measured at the end of the study period, and R_{10}, Q_{10}, and qCO_2 values. General linear models were used to assess the effect of soil origin, incubation site, and their interaction effects. Linear regression analysis was performed between CO_2 flux (average between August 13 and September 17, 2009, which were the days closest to the soil sampling day for K_2SO_4-C and MBC analysis) and K_2SO_4-C and MBC, and between Q_{10} values and qCO_2. All statistical analysis was performed by use of SPSS 13.0 software for Windows (SPSS, Chicago, USA).

Results

Soil micro-environment

T_5, measured at the same time as CO_2 flux, was higher (a warming effect) for TR_{H-L} (mean = 16.54 °C) than for IS_{HE} (13.27 °C) ($P < 0.01$, Fig. 1a) and lower (a cooling effect) for TR_{L-H} (13.31 °C) than for IS_{LE} (16.99 °C) ($P < 0.01$, Fig. 1b). SWC was lower for TR_{H-L} (0.23 cm^3 cm^{-3}) than for IS_{HE} (0.27 cm^3 cm^{-3}) ($P < 0.01$, Fig. 1c) but higher for TR_{L-H} (0.27 cm^3 cm^{-3}) than for IS_{LE} (0.24 cm^3 cm^{-3}) ($P < 0.01$, Fig. 1d), indicating wetter conditions in the high-elevation site than in the low-elevation site. T_5 for trenched and in-situ treatments for both sites was no different (Fig. 1a, b), and we did not find
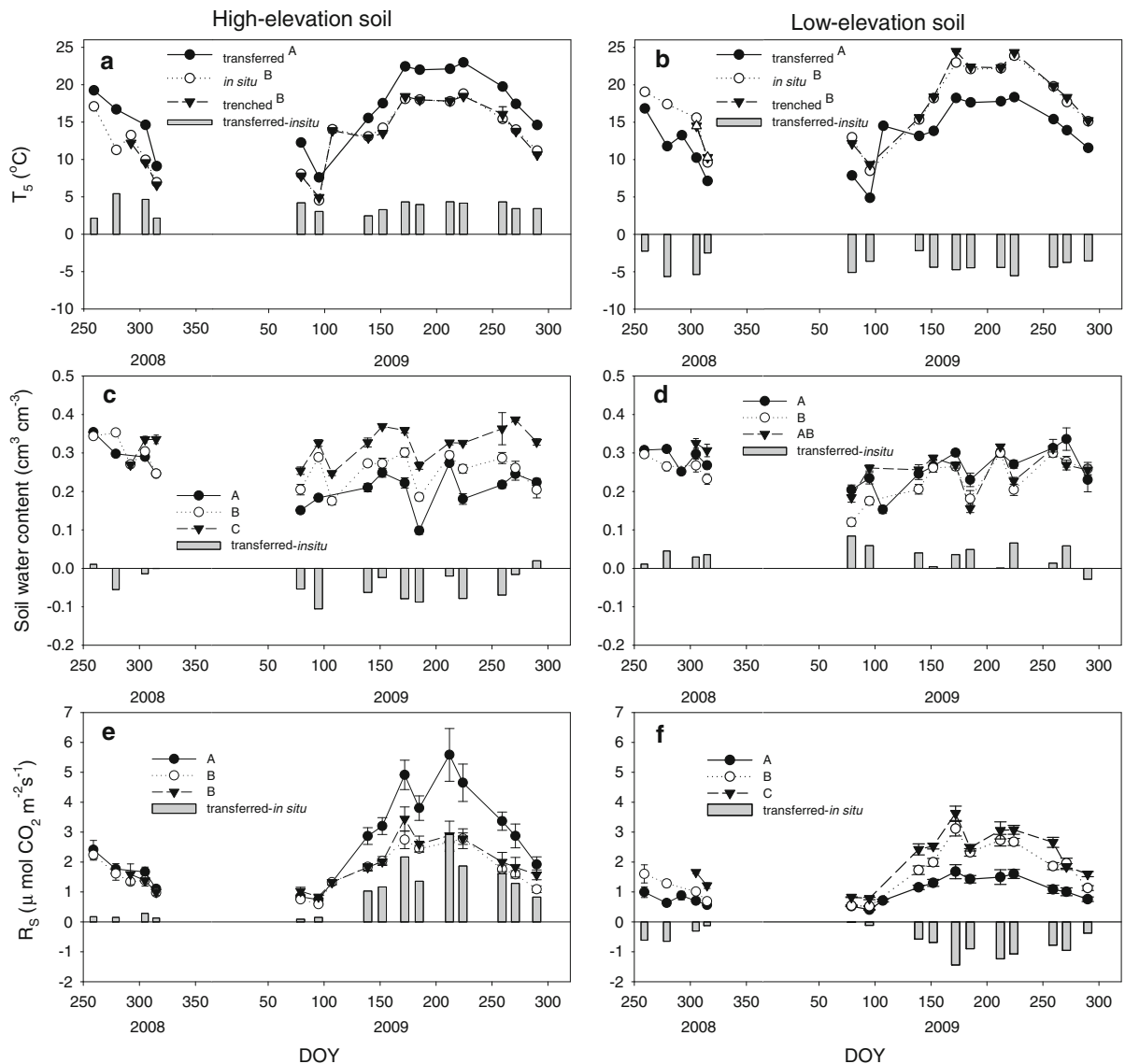
Fig. 1 Seasonal patterns of soil temperature at 5 cm depth (T_5) and soil water content (SWC) among different treatments for the high and low-elevation sites. Soils were subjected to three treatments: transferred (soil monoliths incubated at the other forest site), in-situ (soil monoliths incubated in situ), and trenched (trenched to exclude root growth). The difference between transferred and in situ measurements is plotted as *bars*.

