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Research Paper

Grassland types and season-dependent response of ecosystem respiration to experimental warming in a permafrost region in the Tibetan Plateau

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ABSTRACT

Information regarding the response of ecosystem respiration (ER) to various warming levels, especially in different grassland types and seasons, is scarce at the field scale in the permafrost region of the Tibetan Plateau (TP). In this study, we examined how different warming levels during different seasons affected ER in Tibetan alpine meadow and swamp meadow after 6 years experimental warming. The interpolated annual ER of swamp meadow (387.0 $\mathrm{gC\,m^{-2}}$) was higher than that of alpine meadow (284.5 $\mathrm{gC\,m^{-2}}$) in natural conditions. A moderate warming of 2.4 °C increased ER by 62.2% and 36.6%, and a high warming of 5.3 °C increased ER by 101.3% and 52.0% in alpine meadow and swamp meadow, respectively. The warming effects on ER were greater in the non-growing season compared with the growing season; this significantly increased the contribution of non-growing season emissions to annual ER from 25% in natural conditions to 31% in high warming treatments. ER was significantly affected by soil temperature, aboveground biomass and the duration of thaw days. The temperature sensitivity of ER (Q_{10}) was higher in the non-growing season (3.02–5.02) than in the growing season (2.11–2.75) and decreased with increasing temperature. Our results indicated that the magnitude of warming-induced increases in ER differed by grassland type and season, and there was strong potential for the non-growing season to serve as a positive feedback to annual carbon balance.

1. Introduction

Permafrost soil contains a large amount of carbon (1700 Pg) (Ding et al., 2016; Tarnocai et al., 2009) and temperatures in permafrost regions are increasing faster than the global average. High northern latitudes are predicted to increase 5–9 °C over the next century (IPCC, 2013). Warming could accelerate the permafrost thaw and result in degradation of 37–81% of surface permafrost at the end of this century (IPCC, 2013; Schuur et al., 2013). When permafrost degradation occurs, there is a high risk of ecosystem carbon loss. Climate warming will probably have particularly large impacts on ecosystem respiration (ER) in arctic and alpine ecosystems due to permafrost thaw and the microbial decomposition of previously frozen soil (Hagedorn et al., 2010; Natali et al., 2014; Schuur et al. 2009), potentially creating a positive feedback to climate warming (Fouche et al., 2014; Schuur et al., 2015).

Many studies at the field scale have addressed the potential responses of ecosystem carbon exchange to simulated climate warming. Most previous *in situ* studies have focused on a single warming level (Dorrepaal et al., 2009; Fouche et al., 2014; Peng et al., 2015; Qin et al., 2015) but have ignored the ecosystem responses to various warming amplitudes with the exception of several incubation experiments in the laboratory (Hopkins et al., 2014; Treat et al., 2014; Tucker et al., 2013). Changes in the rate of permafrost degradation and the thawing and freezing time of the soil active layer could be different under different warming amplitudes. Thus, quantifying how these changes regulate ER intensity and its seasonal distribution is important to understanding potential permafrost carbon exchange in a warmer future.

The majority of previous studies have generally reported positive warming effects on ER (Fouche et al., 2014; Natali et al., 2014; Qin et al., 2015; Wu et al., 2011), although some studies have shown negative (Fu et al., 2013) or null effects (Lin et al., 2011) in arctic and alpine ecosystems. These varied results may stem from the various ecosystem responses generated by experimental warming-induced changes in soil temperature and moisture as well as soil properties, plant biomass and their complex interactions (Fouche et al., 2014; Treat et al., 2014; Xu et al., 2015a). The effect of warming on ER may vary

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Table 1
Aboveground and belowground biomass in no warming (NW), moderate warming (MW) and high warming (HW) treatments.

Treatment	Aboveground biomass(g m^{-2})		Belowground biomass(g m^{-2})	
	Alpine meadow	Swamp meadow	Alpine meadow	Swamp meadow
NW	137.57 ± 4.75c	305.08 ± 17.19b	1464.06 ± 98.41b	10460.21 ± 217.86a
MW	378.59 ± 23.04a	400.07 ± 28.97a	2016.98 ± 33.54a	10910.05 ± 139.87a
HW	284.05 ± 11.56b	445.89 ± 20.24a	2508.21 ± 172.12a	10629.55 ± 254.57a

The difference lowercase in the same line were significant ($P < 0.05$), the values was means ± SE.

