



Differential responses of ecosystem respiration components to experimental warming in a meadow grassland on the Tibetan Plateau



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ABSTRACT

Global warming is anticipated to have profound effects on terrestrial carbon fluxes and thus feed backs to future climate change. Ecosystem respiration (R_{eco}) is one of the dominant components of biosphere CO_2 fluxes, but the effects of warming on R_{eco} are still unclear. A field warming experiment using open top chambers (OTCs) was conducted in a meadow grassland on the Tibetan Plateau to study the effects of warming on the components of R_{eco} . Warming significantly enhanced above-ground plant respiration (R_{agb}) and total autotrophic plant respiration (R_{plant}) by 28.7% and 19.9%, respectively, but reduced heterotrophic respiration (R_{h}) by 10.4%. These different responses resulted in the insensitive responses of R_{eco} and soil respiration (R_{s}) to the experimental warming. The warming treatment also increased $R_{\text{plant}}/R_{\text{eco}}$ and $R_{\text{agb}}/R_{\text{eco}}$ by 8.4% and 17.3%, respectively, while decreasing $R_{\text{h}}/R_{\text{eco}}$ by 19.0%, suggesting that warming could eventually cause R_{eco} to be dominated by R_{plant} . Enhancements in R_{plant} and R_{agb} were related to the warming-induced increases in aboveground biomass (AGB) while reduced R_{h} was closely coupled with warming-induced decrease of microbial biomass carbon. Our results highlight that the differential responses of the components of R_{eco} to different environmental physics under warming scenarios should be taken into consideration to project the future carbon-climate feed backs.

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1. Introduction

The global mean air temperature has increased continuously since the industrial revolution (IPCC, 2014), and the rising temperatures can impact ecosystem CO_2 exchanges, potentially causing both positive and negative feed backs to future climates (Brient and

Bony, 2013; Luo, 2007). Ecosystem respiration (R_{eco}) is one of the largest terrestrial carbon fluxes, and thus small fluctuations in R_{eco} can lead to significant changes in atmospheric CO_2 concentration (Luo, 2007). Results from both modeling and field observations suggest that the current annual variations in atmospheric CO_2 are closely related to climate-induced changes in R_{eco} (Cox et al., 2000; Kato et al., 2004; Luo, 2007; Niu et al., 2013). Recent meta-analyses have shown that warming significantly increased R_{eco} (Lu et al., 2013; Wang et al., 2014), but the responses of R_{eco} to warming in individual studies have been highly variable. For example, warming significantly increased R_{eco} in a tall grass prairie in the USA (Niu et al., 2013), had no effect on R_{eco} in a temperate grassland (Xia et al., 2009), and a negative effect in an alpine meadow on the Tibetan Plateau (Fu et al., 2013). Such inconsistent responses in R_{eco} might be largely related to the differential responses of autotrophic plant respiration (R_{plant}) versus heterotrophic respiration (R_{h}) because R_{eco} responds as

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the combination of R_{plant} and R_{h} (Luo and Zhou, 2006; Pries et al., 2013). Therefore, understanding how R_{eco} and its components respond to climatic change is critically important for predicting the carbon-climate feed backs over regional to global scales.

The effects of warming on R_{eco} are driven by its components. R_{plant} derives from both above-ground plant (R_{agb}) and below-ground root (R_{bgb}) respiration while R_{h} mainly results from the decomposition of litter and soil organic matter (Luo and Zhou, 2006). However, previous studies on the responses of the components of R_{eco} to warming were highly contrasting. For example, experimental warming increased R_{h} , but not R_{bgb} in a prairie dominated by winter annual grass; this was attributed to the decreased plant productivity and possibly changes in the microbial community (Li et al., 2013). Results from a tall grass prairie ecosystem, in contrast, showed that both R_{h} and R_{bgb} were significantly enhanced by experimental warming likely due to a longer growing season and increased above-ground biomass (Zhou et al., 2007). Studies using a deconvolution method indicated that warming decreased both R_{bgb} and R_{h} largely as a result of decreases in canopy greenness and plant biomass (Zhou et al., 2010). In any case, there remains a lack of information about the underlying mechanisms responsible for the changes in the components of R_{eco} , and this has led to limits in our understanding of how R_{eco} responds to climate warming at present and what the implications of these relationships hold for the future.

Experimental warming can influence R_{eco} and the components of R_{eco} through both direct and indirect mechanisms. Elevated temperatures can directly increase plant growth and R_{plant} , particularly in areas like the cold Tibetan Plateau (Kato et al., 2004; Lin et al., 2011). Similarly, litter and soil organic matter decomposition can be stimulated directly by experimental warming, resulting in positive responses of soil respiration (R_{s}) and R_{h} to warming (Chen et al., 2015a; Lu et al., 2013; Luo, 2007). Concurrently, there is also evidence that warming has profound indirect effects on the components of R_{eco} by decreasing soil moisture or microbial biomass carbon (MBC) (Frey et al., 2008; Lin et al., 2011; Moyano et al., 2013; Suseela et al., 2012; Xu et al., 2012). Furthermore, the mechanisms involved in warming responses vary among the components of R_{eco} ; for example, studies have shown that R_{plant} is closely coupled with plant productivity, photosynthesis and soil temperature (Li et al., 2013; Lin et al., 2011), while R_{h} can respond to warming by depletion of MBC, labile carbon, or especially soil moisture (Heskel et al., 2014; McDaniel et al., 2014; Tucker et al., 2013). Most of the current Earth system models suggest that terrestrial ecosystems would show a net carbon loss in response to climate warming and in so doing possibly exacerbate the increases in air temperature (Friedlingstein et al., 2006; Luo, 2007). Nonetheless, the magnitudes of these feed backs are not well understood, mainly due to the complex mechanisms involved in the components of R_{eco} .