For a given soil sample, treatments followed by different superscript letters denote significant differences ($P < 0.05$) among treatments (RM ANOVA, Tukey's test). *Vertical bars* denote SE of the mean ($n = 8$ or 7 for high or low-elevation sites, respectively). Net CO_2 flux from soils for **e** high and **f** low-elevation oak forest sites. *Vertical bars* denote SE of the mean ($n = 8$ or 7 for high or low-elevation sites, respectively)

significant differences between SWC for in-situ and trenched treatments at the low-elevation site (Fig. 1d). No clear seasonal trend was observed for T_5 or SWC differences between the transferred and in-situ treatments for monoliths from high and low-elevation sites (Fig. 1a–d).

CO_2 flux

Transfer of soil monoliths from the high to the low-elevation site resulted in an increase in CO_2 flux of approximately 44 % over the 13-month incubation period compared with IS_{HE} (911 and 633 g C m^{-2}

Fig. 2 Relationships between soil CO_2 flux and soil temperature at 5 cm depth for soil monoliths originally from **a** the high-elevation site and **b** the low-elevation site. Relationships between soil CO_2 flux and soil water content for soil monoliths originally from **c** the high-elevation site and **d** the low-elevation site
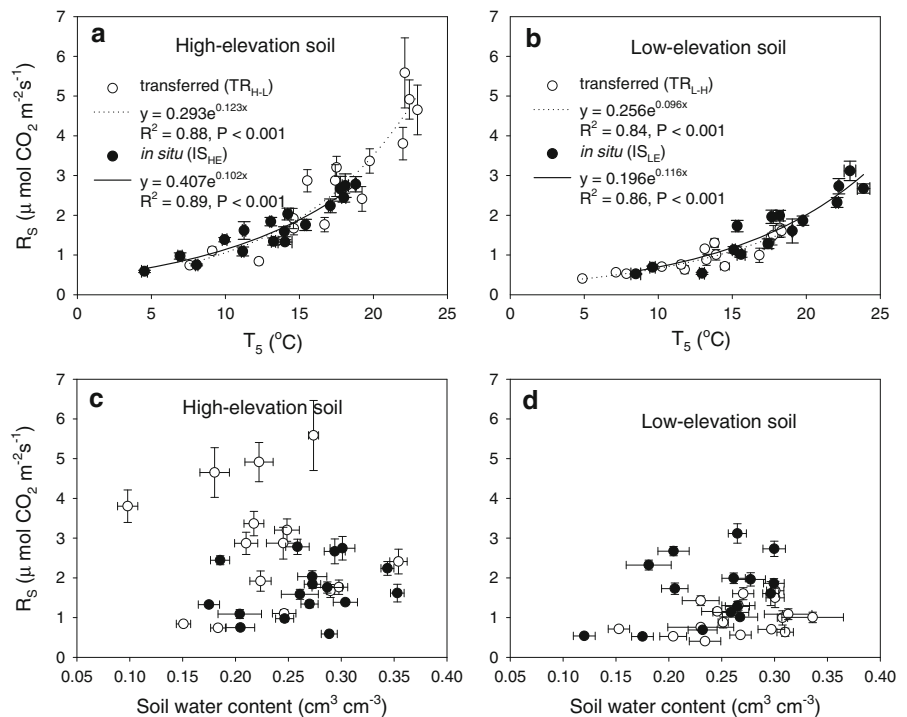
13 months^{-1}, respectively). Transfer of soil monoliths from the low to the high-elevation site, however, resulted in a decrease in net CO_2 flux of approximately 30 % compared with IS_{LE} (383 and 550 g C m^{-2} 13 months^{-1}, respectively). Soil containment had no effect on net CO_2 flux from soil monoliths at the high-elevation site, whereas a reduction was found at the low-elevation site (Fig. 1e, f). The difference between soil CO_2 flux for the transferred and in-situ treatments for both the high and low-elevation sites had similar seasonal patterns to those of soil temperature (Fig. 1e, f). T_5 is a good indicator for explaining the seasonal variation of CO_2 flux in the transferred and in-situ treatments for both the high and low-elevation sites ($R^2 = 0.84$–0.89, $P < 0.001$; Fig. 2a, b), whereas SWC had no relationship with seasonal variations of CO_2 flux for each treatment (Fig. 2c, d). Exclusion of precipitation led to a rapid decrease of SWC and soil CO_2 flux, which were significantly different between the control and the precipitation exclusion treatments (Fig. 3).