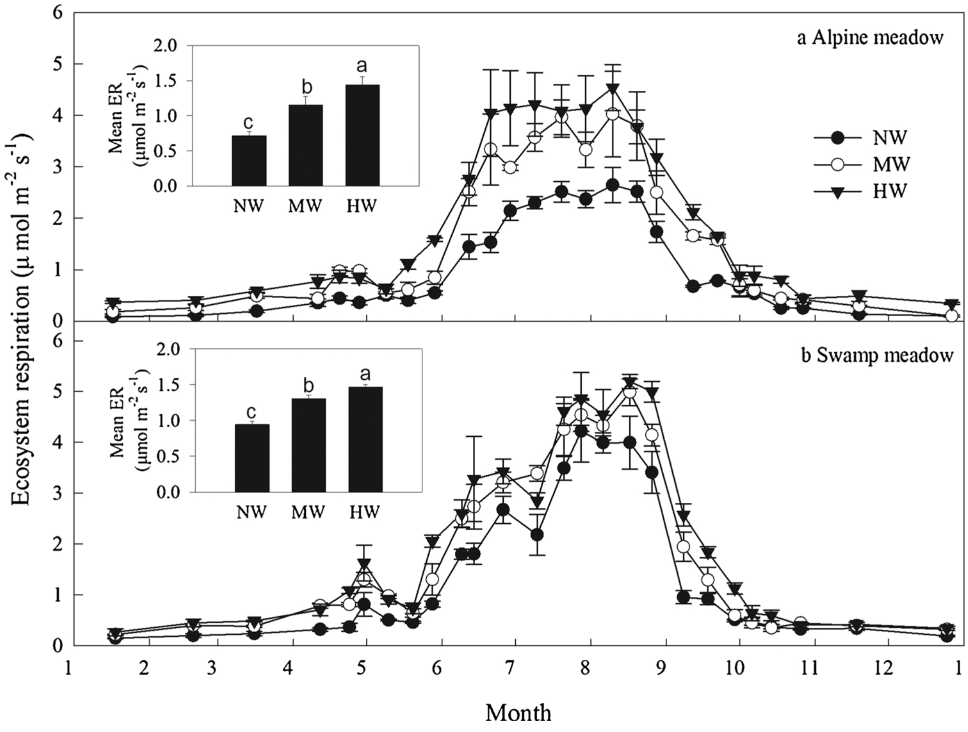

Fig. 1. Seasonal changes of ecosystem respiration (ER) in no warming (NW), moderate warming (MW) and high warming (HW) treatments in alpine meadow (a) and swamp meadow (b). The panel is annual average ER. Error bars show standard error.

Table 2
Results of repeated-measure ANOVA on the effects of grassland type, warming and sampling date, and their interactions on ecosystem respiration.

Variance source	*F*	*P*	*d.f.*
Grassland type (S)	29.12	0.033	1
Warming(W)	138.58	< 0.001	2
Date(D)	84.18	< 0.001	25
S*W	4.08	0.108	2
S*D	9.77	< 0.001	25
S*W*D	1.59	0.025	50

with ecosystem and vegetation types due to microenvironment differences (Oberbauer et al., 2007; Sharkhuu et al., 2013). For example, warming may increase net CO_2 uptake in wet tundra, but increase losses from dry tundra (Oberbauer et al., 2007); drier soil conditions will accelerate decomposition, with concomitant increases in CO_2 emissions (Lawrence et al., 2015), emphasizing the importance of soil moisture-dependence for predicting warming effect on ER. However, the effect of soil moisture regulation on the response of ER to different warming amplitudes is not well understood in permafrost ecosystem at the field scale.

Non-growing season respiration is an important component of the global carbon cycle (Monson et al., 2006). Although the response of ER to climate warming has been studied in various ecosystems, non-growing season respiration has received less attention because of budget/logistical constraints and the overall hypothesis that winter respiration rates are much lower than those during the growing season (Elberling, 2007; Trucco et al., 2012). However, we have long known that respiration continues to occur at cold winter temperatures (Coyne and Kelley, 1971); recent studies have shown that some microorganisms metabolize at extremely low temperatures in permafrost (Jansson and Tas, 2014). Some studies have shown large contributions of non-growing season CO_2 fluxes to annual emissions in alpine (Wang et al., 2014b; Zhang et al., 2015) and Arctic (Euskirchen et al., 2012; Merbold et al., 2012; Schuur et al. 2009) tundra. The warming-induced increase in growing-season carbon gain may be offset by the warming-derived non-growing season respiration; increased non-growing season CO_2 loss to warming has been reported in permafrost regions (Belshe et al., 2013; Webb et al., 2016). Warming could cause huge changes in non-growing season respiration and could alter the annual C balance from its historical C sink to source in Arctic tundra (Natali et al., 2011). Therefore, the non-growing season ER is an important part in quantifying the annual carbon budget of permafrost ecosystems in response to climate warming.

