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Response of ecosystem respiration to experimental warming and clipping in Tibetan alpine meadow at three elevations

G. Fu[1], Y.-J. Zhang[1], X.-Z. Zhang[1], P.-L. Shi[1], Y.-T. Zhou[2], Y.-L. Li[1,3], and Z.-X. Shen[1]

[1] Lhasa Plateau Ecosystem Research Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China
[2] Department of Microbiology and Plant Botany, Center for Spatial Analysis, University of Oklahoma, Norman, Oklahoma 73019, USA
[3] University of Chinese Academy of Sciences, Beijing 100049, China

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Correspondence to: Z.-X. Shen (shenzx@igsnrr.ac.cn)

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Abstract

This study aims to understand the response of ecosystem respiration (R_{eco}) to warming and clipping in the alpine meadow of Tibet. A field warming experiment using open top chambers was conducted in three alpine meadow sites at elevation 4313 m, 4513 m and 4693 m on the Tibetan Plateau since July 2008. Clipping was conducted three times a year since 2009. R_{eco} was measured from June to September in 2010–2012. For most cases, the seasonal variation of R_{eco} was mainly affected by soil water content rather than soil and air temperature, especially under warmer environment. Experimental warming tended to decrease seasonal average R_{eco} by 21.6 % and 10.9 % at elevation 4313 m and 4513 m, respectively, but significantly increased seasonal average R_{eco} by 11.3 % at elevation 4693 m. The different responses of R_{eco} to experimental warming could be mainly dependent on temperature and water availability condition. Clipping decreased seasonal average R_{eco} by 6.9 %, 36.9 % and 31.6 % at elevation 4313 m, 4513 m and 4693 m. The consistent declines caused by clipping may be mainly attributed to clipping-induced decline in aboveground biomass. Our findings suggested that the response of R_{eco} to warming differed among the alpine meadow and was regulated by soil water content on the Tibetan Plateau.

1 Introduction

Global surface temperature is predicted to increase 1.8–4 °C by the end of this century and the expected warming magnitude on the Tibetan Plateau is much greater than the global average (IPCC, 2007). The Tibetan Plateau ecosystem is one of the systems most sensitive to global climate change (Miehe et al., 2011; Yu et al., 2012; Sun et al., 2013). Ecosystem respiration (R_{eco}) is an important carbon flux in the carbon cycling of terrestrial ecosystems, and is related to primary production and net ecosystem exchange (Oberbauer et al., 2007; Welker et al., 2004; Wu et al., 2011b). Few studies have reported the effects of warming on R_{eco} under controlled warming and clipping conditions, especially along an elevation gradient.

Inconsistent results on the responses of R_{eco} to climate warming and clipping have been reported for different vegetation types and climate conditions (Welker et al., 2004; Grogan et al., 2001; Wu et al., 2011a). Temperature and water availability have been found to be the two most important abiotic factors controlling R_{eco} (Shi et al., 2006; Wu et al., 2011b) and their relative contributions can vary with the related environment conditions (Wohlfahrt et al., 2008; Lin et al., 2011). Generally, R_{eco} increases exponentially with temperature when water availability is not limited (Shi et al., 2006; Lin et al., 2011). Experimental warming-induced soil drying has been observed in various terrestrial ecosystems worldwide (Luo et al., 2001; Li et al., 2011), which may dampen the positive direct effect of experimental warming on R_{eco} and thereby leads to no significant change in R_{eco} (Xia et al., 2009; Lin et al., 2011). Climate warming and clipping would lead to changes in nitrogen, microbial biomass, litter, biomass and primary production (Klein et al., 2007; Cheng et al., 2010; Fu et al., 2012b), which would in turn influence R_{eco} (Lin et al., 2011; Yan et al., 2011).

In China, the alpine meadow is concentrated in the western and south-western regions, mostly on the Tibetan Plateau (Ni, 2002). The alpine meadow covers about one-third of the Tibetan Plateau and is a major type of pastureland on the Tibetan Plateau (Cao et al., 2004). The alpine meadow stores a large amount of soil organic carbon (SOC) (4.68 Pg) with SOC density of 9.05 kg m^{-2} at depth of 0–100 cm (Yang et al., 2008). Understanding the effect of warming on R_{eco} for the alpine meadow on the Tibetan Plateau is crucial to predict its future status and implement effective restoring and reserving measures under global warming (Yu et al., 2012; Miehe et al., 2008).

In this study, we set up an experiment in three alpine meadow sites along an elevation gradient (4313–4693 m) on a south-facing slope on the Nyainqentanglha Mountains of the Northern Tibetan Plateau to achieve the following objectives: (1) to compare the response of R_{eco} to experimental warming and clipping among the three alpine meadows and (2) to investigate correlations among soil and air temperatures and soil water content on seasonal variation of R_{eco} during the growing season for the alpine meadow of Tibet.

Temperature sensitivity of respiration declined with increasing temperature (Luo et al., 2001; Zhou et al., 2006) and decreasing elevation (Zimmermann et al., 2009). Additionally, temperature generally decreased with increasing elevation. Therefore, we hypothesized that the response of R_{eco} to warming could differ among the three alpine meadow sites. Considering aboveground biomass was the substrate of R_{eco}, we hypothesized that clipping could decrease R_{eco} by removing parts of aboveground biomass. Thirdly, we hypothesized that soil water content could regulate the effects of warming on R_{eco} because warming may result in soil drying, which in turn suppress R_{eco}.

2 Materials and methods

2.1 Study area

The study area (30°30′–30°32′ N, 91°03′–91°04′ E) was located at Damxung Grassland Observation Station, Tibet Autonomous Region of China. The annual mean sunlight is 2880.9 h and the annual mean solar radiation is 7527.6 $\mathrm{MJ\,m^{-2}}$. The annual mean air temperature is 1.3 °C, ranging from the lowest value (–10.4 °C) in January to the maximum (10.7 °C) in July. Annual mean precipitation is around 476.8 mm, with over 80 % occurring in the period from June to August (Fu et al., 2012a). The annual potential evapotranspiration is about 1725.7 mm. The soil freezing duration is from November to January. The soil texture is sandy loam. The soil layer is 0.5–0.7 m thick, with organic matter of 0.3–11.2 %, total nitrogen of 0.03–0.49 % and pH of 6.0–6.7 (Fu et al., 2012c). The typical vegetation type in the study area is *Kobresia*-dominated alpine meadow (Table 1). Roots are mainly concentrated in the topsoil layer (0–20 cm).