Located in the central Asia, the Tibetan plateau is regarded as the highest unique terrestrial ecosystem in the world. The alpine meadow grassland is one of the most widespread vegetation types on the Plateau, covering an area of $\sim 1.2 \times 10^6$ km² and accounting for about half of its land area (Hu et al., 2004). Low temperatures are the primary factor limiting both plant growth and the decomposition of litter and soil organic matter. The Tibetan Plateau also contains large stores of soil carbon, which prompts research into the response of ecosystem carbon exchanges to rising temperature. Moreover, the projected increase in surface air temperature on the Plateau is higher than the global average (IPCC, 2014), and if this occurs, rendering the ecosystems more vulnerable and sensitive.

In this study, a field-manipulative warming experiment was conducted by using open top chambers (OTCs). In light of previous observations and modeling results, this study tested the following hypotheses: (1) warming would have asymmetrical effects on the components of R_{eco} and (2) R_{eco} and its components would be

controlled by warming-induced changes on both biotic and abiotic factors, (2) warming may have no effect on R_{eco} if the responses of R_{plant} and R_{h} counteract with each other, (3) R_{eco} and its components could be controlled by different factors as experimental warming has different effects on various biotic and abiotic factors.

2. Measurements

2.1. Study site

This study was conducted at the Haibei Grassland Ecological Monitoring Station, which is operated by the China Meteorological Administration in Haibei Prefecture, Qinghai Province, China (100°51' E, 36°57' N, 3140 m). Located in a remote part of Eurasia, the study area has a typical plateau continental climate. Data collected at the station show that the mean annual precipitation from 1995 to 2013 was 408.45 mm, the annual average air temperature was 1.34 °C, and the monthly mean air temperature ranged from –23.35 °C in January to 22.88 °C in July. The soil pH was 7.77, and soil bulk density was 0.95 g cm⁻³. The soil is a sandy loam, and it is classified as mountain brown based on the Chinese soil classification. Vegetation is typical of a meadow grassland, and it is dominated by *Stipa sareptana* var. *krylovii*, *Stipa purpurea*, *Koeleria cristata*, *Poa crymophila*, *Kobresia humilis*, *Artemisia scoparia*, *Aster tataricus*, *Medicago ruthenica*, etc. More detailed and longer-term information about the study site can be found in Chen et al. (2015b) and Chen et al. (2016).

2.2. Experimental design

Open-top chambers (OTCs) were used as passive warming devices which were modified from the methods developed by the International Tundra Experiment (Marion et al., 1997). The OTCs used in the current study were similar to those described in other studies (Dabros and Fyles, 2010; De Frenne et al., 2010). The OTCs were made of 6 mm thick solar transmitting material; they were conical in shape, 40 cm in height, and covered an area of 2.01 m² at the ground.

The study site (200 m × 400 m) was selected in 2008, and after selection, it was fenced to provide a relatively stable environment. Before fencing, it was freely grazed as winter pasture, but after fencing all livestock grazing was excluded. There were 10 m wide buffer zones along the four sides of the study site. We divided the study site into 6 replicate grids (about 180 m × 60 m for each), and each of these grids was divided into two subgrids (about 90 m × 60 m for each), one used as a control and the other one for the experimental warming treatment.

In August 2010, 6 OTCs were installed in six randomly-selected warming subgrids, and the other six subgrids were used as controls. Aluminum frames (0.5 m for each side) were inserted 2–3 cm into the soil to provide a flat base for R_{eco} measurements in both the control and warming subgrids. Polyvinylchloride (PVC) collars (5 cm in height and 20 cm in internal diameter) were inserted to depths of 2–3 cm adjacent to the aluminum frames for R_{s} measurements. Another kind of PVC collars (70 cm in height and 20 cm in internal diameter) were also permanently inserted into soil adjacent to the aluminum frames for R_{h} measurements (Li et al., 2013; Zhou et al., 2007). Previous root exclusion studies have shown that 70 cm PVC collars were deep enough to exclude most living roots in grassland ecosystems (Zhou et al., 2007). These OTCs remained in place for the entire length of the experiment.

2.3. Measurements and calculations of respiration

Measurements of R_{eco} were made twice each month from April to October over periods of 24 h at 3-h intervals. For this

procedure, we first measured R_{eco} with a cubic 0.125 m³ opaque chamber (0.5 m on each side) attached to an infrared gas analyzer (LI-8100, LI-COR, Inc., Lincoln, NE, USA) that covered all the vegetation within the aluminum frames. Two small fans were used to mix the air inside the chamber during the measurements. Previous studies reported that this static-chamber method can be successfully used to measure CO₂ fluxes in grassland ecosystems (Xia et al., 2009).

Consecutive recordings of CO₂ concentrations were taken during 120 s periods after steady-state conditions were achieved (usually, it takes another 10–30 s before the measurements). Increases in air temperature within the chamber during the measurement intervals were less than 0.2 °C. The build ups or draw downs of CO₂ were not enough to significantly alter stomatal conductance, canopy photosynthesis, or respiration (Niu et al., 2008; Xia et al., 2009).

R_s and R_h were also measured twice each month over periods of 24 h at 3-h intervals. For this, all living plants inside the PVC collars were cut to the ground at least one day before the measurements to eliminate the effects of plant respiration (Zhou et al., 2007), but the plant cuttings were left in the collars to decompose. The 70 cm PVC collars cut off old plant roots and prevented new ones from growing, and thus respiration inside these collars represented R_h (Zhou et al., 2007). A soil CO₂ flux chamber attached to an infrared gas analyzer (LI-8100, LI-COR, Inc., Lincoln, NE, USA) was placed on each collar for the measurements of R_s and R_h , and then the chamber was moved to the next collar. R_{agb} was calculated as the difference between R_{eco} and R_s ($R_{\text{agb}} = R_{\text{eco}} - R_s$), and R_{bgb} was calculated as the difference between R_s and R_h ($R_{\text{bgb}} = R_s - R_h$). R_{plant} was the sum of R_{agb} and R_{bgb} ($R_{\text{plant}} = R_{\text{agb}} + R_{\text{bgb}}$).

2.4. Soil sampling and microbial biomass carbon

Soil samples were collected from all 12 subgrids on four occasions 20 June, 27 July, 31 August and 14 October, all in 2013. In each subgrid, soil samples (0–10 cm depth) were collected with the use of a soil auger (4 cm in diameter) after removal of all surface litter, and then all visible plant materials and large stones were manually removed from the collected soil samples. The soil samples were then packed into a portable refrigerated box and immediately transported to the laboratory where they were stored at 4 °C prior to analysis.

