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Climate change affects soil labile organic carbon fractions in a Tibetan alpine meadow

Yigang Hu[1,2] · Zengru Wang[1,2] · Qi Wang[3,4] · Shiping Wang[3,5] · Zhishan Zhang[1,2] · Zhenhua Zhang[6] · Yang Zhao[1,2]

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Abstract

Purpose Changes in bioactive soil C pools and their temperature sensitivities will dominate the fate of soil organic C in a warmer future, which is not well understood in highland ecosystems. This study was conducted in order to evaluate climate change, especially cooling effects, on soil labile organic C (LOC) pools in a Tibetan alpine meadow.

Materials and methods A short-term reciprocal translocation experiment was implemented to stimulate climate warming (downward translocation) and cooling (upward translocation) using an elevation gradient on the Tibetan Plateau. Variations in soil microbial biomass C (MBC), dissolved organic C (DOC) and LOC were analyzed.

Results and discussion Over the range of soil temperature from 0.02 to 5.5 °C, warming averagely increased soil MBC, DOC and LOC by 15.3, 17.0 and 3.7 % while cooling decreased them by 11.0, 11.9 and 3.2 %, respectively. Moreover, warming generally increased the proportion of DOC in LOC but cooling had an opposite effect, while the response of the MBC proportion to DOC and LOC varied depending on vegetation type. Soil MBC, DOC and LOC pools were positively related to soil temperature and showed a hump-shaped relationship with soil moisture with a threshold of about 30–35 %. Although soil DOC was more sensitive to warming (5.1 % $°C^{-1}$) than to cooling (3.0 % $°C^{-1}$), soil LOC showed a symmetrical response due to regulation by soil moisture.

Conclusions Our results indicated that climate change would not only change the size of soil LOC pools but also their quality. Therefore, cooling effects and regulation of soil moisture should be considered to evaluate the fate of soil organic C in Tibetan alpine meadows in a warmer future.

Keywords Alpine meadow · Climate change · Reciprocal translocation · Soil labile organic C

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✉ Yigang Hu
huyig@lzb.ac.cn

✉ Shiping Wang
wangsp@itpcas.ac.cn

1 Shapotou Desert Experiment and Research Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China

2 Key Laboratory of Stress Physiology and Ecology in Cold and Arid Regions of Gansu Province, Lanzhou 730000, China

3 Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100085, China

4 University of the Chinese Academy of Sciences, Beijing 100049, China

5 CAS Center for Excellence in Tibetan Plateau Earth Science, Beijing 100101, China

6 Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China

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1 Introduction

Large amounts of C are stored in the soil of upland and arctic ecosystems in the form of soil organic C (SOC) (Eville 1991; Ping et al. 2008; Yang et al. 2008). SOC can be divided into a labile organic C (LOC) pool with a rapid turnover rate and a recalcitrant C pool with much slower turnover times ranging from decades to centuries (Rovira and Vallejo 2007; Belay-Tedla et al. 2009). Chemically, soil LOC is mainly composed of polysaccharides derived from plant litter and root exudates (hemicellulose, cellulose, and starch residues) and microbial biomass (microbial cell walls) (Rovira and Vallejo 2007). Although the LOC is a relatively small fraction of the full SOC pool, it plays an important role in the exchange of CO_2 between ecosystems and the atmosphere (Bengtson and Bengtsson 2007; Belay-Tedla et al. 2009), with large amounts of LOC stored in alpine meadow and permafrost soils (Budge et al. 2011; Mueller et al. 2015). The fate of SOC in a warmer future relies on its decomposition rate and the temperature sensitivity of different C fractions (Hartley and Ineson 2008; Eberwein et al. 2015). However, only a few field studies (Luo et al. 2009; Rui et al. 2011; Jing et al. 2014) have focused on the responses of different C fractions to climate warming in alpine meadows, and there is much uncertainty about the response of these ecosystems to climate change.

Plants provide a primary input of organic C into soil via root turnover, exudation and litter supply (Khalid et al. 2007), and the amount of C stored in the soil relies on the balance of C inputs and respiration in the long-term (Belay-Tedla et al. 2009). Previous studies have demonstrated that changes in soil microbial C (MBC) and dissolved organic C (DOC) are closely related to environmental conditions, such as soil temperature (Li and Chen 2004; Jiang and Xu 2006), soil moisture (Freeman et al. 2004; Li and Chen 2004), and precipitation (Li and Chen 2004; Harrison et al. 2008), as well as biotic factors including SOC content (Rui et al. 2011; Xu et al. 2013), biomass (Belay-Tedla et al. 2009; Luo et al. 2009) and quality of litter (Jiang and Xu 2006; Luo et al. 2009). Many studies have demonstrated that warming increased aboveground and belowground biomass in the upper soil (Luo et al. 2009; Hu et al. 2016a), leading to an increase in soil MBC (Belay-Tedla et al. 2009; Rui et al. 2011), DOC (Luo et al. 2009) and other forms of LOC (Belay-Tedla et al. 2009). On the other hand, warming has a weak impact on soil extracellular enzyme activity (Jing et al. 2014), MBC and DOC (Luo et al. 2009; Rui et al. 2011; Jing et al. 2014) in an alpine meadow due to the reduction of soil moisture caused by warming. Similarly, no effect on mean seasonal ecosystem respiration was found (Lin et al. 2011) because reduction of soil moisture caused by warming may have limited the decomposition rates of the labile and recalcitrant C pools. Recently, opposite effects of warming and cooling on aboveground biomass and ecosystem respiration have been reported, which showed an asymmetric response to warming and cooling in the Tibetan alpine meadow (Hu et al. 2016a). This asymmetrical response may have resulted from changes in soil LOC pools in response to warming and cooling.

The Tibetan Plateau is the largest and highest geoform on the Eurasian continent that covers an area of about 2.5 million km^2 with a mean elevation of about 4000 m a.s.l. Alpine meadow is one of the most widespread vegetation types, accounting for nearly 35 % of the Tibetan Plateau (Zheng et al. 2000). The Tibetan plateau has been subjected to significant climate warming over the last few decades (IPCC 2013) and a large temperature increase is expected in the future (Hansen et al. 2006). However, the temperature and rainfall showed large variations at the scales of years or decades with higher or lower values than the average over the last 44 years (Li et al. 2004), suggesting that Tibetan Plateau has been subjected to climate warming and cooling synchronized by wetter and drier climate scenarios. Although impacts of warming on SOC in the Tibetan alpine meadow have been intensively studied (Luo et al. 2009; Xu et al. 2010; Rui et al. 2011), cooling effects remains much less studied to date, which may cause an inaccurate estimation about long-term warming effects according to the recent report (Hu et al. 2016a).

In this study, we investigated warming and cooling effects coupled with variations in soil moisture on soil MBC, DOC and LOC in a Tibetan alpine meadow using a reciprocal translocation method. Two following hypotheses will be tested in this study. First, warming leads to an increase in soil LOC pools while cooling has an opposite effect, which could be regulated by soil moisture. Second, soil LOC fractions have varied responses to warming and to cooling due to their differences in composition and quality.

2 Materials and methods

2.1 Site description

The experiment was conducted using a reciprocal translocation climate change platform along the southern slope of Qilian Mountains, situated in the northeastern part of the Tibetan Plateau near the Haibei Alpine Meadow Ecosystem Research Station of the Chinese Academy of Sciences (37° 37′ N, 101° 12′ E; 3250 m a.s.l.). The climate is typical continental climate dominated by the southeast monsoon in summer and high pressure from Siberia in winter. Mean annual air temperature is −1.7 °C, with a maximum monthly mean temperature of 10 °C in July and a minimum of −15 °C in January. Annual mean precipitation is 500 mm, with about 80 % of fallings during the growing season (May–September). The soil is a clay loam and classified as Mat Cry-gelic Cambisols

(The Institute of Soil Science and the Chinese Academy of Sciences 2001).