Results for soil decomposition and labile organic C

Transfer of soil monoliths from the high to the low-elevation site reduced soil MBC and increased Q_{10}

values (calculated on the basis of both the van't Hoff and Lloyd and Taylor equations), K_2SO_4-C, and qCO_2 compared with the IS_{HE} treatment ($P < 0.05$, Table 2). In contrast, transferring soil monoliths from the low to the high-elevation site did not affect Q_{10}, K_2SO_4-C, and MBC (Table 2). Soil origin significantly affected K_2SO_4-C, MBC, and R_{10}, but not Q_{10} values (calculated on the basis of both the van't Hoff and Lloyd and Taylor equations) and qCO_2 (Table 3). In contrast, incubation site significantly affected Q_{10}, MBC, and qCO_2 (Table 3). Significant linear relationships were found between qCO_2 and Q_{10} values calculated by use of both the van't Hoff and Lloyd and Taylor equations (Fig. 4).

Discussion

Soil micro-environment

In our study, significant exponential relationships between soil respiration and soil temperature (Fig. 2a, b) and lack of relationships between soil respiration and soil moisture content (Fig. 2c, d) illustrate that soil temperature was the dominant factor regulating soil organic matter decomposition in the forest ecosystems
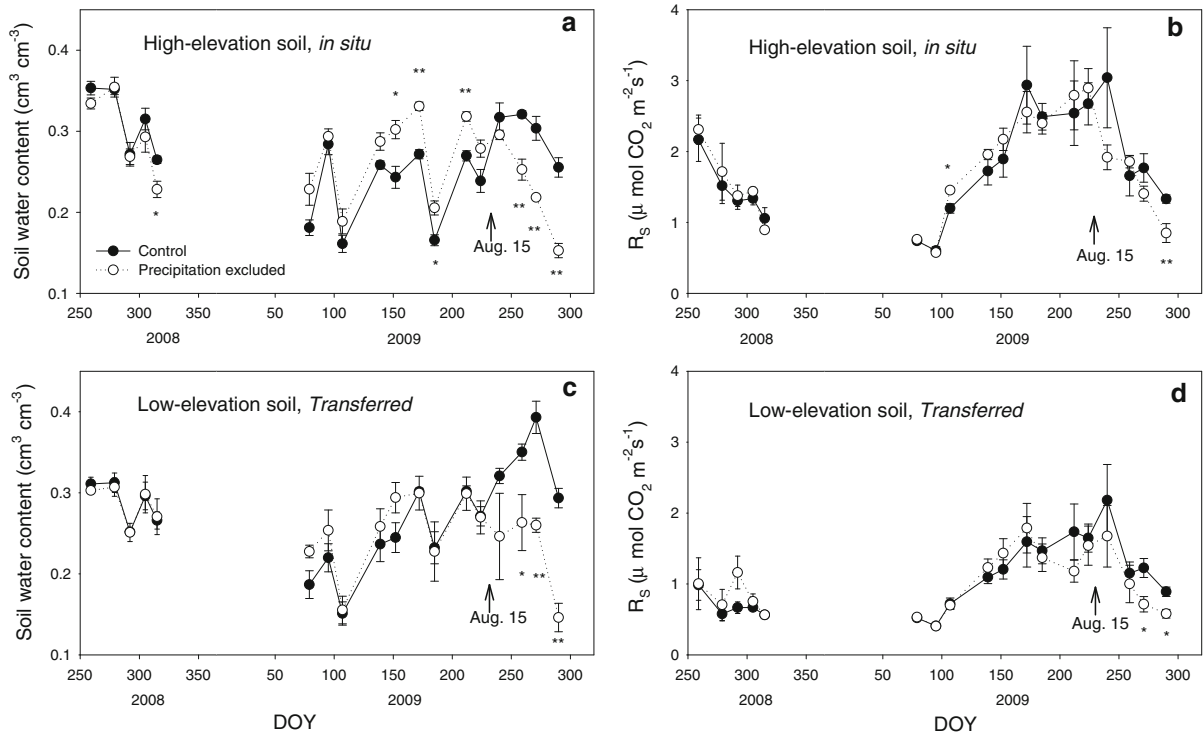
Fig. 3 Seasonal pattern of soil water content (**a**) and soil respiration (**b**) in control and precipitation exclusion treatments for high-elevation soil monoliths incubated in situ (*bars* denote SE of the mean, $n = 4$). Seasonal pattern of soil water content (**c**) and soil respiration (**d**) in control and precipitation exclusion treatments for low-elevation soil monoliths incubated at the high-elevation site (*bars* denote SE of the mean, $n = 3$). * and ** denote significantly different SWC or R_S between the control and precipitation exclusion treatments at $P < 0.05$ and $P < 0.01$, respectively