Soil MBC was measured by the chloroform fumigation–extraction method (Brookes et al., 1985). Briefly, a 10 g aliquot of moist soil was fumigated with chloroform for 24 h and extracted with 0.5 M K₂SO₄ in an end-to-end shaker for 1 h. A second 10 g moist soil aliquot was directly extracted as above, but this aliquot was not fumigated. The amounts of total carbon in both the fumigated and un-fumigated soil extracts were determined using a TOC analyzer (Multi N/C 3100, Analytik Jena, Germany). To account for incomplete extractions, we used an extraction efficiency factor of 0.45 (Brookes et al., 1985). A third 10 g soil aliquot was oven-dried at 105 °C for 48 h for soil moisture determinations. The MBC concentrations were converted to a dry mass basis (mg kg⁻¹) using the soil moisture results. Seasonal MBC were measured only in 2013.

2.5. Plant biomass

A non-destructive sampling method was used to estimate AGB for both the control and warming treatments using procedures similar to those of (Klein et al., 2007; Wang et al., 2012). Briefly, we sampled three quadrats in each of control subgrids by using a frame (1 m × 1 m) divided into 400 equally distributed squares (5 cm × 5 cm) for each year of warming. Before clipping, the vegetative coverage and heights were

recorded. After clipping, all aboveground plant matter was oven dried at 65 °C for 72 h before being weighed. We then constructed regression relationships between the coverage, height and dry weight biomass ($\text{AGB} = -26.236 + 2.242 C + 7.216 H$, $n = 54$, $R^2 = 0.947$, $p < 0.001$, where C and H stand for the averaged coverage and height, respectively) to estimate AGB both for the control and warming groups. This method has been successfully used in many previous studies (Harte and Shaw, 1995; Klein et al., 2007; Wang et al., 2012). BGB was measured by first collecting six replicate soil samples (4 cm in diameter) from depths of 0–40 cm and then picking, washing, oven drying (65 °C for 72 h), and weighing the roots.

2.6. Soil temperature and water content

Soil temperature and soil moisture were recorded with the use of HOBO data loggers (Onset Computer Company, Pocasset, MA, USA) at a soil depth of 10 cm. Soil temperature was measured using a thermocouple probe, and soil volumetric water content was measured using gypsum cast around two concentric stainless-steel electrodes. Data loggers recorded averaged soil temperature and soil moisture every 5 min during the entire experiment.

2.7. Data analysis

Daily, monthly and annual mean values were calculated from the diurnal measurements for each replicate (Xia et al., 2009). Two-way analyses of variance (two-way ANOVAs) were used to examine the effects of warming, year, and their interactive effects on soil temperature, soil moisture, R_{eco} , the components of R_{eco} , and the contributions of each component to R_{eco} . For the seasonal variations in each year, repeated measures ANOVAs were used to examine the effects of sampling date, warming, and their interactive effects on soil temperature, soil moisture, R_{eco} , the components of R_{eco} , and the contributions of each component to R_{eco} . Paired-*T* test was adopted to compare the difference of annual mean values of AGB and BGB in each year, and the MBC in each month in 2013 for the paired control and warming treatments. Significant differences were evaluated at the level $p < 0.05$.

Exponential and linear regression analyses were used to determine whether significant relationships existed between R_{eco} and the components of R_{eco} versus both soil temperature and moisture. Multiple regression analysis was used to evaluate the seasonal variations of soil temperature, soil moisture and MBC on R_{eco} and its components using the data in 2013. Multiple regression analysis also was used to evaluate the annual variations of AGB, BGB, soil temperature and soil moisture on R_{eco} and the components of R_{eco} across the whole three experimental years.

3. Results

3.1. Variations in microclimate and plant productivity

Precipitation showed one annual peak, with higher values during the growing season (April–October) compared with non-growing season (Fig. S1): the precipitation during the growing season accounted for 95.6%, 95.0% and 94.8% of the total annual precipitation of 447.30, 471.20 and 454.80 mm in 2011, 2012 and 2013, respectively. Air temperature also showed a single annual peak with the highest temperatures in July. The mean growing season air temperatures were 8.79, 9.04 and 9.67 °C in 2011, 2012 and 2013, respectively (Table 1).

Deployment of the OTCs resulted in increases of 1.03 °C in the average soil temperature at 10 cm depth during the growing seasons, and the experimental warming also led to decreases in soil

Table 1
Annual and growing season air temperature (AT), precipitation (Ppt), soil temperature (ST) and soil moisture (SM). Δ ST: soil temperature from OTC – soil temperature from control; Δ SM: soil moisture from OTC – soil moisture from control. Data presented are means \pm stand errors for six replicates. ** indicates significant difference at $p < 0.001$. Detailed seasonal variations can be found in figures S1 and S2.

Year	Annual			Growing season			
	AT ($^{\circ}$ C)	Ppt (mm)	ST ($^{\circ}$ C)	AT ($^{\circ}$ C)	Ppt (mm)	Δ ST ($^{\circ}$ C)	Δ SM (%)
2011	1.47	447.30	13.44	8.79	427.70	$0.99 \pm 0.01^{**}$	$-4.3 \pm 0.10^{**}$
2012	1.42	471.20	13.38	9.04	447.70	$1.06 \pm 0.02^{**}$	$-3.3 \pm 0.10^{**}$
2013	2.02	454.80	12.77	9.67	431.30	$1.03 \pm 0.01^{**}$	$-3.5 \pm 0.10^{**}$
Mean	1.64	457.77	13.20	9.17	435.57	$1.03 \pm 0.02^{**}$	$-3.7 \pm 0.17^{**}$