2.2 Experiment design

During the growing season (May–September) in 2009, a reciprocal translocation experiment was implemented along an elevation gradient from 3200 to 3800 m a.s.l. to imitate climate change. Four sites at 3200 (37° 36′ 42.3′ ′N, 101° 18′ 47.9″ E), 3400 (37° 39′ 55.1″ N, 101° 19′ 52.7″ E), 3600 (37° 41′ 46.0″ N, 101° 21′ 33.4″ E) and 3800 m a.s.l. (37° 42′ 17.7″ N, 101° 22′ 09.2″ E) were selected. These four sites consisted of four different vegetation communities within 9 km in distance and named as vegetation type V2, V4, V6 and V8. At 3200 m, the vegetation is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa* spp., *Carex* spp., *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontopo diumnanum*, and *Potentilla nivea*. At 3400 m, the vegetation is dominated by the alpine shrub *Prunus fruticosa*, *Kobresia capillifolia*, *K. humilis*, and *Saussurea superba*. At 3600 m, the vegetation is dominated by *K. humilis*, *Saussurea katochaete Maxim*, *P. nivea*, *Thalictrum alpinum*, *Carex* spp., *Poa* spp., and *P. fruticosa*. At 3800 m, the vegetation is dominated by *K. humilis*, *Leontopo odiumnanum*, and *Poa* spp. More detailed information about the sites can refer to Wang et al. (2014a).

The translocation was implemented for three times on May 7th, June 26th, and August 10th, respectively. On each date, 16 intact soil columns (diameter × height = 10 × 20 cm) at each site were cut off using PVC tubes. Four of these intact soil columns were reinstated at the same site (home plots) and handled similarly as columns that were moved to other elevations. The other 12 intact soil columns were equally distributed among the other three elevation sites (away plots). All intact soil columns were installed in a fully randomized design and capped with lids that had some holes on the side wall for aeration. Thus, there were a total of 64 soil columns (four home plots × four away plots × four replicates) for each translocation. After 49-, 43- and 46-day incubation for the first, second and third translocation, all soil columns were taken back to the laboratory and sieved timely in a day or two. DOC and LOC were measured for all three translocations, while MBC was only analyzed in the second translocation.

2.3 Soil temperature and moisture

At each elevation site, HOBO weather stations (Onset Computer Corporation, Cape Cod, MA, USA) were installed to monitor soil temperature at 5-cm depth and soil moisture at 20-cm depth. The sensors were connected to a CR1000 datalogger. Detailed information about the temperature and soil moisture sensors can be found in Wang et al. (2014b). Soil temperature and soil moisture were measured every 1 min, and then 30-min averages were stored.

2.4 Measurements of SOC, aboveground and belowground biomass

In the middle of August 2009, ten 0.5 m × 0.5 m quadrats were set every 5 m along a 50-m transect for measurements of aboveground biomass. All aboveground biomass was clipped from the soil surface. In the center of each quadrat, belowground biomass within 0–20 cm depth was collected using an 8-cm-diameter soil auger. All soil cores were sieved through a 2-mm mesh and then washed to remove soil in the laboratory. Aboveground and belowground biomasses were dried at 80 °C for about 48 h to a constant weight. The sieved soil was air-dried for analysis of SOC on a TOC-5000A analyzer (Shimadzu Corp., Kyoto, Japan).

2.5 Analysis of soil MBC, DOC and LOC

Incubated soil columns were taken back from the field at the end of each translocation, and sieved through a 2-mm mesh and fully mixed for further analysis. Any visible plant materials were manually removed from the sieved soil. One half of sieved soil sample (about 500 g) was stored at 4 °C for several days and subsequently used for the extraction and measurement of MBC and DOC. The remaining material from each soil sample was air-dried for LOC measurement.

Soil MBC was determined using the chloroform fumigation extraction method (Vance et al. 1987). Briefly, one soil sub-sample (16 g) was fumigated with ethanol-free $CHCl_3$ for 24 h at 25 °C, and another one was also treated in the same manner without $CHCl_3$ (non-fumigated). The extractable C in soil samples was determined by adding 40 mL 0.5 M K_2SO_4, shaking for 30 min and filtered through Whatman # 40 filter paper. The difference in extractable C between fumigated and non-fumigated samples was assumed to be released from lysed soil microbes and converted to soil MBC using an extraction factor of 2.64 (Vance et al. 1987). Soil DOC was extracted according to Jones and Willett (2006). In brief, 20 g fresh soil sample was extracted with 100 mL 2 M KCl (1:5 *w*/*v* soil-to-solution ratio) by shaking for 60 min and filtering using Whatman # 40 filter paper.

Soil LOC was measured using a two-step acid hydrolysis method. In this method, soil LOC was divided into two different pools (i.e., LOCI and LOCII). Details of the method can be found in Belay-Tedla et al. (2009). In brief, 20 mL of 5 N H_2SO_4 was added to 0.5 g air-dried soil, and the samples were hydrolyzed for 30 min at 105 °C in sealed Pyrex tubes, after which the hydrolysate was recovered by centrifugation and decantation. The residue was washed with 20 mL of deionized water and the washing was added to the hydrolysate that was analyzed as LOCI. The remaining residue was hydrolyzed with 2 mL of 26 N H_2SO_4 overnight at room temperature under continuous shaking. The concentration of the acid was then brought down to 2 N by dilution with deionized water and the sample was hydrolyzed for another 3 h at 105 °C with occasional shaking. The hydrolysate was recovered in the same manner as for the LOCI and analyzed as LOCII.

All extracts and hydrolysates were stored at 4 °C for 2–3 days until the concentration of C was measured on a Shimadzu 5000 TOC analyzer (Shimadzu Corp., Kyoto, Japan).

2.6 Temperature sensitivity of MBC, DOC and LOC

Temperature sensitivity (% $°C^{-1}$) is defined as the change in MBC, DOC, LOCI and LOCII (%) per 1 °C temperature increase. To calculate the temperature sensitivity of soil MBC, DOC, LOCI and LOCII, we took the slope of a linear regression equation between the difference (%) in soil MBC, DOC, LOCI, LOCII and the difference (°C) in soil temperature between away plots and home plots.

2.7 Statistical analysis

Shapiro-Wilk and Levene's test of SPSS V. 16.0 (SPSS Inc. 2007) were used to test the normality and check homogeneity of variances to data of MBC, DOC, LOCI and LOCII. A univariate General Linear Model of SPSS V. 16.0 (SPSS Inc. 2007) was used to analyze the main and interactive effects of sampling date, vegetation type and elevation on soil DOC, LOCI and LOCII content in away plots. A similar model was used for MBC, but without sampling date. For analyses of the home plots only, the same models were used, but with elevation excluded. To test for vegetation type and date effects on DOC, LOCI and LOCII in home plots and vegetation type was taken as the between-subject factor and date as the within-subject factor. For warming and cooling effects caused by translocation (away plots), vegetation type and elevation were taken as the between-subject factors, and date was the within-subject factor. One-way ANOVA and least significance difference (LSD) were used to test how soil MBC, DOC, LOCI, LOCII and ratios of MBC to DOC, MBC to LOCI, MBC to LOCII, DOC to LOCI, DOC to LOCII and LOCI to LOCII differed among vegetation types in home plots, and how they differed between home and away plots at different elevations. Non-linear regression was performed to test the relationship between soil MBC, DOC, LOCI, LOCII and soil temperature and soil moisture. Linear regression was used to examine the relationship between differences in soil MBC, DOC, LOCI, LOCII and differences in soil temperature between away plots and home plots. All significances mentioned in the text were at the 0.05 level.

