Different responses of soil respiration and its components to experimental warming with contrasting soil water content

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Abstract

Soil water content (SWC) regulation on the responses of soil respiration (Rₐ), autotrophic respiration (Rₐ), and heterotrophic respiration (Rₜ) to warming are rarely investigated in alpine meadow ecosystem in the Qinghai-Tibet Plateau (QTP). We conducted a warming experiment to investigate how SWC regulates the responses of Rₐ and its components (Rₐ and Rₜ) to warming. Infrared heaters were used to simulate climatic warming. Soil respiration was measured inside surface collars (2–3 cm deep) and Rₐ was measured inside deep collars (50 cm deep), which excludes root respiration. Autotrophic respiration was calculated by subtracting Rₐ from Rₜ. Warming increased the average Rₐ and Rₜ by 9.9% and 12.7% but had no significant effect on Rₜ. Interaction between warming and SWC had significant effect on Rₐ and its components. Soil respiration and Rₐ decreased by 5.8% and 36.3% in dry conditions, but they increased by 23.5% and 47.7% in wet conditions. Growing season above-ground biomass was enhanced by 0.1 kg m⁻² in wet conditions but reduced by 0.10 kg m⁻² in dry conditions under warming manipulation. The estimated net ecosystem carbon (C) balance was 0.65 and –0.16 kg m⁻² in wet and dry conditions, respectively, which indicates a net C emission of alpine meadow in wet but a net C sequestration in dry conditions. Our results emphasize the importance of incorporating SWC in simulation of ecosystem carbon balance under a warming climate.

Introduction

Soil contains the largest carbon (C) pool on the Earth and emits 68 to 80 Pg C per year to the atmosphere by soil respiration (Rₛ), which is the second largest C flux between the atmosphere and terrestrial ecosystems (Raich and Schlesinger, 1992). The annual C efflux from soil is ten times greater than the C emission from fossil fuel combustion. Thus a small warming-induced change in Rₛ could significantly aggravate or mitigate the buildup of CO₂ in the atmosphere (Cox et al., 2000; Friedlingstein et al., 2006). For example, an increase of 1 °C in air temperature would cause 10%–28% more C release (11–34 Pg C yr⁻¹) to the atmosphere (Schimel et al., 1994).

Soil respiration consists of two major components: autotrophic respiration (Rₐ) from plant roots and their symbionts, and heterotrophic respiration (Rₜ) from litter and soil organic C decomposition (Hanson et al., 2000), which have different implications for ecosystem C balance. In general, Rₛ consumes photosynthate recently fixed by the canopy, hence it has little impact on annual net ecosystem C balance (Hogberg et al., 2001), whereas Rₛ decomposes old C in the form of soil organic C and litter, which might activate more C into the ecosystem C cycling (Trumbore, 2000). Responses of Rₛ and Rₜ to warming could be consistent increase (Schindlbacher et al., 2009; Zhou et al., 2007), consistent decline (Zhou et al., 2010), or contrast (Li et al., 2013). The consistent or contrasting responses of Rₛ and Rₜ bring about diverse response of Rₛ to climatic warming. Most studies show significant increase in Rₛ (Rustad et al., 2001; Wu et al., 2011) due to higher activity of microbes and roots (Biasi et al., 2008; Emmett et al., 2004), or due to enhanced C input from plant uptake and allocation to the roots (Luo et al., 2009). However, some studies also find a decrease in dry condition because of the reduction in above-ground plant activity and the corresponding decline in Rₛ resulted from soil water stress, or because soil drying inhibited Rₛ more than soil warming enhanced it (Saleska et al., 1999), or owing to limitation in gas diffusion, nutrients availability to plants and microorganisms, and the potential for soil anoxia in wet condition (Pacifici et al., 2009).

Permafrost thaw affects the soil water saturation and thus will change the soil oxygen and influence soil C decomposition in tundra under a warming climate (Schuur et al., 2009). Decomposition in oxic soils releases primarily CO₂, whereas anoxic decomposition produces both CH₄ and CO₂ but at a lower emission rate. Ecosystem respiration is inhibited in wet and moist tundra because of soil anoxia resulted from soil water saturation, whereas it is stimulated in dry tundra (Oberbauer et al., 2007; Shaver et al., 2000). Alpine meadow in the permafrost area in the Qinghai-Tibet Plateau (QTP) stores 0.22 Pg C (Tao et al., 2007) and is estimated to lose 0.18 Pg C from 1986 to 2000 due to warming and grazing (Wang et al., 2008). Studies show a decrease of soil moisture in surface layer (Klein et al., 2005; Lin et al., 2011) but an increase in deep layers under warming (Xu et al., 2015). Compared to the Arctic tundra, alpine meadow is well drained, thus we hypothesize that responses of Rₛ and its components to warming in alpine meadow are different from those in Arctic tundra in sites with different soil water content (SWC).
SITE DESCRIPTION