studied, similar to previous studies of those ecosystems (Luan et al. 2011a, b). Therefore, the appreciable response of soil respiration to the translocation treatment (Table 2) was mainly caused by changes in soil temperature rather than soil moisture content, even though there was a significant treatment effect on soil moisture content (Fig. 1c, d). In this study, SWC ranged between 0.15 and 0.35 cm^3 cm^{-3} (except on July 4th when it dropped below 0.10 cm^3 cm^{-3}), which was likely to be within the optimum range for soil microbial activity (Luan et al. 2012). In our precipitation exclusion experiment, CO$_2$ flux decreased after the SWC dropped to a critically low value (e.g., 0.15 cm^3 cm^{-3}; Fig. 3). These results further illustrate that soil temperature change had a crucial effect on responses of soil organic matter decomposition to the transfer treatment. In addition, the lack of containment effects on soil temperature in either the high or low-elevation sites indicates that we can exclude the containment effect on soil respiration

from our analysis, enabling us to conduct the following more detailed analyses.

Soil CO$_2$ flux

Our hypothesis that both warming and cooling affect soil CO$_2$ flux is supported by the results of this study (Table 2). Soils in the high-elevation site will be vulnerable to large C losses under future warming conditions. Simulated warming led to 44 % more C being released as CO$_2$ whereas simulated cooling led to 30 % less C being released as CO$_2$ during the 13 months incubation, indicative of different effects of cooling and warming of the soils studied. Different soil characteristics between the high and low-elevation sites (Table 1) might have led to the different responses. Higher qCO$_2$ in the warmer site (Table 2) might also explain the increase of CO$_2$ flux, as a positive linear relationship was found between qCO$_2$ and CO$_2$ flux, irrespective of soil origin and incubation

Table 2 Reciprocal soil monolith transfer effects on soil respiration rates at 10 °C (R_{10}), Q_{10}, K_2SO_4 extractable C, microbial biomass C (MBC), and microbial metabolic quotient (qCO_2) of the high and low-elevation sites in Baotianman National Nature Reserve