To evaluate the asymmetric pattern that possibly existed in the response of soil MBC, DOC, LOCI and LOCII to a change in temperature, an ANOVA with a linear model was implemented in R-3.1.0 (R Development Core Team 2013), in which difference in soil temperature (d_temp) between away plots and home plots was the covariate and the treatment (i.e., "warming" or "cooling") was the categorical variable. If significant interaction between the two variables was attained (at 0.05 level), asymmetry was supported (Wang et al. 2014b; Hu et al. 2016b).

3 Results

3.1 Soil temperature and moisture

In general, soil temperature at 5-cm depth decreased inversely to elevation (Fig. 1). Mean soil temperature at 5-cm depth was 9.4, 8.1, 4.0 and 3.9 for the first translocation from May 7th to June 25th; 13.7, 11.9, 9.8 and 9.1 for the second translocation from June 26th to August 10th; and 11.9, 10.9, 9.2 and 8.2 °C for the third translocation from August 11th to September 25th at 3200, 3400, 3600 and 3800 m elevation, respectively. The corresponding mean soil moistures at 20-cm depth were 38.1, 31.5, 55.6 and 15.9; 34.2, 27.2, 40.6 and 16.0; 34.0, 26.8, 29.6 and 16.7 % at 3200, 3400, 3600, and 3800 m elevation for the first, second and third translocation, respectively.

3.2 Soil MBC, DOC and LOC along the natural gradient

For home plots with no translocation, soil MBC was significantly affected by vegetation type while DOC, LOCI and LOCII were controlled by sampling date, vegetation type and their interaction (Table 1). The content of soil MBC varied from 67.0 to 199.9 mg C kg^{-1} across all elevations, and generally decreased with an increase in elevation though it was lowest at 3600 m (averaged 83.7 mg C kg^{-1}). Soil DOC content varied from 79.6 (vegetation type V6) to 134.7 mg C kg^{-1} (vegetation type V2) across all vegetation types, and with a peak during the second translocation. Soil DOC showed a significant decrease with an increase in elevation except 3600 m, which was significantly lower than DOC at 3800 m in the first translocation. The content of LOCI varied from 216.1 to 281.3 mg C kg^{-1}, while LOCII varied from 154.4 to 265.7 mg C kg^{-1} across all four elevations. In general, soil LOCI and LOCII decreased with an increase in elevation (Fig. 2).

3.3 Soil MBC, DOC and LOC for the translocation gradient

After being translocated, soil MBC was significantly controlled by vegetation type and elevation while soil DOC,

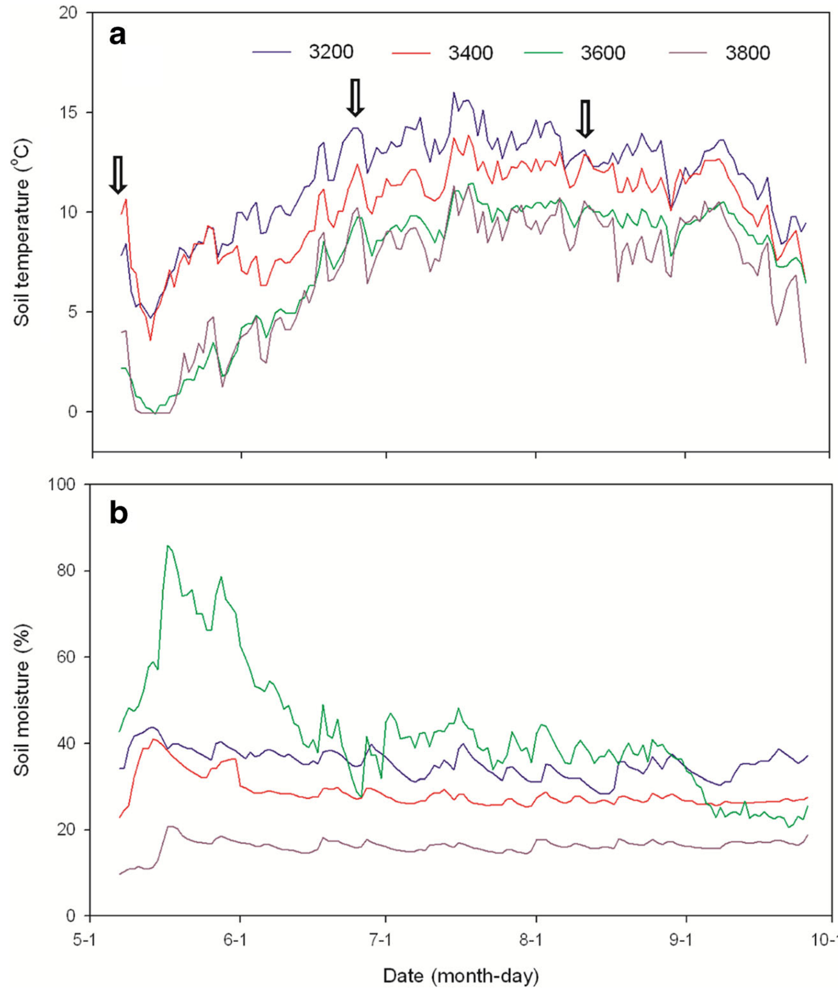


Fig. 1 Daily soil temperature (**a**) at 5-cm depth and soil moisture (**b**) at 20-cm depth at different elevations from May to September in 2009; 3200, 3400, 3600 and 3800 mean different elevations at 3200, 3400, 3600 and 3800 m a.s.l. Arrow indicates the date of reciprocal translocation

LOCI and LOCII were significantly affected by date, vegetation type, elevation and their interactions (Table 2). Warming increased soil MBC, with increases ranging from 0.9 (vegetation type V8 moved downward to 3400 m) to 30.1 % (vegetation type V6 moved downward to 3200 m). By contrast, cooling decreased soil MBC in most cases, with decreases ranging from 0.1 (vegetation type V2 moved upward to 3400 m) to 31.6 % (vegetation type V2 moved upward to 3800 m), but slightly increased soil MBC by 6.3 % for vegetation type V6 moved downward to 3800 m (Fig. 3).

Warming significantly increased soil DOC while cooling had an opposite effect across all vegetation types (Fig. 3). The increase in soil DOC ranged from 1.3 % (vegetation type V8 moved downward to 3600 m) to 33.7 % (vegetation type V8 moved downward to 3200 m), while the decrease ranged from 2.6 % (vegetation type V6 moved upward to 3800 m) to 20.1 % (vegetation type V2 moved upward to 3800 m). The absolute difference in soil DOC between away plots and home plots increased with an increase in elevation difference between away plots and home plots.

Table 1 Summary of univariate analysis on soil MBC, DOC, LOCI and LOCII from general linear model for the natural elevation gradient (i.e., home plots with no translocation)

Source	MBC			DOC			LOCI			LOCII		
	df	*F*	Sig.	df	*F*	Sig.	df	*F*	Sig.	df	*F*	Sig.
Date (*D*)	–	–	–	2	175.922	<0.001	2	11.802	<0.001	2	68.561	<0.001
Vegetation (*V*)	3	8.554	0.003	3	0.00146	<0.001	3	10.993	<0.001	3	128.398	<0.001
D × *V*	–	–	–	6	9.024	<0.001	6	2.517	0.039	6	4.886	0.001