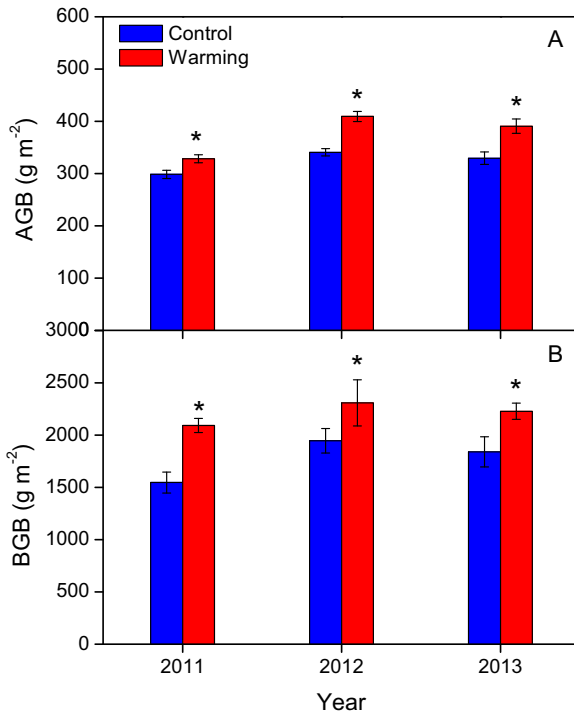


Fig. 1. Warming effects on above-ground biomass (A) and below-ground biomass (B) in the three experimental warming years. Data are arithmetic means \pm stand errors for six replicates. Asterisks indicate significant difference at $p < 0.05$.

moisture (Fig. S2). Compared with the control subgrids, OTCs significantly increased soil temperature by 0.99 ± 0.01 $^{\circ}$ C, 1.06 ± 0.02 $^{\circ}$ C and 1.03 ± 0.01 $^{\circ}$ C in 2011, 2012 and 2013, respectively ($p < 0.001$). There was no significant effect of year or interactive effect of warming and year on soil temperature ($p = 0.91$).

In contrast to soil temperature, soil moisture exhibited pronounced year-to-year variability ($p < 0.001$), with the highest water content in 2012 and lowest water content in 2013 (Fig. S2). The OTCs significantly reduced the soil moisture by $4.3 \pm 0.1\%$, $3.3 \pm 0.1\%$ and $3.5 \pm 0.1\%$ in 2011, 2012 and 2013, respectively ($p < 0.001$). No significant interactive effect of warming and year was found for soil moisture ($p = 0.117$).

The experimental warming significantly increased both AGB and BGB (Fig. 1). Across the 3-years of experimental warming, the average increases for AGB and BGB were 17.4% and 24.3%, respectively. The warming-induced increases in AGB were 12.2%, 20.3% and 19.1% in 2011, 2012 and 2013, respectively, while the corresponding increases in BGB were 35.3%, 18.6% and 21.1%.

3.2. Warming effects on ecosystem respiration and its components

Overall, experimental treatment had no significant effects on R_{eco} or R_s (Table 2), but it significantly increased R_{agb} and R_{plant} by

Table 2

Results (F values) of two-way analysis of variance: effects of warming (W), year (Y) and their interactive effects ($Y \times W$) on ecosystem respiration and respiration components. ** indicates significant difference at $p < 0.001$, and * indicates significant difference at $p < 0.05$. See Fig. 2 for more abbreviations.

	R_{eco}	R_s	R_h	R_{plant}	R_{agb}	R_{bgb}
W	3.273	0.567	4.376*	8.740*	14.503**	0.311
Y	20.880*	23.368**	32.028**	30.962**	15.810**	25.198**
$Y \times W$	1.003	0.433	0.054	2.522	1.87	1.481

Table 3

F values for repeated measures analysis of variance for warming (W), measuring date (D) and their interactive effects ($D \times W$) on ecosystem respiration and its components from 2011 to 2013. ** indicates significant difference at $p < 0.001$ and * indicates significant difference at $p < 0.05$. See Fig. 2 for abbreviations.

Effect	2011					
	R_{eco}	R_s	R_h	R_{plant}	R_{agb}	R_{bgb}
W	1.467	0.160	0.160	3.610	46.013**	0.753
D	46.610**	26.180**	0.391	0.753	0.912	0.912
$D \times W$	0.138	0.391	0.912	0.912	0.912	0.912
Effect	2012					
	R_{eco}	R_s	R_h	R_{plant}	R_{agb}	R_{bgb}
W	7.141*	0.559	1.100	17.911*	20.016**	6.258*
D	71.119**	56.325**	57.201**	64.579**	65.075**	32.957**
$D \times W$	0.172	0.753	0.411	0.816	0.913	0.912
Effect	2013					
	R_{eco}	R_s	R_h	R_{plant}	R_{agb}	R_{bgb}
W	0.241	4.606	8.937*	1.380	3.029	0.259
D	37.100**	23.491**	37.617**	25.970**	26.164**	12.191**
$D \times W$	0.208	1.061	7.543*	0.424	1.187	0.466

28.7% and 19.9% over the three years, respectively, and decreased R_h by 10.4%. No significant treatment effects were found for R_{bgb} (Figs. 2 and 4). There were significant year effects for R_{eco} and all the components of R_{eco} , but no significant interactive effects of warming versus year were found for R_{eco} and all the components of R_{eco} (Table 2).

When analyzed in each year, warming significantly increased R_{eco} only in 2012 ($p < 0.001$), and no significant warming effects on R_s were found in any of the three experimental years (Table 3). Warming also significantly decreased R_h in 2013 by 12.9% but increased R_{agb} , R_{bgb} and R_{plant} in 2012 by 38.6%, 12.8% and 28.5%, respectively. In addition, there were significant effects of measurement date for R_{eco} and all the components of R_{eco} , but no significant interactive effects between warming and measurement date were found apart from the significant interactive effects of warming and measurement date for R_h in 2013 (Table 3).