Based on meteorological observations from 1963 to 2012 at Damxung station (4288 m, approximately 4 km from our study site), annual mean air temperature increased at a rate of 0.37 °C 10 yr^{-1}. However, there was no significant change for annual precipitation ($p > 0.10$).

2.2 Experimental design

The experiment was set up in three alpine meadow sites located at 4313 m, 4513 m and 4693 m, respectively. The field experiment was based on a complete two factorial design (warming and clipping) with three replicates of each of four treatments: no warming and no clipping (NW + NCL), warming and no clipping (W + NCL), clipping and no warming (CL + NW), warming plus clipping (W + CL) at each elevation. In this study, open top chambers (OTCs) were used to increase temperature by trapping solar energy (Marion et al., 1997). Six OTCs were randomly set up at each elevation in July 2008. The OTCs remained on the plots year round. The bottom and top diameters and the height of OTCs are 1.45, 1.00 and 0.40 m, respectively (Fu et al., 2012b). There was one unwarmed plot in the vicinity of each OTC. Three of the six OTCs and their paired unwarmed plots were clipped, but the other OTCs and their unwarmed paired plots were not clipped. Clipping was conducted three times a year (generally in June, July and September) for the clipped plots (i.e., CL + NW and W + CL) during the growing season since 2009. The aboveground parts of live vegetation were clipped to about 0.01 m in height for the clipped plots. The clipped aboveground biomass was removed, oven-dried at 65 °C for 48 h and weighted. The removed aboveground averaged biomass (mean ± SE) was $34.48 \pm 10.91\,\mathrm{g\,m^{-2}\,yr^{-1}}$ and $30.94 \pm 8.20\,\mathrm{g\,m^{-2}\,yr^{-1}}$, $34.28 \pm 3.84\,\mathrm{g\,m^{-2}\,yr^{-1}}$ and $29.69 \pm 1.64\,\mathrm{g\,m^{-2}\,yr^{-1}}$ and $37.48 \pm 4.90\,\mathrm{g\,m^{-2}\,yr^{-1}}$ and $52.01 \pm 13.32\,\mathrm{g\,m^{-2}\,yr^{-1}}$ for CL + NW and W + CL treatments during the three growing seasons of 2010–2012 at elevation 4313 m, 4513 m and 4693 m, respectively.

Soil temperature (T_s) at a depth of 0.05 m (S-TMB-M006), soil water content (SWC) at a depth of 0.10 m (S-SMC-M003), air temperature (T_a) and relative humidity at a height of 0.15 m (S-THB-M008) were measured continuously for all treatments at each elevation during the whole study period. All the channels were connected to data loggers (HOBO weather station, Onset Computer Corporation, USA). OTCs increased seasonal average T_s by 1.13 °C, 1.34 °C and 1.09 °C and T_a by 1.04 °C, 1.41 °C and 1.01 °C across the three consecutive growing seasons in 2010–2012 at elevation 4313 m, 4513 m and 4693 m, respectively ($p < 0.05$). The seasonal average SWC values outside OTCs were $0.16\,\mathrm{m^3\,m^{-3}}$, $0.20\,\mathrm{m^3\,m^{-3}}$ and $0.19\,\mathrm{m^3\,m^{-3}}$, whereas those inside OTCs were $0.11\,\mathrm{m^3\,m^{-3}}$, $0.16\,\mathrm{m^3\,m^{-3}}$ and $0.14\,\mathrm{m^3\,m^{-3}}$ across the three consecutive growing seasons in 2010–2012 at elevation 4313 m, 4513 m and 4693 m, respectively ($p < 0.05$). The absolute differences of SWC between inside and outside OTCs ($-0.05\,\mathrm{m^3\,m^{-3}}$, $-0.04\,\mathrm{m^3\,m^{-3}}$ and $-0.05\,\mathrm{m^3\,m^{-3}}$ at elevation 4313 m, 4513 m and 4693 m, respectively) were close to the observations in an alpine meadow on the Tibetan Plateau (Rui et al., 2011). OTCs-induced increment in T_s and T_a and decrement in SWC were in line with previous studies which showed the warming and drying trends across the Tibetan Plateau (Xie et al., 2010; Zhang et al., 2013). Additionally, T_s and T_a both decreased with increasing elevation during the whole study period ($p < 0.05$). Precipitation increases with increasing altitude along the elevation gradient (Wang et al., 2013).

2.3 Ecosystem respiration (R_{eco}) measurement

A soil CO_2 flux system (LI-8100, LI-COR Biosciences, Lincoln, NE, USA) with an opaque survey chamber of 20 cm in diameter was used to measure R_{eco}. The measurement time was 90 s for each sampling. The R_{eco} was calculated based on CO_2 concentration in the opaque survey chamber during the measurement and this process was auto-completed by the LI-8100. One polyvinyl chloride (PVC) collar (20 cm in diameter and 5 cm in height) was inserted about 2 ~ 3 cm into the soil for each plot in 15 May 2010. Insertion of PVC collars into the soil can disturb soil and plant and then affect R_{eco} measurement. In order to reduce or even eliminate this effect, we started to measure R_{eco} on 6 June 2010. The opaque survey chamber was manually mounted on PVC collar in each plot for R_{eco}. The internal height of the opaque survey chamber is approximately 25 cm, thus the opaque survey chamber is high enough to enclose all the plants within it. R_{eco} was measured during the growing season (from June to September). Diurnal cycles of R_{eco} measurements were generated from 08:00 to 20:00 (Beijing Standard Time, BST) with a 2 h interval at each elevation in 2010–2012 (Fig. 1).

2.4 Soil sampling and analysis

Soil samples (0–20 cm depth) were collected (with a probe of 5.0 cm diameter) along the elevation gradient on 11 August 2012. For each of the three replicates, two soil subsamples were randomly sampled and composited into one soil sample at each plot. The soil samples were immediately stored in an icebox and then transferred to laboratory. Each composited soil sample was passed through a sieve (1 mm diameter) and any visible roots were picked out from the sieved soil. Then subsamples of the sieved soil were used to measure microbial biomass carbon (MBC) and dissolved organic carbon (DOC). Subsamples of the sieved soil were air-dried for the measurement of SOC. All the visible roots in the soil samples were washed, oven-dried at 65 °C for 48 h and then weighted. The oven-dried roots were belowground biomass (BGB).

