



Article ID 1007-1202(2023)01-0077-11

DOI <https://doi.org/10.1051/wujns/2023281077>

# Warming Stimulated Soil Respiration in a Subalpine Meadow in North China

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**Abstract:** In order to explore the response of soil respiration in grassland to global warming, we carried out a warming experiment with open top chambers (OTCs) in the subalpine meadow, Mount Wutai in north China. Our results showed in the subalpine meadow across 2 500-2 700 m above the sea level (ASL), with OTCs, soil respiration increased by  $2.00 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  as soil temperature increased by  $1.25 \text{ }^\circ\text{C}$  on average. Warming decreased soil moisture over the experiment periods except in October 2019 when snow melted in OTCs. Warming effect on soil respiration peaked at 178.31% in October 2019. In control and warming treatment, based on exponential regression equations, soil temperature alone accounted for 85.3% and 61.2% of soil respiration variation, respectively. In control treatment soil moisture alone explained 23.2% of soil respiration variation based on the power regression equation while in warming treatment they were not significantly correlated with each other. The response of soil respiration to warming relied on altitudes as well as the time of the year, but was not inhibited by soil moisture, labile carbon pool, and available nitrogen. We concluded soil temperature was the main factor influencing soil respiration, and global warming would stimulate soil respiration in the subalpine meadows of Mount Wutai in the future. Our analysis provided new data on characteristics and mechanisms of the response of soil respiration to warming, and helped to further understand the relationship between carbon cycle and climate change.

**Key words:** global warming; soil respiration; open top chambers (OTCs); the subalpine meadow; Mount Wutai

**CLC number:** Q 148; X 24

## 0 Introduction

Grassland is an important terrestrial ecosystem. In the world, grassland covers 25% of the terrestrial land and accounts for about 25%-30% of total soil carbon storage<sup>[1-3]</sup>. In China, grassland, as the largest terrestrial ecosystem, covers 41.7% of the national land area<sup>[4]</sup>, and

stores 9%-16% of global organic carbon<sup>[5]</sup>. Soil respiration is defined as the  $\text{CO}_2$  flux released from the soil surface<sup>[6]</sup>. Soil respiration is the main way of carbon output in grassland, and is a significant source of greenhouse gases. The global surface temperature could increase 1.4-5.8  $^\circ\text{C}$  from 1999 to 2100 according to prediction from Intergovernmental Panel on Climate Change (IPCC)<sup>[7]</sup>.

**Received date:** 2022-07-16

**Foundation item:** Supported by Xinzhou Teachers University Project (2018KY02), Shanxi Province Colleges/Universities Discipline Group Construction Plan Project for Service and Industry Innovation "Ecology and Cultural Tourism Discipline Group for Mount Wutai", and Program for the Philosophy and Social Sciences Research of Higher Learning Institutions of Shanxi (20210122)

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To evaluate the response of soil respiration to global warming accurately is an urgent and challenging task in carbon cycle research<sup>[8]</sup>.

The response of soil respiration to climate change has attracted extensive attentions with lots of significant research results. However, there are still great uncertainties in the response due to insufficient understanding of carbon cycle in terrestrial ecosystems.

First, there are great uncertainties in direction as well as magnitude of feedback between carbon cycle and climate change<sup>[9]</sup>. Some studies supported that global warming promoted soil respiration, driving positive feedback between terrestrial carbon cycle and climate change<sup>[10,11]</sup>. Some studies supported that soil respiration acclimated to increasing temperature after varied with climate change over a period of time due to adaptation of microbial activities and exhaustion of labile carbon pools<sup>[12]</sup>. Other studies suggested soil respiration decreased while temperature increased as a result of limited soil moisture<sup>[13,14]</sup>.

Second, altitude variations drive differences in the response of soil respiration to climate change. The lower the temperature, the higher the temperature sensitivity of soil respiration<sup>[15,16]</sup>. At different altitudes, long-term temperature differences are responsible for differences in the sensitivity of soil respiration to temperature as well as to climate change. At different altitudes, the response of soil respiration to climate change is different owing to the differences in short-term temperature increase with climate change<sup>[17,18]</sup>, biodiversity, plant growth, species distribution and soil properties. More warming experiments on soil respiration *in situ* should be conducted so as to further explore the response of soil respiration to climate change.

Mount Wutai, a Buddhist holy place, appeared in world heritage list in 2009. Its highest altitude is 3 061.1 meters above the sea level (ASL)<sup>[19]</sup>. It retains relatively intact and stable montane meadows above the altitude of 2 000 m<sup>[20,21]</sup> and provides an ideal natural laboratory for studying the response of soil respiration to climate change. However, inconvenient transportation and strict entry policy stop conducting long-time field experiments. To our knowledge, soil respiration in the montane meadows, Mount Wutai has not been measured *in situ* to date. Here, we set up control and warmed plots *in situ* across an altitude gradient of about 200 m in the subalpine meadow, Mount Wutai. Our study aimed to 1) measure soil respiration and analyze its relationship with en-

vironment factors, 2) test whether temporal and spatial differences exist in the response of soil respiration to warming, and 3) predict how soil respiration in the subalpine meadow responds to global warming.