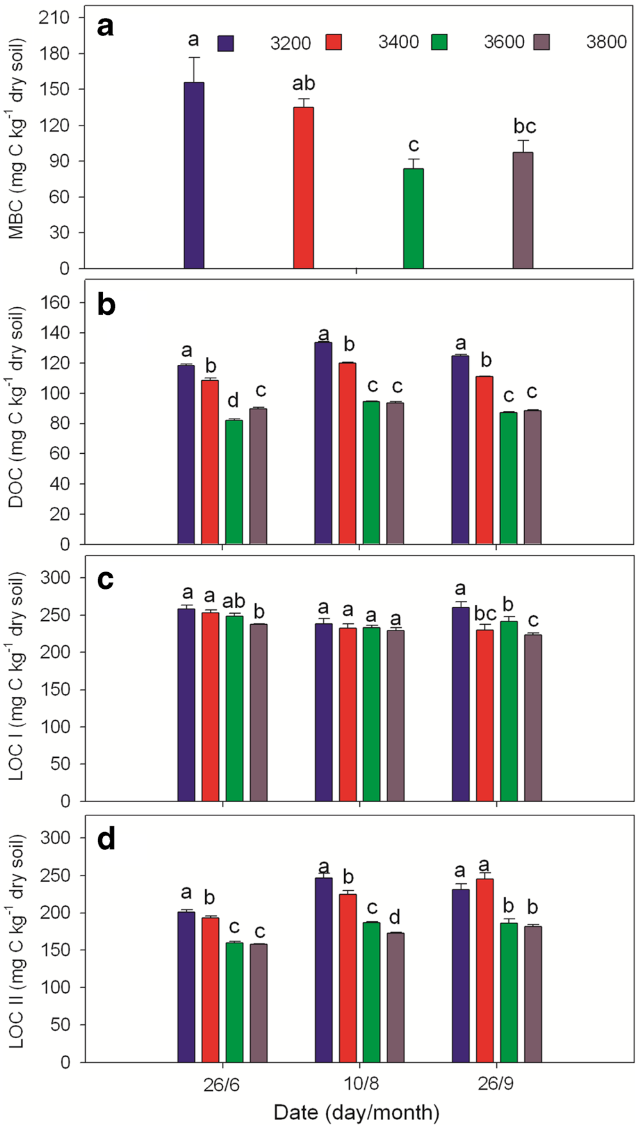


Fig. 2 Soil MBC (**a**), DOC (**b**), LOCI (**c**) and LOCII (**d**) in home plots with no translocation; 3200, 3400, 3600 and 3800 mean different elevations at 3200, 3400, 3600 and 3800 m a.s.l. Different letters indicate significant differences between different elevations. Mean ± SE are shown

Warming increased soil LOCI ranging from 0.2 % (vegetation type V8 brought down to 3600 m on September 26th) to 9.7 % (vegetation type V6 brought down to 3200 m on August 10th) across all vegetation types. In most cases, cooling decreased soil LOCI ranging from 0.4 % (vegetation type V2 brought up to 3800 m on September 26th) to 12.1 % (vegetation type V2 brought up to 3600 m on August 10th). However, cooling increased soil LOCI by 0.7 and 0.3 % at 3400 and 3600 m on June 26th for vegetation type V2; and by 3.5 and 1.2 % at 3600 m on September 26th for vegetation type V2 and V4; and also by 0.3 and 0.5 % at 3800 m on August 10th and September 26th for vegetation type V6. No significant difference was found between home plots and away plots with cooling except for vegetation type V2 brought up to 3600 m on August 10th (Fig. 3).

Similar to the variations in LOCI, warming increased soil LOCII ranging from 0.1 (vegetation type V8 brought down to 3600 m on August 10th) to 13.6 % (vegetation type V8 brought down to 3200 m on August 10th), while cooling decreased it with the average ranged from 0.1 % (vegetation type V4 brought up to 3600 m on August 10th) to 11.8 % (vegetation type V2 brought up to 3800 m on September 26th). By contrast, warming decreased soil LOCII by 2.2 % at 3200 m and 2.9 % at 3400 m for vegetation type V6 on August 10th, and by 0.04 % on August 10th and 2.9 % on September 26th at 3200 m for vegetation type V4, respectively. Cooling increased it by 2.9 % at 3400 and 7.6 % at 3600 m for vegetation type V2 on August 10th.

3.4 The ratios among MBC, DOC and LOC

For home plots with no translocation, the ratios of MBC to DOC, LOCI and LOCII, as well as the ratios of DOC to LOCI and DOC to LOCII generally decreased with an increase in elevation with the minimum at 3600 m. Warming and cooling effects on the ratios of MBC to DOC, LOCI and LOCII varied

Table 2 Summary of univariate analysis on soil MBC, DOC, LOCI and LOCII from general linear model and type III test for warming and cooling effects (i.e., away plots with translocation)

Source	MBC			DOC			LOCI			LOCII		
	df	*F*	Sig.	df	*F*	Sig.	df	*F*	Sig.	df	*F*	Sig.
Date (*D*)	–	–	–	2	513.425	<0.001	2	86.355	<0.001	2	354.204	<0.001
Vegetation (*V*)	3	19.172	<0.001	3	711.001	<0.001	3	30.021	<0.001	3	374.640	<0.001
Elevation (*E*)	3	8.351	<0.001	3	0.00176	<0.001	3	17.344	<0.001	3	47.749	<0.001
D × *V*	–	–	–	6	8.039	<0.001	6	20.666	<0.001	6	32.480	<0.001
D × *E*	–	–	–	6	5.790	<0.001	6	1.429	0.208	6	3.042	0.008
V × *E*	9	1.213	0.309	9	8.535	<0.001	9	1.148	0.333	9	2.407	0.014
D × *V* × *E*	–	–	–	18	1.696	0.046	18	1.747	0.038	18	1.842	0.026