The study site is situated in the source region of the Yangtze River and in the middle of the QTP (Fig. 1, part A, 92° 56′ E, 34° 49′ N) with a mean altitude of 4635 m and typical alpine climate (Fig. 1, part B). Mean annual temperature is −3.8 °C with a minimum of −27.9 °C in January and a maximum of 19.2 °C in July. Mean annual precipitation is 290.9 mm with 95% falling from May to October. Mean potential annual evaporation is 1316.9 mm, mean annual relative humidity is 57%, and mean annual wind velocity is 4.1 m s −1 (Lu et al., 2006). The study site is a winter-grazed range, dominated by alpine meadow species: Kobresia capillifolia, Kobresia pygmaea, Carex moroeriflora, with mean plant height of 5–10 cm. Plant roots are mainly at 0–20 cm soil depth with an average soil organic C of 1.5%. Soil development is weak and belongs to the alpine meadow soil (soil taxonomy in China, and cryosolos in World Reference Base taxonomy) with a matted epipod at approximately 0–10 cm depth and organic-rich layer at the depth of 20–30 cm (Wang et al., 2007). The parent soil material is of fluvial-glacial origin and sand (>0.05 mm) contents reach to 95%. Permafrost thickness near the experimental site is 60–200 m and the active layer is 2.0–3.2 m (Pang et al., 2009), which has been increased at the rate of 3.1 cm yr −1 from 1995 to 2000 (Wu and Liu, 2004). The experimental field was on a mountain slope with a mean inclination of 5°. Detailed information about soil properties in the 0–20 cm layer and plant features in dry and wet conditions are in Table 1. Species composition was similar but with higher coverage and plant height in wet than in dry conditions. Average elevation difference between plots in wet and dry conditions was about 1 m (Fig. 1).

EXPERIMENTAL DESIGN AND MEASUREMENT PROTOCOL

Experimental Design

We used a split-plot experimental design with soil moisture condition as the main factor and warming as the secondary factor in this study. Four pairs of control (unwarmed) and warmed plots were in a dry site and five of them were in a wet site (Fig. 1, part C). In each warmed plot, one 165 cm × 15 cm infrared heater (MR-2420, Kalgoorlie Electronics, Utah, U.S.A.) was suspended in the middle of the plot at a height of 1.5 m above the ground with a radiation output of 150 W m −2. The heating was operated year-round since 1 July 2010. To simulate the shading effect of heaters, one “dummy” heater made of metal sheet with the same shape and size as the heater was also installed in the control plot. For each of the paired plots, distance between the control and the warmed plots was at least 4 m to avoid the heating of the control plot by the infrared heater. The distance between the paired plots varied from 20 to 50 m (Fig. 1).

MEASUREMENT PROTOCOL

A polyvinyl chloride (PVC) collar (80 cm 2 in area and 5 cm in depth) was permanently inserted 2–3 cm into soil at the center of each plot for measuring R s. Small living plants were removed at the soil surface at least one day before the R s measurement to eliminate the effect of above-ground biomass respiration (Zhou et al., 2007). A deep PVC tube (80 cm 2 in area and 50 cm in depth) was inserted into the soil in each plot near the shallow collar in July 2010 for measuring R c. The deep PVC tube cuts off old plant roots and prevents new roots from growing inside the tube. Carbon dioxide efflux measured above deep tubes was used to represent the effect of above-ground biomass respiration (Zhou et al., 2007). A deep PVC tube (80 cm 2 in area and 50 cm in depth) was permanently inserted 2–3 cm into soil at the center of each plot near the shallow collar in July 2010. The increasing magnitude had no difference between the dry and wet sites (1.75 and 1.76 °C in wet and dry).

Three months of deep collar insertion. The R c value was calculated as the difference between R s and R c, which was measured once or twice a month between 10:00 and 15:00 hours (local time), using a Li-COR 6400 portable photosynthesis system attached to a soil CO2 flux chamber (Li-COR, Lincoln, Nebraska, U.S.A.).