## 1 Methods

### 1.1 Study Area

Mount Wutai (113° 24'51" -113° 44'21"E, 38° 50'11" -39° 8'22"N) is located in Xinzhou City, Shanxi Province, China (Fig. 1). Based on data over the period of 1998-2019 from the China Meteorological Data Service Center, the annual average air temperature is 2.15 °C. The maximum and minimum of air temperature are respectively 29.6 °C and -32.3 °C. The annual average precipitation is 673 mm. Rain mainly falls from June to September. The annual average sunshine hours are 2 632 h, the average relative humidity is 60%, and the maximum wind speed is 30.3 m/s. In the subalpine meadow, Mount Wutai, the dominant species are *K. pusilla* and *K. myosuroides*. Other species include *Carex spp.* and *Polygonum viviparum*<sup>[22]</sup>.

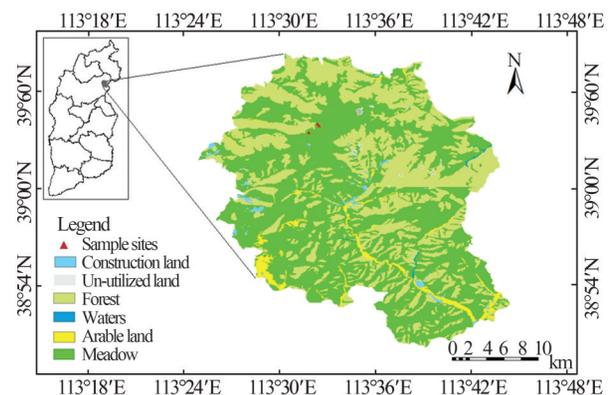


Fig. 1 The location of the study area and the sample sites

### 1.2 Plot Design

In April 2019, we designed and made the open top chambers (OTCs) for warming *in situ* in our experiment. The making processes are as following: first, two regular hexagons were made from stainless steel square tubes, one for the base of a chamber with side length of 0.75 m, the other for the top of the chamber with side length of 0.40 m; second, two regular hexagons were connected by the stainless steel square tubes with the height between them being 0.65 m; third, glass was fixed to the side of the chamber (Fig. 2).

In August 2019, three plots (50 m × 50 m) were se-



**Fig. 2** The open top chamber for warming in the field

lected along altitudes in the subalpine meadow, Mount Wutai (Fig. 1). Their geographical coordinates were shown in Table 1. In each plot, twelve subplots (1.5 m × 1.5 m) were established, half of them were set as control plots and the other half were set as warmed plots. On each warmed plot, one open top chamber was placed. In the subplots, in order to support and seal the Li-cor 8100 portable infrared gas analyzer, polyvinyl chloride collars, 8 cm tall and 20 cm in inner diameter, were inserted into soil, keeping the collars 3 cm above soil surface. Before measurements, green plants in the collars were cut to eliminate photosynthesis.

**Table 1** The geographical coordinates of three plots in Mount Wutai

Longitude	Latitude	Altitude/m
113°32'23.05"E	39°4'1.14"N	2 544
113°32'29.53"E	39°3'53.58"N	2 631
113°31'50.71"E	39°3' 28.28"N	2 700

### 1.3 Field Measurements

Soil respiration was measured by the Li-cor 8100 portable CO<sub>2</sub> analyzer (Li-cor Biosciences, Lincoln, Nebraska). Soil moisture at 5 cm was tested by soil moisture probe, 8100-204 Delta-Theta. Soil temperature at 5 cm was tested using the soil temperature probe, 6000-09TC.

### 1.4 Soil Property Analyses

In September 2020, soil at 0-10 cm was dug with soil drills, put into plastic sealed bags, and then stored in a refrigerator for chemical properties analyses. NH<sub>4</sub><sup>+</sup>-N and NO<sub>3</sub><sup>-</sup>-N were measured by flow injection method by Continuous Flow Analyzer (Auto Analyzer 3, Germany). Microbial biomass carbon (MBC) and microbial bio-

mass nitrogen (MBN) were tested by fumigation extraction method with Total Organic Carbon Analyzer (multi N/C 3100, Germany).

### 1.5 Warming Effect on Soil Respiration

Warming effect on soil respiration (WE<sub>r</sub>) was quantified using  $WE_r = (R_w/R_c - 1) \times 100\%$ , where WE<sub>r</sub> is warming effect on soil respiration,  $R_w$  is soil respiration in warming treatment,  $R_c$  is soil respiration in control treatment.

### 1.6 Statistical Analysis

SPSS 20 was used to analyze statistically. Shapiro-Wilk analysis was used to test whether data distributed normally. The independent sample *t* test or the nonparametric test was applied to tell if significant differences existed in data between control and warmed plots. Correlation of different variables was analyzed using spearman correlation coefficient. The exponential model and the power model in regression analysis further described soil respiration's relationship with soil temperature and moisture.

## 2 Results

### 2.1 Influences of Warming on Soil Properties

At altitudes of 2 500, 2 600 and 2 700 m, NH<sub>4</sub><sup>+</sup>-N was on average 12.50 ± 2.71, 10.91 ± 3.71 and 17.24 ± 2.89 mg/kg in control plots and was on average 17.87 ± 3.91, 14.49 ± 2.47 and 12.10 ± 2.32 mg/kg in warmed plots, respectively. NO<sub>3</sub><sup>-</sup>-N varied from 2.91 ± 0.69 to 9.09 ± 2.27 mg/kg in control plots, and from 4.97 ± 3.06 to 9.73 ± 2.20 mg/kg in warmed plots. In control plots, the maximum and minimum of MBC were 961.62 ± 157.48 mg/kg at 2 700 m ASL and 607.83 ± 252.72 mg/kg at 2 600 m ASL, respectively. In warmed plots, the highest value was 913.11 ± 221.53 mg/kg at 2 700 m ASL, and the lowest value was 710.16 ± 288.33 mg/kg at 2 500 m ASL. MBN was higher than 91.27 ± 34.35 mg/kg in control plots, and higher than 98.41 ± 37.84 mg/kg in warmed plots. Warming did not significantly affect NH<sub>4</sub><sup>+</sup>-N, NO<sub>3</sub><sup>-</sup>-N, MBC or MBN (Table 2).