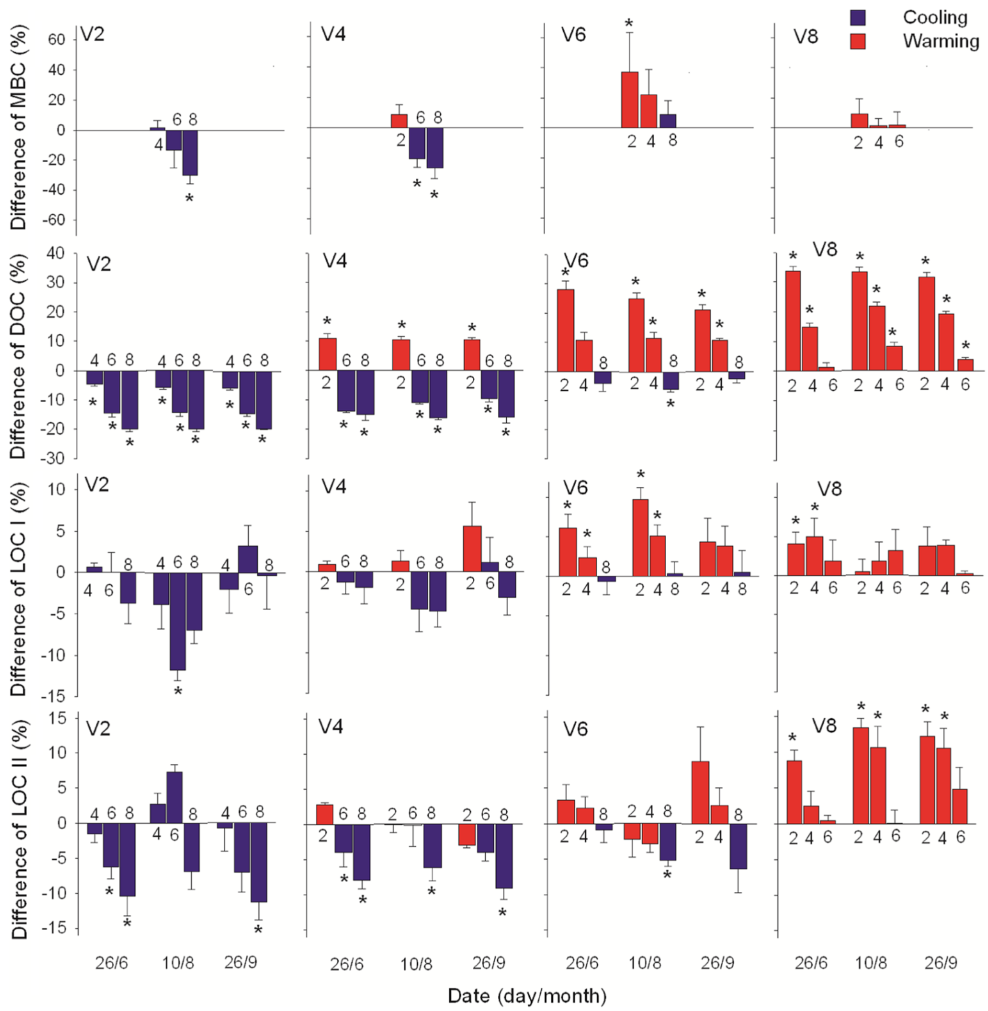


Fig. 3 Difference in soil MBC, DOC, LOCI and LOCII between away plots and home plots. V2, V4, V6 and V8 represent vegetation type at 3200, 3400, 3600 and 3800 m elevation, respectively; 2, 4, 6 and 8 represent away site elevation of 3200, 3400, 3600 and 3800 m a.s.l. *Asterisk* indicates significant difference between away plots and home plots at 0.05 level. Mean ± SE are shown

depending on vegetation type and elevation. For example, warming significantly increased the ratio of MBC to LOCI but had no effects on the ratio of MBC to LOCII for vegetation type V8, while cooling significantly increased the ratio of MBC to LOCI but decreased the ratio of MBC to LOCII and had no effect on MBC to DOC. However, warming generally increased the ratios of DOC to LOCI and DOC to LOCII while cooling decreased these ratios. However, neither warming nor cooling affected the ratio of LOCI to LOCII (Table 3).

3.5 Relationships between different soil organic C pools and soil temperature and moisture

When all data from home plots with no translocation and away plots with warming and with cooling were considered together, soil MBC was positively related to soil DOC and LOCII but not related to LOCI. DOC and LOCII explained 44 and 36 % of the variations in soil MBC, respectively. Soil DOC was also not related to LOCI but positively related to soil LOCII explaining 38 % of the variation in soil DOC. However, soil LOCI was negatively related to LOCII with the explanation of 17 %. No relationship was found between LOCI and soil moisture for home plots with no translocation and away plots with warming (Fig. 4).

Soil MBC, DOC, and LOCII were positively related to soil temperature while soil LOCI showed a very weak negative relationship with soil temperature (R^2 = 0.029, P = 0.018) for all data from home plots and away plots. Soil temperature at 5-cm depth explained 17, 53 and 28 % of the variations in MBC, DOC and LOCII, respectively. A quadratic relationship was found between MBC, DOC, LOCI, LOCII and soil moisture, explaining 16, 43, 0.5 and 14 % of the variations in MBC, DOC and LOCII, respectively. No relationship was found between LOCI and soil moisture for away plots with warming and away plots with cooling (Fig. 5).

3.6 Temperature sensitivity of soil MBC, DOC and LOC

Positively linear relationships between the differences (%) in soil MBC, DOC, LOCI, LOCII and differences

Table 3 The ratios of soil MBC, DOC, LOC, LOCI and LOCII for home plots (H) and away plots with warming (W) and cooling (C). Different lower case letters mean significant difference between various elevations at 0.05 level

Vegetation	Elevation	Treatment	MBC/DOC	MBC/LOCI	MBC/LOCII	DOC/LOCI	DOC/LOCII	LOCI/LOCII
V2	3200	H	1.17 (0.15) a	0.65 (0.09) a	0.64 (0.09) a	0.50 (0.02) a	0.56 (0.01) a	1.13(0.05)a
	3400	C	1.24 (0.13) a	0.68 (0.06) a	0.62 (0.07) a	0.48 (0.02) ab	0.53 (0.01) b	1.11(0.05)a
	3600	C	1.12 (0.05) a	0.61 (0.02) a	0.48 (0.03) a	0.45 (0.02) bc	0.49 (0.01) c	1.14(0.08)a
	3800	C	1.01 (0.15) a	0.49 (0.07) b	0.47 (0.07) a	0.42 (0.01) c	0.50 (0.01) c	1.21(0.06)a
V4	3200	W	1.10 (0.03) a	0.62 (0.03) a	0.65 (0.02) a	0.52 (0.02) a	0.57(0.01) a	1.12(0.05)a
	3400	H	1.13 (0.06) a	0.30 (0.01) c	0.60 (0.03) a	0.48 (0.01) b	0.52 (0.02) b	1.09(0.05)a
	3600	C	1.00 (0.07) a	0.48 (0.03) b	0.48 (0.04) b	0.43 (0.02) c	0.47 (0.01) c	1.11 (0.06)a
	3800	C	0.98 (0.09) a	0.45 (0.05) b	0.47 (0.04) b	0.42 (0.01) c	0.47 (0.01) c	1.15 (0.06)a
V6	3200	W	0.92 (0.11) a	0.43 (0.04) a	0.60 (0.07) a	0.43 (0.01) a	0.60 (0.02) a	1.42 (0.05)a
	3400	W	0.93 (0.04) a	0.40 (0.02) a	0.54 (0.03) ab	0.39 (0.01) b	0.55 (0.01) b	1.41 (0.04)a
	3600	H	0.89 (0.08) a	0.20 (0.02) b	0.45 (0.04) b	0.37 (0.01) bc	0.50 (0.01) c	1.37 (0.05)a
	3800	C	1.00 (0.03) a	0.38 (0.01) a	0.50 (0.02) ab	0.35 (0.01) c	0.50 (0.00) c	1.42 (0.03)a
V8	3200	C	0.77 (0.03) b	0.42 (0.01) a	0.49 (0.02) a	0.51 (0.01) a	0.64 (0.02) a	1.25 (0.04)a
	3400	C	0.79 (0.04) ab	0.39 (0.02) a	0.47 (0.04) a	0.45 (0.01) b	0.59 (0.02) b	1.31 (0.06)a
	3600	C	0.90 (0.09) ab	0.39 (0.05) a	0.52 (0.05) a	0.40 (0.01) c	0.55 (0.01) bc	1.36 (0.05)a
	3800	H	0.95 (0.06) a	0.22 (0.01) b	0.52 (0.04) a	0.39 (0.00) c	0.53 (0.01) c	1.36 (0.04)a

(°C) in soil temperature at 5-cm depth between away plots and home plots were found for all vegetation types considered together (Fig. 6) and for each vegetation type separately, except for soil MBC of vegetation types V6 and V8 and soil LOCI of vegetation types V4 and V6 (Appendix 1, Electronic Supplementary Material). Difference in soil temperature explained 47–87, 64–89, 19–28 and 8–38 % of the variations in soil MBC, DOC, LOCI and LOCII. The slopes of regression equations between the difference (%) soil MBC, DOC, LOCI, LOCII and the differences (°C) in soil temperature at 5-cm depth between home plots and away plots revealed the temperature sensitivity of these C pools. The temperature sensitivity of soil MBC, DOC, LOCI and LOCII was 5.0, 5.1, 0.9 and 1.5 % °C^{-1} for all vegetation types with warming and cooling considered together, respectively. The temperature sensitivity of DOC was 3.0, 4.6, 5.3 and 5.3 % °C^{-1}; 4.9, 5.8, 6.8 and 6.6 % °C^{-1}; 5.2, 7.1, 6.0 and 10.0 % °C^{-1} for vegetation type V2, V4, V6 and V8 for the first (June 26th), second (August 10th) and third (September 26th) translocation, respectively. When separated by warming and cooling, the temperature sensitivity of DOC was 5.1 % °C^{-1} under warming and 3.0 % °C^{-1} under cooling, and the temperature sensitivity of LOCII was 1.1 % °C^{-1} under warming and 1.4 % °C^{-1} under cooling, respectively. The interaction between d_temp and treatment was significant for DOC while it was not significant for MBC, LOCI and LOCII (Table 3), suggesting that the response of DOC was asymmetric but symmetric for MBC, LOCI and LOCII to warming and cooling.