3.3. Warming effects on the contributions of ecosystem respiration components

The annual mean R_h/R_{eco} , R_s/R_{eco} and R_h/R_s ratios of both control and experimental warming treatments varied from 25.0% to

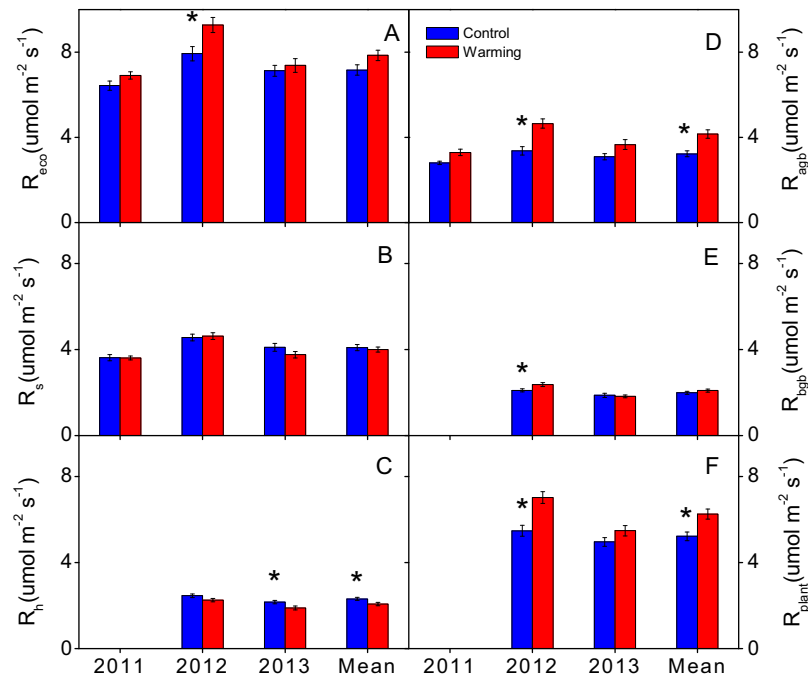


Fig. 2. Annual and mean variations of ecosystem respiration (R_{eco} , A), soil respiration (R_s , B), heterotrophic respiration (R_h , C), aboveground plant respiration (R_{agb} , D), belowground plant respiration (R_{bgb} , E) and total autotrophic respiration (R_{plant} , F) for both control and warming treatments. Data are arithmetic means \pm stand errors for six replicates. Asterisks indicate significant difference at $p < 0.05$.

33.4%, 50.6% to 59.0% and 49.8% to 56.8%, respectively, and warming significantly decreased these ratios by 19.0%, 10.8% and 7.5%, respectively. When analyzed in each year, warming significantly decreased R_h/R_{eco} , R_s/R_{eco} and R_h/R_s by 25.1% and 16.3%, 14.2% and 11.3%, and 12.3% and 5.7% in 2012 and 2013, respectively, but it had no effect on R_s/R_{eco} in 2011 (R_h was not measured in 2011) (Fig. 3).

Annual averages for R_{plant}/R_{eco} , R_{agb}/R_{eco} and R_{bgb}/R_{eco} of both control and experimental warming ranged from 66.6% to 73.9%, 41.0% to 49.4% and 25.6% to 27.6%, respectively. In contrast to R_h/R_{eco} and R_s/R_{eco} , which both decreased following the experimental manipulations, warming significantly increased R_{plant}/R_{eco} by 8.4% and R_{agb}/R_{eco} by 17.3%, respectively, but it had no effect on R_{bgb}/R_{eco} . The annual average R_{plant}/R_{eco} ratio of both control

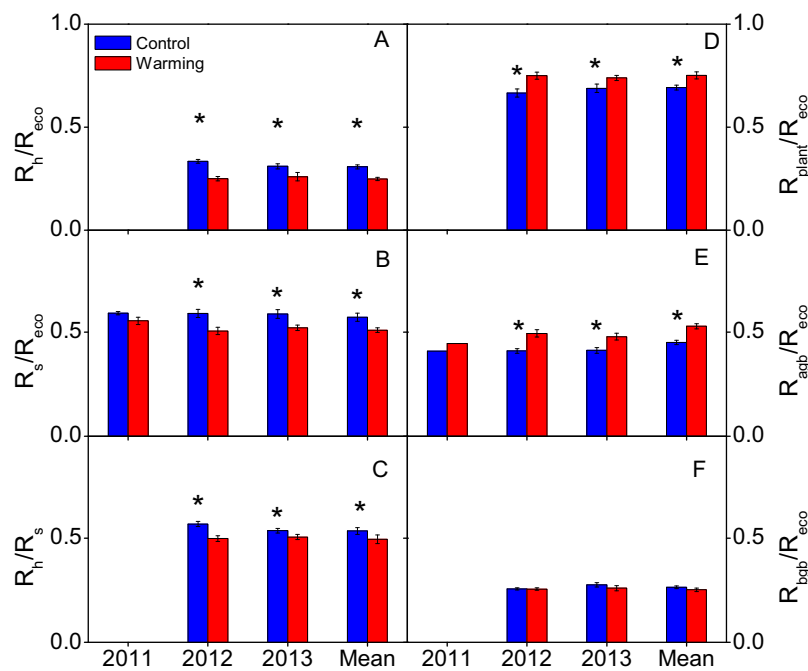


Fig. 3. Annual and mean contributions of heterotrophic respiration to ecosystem respiration (R_h/R_{eco} , A), soil respiration to ecosystem respiration (R_s/R_{eco} , B), heterotrophic respiration to soil respiration (R_h/R_s , C), total autotrophic respiration to ecosystem respiration (R_{plant}/R_{eco} , D), above-ground plant respiration to ecosystem respiration (R_{agb}/R_{eco} , E) and below-ground plant respiration to ecosystem respiration (R_{bgb}/R_{eco} , F) in both control and warming treatments. Data are arithmetic means \pm stand errors for six replicates. Asterisks indicate significant difference at $p < 0.05$.