Soil treatment	CO_2 g C m^{-2} 13 months^{-1}	R_{10} μ mol CO_2 m^{-2} s^{-1}	van't Hoff Q_{10}	Lloyd and Taylor Q_{10}	K_2SO_4 C mg g^{-1} soil	MBC mg g^{-1} soil	qCO_2 μg CO_2 h^{-1} μg microbial C^{-1}
High-elevation soil							
In situ (IS[HE])	633[a] (34)	1.12[a] (0.05)	2.73[a] (0.46)	2.72[a] (0.19)	0.23[a] (0.03)	1.14[a] (0.48)	0.010[a] (0.002)
Transferred (TR[H-L])	911[b] (85)	0.97[a] (0.07)	3.42[b] (0.48)	3.75[b] (0.33)	0.27[b] (0.03)	0.73[b] (0.08)	0.023[b] (0.003)
F	9.107	2.976	8.74	6.08	10.332	5.472	12.14
P value	0.009	0.107	0.01	0.007	0.006	0.035	0.004
Low-elevation soil							
In situ (IS[LE])	550[a] (23)	0.61[a] (0.03)	3.10[a] (0.28)	3.31[a] (0.11)	0.09[a] (0.04)	0.40[a] (0.21)	0.019[a] (0.003)
Transferred (TR[L-H])	383[b] (23)	0.54[a] (0.06)	2.69[a] (0.65)	3.03[a] (0.42)	0.10[a] (0.04)	0.59[a] (0.19)	0.0065[b] (0.0006)
F	22.43	1.215	2.278	0.429	0.109	3.348	16.32
P value	<0.001	0.292	0.157	0.525	0.746	0.092	0.002

IS[HE], high-elevation soil monoliths incubated in situ; IS[LE], low-elevation soil monoliths incubated in situ; TR[H-L], high-elevation soil monoliths transferred to the low-elevation site; TR[L-H], low-elevation soil monoliths transferred to the high-elevation site

Values in parentheses are SE. Different lowercase letters within each column indicate significant difference at $P = 0.05$ level

site (CO_2 flux $= 399.6 + 14081 \times qCO_2$, $R^2 = 0.33$, $P = 0.001$).

Interestingly, CO_2 flux rates were similar for the two soils in their initial elevations even though there were apparent differences in soil characteristics (i.e., lower SOC, K_2SO_4-C and MBC at the low-elevation site, Table 2). In addition, if we do not consider the direction of soil monolith transfer, both high and low-elevation soils had 44 % greater CO_2 flux when they were incubated in the low-elevation site than those incubated in the high-elevation site, indicating that the temperature difference between the two sites determined the different CO_2 flux rates. In combination with higher soil C stock at the higher-elevation site (Table 1), similar CO_2 flux rate between both soils incubated in situ implies that more C would be stored in the soil at the high-elevation site (Zimmermann et al. 2009, 2010).

Soil heterotrophic respiration is determined by temperature and many other factors other than temperature, for example C substrate supply, microbial biomass, and climatic conditions (Davidson et al. 2006). In our study, a 3.27 °C soil temperature increase led to a 44 % increase in soil CO_2 flux, which was much less than the 120 % increase reported in a spruce–fir forest as the result of a 2.5 °C increase in soil temperature (Hart 2006). The different responses might be caused by different soil quality. For example, the soil in the Hart (2006) study had a higher C:N ratio (24.4–41) than that in our study (14.6–15.6). Increased substrate availability was also linked to the increase of CO_2 flux caused by warming in our study (Fig. 5a).

The transferred soils underwent a change in air and soil temperatures, and soil CO_2 flux rates. However, in our reciprocal soil-transfer experiment, the transfer of soil monoliths to either a warmer or cooler site resulted in comparably stable seasonal warming or cooling effects (soil temperature difference between transferred and in-situ treatments; Fig. 1a, b) and it was not accompanied by similar stable seasonal variation of differences in soil CO_2 flux between the transferred and in-situ treatments (Fig. 1e, f). Both warming and cooling effects on soil CO_2 flux were more apparent during the summer, which could be attributed to higher microbial activity in the summer when soil moisture availability was not limiting (Martin and Bolstad 2005). The effect was clearly demonstrated at the high-elevation site (Table 2) where more substrate supply occurred and substrate availability (e.g.,

Table 3 Significance of general linear model (two-factor ANOVA) for evaluation of soil origin (i.e., high-elevation vs. low-elevation) effects, and their interactions with soil decomposition conditions ($df = 1$ for all factors)