### 2.2 Warming Responses of Soil Respiration, Temperature and Moisture

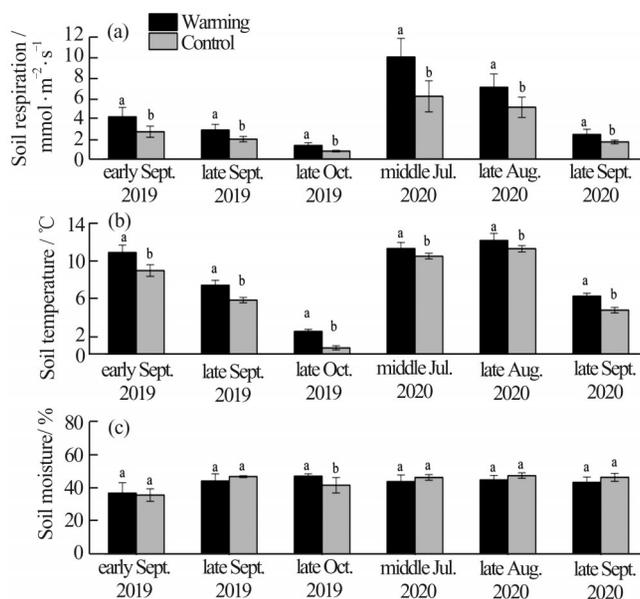
At an altitude of 2 500 m, OTCs significantly promoted soil respiration as well as soil temperature ( $p < 0.05$ ,  $n = 6$ ). In control and warming treatment, soil respiration peaked in middle July 2020, the value was 6.21±

**Table 2** Soil chemical properties in warmed and control plots at different altitudes

Altitude /m	Treatment	NH <sub>4</sub> <sup>+</sup> -N /mg·kg <sup>-1</sup>	NO <sub>3</sub> <sup>-</sup> -N /mg·kg <sup>-1</sup>	MBC /mg·kg <sup>-1</sup>	MBN /mg·kg <sup>-1</sup>
2 500	Warming	17.87 ± 3.91a	5.41 ± 2.44a	710.16 ± 288.33a	150.72 ± 52.96a
2 500	Control	12.50 ± 2.71a	2.91 ± 0.69a	928.02 ± 231.81a	165.53 ± 51.40a
2 600	Warming	14.49 ± 2.47a	9.73 ± 2.20a	797.01 ± 257.74a	98.41 ± 37.84a
2 600	Control	10.91 ± 3.71a	9.09 ± 2.27a	607.83 ± 252.72a	91.27 ± 34.35a
2 700	Warming	12.10 ± 2.32a	4.97 ± 3.06a	913.11 ± 221.53a	131.22 ± 34.52a
2 700	Control	17.24 ± 2.89a	6.51 ± 1.78a	961.62 ± 157.48a	128.00 ± 27.90a

Mean ± standard deviation ( $n = 6$ ); a indicates no significant difference between the two treatments

1.530 and  $10.09 \pm 1.831 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , respectively. The minimum value was  $0.80 \pm 0.082 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  in control treatment and  $1.37 \pm 0.269 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  in warming treatment in late October 2019 (Fig. 3(a)). Soil temperature peaked in late August 2020, and the highest value was  $11.31 \pm 0.329$  and  $12.20 \pm 0.736$  °C in control and warming treatment, respectively. The lowest soil temperature appeared in late October 2019, and was  $0.79 \pm 0.213$  and  $2.53 \pm 0.214$  °C in control and warming treatment respectively (Fig. 3(b)). No significant difference existed ( $p > 0.05$ ,  $n=6$ ) between soil moisture in the two treatments over the measurement period except in late October 2019 when OTCs promoted soil moisture significantly ( $p < 0.05$ ,  $n=6$ ). Soil moisture varied in the range of 35.5%–47.3% in control plots and 36.7%–47% in warmed plots (Fig. 3(c)).



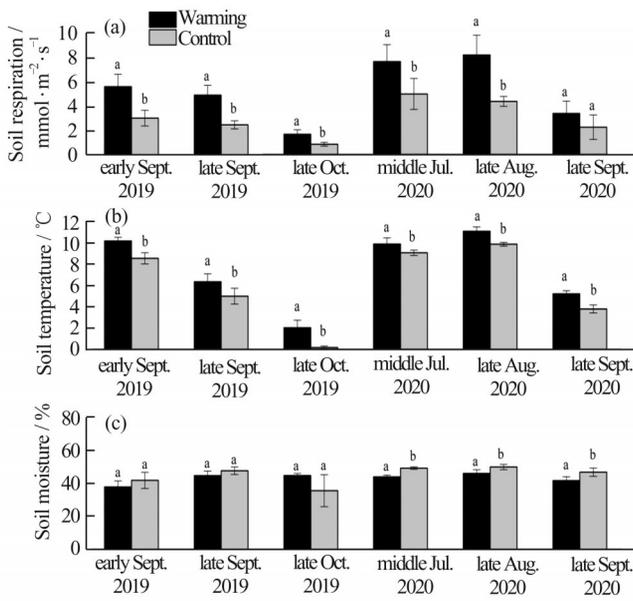
**Fig. 3** Soil respiration(a), soil temperature(b) and soil moisture(c) in warming and control treatment at 2 500 m ASL

a, b indicate significant differences between warming and control treatment; The data are mean ± standard deviation