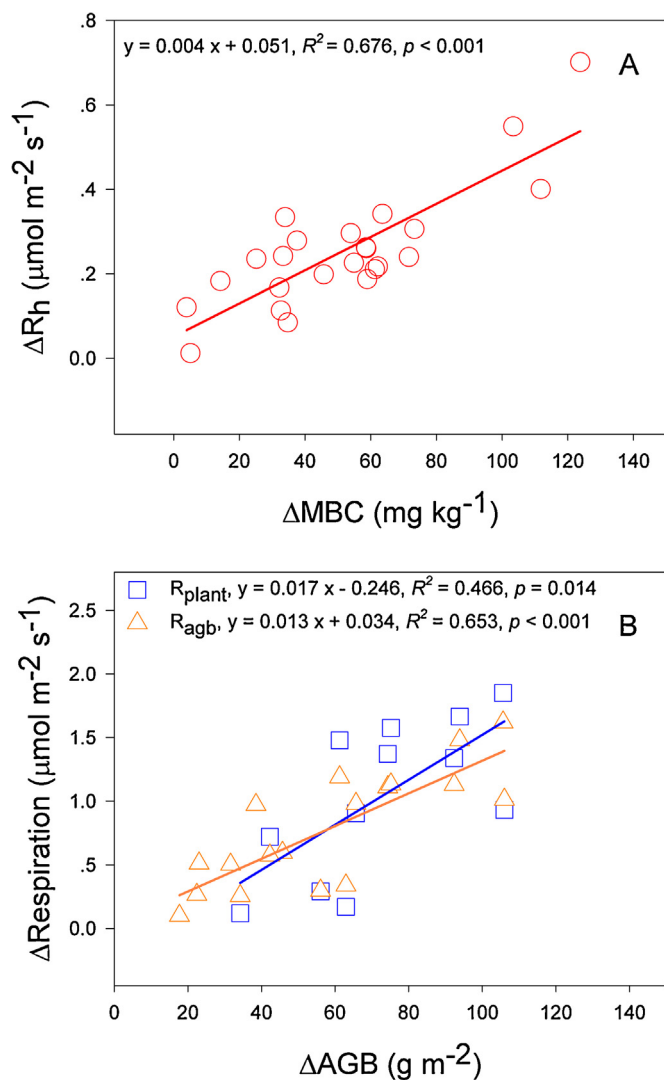


Fig. 4. (A) Warming effects on heterotrophic respiration (R_h) and microbial biomass carbon (MBC) during the growing season in 2013, and (B) warming effects on total autotrophic respiration (R_{plant}) and aboveground biomass (AGB) across the warming years. The delta terms indicate the difference between the OTC and control, for example, $\Delta\text{AGB} = \text{OTC (AGB)} - \text{Control (AGB)}$.

and experimental warming varied from 66.6% to 73.9%. Specifically, warming increased $R_{\text{plant}}/R_{\text{eco}}$ both in 2012 by 12.6% and in 2013 by 7.3%. Warming also enhanced $R_{\text{agnb}}/R_{\text{eco}}$ by 20.7% in 2012 and 16.0% in 2013 (Fig. 3).

3.4. Factors affecting ecosystem respiration and its components

Multiple regression analysis for soil temperature, soil moisture, and MBC in 2013 showed that the changes in R_{eco} , R_{plant} and R_{agnb} were mainly related to soil temperature ($R^2 = 0.682$, 0.674 , and 0.681 , $p < 0.001$, respectively) while R_s and R_{bgb} were more closely coupled with soil moisture ($R^2 = 0.559$ and 0.307 , $p < 0.001$, respectively), and R_h was strongly correlated with both soil temperature and MBC ($R^2 = 0.607$, $p < 0.001$). Furthermore, there were significant warming effects on R_h and MBC ($R^2 = 0.676$, $p < 0.001$) (Fig. 4A).

Multiple regression analysis across the three experimental warming years with AGB, BGB, soil temperature and soil moisture as the predictors showed that R_{eco} , R_s and R_{agnb} were mainly related to soil moisture and AGB ($R^2 = 0.612$, 0.623 , and 0.549 , $p < 0.001$, respectively); R_h was correlated with soil moisture ($R^2 = 0.571$, $p < 0.001$); R_{plant} was primarily related to soil temperature, soil

Table 4

Multiple stepwise regression analysis of ecosystem respiration (R_{eco}) and the components of R_{eco} with soil temperature (ST), soil moisture (SM), aboveground biomass (AGB) and belowground biomass (BGB) across the experimental warming years. + indicates entered variables. ** indicates significant difference at $p < 0.001$. BGB was not included in any model. See Fig. 2 for other abbreviations.

	Variable			R^2	F
	ST	SM	AGB		
R_{eco}		+	+	0.611	25.864**
R_s		+	+	0.623	27.282**
R_h		+		0.571	29.327**
R_{plant}	+	+		0.638	11.730**
R_{agnb}			+	0.551	41.511**
R_{bgb}	+	+		0.583	14.706**

moisture, and AGB ($R^2 = 0.638$, $p < 0.001$); and R_{bgb} was closely coupled with soil temperature and soil moisture ($R^2 = 0.583$, $p < 0.001$) (Table 4). There also were significant warming effects on the relationship between the treatment effects on R_{plant} , R_{agnb} and AGB ($R^2 = 0.466$, $p = 0.014$ for R_{plant} and $R^2 = 0.653$, $p < 0.001$ for R_{agnb}) (Fig. 4B).

4. Discussion

4.1. Insensitive response of R_{eco} and R_s to warming

We found non-significant responses of R_{eco} or R_s to 3-years of experimental warming in our study of a meadow grassland on the Tibetan Plateau. Our results are consistent with those from a temperate steppe (Xia et al., 2009), an alpine meadow (Lin et al., 2011), and a high arctic grassland (Lamb et al., 2011). In contrast, several studies have shown that experimental warming can either increase R_{eco} and R_s due to positive effects on autotrophic respiration (Flanagan et al., 2013a; Lin et al., 2011; Vogel et al., 2014), or have negative effects on R_{eco} and R_s due either to the suppression of R_h or to acclimation by both plants and soil microbial activities (Fu et al., 2013; Zhou et al., 2010). It is worth mentioning that different mechanisms can control the components of R_{eco} (Li et al., 2013; Wang et al., 2014), but even so, the lack of responses of R_{eco} and R_s to warming was somewhat surprising given the low temperatures and the large amount of carbon stocked on the Tibetan Plateau. The lack of significant responses of R_{eco} and R_s to warming in the current study is due to the contrasting responses of R_{plant} and R_h to the experimental treatment (Fig. 5). Our results therefore suggest that the R_{eco} and R_s have the potential to resist to climate warming through adjusting the responses of their endogenous components.