Soil temperature was monitored by thermo-probes (Model 109, Campbell Scientific, Utah, U.S.A.) installed at 5.0 cm depth in the center of each plot. Volumetric SWC (v v% −1) was measured based on frequency domain reflectometry (FDR; Sentek Pty, Stepney, Australia) at 0–10, 10–20, 20–40, 40–60, and 60–100 cm depths in each plot. The daily average data of soil temperature and moisture were recorded in a CR 1000 data logger (Campbell Scientific, U.S.A.).

Above-ground biomass (AGB) in each plot was obtained indirectly from a step-wised multiple linear regression (AGB = 22.76 × plant height + 308.26 × Coverage – 121.80, R 2 = 0.74, P < 0.01, n = 100). In each month of the growing season, we took eight repeated measurements of plant coverage and forty measurements of plant height in each plot. The average plant coverage and height were substituted into the linear function to get the monthly AGB data of each plot. Root biomass (RB) was obtained from soil samples at 0–10, 10–20, 20–30, 30–40, and 40–50 cm depths. The soil samples were air-dried for one week and passed through a 2-mm-diameter sieve to remove large particles. Procedure of separation of roots from soil and the separation of living roots from dead roots can be found in Yang et al., 2009a.

DATA ANALYSIS

Soil respiration and its components were fitted exponentially and linearly with soil temperature. Determinant coefficient was used to examine which model was better for deriving their temperature sensitivity (Q 10). If the linear fitting performed better than did exponential model, Q 10 would be obtained by multiplying the slope of linear fitting with 10.

Daily soil temperature and SWC data were used and analyzed with a two-way ANOVA analysis. The measured R s, R c, AGB, and RB in each replicate were averaged to get the monthly data, and the monthly data were analyzed by variance analysis of split-plot design in SPSS 16.0 when investigating the effects of warming, soil moisture condition, and their interaction on these parameters.

Fourteen measurements of R s and R c, and the calculated R c were averaged. Mean R s, R c, and R c were multiplied by growing season length to estimate the total C release. AGB and RB change in growing season was the sum of difference in five months between control and warming plots (May–September).

Results

MICROCLIMATE

Mean soil temperature was higher in dry (0.32 °C) than in wet sites (−0.16 °C; Fig. 2, part A) in control plots, which significantly increased by warming in both conditions (P < 0.01; Fig. 2, part A). The increasing magnitude had no difference between the dry and wet sites (1.75 and 1.76 °C in wet and dry). Soil water content was higher in wet than in dry sites in control plots (Fig. 2, part B), which significantly decreased by 0.89% and 2.0% in 0–10 cm but increased by 2.62% and 2.99% (v v% −1) in 60–100 cm layer in wet and dry conditions (Fig. 2, part B), respectively.
FIGURE 1. (A) Location, (B) warming equipment installation, and (C) plots distribution of the experimental site.
RELATIONSHIP OF SOIL RESPIRATION AND ITS COMPONENTS WITH ABIOTIC FACTORS

Soil temperature was positively correlated with $R_s$ and its components in wet conditions, whereas it only correlated with $R_s$ and $R_h$ in dry conditions (Fig. 3, parts A, C, and E). $Q_{10}$ of $R_s$ was higher in wet than in dry conditions (4.67 vs. 3.55), but that of $R_h$ was higher in dry than in wet conditions (2.87 vs. 3.44). No obvious relationship was observed between SWC and $R_s$ and its components in wet conditions but a positive correlation occurred between SWC and $R_a$ and $R_h$ in dry conditions (Fig. 3, parts B, D, and F).

RESPONSES OF SOIL RESPIRATION AND ITS COMPONENTS TO WARMING

Soil respiration and its components were higher in summer and lower in winter (Fig. 4). Soil respiration and $R_h$ had no significant differences between the two sites (Table 2), while $R_s$ was marginally higher in wet than in dry conditions (Table 2). Warming significantly increased $R_s$ and $R_h$ but had no effect on $R_a$ (Table 2). On average $R_s$ and $R_h$ increased by 9.9% and 12.7% in both wet and dry conditions. The interaction between warming and SWC had a significant effect on $R_s$ and $R_h$ but had no effect on $R_a$ (Fig. 5; Table 2). Both $R_s$ and $R_h$ decreased in dry but increased in wet condition. On average $R_s$ and $R_h$ decreased by 5.8% and 36.3% in dry but increased by 23.5% and 47.7% in wet. The estimated increase in soil C emission in growing season was 0.65 kg m$^{-2}$ in wet condition, of which $R_h$ increased contributed to 0.33 kg C m$^{-2}$. The estimated reduction in soil C emission was 0.16 kg C m$^{-2}$ in dry condition, among which $R_a$ decrease accounted for 0.17 kg C m$^{-2}$.