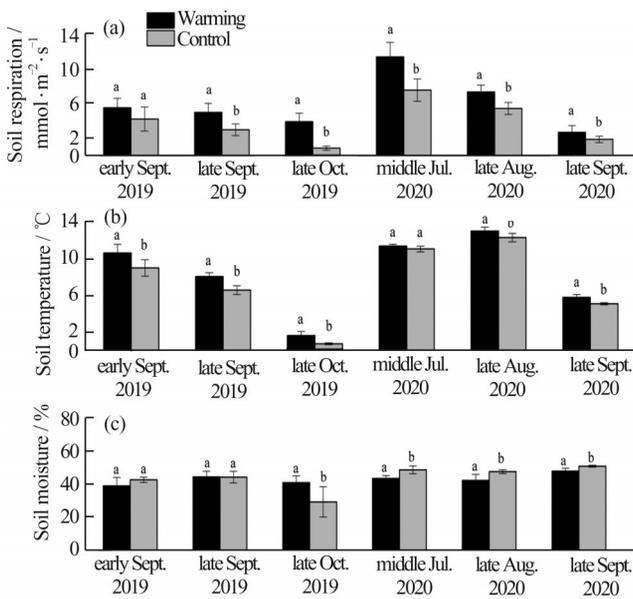
At an altitude of 2 600 m, warming increased soil respiration. The increases were significant ( $p < 0.05$ ,  $n=6$ ) during the measurement period except in late September 2020 ( $p > 0.05$ ,  $n = 6$ ). Control plots recorded the highest soil respiration of  $5.04 \pm 1.285 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  in middle July 2020 and the lowest value of  $0.87 \pm 0.159 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  in late October 2019. Warmed plots recorded the highest soil respiration of  $8.27 \pm 1.645 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  in late August 2020 and the lowest value of  $1.69 \pm 0.377 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  in late October 2019 (Fig. 4(a)). Warming consistently elevated soil temperature ( $p < 0.05$ ,  $n = 6$ ). In control and warming treatment, the highest soil temperature was  $9.89 \pm 0.177$  °C and  $11.10 \pm 0.399$  °C in late August 2020 and the lowest value was respectively  $0.20 \pm 0.136$  °C and  $2.05 \pm 0.707$  °C in late October 2019 (Fig. 4(b)), respectively. Soil moisture was above 36% in the two treatments. Not all differences in soil moisture between the two treatments were significant (Fig. 4(c)).

At an altitude of 2 700 m, soil respiration increased under OTCs. The effects of OTCs were significant over the measurement period ( $p < 0.05$ ,  $n = 6$ ) with the exception of early September in 2019 ( $p > 0.05$ ,  $n = 6$ ) (Fig. 5 (a)). Except in middle July 2020, soil temperature significantly increased under warming condition ( $p < 0.05$ ,  $n = 6$ ). In middle July 2020, soil temperature was  $11.46 \pm 0.196$  °C and  $11.14 \pm 0.323$  °C under warming and control treatment, respectively (Fig. 5(b)). Under warming condition, soil moisture varied from 39.0% to 48.0%, and under control condition, it varied from 29.2% to 51%. Warming influenced soil moisture significantly ( $p > 0.05$ ,  $n = 6$ ) over the measurement period except in early and late September 2019 ( $p < 0.05$ ,  $n = 6$ ) (Fig. 5(c)).

At 2 500–2 700 m ASL, warming promoted soil respiration and temperature significantly ( $p < 0.05$ ,  $n = 6$ ) (Fig. 6(a) and (b)). Soil moisture between the two treat-



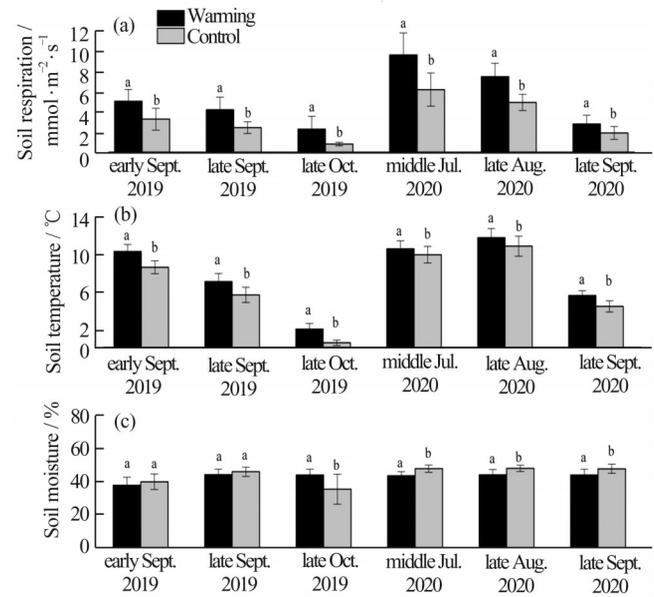
**Fig. 4** Soil respiration(a), soil temperature(b) and soil moisture(c) in warming and control treatment at 2 600 m ASL  
a, b indicate significant differences between warming and control treatment; The data are mean ± standard deviation