The lack of responses of R_{eco} and R_s to warming also could be related to warming-induced reduced soil moisture. This possibility is supported by our multiple regression analyses which showed that soil moisture played a critical role in terms of the effects of warming on R_{eco} and all the components (apart from R_{agnb}) (Table 4). Low soil moisture is one of the primary factors that limits the growth and productivity of alpine meadow ecosystems on the Tibetan Plateau (Chen et al., 2015b), and this may have been affected by the experimental warming (Lin et al., 2011). Seasonal and inter-annual dynamics of R_{eco} and the components of R_{eco} also followed the seasonal variations in precipitation, and some of the decreases we observed were coherent with the lower precipitation and soil moisture (Fig. S3). Moreover, a significant experimental warming effect on R_{eco} was found only in 2012, synchronizing with higher precipitation (Table 3, Fig. S1). Indeed, previous studies have shown that inter-annual variations in respiration can be linked to changes in precipitation (Marcolla et al., 2011; Nijp et al., 2014; Ryan et al., 2015; Slot et al., 2014; Yan et al., 2014; Zhou et al., 2007). These results further highlight that soil moisture played an

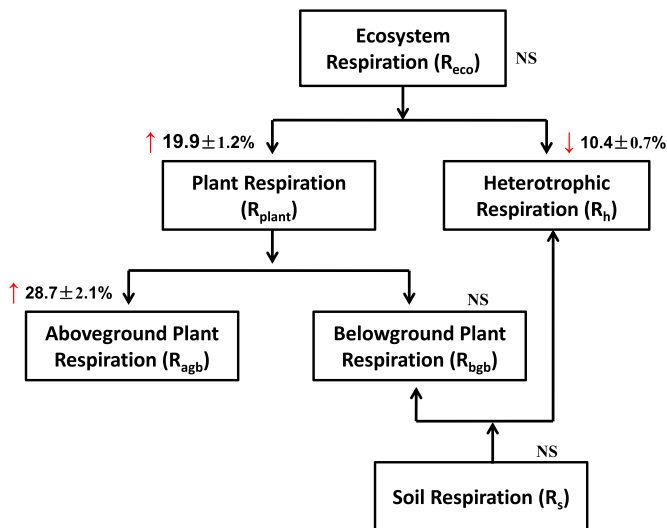


Fig. 5. A diagram showing the mechanisms and magnitudes of warming effects on ecosystem respiration (R_{eco}) and its source components. We only present significant difference, NS indicates no significant difference. Data are means \pm stand errors for six replicates. Arrows in the figure indicate the components of respiration, for example, R_s can be partitioned into R_h and R_{bgb} .

important role in the changes in R_{eco} and the components of R_{eco} that were caused by the experimental warming.

4.2. The effects of warming on autotrophic respiration

Experimental warming significantly enhanced R_{plant} and R_{agb} for each of the experimental years (Table 2). Our regression analysis showed that there were significant positive relationships between experimental warming-induced increases in both R_{plant} versus AGB and R_{agb} versus AGB (Fig. 4). These relationships suggest that experimental warming-induced indirect impacts on plant productivity have the potential to influence R_{plant} and R_{agb} . These might be primarily related to the experimental warming-induced changes in microclimate which could favor plant growth as well as trigger shifts in plant functional groups in this temperature- and vegetation-sensitive region and thereby promote plant productivity and respiration (Kardol et al., 2010). We further found larger increases in R_{agb} in 2012 and 2013 compared with 2011 (Fig. 2), which is in contrast to what one would expect if acclimation occurred (Atkin and Tjoelker, 2003; Slot and Kitajima, 2015). On the other hand, if growth were stimulated by warming (Fig. 1) (Lin et al., 2010; Way and Oren, 2010), then it is possible that warming-induced increases in AGB could lead to an increase in R_{agb} even if some degree of acclimation occurred (Smith and Dukes, 2013). Therefore, our results suggest that indirect effects of warming on plant productivity could have large impacts on R_{plant} and even R_{eco} .

The observed differences in the responses of R_{agb} and R_{bgb} (Table 2 and Fig. 2) to warming could be due to the fact that experimental warming by OTCs have been found to have more pronounced effects on air temperature than soil temperature (Klein et al., 2004; Kudo and Suzuki, 2003; Marion et al., 1997). Thus, it is possible that the relatively strong effects of the OTCs on air temperature are more likely causing significant positive impacts on R_{agb} compared with R_{bgb} . In addition, R_{bgb} can be constrained by a variety of other factors, such as reduced soil moisture and microbial activities (Moyano et al., 2008; Schindlbacher et al., 2009), and thus the R_{bgb} might more easily acclimate to warming compared with R_{agb} , even though warming increased BGB (Atkin et al., 2000; Burton et al., 2002). Therefore, the OTC-induced increase in R_{plant} could be mainly resulted from the positive responses of R_{agb} .

4.3. The effects of warming on heterotrophic respiration

Experimental warming significantly decreased R_h over the course of experiment (Table 2), and this was likely due, at least in part, to warming-induced reductions in MBC (Fig. 4). Our results agree with previous results which showed that experimental warming significantly decreases R_h due to the corresponding reductions in MBC (Fig. 4 and S5) (Lamb et al., 2011; Liu et al., 2009). R_h derives from the microbial decomposition of root exudates in the rhizosphere, above-ground and below-ground litter, and soil organic matter. Reductions in MBC could result from depletion of labile soil carbon (Song et al., 2012; Tucker et al., 2013), alterations of microbial communities (Frey et al., 2008), or limitations in soil moisture (Curtin et al., 2012; Liu et al., 2009); these factors in turn also could impact microbial activities and respiration. Our results concerning R_h were at odds with a study from a permafrost region where warming profoundly increased R_h (Peng et al., 2014). In contrast to our site, warming of the permafrost soils may have increased the active layer where microbial activity was likely not water limited and where respiration was enhanced. The permafrost study also showed that enhancements in R_h were closely coupled with increased microbial activities and the availability of labile substrates, and this is further evidence suggesting that the effects of warming on R_h can be modulated by warming-induced changes in MBC.