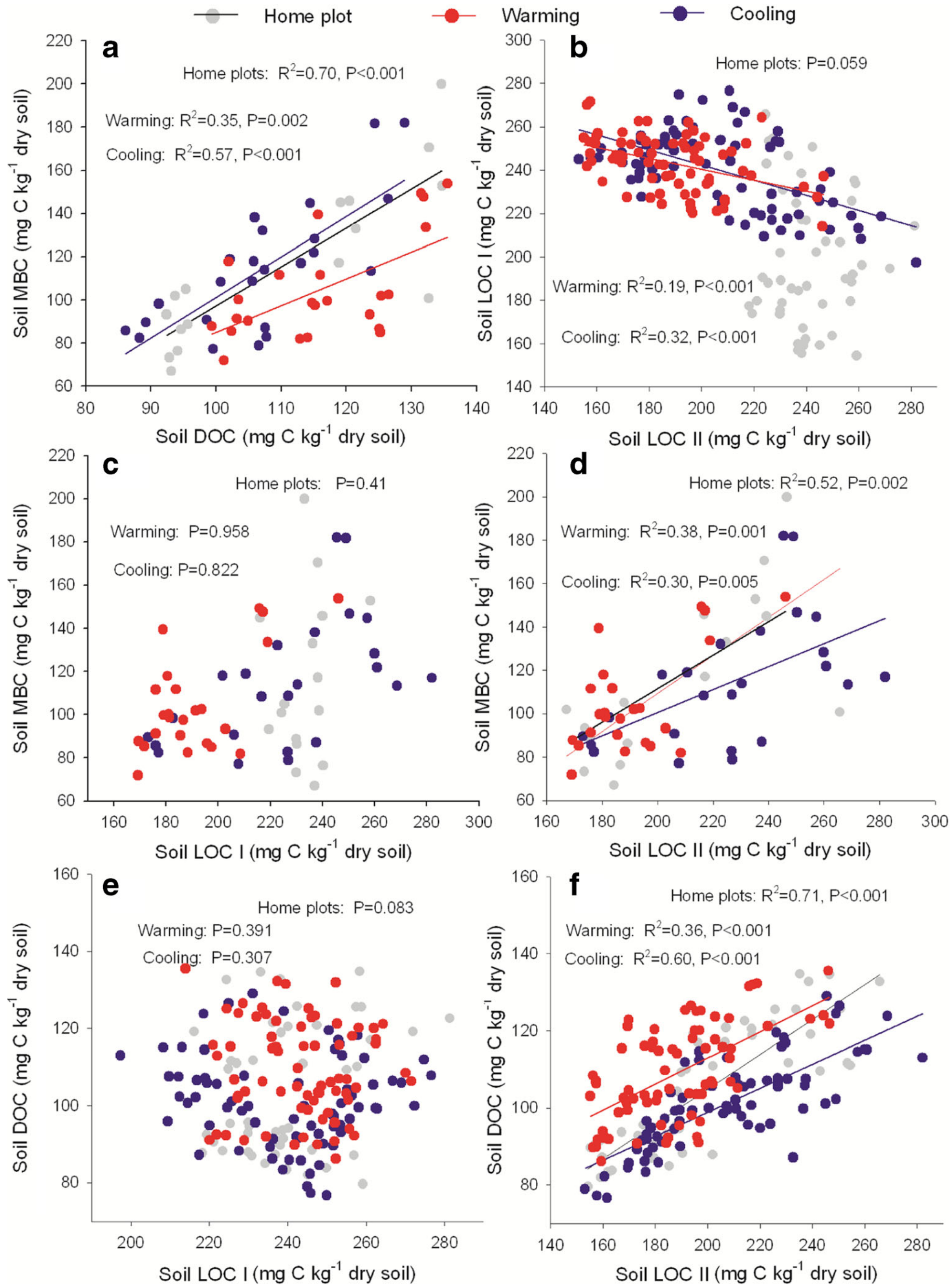
4 Discussion

4.1 Temperature effects

Consistent with previous studies (Belay-Tedla et al. 2009; Luo et al. 2009; Rui et al. 2011), our results showed that soil DOC, LOCI and LOCII were related to SOC, aboveground biomass and belowground biomass for the natural elevation gradient (Table 4). In agreement with previous studies (Liechty et al. 1995; Luo et al. 2009), soil LOC pools were generally positively correlated with soil temperature for home plots without translocation (Fig. 5). Therefore, the decreased soil LOC pools with an increase in elevation for home plots (Fig. 2) could be explained by a decrease in aboveground and belowground biomass (Table 5). The decreased biomass may reduce C substrate input and accumulation of SOC and DOC, and thereby limit available C substrate supply to soil microbes.

Some previous studies indicated that an increase in temperature may increase soil MBC (Belay-Tedla et al. 2009; Ziegler et al. 2013), DOC (Harrison et al. 2008; Luo et al. 2009) and LOC (Belay-Tedla et al. 2009) in different ecosystems. Similarly, we also found that warming generally increased LOC pools while cooling decreased them (Fig. 3). These results supported the first hypothesis and suggested that soil LOC pools of alpine meadow are very sensitive to temperature change. Probably, higher soil temperature may stimulate production of root exudates (Uselman et al. 2000) that is beneficial to microbial growth and reproduction

Fig. 4 Relationships among soil MBC, DOC, LOCI and LOCII for home plots and away plots with warming and with cooling



(Waldrop and Firestone 2006; Rui et al. 2011) and even that can stimulate decomposition of recalcitrant C (Knorr et al. 2005; Ziegler et al. 2013). Furthermore, higher soil LOC availability may have speeded decomposition of SOC (Zhu and Cheng 2011; Pang et al. 2015). By contrast, cooling significantly decreased soil LOC pools due to inverse effects. In this study, soil temperature explained a larger part (15–64 %) of the variations in soil LOC pools (Fig. 5) than previous reports (Luo et al. 2009; Rui et al. 2011; Jing et al. 2014). This difference was likely caused by the fact that our study largely excluded plants uptake of dissolved organic compounds (Schimel and Chapin 1996; Ma et al. 2015) and leaching of LOC due to rainfall (Harrison et al. 2008). Furthermore, warming caused soil drying that might have offset positive effects of warming on soil enzyme activity (Jing et al. 2014) and thus may have limited SOM decomposition. Notably, warming and cooling also changed the ratios of different C fractions via changing the ratios of MBC and DOC to LOCI and LOCII rather than LOCI and LOCII depending on vegetation types and elevations (Table 2), indicating