Factor	CO_2		K_2SO_4 extractable C		MBC		R_{10}		Van't Hoff Q_{10}		Lloyd and Taylor Q_{10}		qCO_2	
	P value	F	P value	F	P value	F	P value	F	P value	F	P value	F	P value	F
Soil origin effect	0.011	7.6	<0.001	17.17	0.07	3.59	0.003	10.66	0.47	0.55	0.95	0.005	0.646	0.216
Incubation site	<0.001	17.6	0.19	1.82	0.01	7.81	0.504	0.459	0.005	9.27	0.034	5.03	0.001	14.79
Soil origin × Incubation site	0.304	1.1	0.072	3.5	0.32	1.04	0.065	3.74	0.43	0.644	0.21	1.64	0.976	0.001

C was included in the GLM as a covariate variable
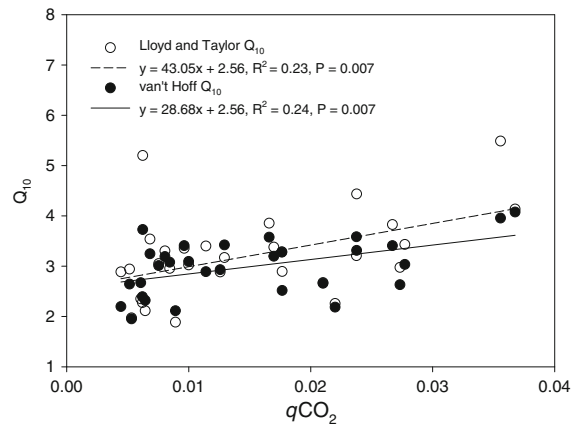
Fig. 4 Relationships between average CO_2 flux (samples were collected on Aug. 13 and Sept. 17 near fresh soil sampling day) and K_2SO_4-C (**a**), and MBC (**b**) for soil monoliths originally from the high and low-elevation sites

K_2SO_4-C) has a strong effect on soil respiration (Curiel Yuste et al. 2007; Grogan and Jonasson 2005).

Labile organic carbon

The significant reduction in MBC in the soil caused by the warming treatment (Table 2) was consistent with the effect of 12 years of soil warming of approximately 5 °C at the Harvard Forest (Bradford et al. 2008; Smith et al. 2004). However, the reduction in microbial biomass did not imply a reduction in substrate supply as there was a significant increase in K_2SO_4-C, or a reduction in microbial activity as CO_2 flux increased after transfer from the high to the low-elevation site (Fig. 5a). Our results partially support the idea that the reduction in the increment of respiration rates after prolonged soil warming was caused by substrate loss (Kirschbaum 2004; Knorr et al. 2005), because the increase of CO_2 flux eventually reduced substrate availability. Rey et al. (2007) found that relative emissions per unit of C depended mostly on climate and there was a clear reduction of absolute emissions with decreasing labile C content. The changes in CO_2 flux after translocation may also be attributed to the changes in microbial metabolic quotient (Table 2) and shifts in microbial community composition (Budge et al. 2011).

In contrast, transferring soil monoliths from the low to the high-elevation site (i.e., cooling) did not result in expected changes in MBC and K_2SO_4-C. It is

Fig. 5 Relationships between qCO_2 and Q_{10} values calculated on the basis of both the van't Hoff and Lloyd and Taylor equations
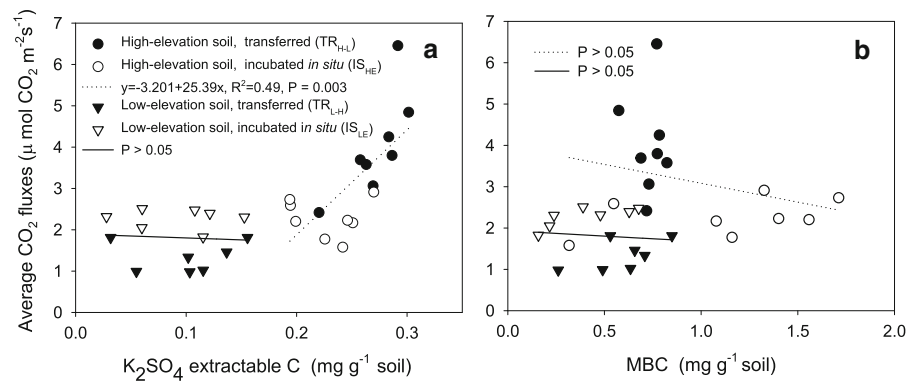
plausible that soils from the low-elevation site with poor labile-C and a smaller microbial population, were less responsive to the change in temperature, and required a longer time to adapt to the new (cooler) environment. We found that neither MBC nor K_2SO_4-C could explain the reduction of CO_2 flux after transferring soil monoliths from the low to the high-elevation site (Fig. 5a, b). Therefore, only part of our hypothesis was supported—that warming will affect labile organic C and subsequently CO_2 flux; however, the corresponding responses did not occur in the cooling treatment, rejecting part of the hypothesis.