**Fig. 5** Soil respiration(a), soil temperature(b) and soil moisture(c) in warming and control treatment at 2 700 m ASL  
a, b indicate significant differences between warming and control treatment; The data are mean ± standard deviation

ments was not significantly different in early or late September 2019 ( $p > 0.05$ ,  $n = 6$ ) while it was significantly different in other measurement time ( $p < 0.05$ ,  $n = 6$ ) (Fig. 6(c)). In control and warmed plots, soil respiration was averagely  $3.30 \pm 2.008$  and  $5.29 \pm 2.851 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , soil temperature was averagely  $6.87 \pm 4.018$  °C and  $8.12 \pm 3.828$  °C, soil moisture was averagely 44.53% ±

5.939% and  $43.30\% \pm 2.608\%$ , respectively (Fig. 6 (a)-(c)).



**Fig. 6** Soil respiration(a), soil temperature(b) and soil moisture(c) in warming and control treatment at 2 500-2 700 m ASL  
a, b indicate significant differences between warming and control treatment; The data are mean ± standard deviation

### 2.3 Differences in Warming Effects

With OTCs, soil temperature increased by 1.40 °C at 2 500 m ASL, 1.38 °C at 2600 m ASL and 0.97 °C at 2 700 m ASL. Warming averagely increased soil temperature by 1.25 °C at 2 500-2 700 m ASL. Warming promoted soil respiration by  $1.59 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  at 2 500 m ASL,  $2.26 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  at 2 600 m ASL,  $2.15 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  at 2 700 m ASL respectively, and by  $2.00 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  on average at 2 500-2 700 m ASL. In late October 2019, warming effect on soil respiration ( $WE_r$ ) reached a maximum of 71.25% at 2 500 m ASL and 373.17% at 2 700 m ASL. At 2 600 m ASL,  $WE_r$  in late October 2019 was 94.25% that was slightly lower than the highest value of 100% in late September 2019. At 2 500-2 700 m ASL,  $WE_r$  peaked at 178.31% in late October 2019, the second largest  $WE_r$  was 72.06% in late September 2019, and other values ranged from 46.39% to 55.36% (Fig. 7).

### 2.4 Regression Models

At 2 500 m ASL, soil respiration correlated with soil temperature significantly and positively in control and warming treatment ( $p < 0.01$ ,  $n = 36$ ). The regression model was  $y = 0.689e^{0.180x}$  in control treatment ( $R^2 = 0.887$ ,  $p = 0$ ,  $n = 36$ ) (Fig. 8(a)) and was  $y = 0.806e^{0.181x}$

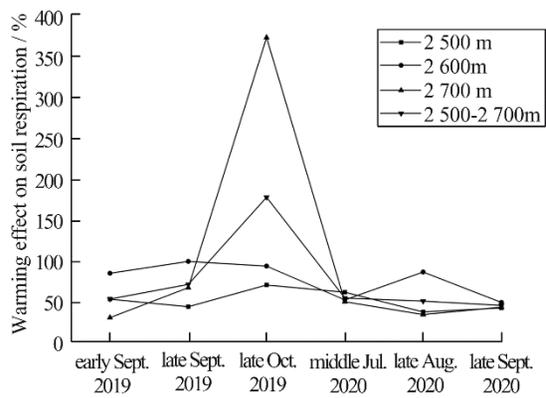


Fig. 7 Warming effect on soil respiration

in warming treatment ( $R^2 = 0.807$ ,  $p = 0$ ,  $n = 36$ ) (Fig. 8 (b)), where  $y$  was soil respiration,  $x$  was soil temperature, indicating that soil temperature alone accounted for 88.7% and 80.7% of the variation in soil respiration in control and warming treatment, respectively. Soil respiration and soil moisture were negatively correlated ( $p < 0.05$ ,  $n = 36$ ) under warming treatment and not corre-

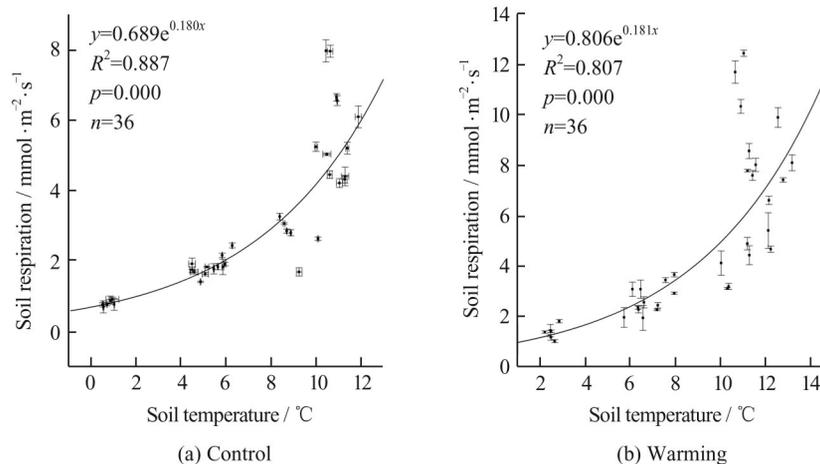


Fig. 8 Regression models between soil respiration and soil temperature in control(a) and warmed(b) plots at 2500 m ASL

At 2700 m ASL, in control plots soil respiration had a significant positive correlation with soil temperature ( $p < 0.01$ ,  $n = 36$ ) as well as soil moisture ( $p < 0.01$ ,  $n = 36$ ). The function  $y = 0.757e^{0.182x}$  ( $R^2 = 0.888$ ,  $p = 0$ ,  $n = 36$ ), where  $y$  was soil respiration,  $x$  was soil temperature, further described soil respiration's relationship with soil temperature (Fig. 10(a)).