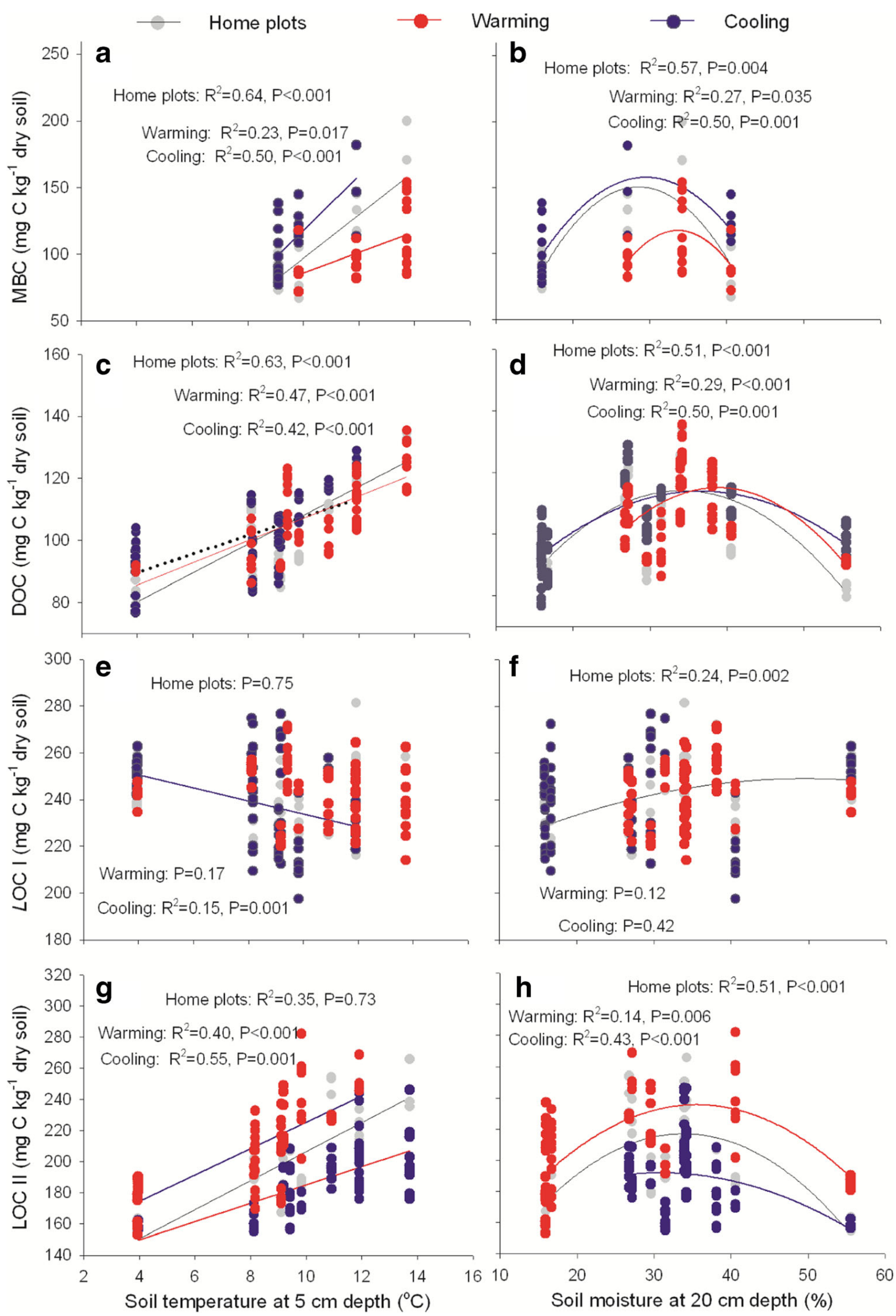


Fig. 5 Relationships between soil MBC, DOC, LOCI, LOCII and soil temperature (**a**, **c**, **e**, and **g**) and soil moisture (**b**, **d**, **f**, and **h**) for home plots and away plots with warming and with cooling

that climate change would not only change the size of soil LOC pools but also soil C quality and composition.

4.2 Moisture effects

The status of soil moisture may affect the response of soil LOC to warming (Kalbitz et al. 2000). For the sites at 3600 and 3800 m, mean soil temperature was almost the same (4.0 °C for 3600 m and 3.9 °C for 3800 m) while soil conditions were much drier at 3800 m (15.9 %) than 3600 m (55.6 %) during the first translocation. However, soil DOC, LOCI and LOCII decreased for vegetation V6 brought up to 3800 m but increased for vegetation V8 moved down to 3600 m (Fig. 3), suggesting that dry conditions likely caused the decreases but wet conditions caused the increases in these LOC pools. However, several increases and decreases in MBC, LOCI

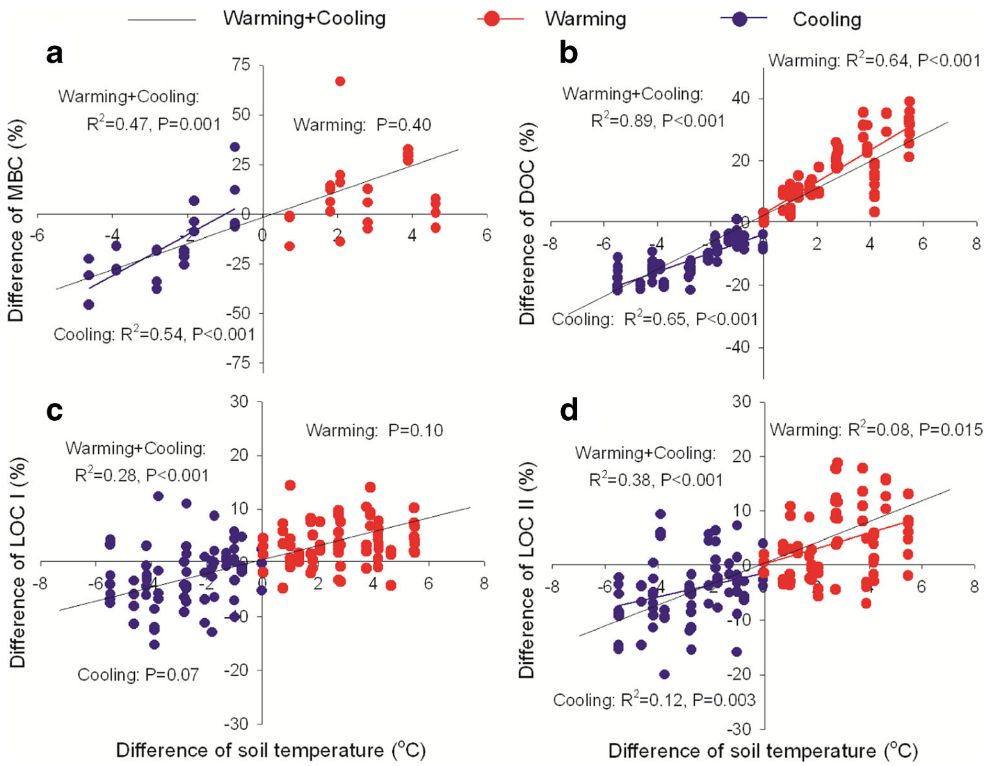


Fig. 6 Relationships between differences in soil MBC (**a**), DOC (**b**), LOCI (**c**), LOCII (**d**) and differences in soil temperature between away plots and home plots with warming, cooling as well as warming and cooling

and LOCII with warming or cooling were detected, especially for vegetation type V6 and other vegetation types translocated to 3600 m (Fig. 3). These results imply that effects of soil moisture may override temperature effects (Luo et al. 2009) depending on soil moisture conditions. On the one hand, higher soil moisture with cooling limited microbial activity and hence limited soil microbes to immobilize labile nutrients. On the other hand, decreased soil moisture with warming might restrict the decomposition of labile and recalcitrant C pools (Skopp et al. 1990). Although few studies have studied the relationships between soil LOC pools and soil moisture, we found that soil LOC showed a hump-shaped relationship with soil moisture with a threshold of about 30–35 % (Fig. 5). These results indicate that soil moisture might modify temperature effects by weakening warming effects but strengthening cooling effects on soil LOC pools when soil moisture exceeded the threshold. Soil moisture explained more variations (14–57 %) in LOC pools than other previous reports (Luo et al. 2009; Rui et al. 2011), indicating that previous warming studies using heaters may have under-evaluated the direct contribution from soil moisture. Probably, drought caused by heaters might have offset warming effects on activity of soil extracellular enzymes and microbial biomass (Jing et al. 2014).