MBC was determined using the chloroform fumigation-extraction method (Vance et al., 1987). Briefly, the fumigated and unfumigated soil samples (20 g) were both extracted using 80 mL 0.5 M K_2SO_4. Then K_2SO_4 extracts were filtered through 0.45 µm filter membrane. The extractable organic carbon in the K_2SO_4 extracts was analyzed on a Liqui TOC II elementar analyzer (Elementar Liqui TOC, Elementar Co., Hanau, Germany). The extractable carbon in the K_2SO_4 extracts was converted to MBC using the conversion factor of 0.45 (Fu et al., 2012b).

DOC was determined using the method of Jones and Willett (2006). Briefly, 20 g fresh soil samples were extracted using 100 mL distilled water and filtered through 0.45 µm filter membrane. The extractable organic carbon in the distilled water extracts was also analyzed on a Liqui TOC II elementar analyzer (Elementar Liqui TOC, Elementar Co., Hanau, Germany). SOC was determined using the potassium dichromate method (Walkley and Black, 1934).

2.5 Aboveground present biomass

A non-destructive approach was used to estimate aboveground present biomass (APB, g D.W. m^{-2}) (Klein et al., 2007). Canopy coverage (CC, %) and height (CH, cm) in a 50 cm × 50 cm subplot in the center of each plot were measured in August of 2010, 2011 and 2012 when maximum APB occurred. Maximum APB during the growing season can be treated as aboveground net primary production (ANPP) in the unclipped plots (Klein et al., 2007). Within each plot, the 50 cm × 50 cm subplot was divided into 10 cm × 10 cm sub-units. The same measurement was also conducted outside the treatment plots and then the aboveground plant parts were harvested, dried and weighed. A regression equation ($\text{APB} = -11.49 + 1.21\text{CC} + 3.75\text{CH}$, $R^2 = 0.73$, $p < 0.001$, $n = 90$) between APB and CC and CH was developed using the data collected from outside the treatment plots across the three alpine meadow sites along the elevation gradient.

2.6 Statistical analysis

Three-way analysis of variance (ANOVA) was used to assess the main and interactive effects of experimental warming, clipping and elevation on SOC, DOC, MBC and BGB. Repeated-measures ANOVA was performed to test effects of year, experimental warming and clipping on APB for each elevation. Repeated-measures ANOVA with elevation, experimental warming and clipping as the between-subject factors and with year as the within-subject factor for growing-season average R_{eco} was conducted (Table 2). Repeated-measures ANOVA was used to estimate the main and interactive effects of measuring date, experimental warming and clipping on diurnal average R_{eco} in 2010, 2011 and 2012, respectively for each elevation (Table 3). For each treatment, a stepwise multiple regression analysis was applied between diurnal average R_{eco} and T_s, T_a and SWC (Table 4), before which natural logarithm transformations were made for R_{eco} and SWC. The temperature sensitivity of R_{eco} was assessed by relating R_{eco} to T_s or T_a as follows for a specific treatment using all measuring data.

$$R_{\text{eco}} = ae^{bT} \qquad (1)$$

where T is T_s or T_a, a is the intercept of R_{eco} when temperature is zero, and b reflects the temperature sensitivity of R_{eco}. The b values were used to calculate the respiration quotient (Q_{10}), which could reflect the change of R_{eco} with a 10 °C increase in T_s or T_a.

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

T test was used to assess the significance of main and interactive effects of experimental warming and clipping on regression coefficient b (Zhou et al., 2006).

All the statistical tests were performed using the SPSS software (version 16.0; SPSS Inc., Chicago, IL).

3 Results

3.1 SOC, MBC, DOC and BGB

SOC increased significantly with increasing elevation ($F_{2,24} = 175.37$, $p < 0.001$). Although MBC, DOC and BGB at elevation 4693 m was significantly higher compared to elevation 4513 m and 4313 m, there were no significant differences between elevation 4313 m and 4513 m. Additionally, no other significant main and interactive effects on SOC, MBC, DOC and BGB were found.

No significant differences of SOC, MBC, DOC and BGB among NW + NCL, W + NCL, CL + NW and W + CL treatments were found (Fig. 2).

3.2 Aboveground present biomass

The responses of APB to experimental warming and clipping varied with year and elevation (Fig. 3). Averaged for the three years, experimental warming significantly decreased APB by 30.5 % at elevation 4313 m, but had little effects on APB at elevation 4513 m and 4693 m. Clipping consistently reduced APB by 50.0 %, 48.0 % and 19.0 % at elevation 4313 m, 4513 m and 4693 m across the three years, respectively ($p < 0.05$).

No significant difference of APB between elevation 4313 m and 4513 m was found, although they were both significantly lower than that of elevation 4693 m, irrespective of experimental warming, clipping and year effects.

3.3 Ecosystem respiration

The responses of growing-season average R_{eco} to experimental warming and clipping varied with elevation and year (Tables 2 and 3). Regardless of clipping effect, experimental warming significantly decreased growing-season average R_{eco} in 2010 by 36.5 % and 22.8 % at elevation 4313 m and 4513 m, respectively, while the decreases caused by experimental warming in 2011 (by 18.4 % for elevation 4313 m and by 5.69 % for elevation 4513 m) and 2012 (by 10.1 % for elevation 4313 m and by 5.68 % for elevation 4513 m) were not statistically significant. In contrast, experimental warming significantly increased growing-season average R_{eco} of elevation 4693 m by 12.2 % and 16.1 % in 2011 and 2012, respectively, whereas the increment (by 5.2 %) in 2010 was not statistically significant. On average, experimental warming significantly increased seasonal average R_{eco} by 11.3 % at elevation 4693 m, but had little effects on seasonal average R_{eco} at elevation 4313 m and 4513 m across the three consecutive growing seasons in 2010–2012.

For the three growing season averages, clipping significantly reduced seasonal average R_{eco} by 36.9 % and 31.6 % at elevation 4513 m and 4693 m, respectively, while had little effect on seasonal average R_{eco} at elevation 4313 m. In detail, growing-season average R_{eco} at elevation 4513 m and 4693 m was significantly reduced by 36.5 % and 24.1 %, 37.5 % and 32.1 % and 36.6 % and 37.2 % in 2010, 2011 and 2012, respectively. Clipping tended to decrease growing-season average R_{eco} by 2.3 %, 5.6 % and 12.4 % in 2010, 2011 and 2012 at elevation 4313 m, respectively, although these declines were not statistically significant.