Another consideration with reference to our results is that there may have been some thermal acclimation of R_h to warming (Bradford et al., 2008; Luo et al., 2001). Warming-induced reductions in soil moisture could facilitate this kind of thermal acclimation, and in fact, this suggestion is consistent with previous studies which showed that the negative warming effects on R_h were linked to warming-induced reductions in soil moisture (Bauer et al., 2012; Moyano et al., 2013; Suseela et al., 2012). Although the mechanisms involved are still unclear, one possibility is that reduced soil moisture could lead to changes in microbial communities and hence enzymatic reactions (Carbone et al., 2011; Flanagan et al., 2013b). Our results suggest that the warming-induced negative effects on R_h may tend to offset the effects of climate warming on R_s and R_{eco} .

4.4. The effects of warming on the contributions of ecosystem respiration components

Warming significantly increased R_{plant}/R_{eco} and R_{agb}/R_{eco} , but it decreased R_h/R_{eco} , R_s/R_{eco} and R_h/R_s (Fig. 3). The contributions of each subcomponent to R_{eco} varied within a similar range as reported previously (Gomez-Casanovas et al., 2012; Hu et al., 2008; Li et al., 2013; Luo and Zhou, 2006; Savage et al., 2013; Zhou et al., 2007). Our results indicate that warming eventually could cause R_{eco} to become dominated by R_{plant} , an idea that has been suggested in previous studies (Hicks Pries et al., 2015; Peng et al., 2014; Suseela and Dukes, 2013). The significant positive effects of experimental warming on AGB may be key to the result of increased R_{plant} or R_{agb} relative to R_{eco} , even though plant respiration acclimates to warming (Lin et al., 2010; Slot and Kitajima, 2015; Way and Oren, 2010). Another possible explanation might be that the varied responses of the components of R_{eco} to changes in soil temperature and moisture (Fig. S4). Previous results have shown that R_{plant} was more temperature sensitive than R_h (Chen et al., 2015b; Lin et al., 2011), and therefore warming was more likely to have more positive effects on autotrophs than heterotrophs.

If one were to extrapolate the results showing positive response of the R_{plant}/R_{eco} to warming (Fig. 3), eventually R_{eco} would become dominated by R_{plant} , and if that were to occur R_{eco} might then increase in response to warming (Hicks Pries et al., 2015; Peng et al., 2014; Suseela and Dukes, 2013). These changes indicate that shifts

in the contributions of the components of R_{eco} caused by warming would potentially alter the ecosystem's carbon balance, and this possibility should be explicitly considered when modeling the carbon–climate feed backs.

4.5. Partitioning method and uncertainties

The root exclusion method is among three widely used methods for distinguishing R_h from R_{bgb} (Zhu and Cheng, 2011). Compared with other methods, this method is simple, cheap and easy to be conducted (Schindlbacher et al., 2009; Subke et al., 2011). Previous root exclusion studies have shown that 70 cm PVC collars were deep enough to exclude most living roots in a tall-grass prairie ecosystem (Zhou et al., 2007). However, the method may cause biases in estimated R_h in a few sources. First, vegetation exclusion (especially aboveground plants) might result in higher soil surface temperature and lower soil moisture, and then increased or decreased R_h depending on the change in soil moisture (Bond-Lamberty et al., 2011; Hanson et al., 2000). Thus, the effects of warming on the other components of R_{eco} could be regulated by the changes in soil temperature and soil moisture. Second, root exclusion was conducted nearly one year before the measurements to exclude the effects of dead root decomposition (Zhou et al., 2007). It also should be noted that this method would underestimate R_h owing to the exclusion of detrital inputs from dead roots and root exudates (Li et al., 2013), and in turn overestimated R_{bgb} . Thirdly, some uncertainties might also stem from possible changes in soil microbial activities and communities, which were not measured in the current study. Therefore, cautions should be taken to extrapolate the proportional changes in Fig. 5.

R_{agb} , R_{bgb} and R_{plant} were calculated by subtraction and thus have relatively high uncertainties because uncertainties in R_{eco} , R_s and R_h would need to be propagated. Even so, this subtraction method has been successfully used in many previous studies (Li et al., 2013; Peng et al., 2014; Zhou et al., 2007), and our results also are in line with a recent study of partitioning above- and below-ground plant respiration by using non-destructive isotopic method (Schindlbacher et al., 2009). Furthermore, the values for R_{agb} , R_{bgb} , R_{plant} and their contributions to R_{eco} in our study were all within the ranges reported in previous studies (Li et al., 2013; Luo and Zhou, 2006; Savage et al., 2013; Zhou et al., 2007), which indicates that any biases caused by the subtraction method are likely minor.

5. Conclusions

The high latitude and elevation of the Tibetan Plateau make it especially more sensitive to climate warming than most other temperate regions. The contrasting responses of R_{plant} and R_h to the experimental treatment with OTCs resulted in non-significant responses in either R_{eco} or R_s . Our results suggest that R_{eco} and R_s may be insensitive to warming as a result of complex changes in the respiration of the various endogenous components of the ecosystem. Increases in R_{plant} and R_{agb} were significantly correlated with the higher AGB, but the effects of warming on R_h evidently were negated by decreases in MBC and soil moisture in the warming treatments. Meanwhile, warming also increased $R_{\text{plant}}/R_{\text{eco}}$ and $R_{\text{agb}}/R_{\text{eco}}$, but it decreased R_h/R_{eco} , R_s/R_{eco} and R_h/R_s . The increase in $R_{\text{plant}}/R_{\text{eco}}$, which presumably reflects a positive response of R_{plant} to warming, suggests that warming could cause R_{eco} to become dominated by R_{plant} . Overall, the lack of significant responses of R_{eco} and R_s , and the complex responses of the components of R_{eco} to the experimental treatment should be taken into account when attempting to predict future warming effects on ecosystem carbon budget.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2016.01.010>.

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