Similar to other studies (Belay-Tedla et al. 2009; Luo et al. 2009; Rui et al. 2011), our results showed that DOC, LOCI and LOCII were related to SOC, aboveground biomass or belowground biomass in home plots, respectively (Table 4). Root growth and root exudates are known to be key processes governing inputs of carbon to soil (Farrar and Jones 2003; Cleveland et al. 2004) and influenced by temperature and solar radiation (Fitter et al. 1998; Harrison et al. 2008). Because plant production from photosynthesis was excluded in this study, the unexplained variations in soil LOC pools might be attributed to changes in belowground biomass that was not measured. Thus, further study is needed to examine

Table 4 Relationships between soil MBC, DOC, LOCI, LOCII and SOC, aboveground biomass (ABS) and belowground biomass (BBS) for the natural elevation gradient (i.e., home plots with no translocation). Pearson correlation coefficients (*r*), stepwise liner regression equations and van't Hoff equations are presented

	r			Stepwise linear regression		
	SOC	ABS	BBS	Equation	Sig.	R^2
MBC	0.936	0.936	0.825	–	–	–
DOC	0.954*	0.959*	0.870	*Y* = 0.163 ABS + 85.324	0.041	0.920
LOCI	0.815	0.933	0.994**	*Y* = 0.005 BBS + 220.392	0.006	0.988
LOCII	0.986*	0.960*	0.907	*Y* = 59.366 SOC − 128.684	0.014	0.972

Significant difference at *0.05 and **0.01 level

Table 5 Soil organic carbon (SOC) within 10-cm depth, aboveground biomass (ABS) and belowground biomass (BBS) within 20-cm depth at 3200, 3400, 3600 and 3800 m a.s.l. in 2009, respectively. Different lower case letters mean significant difference between various elevations at 0.05 level

Elevation (m a.s.l.)	SOC (%)	ABS (g m^{-2})	BBS (g m^{-2})
3200	6.22 (0.01) a	313.49 (8.86) a	3358.12 (238.92) a
3400	6.04 (0.04) b	164.36 (12.81) b	2358.24 (309.97) b
3600	5.39 (0.04) c	85.72 (5.33) c	2281.69 (223.07) b
3800	5.01 (0.03) d	52.08 (4.46) d	1707.28 (211.63) c

the relationships between soil LOC pools and biomass under warming and cooling in the future.

4.3 Temperature sensitivity of different LOC pools

Effects of temperature on biological processes are often non-linear, particularly when the range in temperature is large (Schleip et al. 2008; Iler et al. 2013). Although differences in soil temperature failed to explain difference in MBC with warming and in LOCI with warming and with cooling, variations in these soil LOC pools were well explained by difference in soil temperature when warming and cooling results were considered together (Fig. 6). The temperature sensitivity of soil MBC under cooling was comparable to previous report (about 11 % °C^{-1}) (Rui et al. 2011), but lower (5 % °C^{-1}) when warming and cooling effects were considered together. This might be caused by an offset effect from warming, though soil MBC was not related to changes in soil temperature (Fig. 6). The temperature sensitivities of DOC (5.1 % °C^{-1}), LOCI (0.9 % °C^{-1}) and LOCII (1.5 % °C^{-1}) were much lower than that of previous reports (8–12 % °C^{-1} for DOC, 7–8 % °C^{-1} for LOCI and LOCII) from an alpine meadow (Luo et al. 2009), hardwood forest (Liechty et al. 1995), and tallgrass prairie (Belay-Tedla et al. 2009). This was most likely caused by exclusion of leaching effects and plants photosynthesis, implying that accumulation of photosynthesis products might contribute more to soil LOCI and LOCII than to DOC in response to climate change.

Soil DOC showed an asymmetric response while LOCII had a symmetric response to warming and to cooling (Table 6). Although ANOVA results showed that the responses of MBC and LOCI to warming and to cooling were asymmetric, uncertainties still existed because linear model failed to explain differences in soil temperature and differences in MBC with warming and in LOCI with warming and with cooling (Fig. 6). These results supported our second hypothesis (i.e., soil LOC fractions have varied responses to warming and to cooling). Then, 2 °C of variation in soil temperature corresponded to a 13 % increment of DOC under warming but only to a 2 % decrease of soil DOC under cooling (Fig. 6), indicating that soil DOC was more sensitive to warming than to cooling. Since DOC is the source of respired C and its rapid turnover rate accounts for increased CO_2 production (Bengtson and Bengtsson 2007), this asymmetrical response provided direct evidence for an asymmetrical response of ecosystem respiration to warming and to cooling (Hu et al. 2016a). This asymmetry might be caused by acclimation of plants and soil microbes to cooling due to the cold conditions in this region (Chang et al. 2012) that may have alleviated the reduction in DOC with cooling, as evidenced in the home plots along the elevation gradients (Fig. 5). The most likely explanation for the asymmetry is that higher labile substrate supply in away plots with warming increases the decomposition of SOC with a higher temperature sensitivity (Pang et al. 2015), while reduced labile substrate levels in away plots with cooling limits SOC decomposition (Fissore et al. 2013). Another possible cause is the regulation from moisture because the status of soil moisture may affect the response of soil LOC to warming (Belay-Tedla et al. 2009; Kalbitz et al. 2000). In our study, warming was often synchronized with increased soil moisture while cooling was often coupled to decreased soil moisture, and mean soil moisture was usually below the threshold of 35 %. In this case, soil moisture might strengthen warming effects but weaken cooling effects on DOC. However, a potential lower increase in microbial biomass in away plots with warming than with cooling (Fig. 6a)

Table 6 ANOVA analysis with difference in soil temperature (d_temp) as the covariate and treatment as the categorical variable

Source	MBC			DOC			LOCI			LOCII		
	df	*F*	Sig.	df	*F*	Sig.	df	*F*	Sig.	df	*F*	Sig.
d_temp	1	21.51	3.15e-5*	1	1379.99	<2e-16*	1	56.17	6.88e-12*	1	87.75	<2e-16*
treatment	1	0.17	0.68	1	15.33	1.41e-4*	1	2.45	0.12	1	0.79	0.37
d_temp × treatment	1	0.74	0.40	1	15.63	1.22e-4*	1	0.25	0.62	1	0.27	0.61

*Mean significant difference at 0.001 level may have limited the decomposition of SOM and litter, thereby offsetting warming effects on soil LOCI and LOCII. The temperature for vegetation type V8 was also higher (only warming) than for vegetation type V2 (only cooling) while LOCII showed almost the same temperature sensitivity (Appendix 1, Electronic Supplementary Material). Thus, warming is most likely to accelerate soil C loss from the Tibetan alpine meadow by improving the decomposition of SOC in a warmer future. These results underline that these soil LOC pools would have a different response to warming and to cooling regulated by soil moisture, and that the tradeoff of cooling effects on soil LOC pools should not be ignored in modeling studies.

5 Conclusions

Our study demonstrated that soil MBC, DOC and LOC changed rapidly in response to variation in soil temperature and soil moisture, and were affected by vegetation type and sampling date. In general, warming increased these soil LOC pools while cooling had an opposite effect. Although warming increased and cooling decreased the proportion of DOC in soil LOC, their effects on the proportion of MBC varied depending on vegetation type and elevation. Therefore, climate change would not only have an impact on the size of soil LOC pools but also its quality and composition. Soil LOC content was positively related to soil temperature but showed a hump-shaped relationship with soil moisture with a threshold of about 30–35 %. Soil DOC showed an asymmetric response to warming and to cooling with higher temperature sensitivity under warming than under cooling, while soil LOCII showed a symmetric response. Therefore, cooling effects on soil LOC pools and regulation by soil moisture should be taken into consideration to evaluate the fate of soil organic C in the Tibetan alpine meadow in a warmer future.

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