The responses of diurnal average R_{eco} within one-growing-season to experimental warming and clipping varied with measuring date (Fig. 1, Table 3). Experimental warming significantly decreased diurnal average R_{eco} on 8, 9 and 2 out of the 22 measuring dates at elevation 4313 m, 4513 m and 4693 m, respectively. In contrast, experimental warming significantly increased diurnal average R_{eco} on 8 out of the 22 measuring dates at elevation 4693 m. Clipping significantly reduced diurnal average R_{eco} on all the 22 measuring dates at elevation 4513 m and 4693 m, respectively, but the response magnitudes differed.

No significant difference of R_{eco} between elevation 4313 m and 4513 m was found, although they were both significantly lower than that of elevation 4693 m, irrespective of experimental warming, clipping and year effects.

3.4 Temperature sensitivity

The Q_{10} values based on T_s in NW + NCL, W + NCL, CL + NW and W + CL treatments were 1.32, 1.39, 1.51 and 1.38 at elevation 4313 m, 1.39, 1.21, 1.68 and 1.26 at elevation 4513 m, 2.41, 1.67, 1.99 and 1.75 at elevation 4693 m, respectively. In contrast, the Q_{10} values based on T_a in NW + NCL, W + NCL, CL + NW and W + CL treatments were 1.57, 1.45, 1.68 and 1.46 at elevation 4313 m, 1.55, 1.23, 1.80 and 1.36 at elevation 4513 m and 2.27, 1.72, 2.16 and 1.63 at elevation 4693 m, respectively.

One-way ANOVA showed that elevation had significant effect on the regression coefficient b for the NW + NCL treatment ($F = 6.18$, $p < 0.05$ based on T_a; $F = 12.42$, $p < 0.05$ based on T_s). In detail, the regression coefficients b at elevation 4693 m was significant larger than that at elevation 4513 m and 4313 m, while there was no significant difference between elevation 4513 m and 4313 m. In other words, the Q_{10} at elevation 4693 m was higher in comparison with elevation 4513 m and 4313 m.

The main effect of experimental warming on the coefficient b was statistical significant for elevation 4513 m ($t = -2.91$, $p < 0.05$ based on T_a; $t = -2.37$, $p < 0.05$ based on T_s) and 4693 m ($t = -3.61$, $p < 0.05$ based on T_a; $t = -2.94$, $p < 0.05$ based on T_s), but not 4313 m ($t = -1.33$, $p > 0.05$ based on T_a; $t = -0.21$, $p > 0.05$ based on T_s). The main effect of clipping and its interaction with experimental warming had little effects on the coefficient b.

3.5 Relationships between R_{eco} and T_s, SWC, T_a, APB, ANPP, SOC, DOC, MBC, BGB

With the exception of SWC, T_s and T_a were excluded in the multiple regression analyses for NW + NCL, W + NCL, CL + NW and W + CL treatments at elevation 4313 m, W + NCL and W + CL treatments at elevation 4513 m and W + CL treatment at elevation 4693 m (Table 4). SWC explained more seasonal variation of R_{eco} in the multiple regression equations except the NW + NCL treatment at elevation 4693 m (Table 4).

Growing-season average R_{eco} increased with increasing SOC, DOC, MBC, BGB and ANPP along warming and clipping treatments and elevation (Figs. 4 and 5).

4 Discussion

4.1 Warming effect

Previous studies showed that warming exerted no influence on seasonal average R_{eco} in dry subarctic heath (Illeris et al., 2004) and temperate and alpine grasslands (Xia et al., 2009; Lin et al., 2011), while enhanced R_{eco} throughout growing season in Alaska and Arctic Tundra ecosystems (Welker et al., 1999; Hobbie and Chapin, 1998), and increased R_{eco} in alpine tundra and meadow early in growing season (Welker et al., 1999; Zhuang et al., 2010). Similarly, we also found variable warming effects on seasonal average R_{eco} among the three elevations (Tables 2 and 3), which was in line with our hypothesis. Therefore, warming had ecosystem-specific effects on R_{eco} (De Boeck et al., 2007; Oberbauer et al., 2007; Welker et al., 2004; Wu et al., 2011b).

The Q_{10} values of R_{eco} were larger than 1.0 at the three elevations, which implied warming should increase R_{eco}. However, experimental warming could not increase but even tend to decrease R_{eco} for the two lower elevations. Therefore, inconsistent with our hypothesis, temperature sensitivity of R_{eco} could not explain the variable responses of R_{eco} to warming among the three elevations.

There were similar dominant species at the three alpine meadow sites (Table 1), and there were no significant difference in species richness among the three sites (data not shown). Therefore, species change among the three sites could be not the most important factor controlling the different responses of R_{eco} to warming in this study.

In our study, experimental warming had fractional effects on SOC, MBC, DOC and BGB for the three sites and AGB for the two higher elevations, although SOC, MBC, DOC, BGB and AGB at elevation 4693 m were larger compared to elevation 4513 m and 4313 m. Therefore, soil organic carbon pools and plant biomass could be also not the dominant factor controlling the different warming effects on R_{eco}, at least in the short-term.

The relative contribution of water availability to seasonal variation of R_{eco} at the two lower elevations was larger than that of temperature for the NW + NCL treatment, whereas it showed the quite the contrary result at elevation 4693 m (Table 4). In addition, precipitation increased with increasing elevation, while temperature increased with decreasing elevation (Table 1). These findings implied that seasonal variation of R_{eco} was mainly controlled by water availability for the two relative warmer and drier sites under the untreated conditions, whereas the seasonal variation was mainly controlled by temperature for the one relative colder and wetter site. That is, the main control for the seasonal variation of R_{eco} was dependent on site-specific environmental temperature and water availability conditions.

The net effect of experimental warming on R_{eco} was determined by relative strengths of experimental warming-induced positive effect by enhancing temperature and negative effect by reducing water availability (Wu et al., 2011a; Liu et al., 2009). In our study, the positive effect was larger than the negative effect for elevation 4693 m, while the positive and negative effects had insignificant differences for elevation 4513 m and 4313 m.

Inconsistent with our hypothesis, our findings indicated that R_{eco} did not always have higher temperature sensitivity in colder environments (Kirschbaum, 1995; Wu et al., 2011a). Both temperature and water availability can affect the temperature sensitivity of R_{eco} (Lin et al., 2011; Wen et al., 2006) and it is hard to distinguish their effects (Xu and Qi, 2001). Since SOC, MBC, DOC, BGB and AGB had no significant responses to experimental warming, experimental warming-induced significant declines in Q_{10} at the two higher elevations could be mainly attributed to experimental warming-induced increment in temperature and decrement in soil water content (Lin et al., 2011; Zhou et al., 2006), at least in the short-term. These findings suggested that temperature sensitivity of R_{eco} could be also dependent on environmental temperature and water availability conditions.