Contribution of $R_h$ to $R_s$ ($R_h:R_s$) was significantly different between dry and wet (Table 2). On average $R_h:R_s$ was 76% ± 3% and 63% ± 3% in dry and wet, respectively. Interaction between warming and SWC significantly affected the $R_h:R_s$ (Table 2). Warming increased $R_h:R_s$ (70% ± 4% vs. 82% ± 4% in control and warming, respectively) in dry but decreased it in wet condition.

![Graph](https://bioone.org/journals/Arctic,-Antarctic,-and-Alpine-Research)
in wet condition (67% ± 4% vs. 60% ± 4% in control and warming).

**RESPONSES OF ABOVE-GROUND AND ROOT BIOMASS TO WARMING**

Soil water content and warming had no significant effects on AGB and RB (Table 2). However, their interaction significantly affected AGB. On average, warming increased monthly average AGB by 0.02 kg m⁻² in wet but decreased it by 0.02 kg m⁻² in dry conditions (Fig. 6). The cumulative AGB increase was 0.1 kg m⁻² in wet and the reduction was 0.1 kg m⁻² in dry condition in growing season.

The seasonal variation in Rs and its components were largely (87%, 75%, and 18%) explained by AGB (Fig. 7). Rs and Rh were more sensitive to AGB than was Ra (Fig. 7).

**Discussion**

**RESPONSES OF Rs AND ITS COMPONENTS TO WARMING**

In most field experiments, warming manipulation increases Rs (Rustad et al., 2001; Wu et al., 2011), but the negative warming effect on Rs is also reported (Saleska et al., 1999). We found that warming effects on Rs depend on SWC, which was stimulated in wet but suppressed in dry condition (Fig. 5). The opposite respons-
es of $R_s$ in our study are consistent with results from a semi-arid steppe ecosystem (Mauritz and Lipson, 2013) and an old-field ecosystem dominated by grasses and forbs (Suseela and Dukes, 2013). In a semi-arid area, $R_s$ and its components are inhibited when SWC is less than 10% or more than 15% (Mauritz and Lipson, 2013). The positive relationship between $R_s$ and SWC in dry conditions (Fig. 3, part B) implies the SWC limitation on $R_s$ in dry conditions, therefore $R_s$ reduction is likely the result of lower SWC in dry sites (6.8% in control and decreases under warming). Nevertheless, results in our study are also different with Arctic tundra ecosystem, in which ecosystem respiration is suppressed in wet and moist but stimulated in dry tundra (Oberbauer et al., 2007). Soil water content is generally higher than the field capacity and there is even

<table>
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<th>TABLE 2</th>
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<td>Results ($F$-values) of split-plot variance analysis on the effects of warming, soil moisture condition, and their interaction on soil respiration ($R_s$) and its components ($R_a$ and $R_h$), aboveground biomass (AGB), and root biomass (RB).</td>
</tr>
<tr>
<td>variance source</td>
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<td>-----------------</td>
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<tr>
<td>SWC 0.006</td>
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<td>W 5.3*</td>
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<td>W × SWC 12.9**</td>
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Significance: *, $P < 0.05$; **, $P < 0.01$
Lower water table resulting from warming would lead to saturation stress for ecosystem respiration in wet tundra (Oechel et al., 1998). Saturation stress does not exist in our study because SWC is lower than the field capacity even in the wet site and this led to the $R_s$ increase.
Autotrophic respiration and $R_a$ could both positively or negatively (Schindlbacher et al., 2009; Zhou et al., 2007) or conversely respond to warming (Li et al., 2013). The consistent positive in wet and negative responses in dry of $R_a$ and $R_h$ (Fig. 5) in our study could be caused by the corresponding changes in SWC and biomass. Positive correlation between $R_a$ and soil temperature but no obvious relationship between SWC and $R_a$ either in dry or in wet (Fig. 3, part D) indicates that soil temperature is more important than SWC in regulating soil C decomposition in alpine meadow. $R_a$ is affected by total detritus input or AGB (Bond-Lamberty et al., 2004), and $R_h$ is determined by RB (Zhou et al., 2007) and temperature dependence of specific root respiration (Boone et al., 1998). Possible elevated
detritus input and the associated AGB increase in wet (Fig. 6, part A) therefore would be responsible for the \( R_s \) increase because of the positive relationship between AGB and \( R_s \) (Fig. 7). The effect of AGB decrease on \( R_s \) could be compensated by the increase in RB, thus resulting in non-significant change in \( R_s \) in dry condition. \( R_s \) increase in wet is likely due to the soil temperature increase because of the positive correlation between them (Fig. 3, part E). Soil moisture deficit constrains \( R_s \) through limitation on annual productivity (Li et al., 2013), root growth (Zhou et al., 2007), and specific \( R_s \) rate (Michele and Douglas, 2009). Non-significant change in RB under warming in dry condition suggests the change in specific \( R_s \) rate. We have no direct data on the specific \( R_s \), but the species composition change in our study site (Xu et al., 2014) might change the RB quality, thus resulting in the specific \( R_s \) change under warming.