Temperature sensitivity of soil respiration

Q_{10} values increased when soil monoliths were transferred from the high to the low-elevation site (Table 2) and were affected by incubation site but not by soil origin (Table 3), indicating a higher risk of C loss under future warming conditions. We found a significant linear relationship between Q_{10} values and qCO_2 (Fig. 4), suggesting a connection between temperature sensitivity of soil organic matter decomposition and soil microbial function under warming, because qCO_2 is a useful measure of microbial efficiency in conserving C (Wardle and Ghani 1995). Soil microbes that were adapted to the higher elevation (lower temperature) reduced their biomass and increased qCO_2 when the soil was transferred to the lower-elevation (higher-temperature) site. A moderate shift of microbial communities toward new environmental conditions 11 years after soil translocation was observed by Budge et al. (2011). The increased Q_{10} values with warming might also be linked to the greater amount of respired biochemically recalcitrant

SOM, which has greater temperature sensitivity (Craine et al. 2010). It was very likely that labile C would drastically decline at the end of the warming experiment, forcing microbes to rely on more recalcitrant soil C.

In contrast, Q_{10} and R_{10} were not affected by transferring soil monoliths from the low to the high-elevation site (Table 2), suggesting that the temperature reduction might be within the range of tolerance limits for normal microbial activity, or the phenomenon represented a chronic response (or acclimation, adaptation) of microbial community to cooling. The fact that soils from the high and low-elevation sites differ in their properties, for example soil C and N content, could also cause the different warming and cooling effects observed. However, we did not find significant effect of soil origin on both Q_{10} and qCO_2 (Table 3). Therefore, Q_{10} was mainly affected by transfer of the soils. Although different methods used to calculate Q_{10} might lead to different results (Zimmermann et al. 2009), Q_{10} calculated by use of both the van't Hoff (the most commonly used equation) and the Lloyd and Taylor (suggested to give an unbiased estimate of Q_{10}) equations had consistent responses to the treatments in our study.

The Q_{10} calculation can be affected by the range of temperature considered (Kätterer et al. 1998; Paz-Ferreiro et al. 2012). However, the positive warming effect on Q_{10} in our study was apparently not caused by the different temperature range, because lower temperature sensitivity were estimated at higher temperatures (Kätterer et al. 1998). The positive warming effects on Q_{10} values must be further studied, because this translocation experiment was conducted for one year only. It is reported that a sustained temperature increase may reduce the

temperature sensitivity of soil OM decomposition (Craine et al. 2013). Therefore, the response of soil OM decomposition to warming might be a nonlinear process, along with depletion of soil labile carbon (Bradford et al. 2008) and the adaptation of microbes to the new environment (Bradford et al. 2008; Crowther and Bradford 2013; Luo et al. 2001). The acclimation or adaptation of microbes to warming has been widely reported (Luo et al. 2001; Bradford et al. 2008), and it is important to understand microbial response to cooling, with implications for modeling of paleoclimate (e.g., Holocene), particularly during periods of regional or global cooling. Further research is needed to broaden our understanding of possible mechanisms causing different responses to cooling and warming.

Conclusions

The simulated warming treatment (transfer of soils from the high to the low-elevation site) altered soil OM decomposition processes, including increased soil surface CO_2 flux and labile organic C (i.e., K_2SO_4-C) production. Therefore, a large amount of soil C loss occurred in the early stage of warming and such C losses were linked to the increased extractable organic C (K_2SO_4-C) supply under warming. The simulated cooling reduced CO_2 flux, but the extent of decrease in C loss (30 %) was lower than the extent of increase in C loss (44 %) caused by simulated warming. Furthermore, cooling did not cause the expected opposite changes in labile organic C and decomposition behavior. We therefore conclude that cooling and warming had different effects on soil organic C processes. Such different effects should be taken into consideration in paleoecological modeling when both warming and cooling are involved in changes in the regional and global climate.

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