In general, the variable experimental warming effects on R_{eco} were mainly dependent on environmental temperature and water availability conditions.

We observed a similar interannual variation for the responses of growing-season average R_{eco} to experimental warming along the elevation gradient. The decreased magnitude of R_{eco} caused by experimental warming at elevation 4313 m and 4513 m decreased with year, whereas the increased magnitude of R_{eco} at elevation 4693 m increased with year. This finding implied that warming probably had a lagging effect on R_{eco}, which in line with previous studies (Luo et al., 2001; Wan et al., 2005; Fu et al., 2012b).

4.2 Clipping effect

Many studies showed that clipping decreased R_{eco} and soil respiration (Shahzad et al., 2012; Bahn et al., 2008; Wan and Luo, 2003), whereas some studies found that clipping had little effect on soil respiration (Zhou et al., 2006). The different responses of soil respiration to clipping may be dependent on clipping intensity and frequency (Allaire et al., 2008). Clipping can decrease soil respiration by weakening assimilation supply from photosynthesis (Bahn et al., 2008; Wan and Luo, 2003) and slowing translocation of assimilation supply to rhizosphere (Bremer et al., 1998). In addition, clipping may reduce canopy respiration by decreasing aboveground biomass (Shahzad et al., 2012) and microbial respiration by decreasing microbial biomass (Zhang et al., 2005). In our study, we found that R_{eco} increased significantly with increasing MBC, DOC, BGB

(Fig. 4b–d) and APB (Fig. 5a). Meanwhile, clipping significantly reduced APB (Fig. 3), but had little effects on MBC, DOC and BGB (Fig. 2). Therefore, consistent with our hypothesis, clipping-induced consistent declines in seasonal average R_{eco} at the three alpine meadow sites may be mainly due to the removal of aboveground biomass.

4.3 Water availability

Recent studies have indicated that water availability plays a predominant role in regulating the response of ecosystem carbon flux to climate change in temperate grasslands (Liu et al., 2009; Niu et al., 2008), wet sedge Tundra (Huemmrich et al., 2010) and tallgrass prairie (Xu et al., 2012). Similarly, we also found that SWC was more important than T_s and T_a in regulating the seasonal variation of R_{eco} and that SWC regulated the response of R_{eco} to warming for the alpine meadow (Table 4). This phenomenon could be accounted by the following speculations. Firstly, the effect of photosynthetic substrate supply on soil respiration increased with increasing water availability (Yan et al., 2011). The seasonal variation of primary production was regulated by SWC (Fu et al., 2012a). R_{eco} increased significantly with increasing ANPP and APB (Fig. 5). Meanwhile, ANPP and APB increased with increasing SWC (Fig. 6). Secondly, SOC and its density both increased significantly with increasing SWC (Yang et al., 2008; Liu et al., 2012; Baumann et al., 2009). Similarly, we found that SOC was positively correlated with R_{eco} and SWC (Figs. 4a and 7a). Thirdly, microbial biomass responded quickly to change in SWC (Skopp et al., 1990). The response of MBC to elevated temperature and the seasonal variation of MBC were regulated by SWC (Liu et al., 2009; Fu et al., 2012b). The positive relationships between R_{eco}, MBC and SWC were found (Figs. 4b and 7b). Fourthly, SWC regulated the response of DOC to warming (Christ and David, 1996) and DOC was positively related to R_{eco} and SWC (Figs. 4c and 7c). Therefore, experimental warming-induced soil drying may suppress vegetation production, SOC, MBC and DOC, which in turn can suppress R_{eco} (Wu et al., 2011b; Liu et al., 2009; De Boeck et al., 2007). This supported our hypothesis that soil water content can regulate the warming effect on R_{eco}.

5 Conclusions

In summary, we found that the seasonal variations of R_{eco} were mainly correlated with soil water content in comparison with air and soil temperatures in the alpine meadow of Tibet. Experimental warming significantly increased seasonal average R_{eco} in one of the three alpine meadow sites (i.e. elevation 4693 m), whereas the decreased R_{eco} caused by experimental warming was not obvious for the alpine meadow at elevation 4313 m and 4513 m, this different responses could be mainly attributed to different temperature and water availability conditions among the three sites. This finding suggested that the future studies should consider the different responses of R_{eco} to warming among the alpine meadow on the Tibetan Plateau. Soil water content regulated the response of R_{eco} to warming by modulating soil carbon, root biomass and aboveground net primary production. Clipping consistently reduced seasonal average R_{eco} at the three alpine meadow sites, probably caused by reduced aboveground biomass. Additionally, obvious interactive effect between experimental warming and clipping on R_{eco} was found at elevation 4693 m in 2010. These results suggested that clipping may dampen experimental warming-induced positive effect on R_{eco} in the alpine meadow on the Tibetan Plateau.

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Table 1. Sites description.

Site	Site 1	Site 2	Site 3
Location	30°30′ N 91°04′ E	30°31′ N 91°04′ E	30°32′ N 91°03′ E
Elevation (m)	4313	4513	4693
Dominant species	*Stipa capillacea*, *Carex montis-everestii*, *Kobresia pygmaea*	*Stipa capillacea*, *Kobresia pygmaea*, *Carex montis-everestii*	*Kobresia pygmaea*
Canopy height (cm)	< 10	< 10	< 10
Vegetation coverage (%)	< 50	< 50	> 50
Air temperature (°C)[a]	10.24	9.53	8.23
Precipitation (m)[a]	255.25	282.87	341.43
Soil organic carbon (0–30 cm, $\mathrm{g\,kg^{-1}}$)	19.83 ± 0.36	24.04 ± 0.34	43.74 ± 0.60
Total nitrogen (0–30 cm, $\mathrm{g\,kg^{-1}}$)	2.12 ± 0.19	2.18 ± 0.18	3.32 ± 0.12

[a] Data were average temperature or total precipitation during the period from June to September.

Table 2. Repeated-measures analysis of variance for the main and interactive effects of year (Y), elevation (E), experimental warming (W) and clipping (CL) on growing-season average ecosystem respiration (R_{eco}) in the alpine meadow along an elevation gradient (4313–4693 m) ($n = 3$).