The function  $y = 14.670x^{1.898}$  ( $R^2 = 0.354$ ,  $p = 0$ ,  $n = 36$ ), where  $y$  was soil respiration,  $x$  was soil moisture, expressed its relationship with soil moisture. It was inferred that soil temperature was a stronger controller than soil moisture.

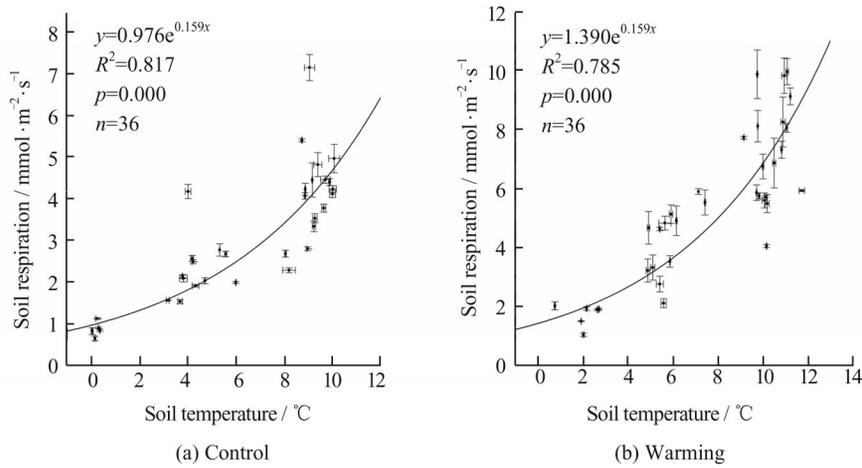
In warmed plots, soil respiration and soil tempera-

lated ( $p > 0.05$ ,  $n = 36$ ) under control treatment.

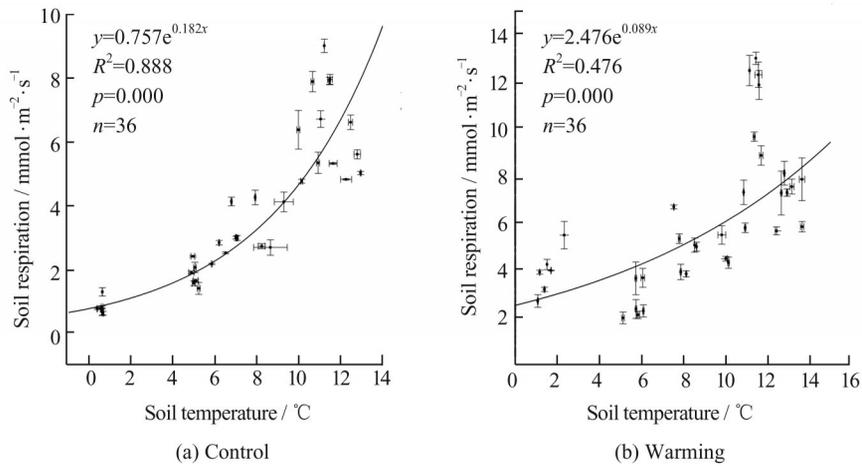
At 2600 m ASL, soil respiration and soil temperature were correlated significantly and positively ( $p < 0.01$ ,  $n = 36$ ) in the two treatments. Their relationship was further described using  $y = 0.976e^{0.159x}$ , where  $y$  was soil respiration,  $x$  was soil temperature, in control treatment ( $R^2 = 0.817$ ,  $p = 0$ ,  $n = 36$ ) (Fig. 9(a)) and  $y = 1.390e^{0.159x}$ , where  $y$  was soil respiration,  $x$  was soil temperature, in warming treatment ( $R^2 = 0.785$ ,  $p = 0$ ,  $n = 36$ ) (Fig. 9(b)). Soil temperature alone accounted for 81.7% and 78.5% of the variance in soil respiration in control and warming treatment, respectively. Soil respiration and soil moisture were correlated significantly and positively in control treatment ( $p < 0.01$ ,  $n = 36$ ) and not correlated in warming treatment ( $p > 0.05$ ,  $n = 36$ ). In control treatment, their relationship was expressed by  $y = 14.122x^{2.137}$  ( $R^2 = 0.367$ ,  $p = 0$ ,  $n = 36$ ), where  $y$  was soil respiration,  $x$  was soil moisture, which meant soil moisture alone explained 36.7% of the variation in soil respiration.

ture had a significant positive correlation ( $p < 0.01$ ,  $n = 36$ ), and their relationship was expressed by  $y = 2.476e^{0.089x}$  ( $R^2 = 0.476$ ,  $p = 0$ ,  $n = 36$ ), where  $y$  was soil respiration,  $x$  was soil temperature, indicating soil temperature was responsible for 47.6% of soil respiration variation (Fig. 10(b)). Soil respiration was not significantly correlated with soil moisture ( $p > 0.05$ ,  $n = 36$ ).