The response of \( R_s \) to warmer soil can affect ecosystem C allocation and the strength of positive feedback of soil CO\(_2\) efflux to climate warming. Both \( R_s \) and \( R_d \) increased with larger relative increase in \( R_s \) in wet (53% vs. 33% in \( R_s \) and \( R_d \)), which suggests that the effect of warming-induced change in biomass on \( R_s \) is larger than direct temperature effect on \( R_s \).

Higher \( Q_{10} \) of \( R_s \) in dry than in wet conditions is similar to the result in an incubation study where \( Q_{10} \) of \( R_s \) decreases as SWC increases (Guntiñas et al., 2013). However, higher \( Q_{10} \) of \( R_s \) in wet than in dry is observed in a desert shrub ecosystem (Wang et al., 2013) and in our study. The higher \( Q_{10} \) of \( R_s \) in dry may be due to the switch in C pool of labile substrate to recalcitrant substrates (Reichstein et al., 2002) because recalcitrant C is more sensitive to temperature change than is labile C (Knorr et al., 2005). Root always exerts a strong influence on \( Q_{10} \) of \( R_s \) (Boone et al., 1998; Zhou et al., 2007). The lower \( Q_{10} \) of \( R_s \) in dry is probably the result of lower RB biomass (Fig. 6, part B). The contrast performance of \( Q_{10} \) of \( R_s \) and \( R_d \) in wet and dry in our study suggests that \( R_s \) has a large effect on apparent \( Q_{10} \) of \( R_s \) and indicates apparent \( Q_{10} \) obtained in field studies without exclusion of \( R_s \) may overestimate the warming effect on soil C output.

**BIOMASS RESPONSES TO WARMING**

In an experimental warming study covering an elevation gradient from 4300-4600 m in alpine meadow, AGB significantly decreased at the 4300 m study site, but had no significant change in the 4600 m site (Fu et al., 2013). Optimum air temperature (\( T_o \)) for AGB is about 5.8 °C (Wang et al., 2012), and AGB increases with increasing water availability in the alpine meadow of Tibet (Yang et al., 2009b). Annual mean \( T_o \) in the present study is ~3.8 °C, which is much lower than the optimum temperature. The elevated temperature is probably the reason for AGB increase in wet condition. The minimum SWC for meadow growth is found to be 11.8% (Ma et al., 2004), which is much higher than the mean SWC in dry condition. Although soil temperature significantly increased in dry condition (Fig. 2, part B), lower SWC and its decrease could result in the AGB decrease (Fig. 6, part A), which suggests that AGB is more sensitive to SWC than temperature change when SWC is lower than a threshold.

**IMPLICATION FOR THE FEEDBACK OF ECOSYSTEM CARBON BALANCE TO WARMING**

The growing season AGB increase in wet (0.1 kg m\(^{-2}\)) and decrease in dry (0.1 kg m\(^{-2}\)) is much lower than the soil C release change under warming (0.65 kg m\(^{-2}\) in wet and ~0.16 kg m\(^{-2}\) in dry). The balance between AGB and \( R_s \) is 0.55 and ~0.06 kg C m\(^{-2}\) in wet and dry conditions, respectively. The results suggest net C release in alpine meadow under warming climate when SWC maintains greater than 10%. Decrease in \( R_s \) especially in \( R_s \) could make the alpine meadow ecosystem serve as a C sink since reduction in \( R_s \) is higher than the decline in C uptake when SWC is less than 10%.

**Conclusion**

Soil water content determines responses of \( R_s \) and its components to warming. \( R_s \) is more sensitive to the decrease in SWC than to the increase in soil temperature when SWC is lower than 10%. AGB increase does not result in a net C gain as \( R_s \) is also largely stimulated when SWC is higher than 10% in alpine meadow. Carbon gain could happen when SWC is less than 10% as decrease in AGB under warming in dry condition would be offset by a substantial decrease in \( R_s \) and the corresponding decline in \( R_s \), SWC difference should be considered in an ecosystem C model when investigating climatic warming effects on terrestrial ecosystem C balance.

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