Model	d*f*	*F*	*p*
W	1, 24	1.96	0.17
CL	1, 24	50.16	< 0.001
E	2, 24	29.62	< 0.001
Y	2, 48	42.41	< 0.001
W × CL	1, 24	0.01	0.93
W × E	2, 24	5.50	< 0.05
CL × E	2, 24	8.10	< 0.01
W × Y	2, 48	7.57	< 0.01
CL × Y	2, 48	5.95	< 0.01
E × Y	4, 48	2.64	< 0.05
W × CL × E	2, 24	2.68	0.09
W × CL × Y	2, 48	0.44	0.65
W × E × Y	4, 48	0.46	0.77
CL × E × Y	4, 48	1.02	0.41
W × CL × E × Y	4, 48	0.26	0.90

Table 3. Repeated-measures analysis of variance for the main and their interactive effects of measuring date (D), experimental warming (W) and clipping (CL) on diurnal average ecosystem respiration (R_{eco}) in the three alpine meadows at elevation 4313 m, 4513 m and 4693 m during the growing season (from June to September) in 2010, 2011 and 2012, respectively ($n = 3$).

Model	2010				2011				2012			
	df	4313	4513	4693	df	4313	4513	4693	df	4313	4513	4693
W	1, 8	5.57^{a}	12.34^{b}	1.59	1, 8	4.64	0.53	5.50^{a}	1, 8	0.61	0.67	5.40^{a}
CL	1, 8	0.02	37.11^{c}	47.41^{c}	1, 8	0.37	32.88^{c}	61.06^{c}	1, 8	0.96	39.34^{c}	50.88^{c}
D	7, 56	22.83^{c}	114.09^{c}	128.78^{c}	6, 48	61.71^{c}	97.87^{c}	60.32^{c}	6, 48	122.60^{c}	148.85^{c}	45.76^{c}
W × CL	1, 8	0.58	0.00	5.95^{a}	1, 8	2.54	0.09	1.83	1, 8	0.78	0.02	4.60
W × D	7, 56	7.93^{c}	5.85^{b}	17.07^{c}	6, 48	2.54^{a}	7.69^{b}	0.69	6, 48	2.56^{a}	9.09^{b}	1.38
CL × D	7, 56	2.29^{a}	8.65^{c}	2.62^{a}	6, 48	1.67	8.04^{b}	4.41	6, 48	3.26^{b}	6.52^{b}	4.60^{a}
W × CL × D	7, 56	0.96	1.97	0.85	6, 48	3.02^{a}	1.71	0.51	6, 48	1.48	5.28^{a}	0.57

[a], [b] and [c] mean significant at 0.05, 0.01 and 0.001 level.

Table 4. Stepwise multiple linear regression analyses between diurnal mean ecosystem respiration (R_{eco}) and soil temperature at the depth of 5 cm (T_s), soil water content at the depth of 10 cm (SWC) and air temperature at the height of 15 cm above the ground (T_a), showing regression coefficient (Coef., mean ± SE), significance probability (p) and coefficient of determination (R^2) change. Natural logarithm transformations were made for R_{eco} and SWC before regression analysis. Diurnal mean T_s, SWC and T_a coincide with diurnal mean R_{eco}. All the 22 diurnal average data were used.

Elevation (m)	Factor	NW + NCL			W + NCL			CL + NW			W + CL		
		Coef.	p	R^2	Coef.	p	R^2	Coef.	p	R^2	Coef.	p	R^2
4313	Constant	1.86 ± 0.22	< 0.001		1.76 ± 0.16	< 0.001		1.76 ± 0.26	< 0.001		1.65 ± 0.23	< 0.001	
	SWC	0.39 ± 0.11	0.003	0.37	0.46 ± 0.07	< 0.001	0.72	0.42 ± 0.13	0.004	0.34	0.34 ± 0.09	0.001	0.45
4513	Constant	2.18 ± 0.32	< 0.001		2.54 ± 0.16	< 0.001		1.21 ± 0.26	< 0.001		1.90 ± 0.21	< 0.001	
	SWC	1.24 ± 0.17	< 0.001	0.67	0.82 ± 0.08	< 0.001	0.83	0.67 ± 0.09	< 0.001	0.66	0.71 ± 0.10	< 0.001	0.71
	T_a							0.05 ± 0.02	0.026	0.08			
	T_s	0.06 ± 0.02	0.021	0.08									
4693	Constant	1.20 ± 0.23	< 0.001		1.62 ± 0.27	< 0.001		1.44 ± 0.26	< 0.001		1.99 ± 0.23	< 0.001	
	SWC	0.89 ± 0.13	< 0.001	0.22	0.50 ± 0.09	< 0.001	0.51	0.69 ± 0.17	0.001	0.24	0.46 ± 0.11	< 0.001	0.47
	T_a							0.06 ± 0.02	0.01	0.23			
	T_s	0.13 ± 0.02	< 0.001	0.49	0.06 ± 0.03	0.018	0.13						