At 2500-2700 m ASL, soil respiration had a significant positive correlation with soil temperature in the two treatments ( $p < 0.01$ ,  $n = 108$ ). The function  $y = 0.811e^{0.172x}$  ( $R^2 = 0.853$ ,  $p = 0$ ,  $n = 108$ ), where  $y$  was soil respiration,  $x$  was soil temperature, and  $y = 1.498e^{0.134x}$  ( $R^2 = 0.612$ ,  $p = 0$ ,  $n = 108$ ), where  $y$  was soil respiration,



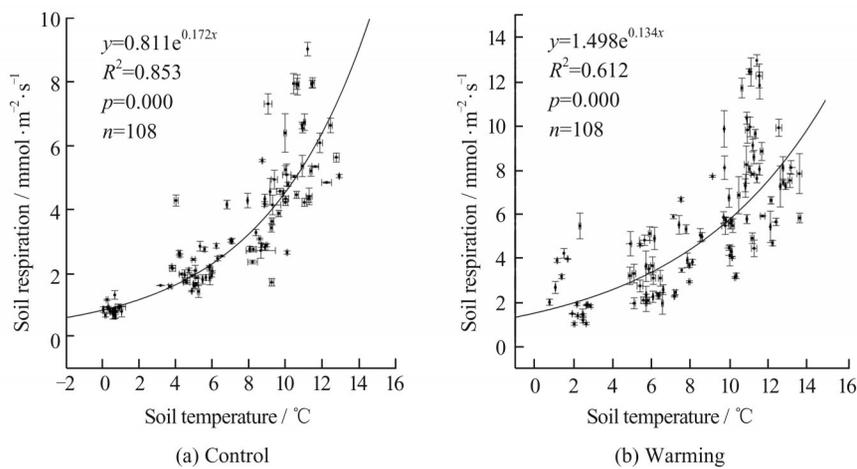
**Fig. 9** Regression models between soil respiration and soil temperature in control(a) and warmed(b) plots at 2 600 m ASL



**Fig. 10** Regression models between soil respiration and soil temperature in control(a) and warmed(b) plots at 2 700 m ASL

$x$  was soil temperature, described their relationship in control and warming treatment respectively (Fig. 11(a) and (b)). It was obvious that 61.2% and 85.3% of the variance in soil respiration were respectively regulated by soil temperature alone with and without warming.

There was a significant positive correlation between soil respiration and soil moisture in control treatment ( $p < 0.01$ ,  $n = 108$ ) but not in warming treatment ( $p > 0.05$ ,  $n = 108$ ). In control treatment, their relationship was described by  $y = 11.764x^{1.809}$  ( $R^2 = 0.232$ ,  $p = 0$ ,  $n = 108$ ),



**Fig. 11** Regression models between soil respiration and soil temperature in control(a) and warmed(b) plots at 2 500-2 700 m ASL

where  $y$  was soil respiration,  $x$  was soil moisture, with 23.2% of the variance in soil respiration explained by soil moisture alone.

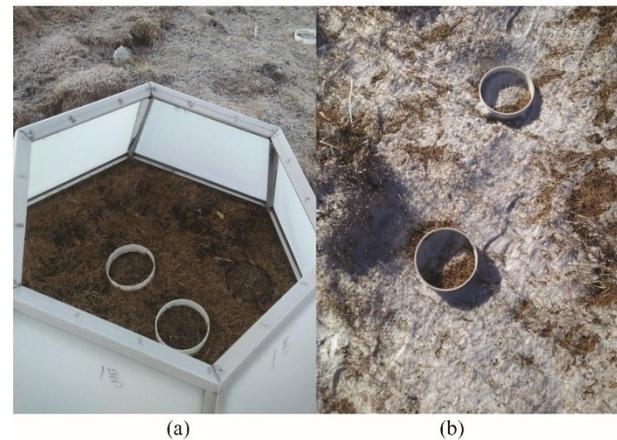
### 3 Discussion

#### 3.1 Factors Affecting the Response of Soil Respiration to Warming

Temperature was one of the most important factors regulating soil respiration. Temperature increase stimulated soil respiration<sup>[23,24]</sup>. Yadugiri and Tiruvaimozhi<sup>[25]</sup> reported soil respiration almost doubled with soil temperature increased by 1.4 °C in a warming experiment with OTCs in tropical montane grasslands. Xu *et al.*<sup>[26]</sup> observed soil respiration significantly increased as temperature was elevated by 2 °C with infrared heaters in a warming experiment for 13 years in a tallgrass prairie in Oklahoma, USA. Lu *et al.*<sup>[27]</sup> suggested warming accelerated soil respiration by 9.0% and used the response ratio to measure warming effect in a meta-analysis. Similarly, we found that temperature was the most important factor regulating soil respiration and warming with OTCs promoted soil respiration in the subalpine meadow, Mount Wutai in this study.