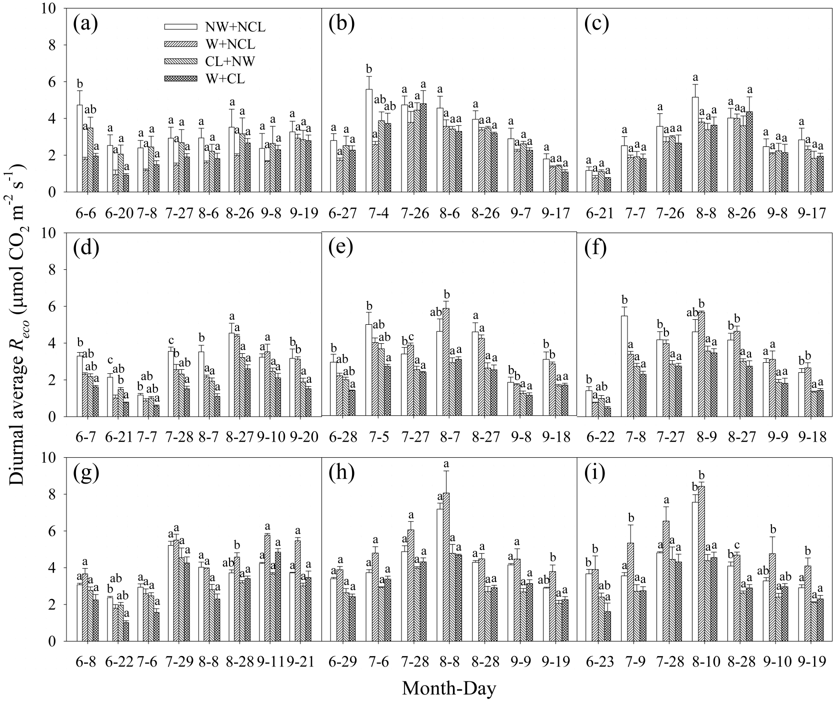

Fig. 1. Diurnal average ecosystem respiration (R_{eco}, µmol $CO_2\,m^{-2}\,s^{-1}$) for the no warming and no clipping (NW + NCL), warming and no clipping (W + NCL), clipping and no warming (CL + NW) and warming plus clipping (W + CL) treatments in the three alpine meadow sites at elevation 4313 m **(a, b, c)**, 4513 m **(d, e, f)** and 4693 m **(g, h, i)** during the three consecutive growing seasons in 2010 **(a, d, g)**, 2011 **(b, e, h)** and 2012 **(c, f, i)**, respectively. Error bars represent standard error ($n = 3$). Different letters mean statistical significant at $p < 0.05$.

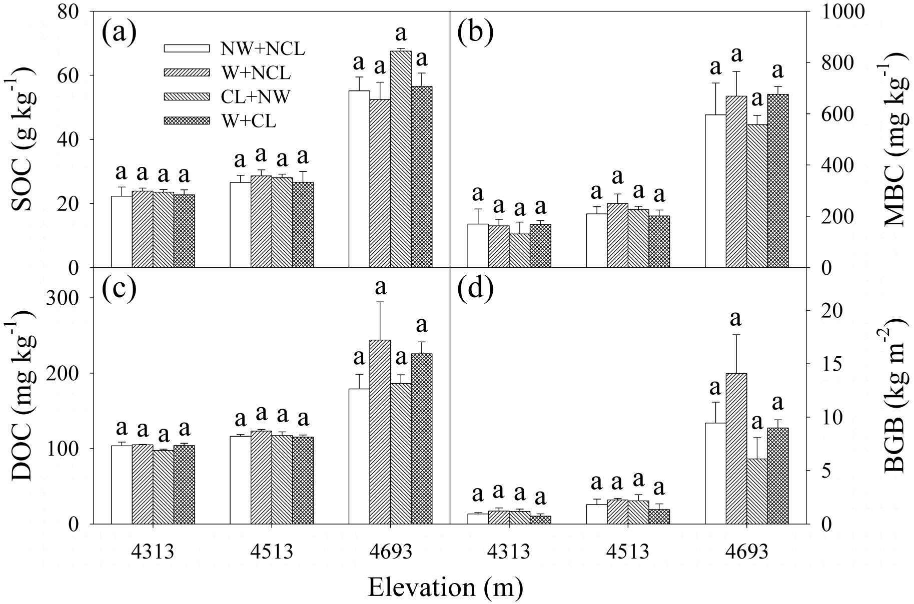

Fig. 2. Topsoil (0–20 cm) soil organic carbon (SOC, $\mathrm{g\,kg^{-1}}$) **(a)**, microbial biomass carbon (MBC, $\mathrm{mg\,kg^{-1}}$) **(b)**, dissolved organic carbon (DOC, $\mathrm{mg\,kg^{-1}}$) **(c)** and belowground biomass (BGB, $\mathrm{kg\,m^{-2}}$) **(d)** in the three alpine meadow sites along an elevation gradient (4313–4693 m) in August 2012. Error bars represent standard error ($n = 3$). Different letters mean statistical significant at $p < 0.05$.

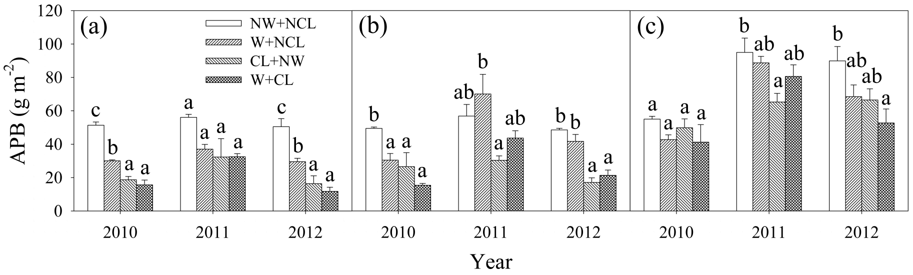

Fig. 3. Aboveground present biomass (APB, g m^{-2}) in the three alpine meadow sites at elevation 4313 m **(a)**, 4513 m **(b)** and 4693 m **(c)** in August 2010–2012. Error bars represent standard error ($n = 3$). Different letters mean statistical significant at $p < 0.05$.

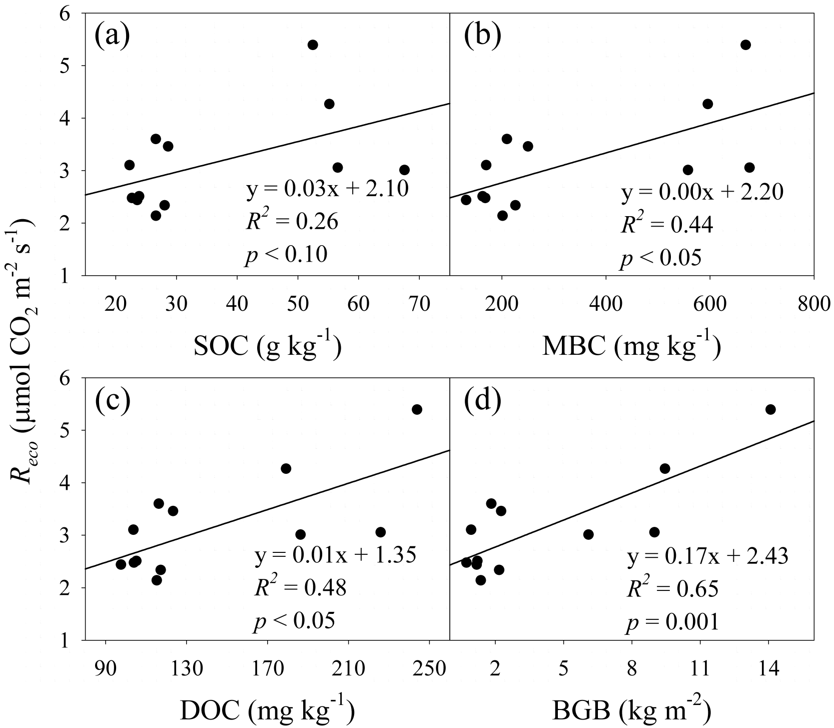

Fig. 4. Relationships between growing-season average ecosystem respiration (R_{eco}, μmol $\text{CO}_2\,\text{m}^{-2}\,\text{s}^{-1}$) and soil organic carbon (SOC, $\text{g}\,\text{kg}^{-1}$) **(a)**; R_{eco} and microbial biomass carbon (MBC, $\text{mg}\,\text{kg}^{-1}$) **(b)**; R_{eco} and dissolved organic carbon (DOC, $\text{mg}\,\text{kg}^{-1}$) **(c)** and R_{eco} and belowground biomass (BGB, $\text{kg}\,\text{m}^{-2}$) **(d)** in the alpine meadow along an elevation gradient (4313–4693 m) in 2012.

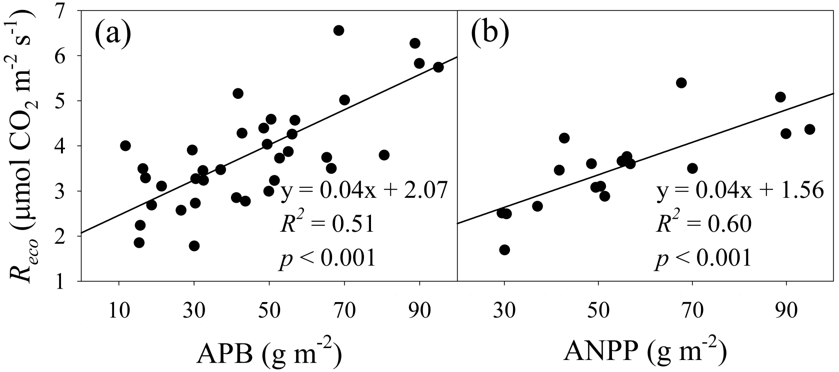

Fig. 5. Relationships between monthly average ecosystem respiration (R_{eco}, µmol CO$_2$ m^{-2} s^{-1}) in August and aboveground present biomass (APB, g m^{-2}) **(a)**; and growing-season average R_{eco} and aboveground net primary production (ANPP, g m^{-2}) in the unclipped plots **(b)** in the alpine meadow along an elevation gradient (4313–4693 m).

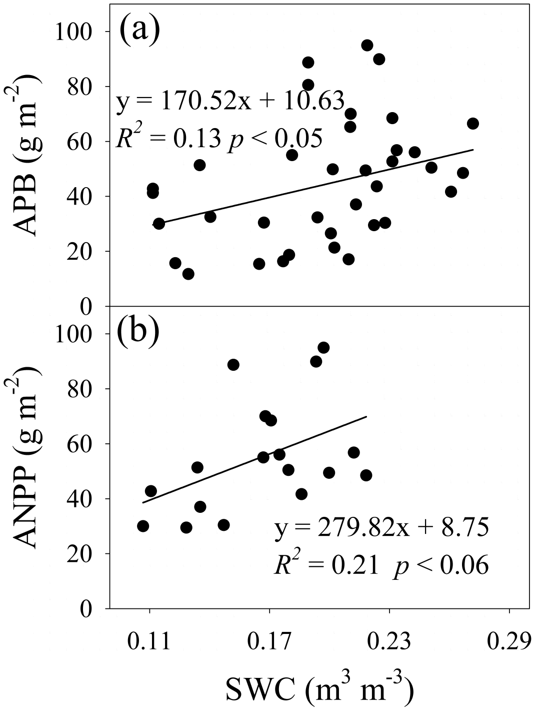

Fig. 6. Relationships between aboveground present biomass (APB, $\mathrm{g\,m^{-2}}$) and monthly average soil water content (SWC, $\mathrm{m^3\,m^{-3}}$) in August **(a)** and aboveground net primary production (ANPP, $\mathrm{g\,m^{-2}}$) in the unclipped plots and growing-season average SWC **(b)** in the alpine meadow along an elevation gradient (4313–4693 m).

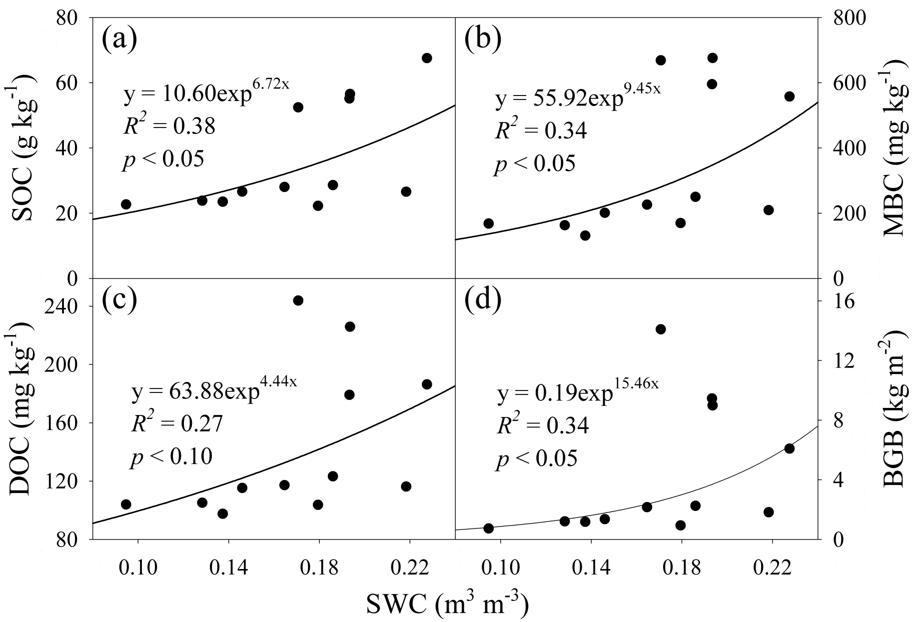

Fig. 7. Relationships between soil organic carbon (SOC, $\mathrm{g\,kg^{-1}}$) and growing-season average soil water content (SWC, $\mathrm{m^3\,m^{-3}}$) **(a)**; microbial biomass carbon (MBC, $\mathrm{mg\,kg^{-1}}$) and growing-season average SWC **(b)**; dissolved organic carbon (DOC, $\mathrm{mg\,kg^{-1}}$) and growing-season average SWC **(c)** and belowground biomass (BGB, $\mathrm{kg\,m^{-2}}$) and growing-season average SWC in 2012.