Soil moisture affected the response of soil respiration to warming. Reynolds *et al.*<sup>[28]</sup> observed warming promoted soil respiration under sufficient soil water, but insufficient soil water reduced respiration. Zhang *et al.*<sup>[13]</sup> and Chen *et al.*<sup>[29]</sup> showed warming decreased soil moisture, and consequently soil respiration reduced in grassland in Inner Mongolia and the Qinghai-Tibet Plateau in China. Zhang and Hong<sup>[30]</sup> found soil respiration did not increase under warming condition with infrared heating devices due to low soil moisture in the desert steppe, Inner Mongolia, China. Yu *et al.*<sup>[31]</sup> suggested soil respiration was more sensitive to warming in wetter environments. In our study, moderate soil moisture ranging from 35.6% to 48.5% had no inhibitory effect on the response of soil respiration to warming. Because of higher evaporation under warming, soil moisture was prone to be higher in control plots than that in OTC plots over experiment period except in late October 2019. In late October 2019, snow melted in OTCs due to warming which increased soil moisture while snow still covered the ground outside the OTCs (Fig. 12). Similarly, Wu<sup>[32]</sup> speculated that soil thawing due to warming might promote soil moisture temporarily in a desert steppe.

Labile carbon pool affected the response of soil res-



**Fig. 12** A warmed plot without snow and a control plot(a) with snow in the subalpine meadow(b), Mount Wutai in late October 2019

piration to warming. Soil contains two carbon pools. One is labile carbon pool, which is sensitive to temperature, the other is recalcitrant carbon pool, which is less or not sensitive to temperature<sup>[17, 33, 34]</sup>. Due to exhaustion of labile carbon pool, soil respiration would become less responsive after a period of time, showing acclimatization to warming. Luo *et al.*<sup>[35]</sup> quantified acclimatization of soil respiration to warming for the first time and speculated that acclimatization might weaken positive feedback between climate change and terrestrial carbon cycle. Liu *et al.*<sup>[36]</sup> revealed that warming reduced decomposable carbon and soil moisture resulting in a weaker response of heterotrophic respiration to warming in alpine meadows, the Qinghai-Tibet Plateau. However, soil respiration did not show acclimatization to warming in our study. The subalpine meadow in Mount Wutai was a natural pasture, the grazing cattle from Grain Buds to White Dew according to China's Twenty-Four Solar Terms could increase belowground biomass or carbon allocation to roots while decrease aboveground plant biomass, thereby increasing labile carbon input to soil<sup>[14,37]</sup>. MBC in soil reflected the size of soil microbial biomass<sup>[38]</sup>, and belonged to labile carbon pool for soil nutrient transformation. In our study, MBC in soil was relatively high and was not significantly different between treatments. We speculated sufficient labile carbon pool due to grazing might be responsible for responsive soil respiration.

Available nitrogen affected the response of soil respiration to warming, too. Plants could only absorb and utilize available nitrogen. Both  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N were the main forms of available nitrogen in soil and

were main nutrients for plants<sup>[39]</sup>. Available nitrogen could affect plant grow and then affect soil respiration<sup>[40]</sup>. In this study, comparatively high  $\text{NH}_4^+$ -N and  $\text{NO}_3^-$ -N indicated sufficient available nitrogen. Therefore, the response of soil respiration to warming could not be inhibited by available nitrogen.

### 3.2 Differences in Warming Effects

Generally, warming effect on soil respiration was stronger in late October 2019 in this study. It averaged 178.31% across the selected altitudes. In late October 2019, the weather was so cold that no green grass left. Soil respiration was low due to limited microbe and root activities in the cold weather. Experimental warming with OTCs at this time of the year effectively increased soil temperature and mainly promoted heterotrophic respiration, resulting in higher warming effect on soil respiration.

During the growing season, warming could improve soil microbial activity and plant root physiological activity, thereby increasing soil heterotrophic and autotrophic respiration<sup>[41]</sup>. Warming-induced increases in soil respiration were largest in middle July, 2020 in this study. Because at this time of the year the biological vitality was vigorous, and both heterotrophic and autotrophic respiration increased greatly with temperature increasing.

An altitude gradient was characterized by obvious climatic changes within a short distance. Microbial composition along an altitude gradient varied as temperature changed<sup>[42-44]</sup>. Patterns of microbial diversity at 2 900-3 055 m were different from those at lower altitudes in Mount Wutai<sup>[45]</sup>. We speculated that soil respiration at higher altitudes (2 800-3 061 m) in the alpine meadow, Mount Wutai should have distinctive features compared with this study. In order to fully understand soil respiration in montane meadow, it is necessary to conduct more warming experiments in higher elevations in future.

### 3.3 Regression Relationships

Li *et al.*<sup>[46]</sup> reported a significant linear regression relationship existed between soil temperature and soil respiration under both warming and control conditions, and their correlation was weaker under warming condition than control condition. Tian *et al.*<sup>[47]</sup> showed that 76.9% and 25.8% of variation in soil respiration were controlled by soil temperature and soil water content alone in the *Abies nephrolepis* forest in Mount Wutai. In our study, soil temperature explained more variations of soil

respiration under control condition than those under warming condition which indicted warming decreased the reliance of soil respiration on soil temperature. Warming also reduced the dependence of soil respiration on soil moisture in this study. Based on regression models, soil respiration was mainly influenced by soil temperature in the subalpine meadow, Wutai Mountain. Therefore, global warming should promote soil respiration in the subalpine meadow, Wutai Mountain in the future.

## 4 Conclusion

Our experimental warming with OTCs *in situ* increased soil respiration and soil temperature in the subalpine meadow, Mount Wutai. Soil temperature was the main factor affecting soil respiration, and warming reduced the reliance of soil respiration on soil temperature as well as soil moisture. Therefore, in the future, global warming should promote soil respiration and alter its relationships with environmental factors in the subalpine meadow, Mount Wutai.

### Acknowledgements

The authors gratefully thank graziers in the grassland, Mount Wutai for their help in the field work.

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