The Tibetan Plateau (TP) is one of the areas impacted by permafrost in this region and sensitive to global climate change (Liu and Chen, 2000). Evidence indicates that the permafrost region in this area exhibited a rapid increase (0.4–0.67 °C/10a) in climate warming over the last 45 years (Wang et al., 2011). Warming has resulted in permafrost thaw in this region (Cheng and Wu, 2007). Although the relationship between ER and climate warming has been widely studied on the TP, most have focused on the growing seasons (Peng et al., 2014; Qin et al., 2015), short-term warming effects (< 5 years) (Peng et al., 2015), and

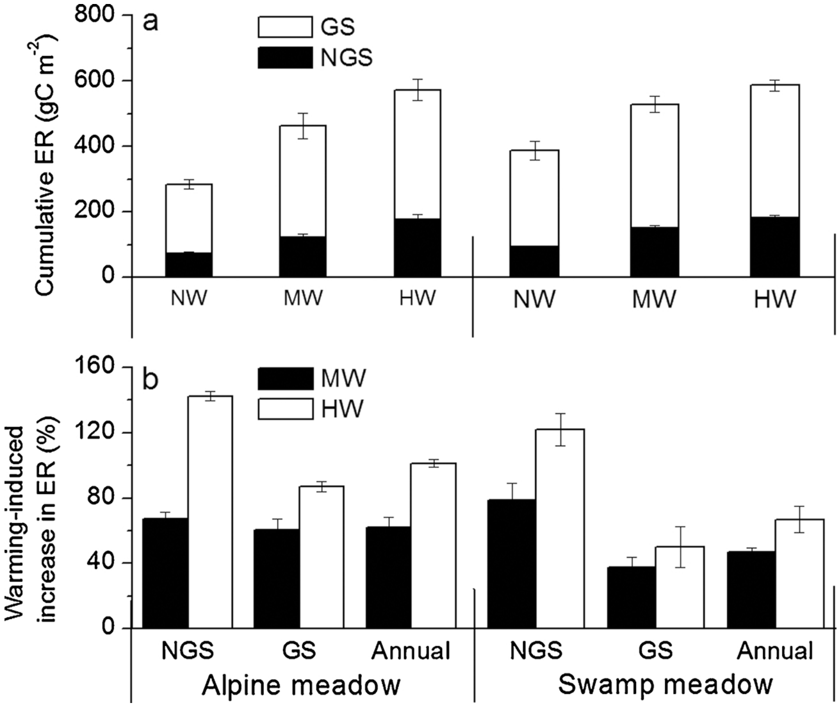

Fig. 2. Interpolated non-growing season (NGS) and growing season (GS) ecosystem respiration (ER) in no warming (NW), moderate warming (MW) and high warming (HW) treatments (a), and the warming-induced increase in ER (b). Warming-induced changes were defined as%effect = ((warming-control)/control)*100. Error bars show standard error.

non-permafrost areas (Lin et al., 2011). In addition, previous studies mainly focused on alpine meadow (dry condition); though the permafrost in this region is largely dominated by alpine meadow (70% of the area), there are also areas of swamp meadow (6.5%) under moist soil conditions (Li et al., 2011). Long-term experimental warming studies have not generally considered the response of growing season and non-growing season ER, under both dry and moist soil conditions, to this warming. In particular, experimental warming studies have not examined changes in ER under an annual freeze-thaw cycle.

To characterize permafrost ER feedback to climate warming across time, seasons and soil moistures, we conducted a full year of measurements of ER in alpine meadow (dry) and swamp meadow (moist) after 6 years of experimental warming; warming treatments included two warming levels in the permafrost region of TP. The objectives of this study were the following: (1) compare the differences of growing and non-growing season ER changes under different warming levels and (2) investigate how soil moisture regulates the responses of ER to long-term experimental warming.

2. Methods

2.1. Study site

This study was conducted on Fenghuo mountain in the permafrost region of the Tibetan Plateau, China (92°50′–93°3′E and 34°40′–34°48′N; 4600–4800 m a.s.l.), located within the region of continuous permafrost with an active layer of 0.8–1.5 m. The mean annual temperature and precipitation are −5.3 °C and 269.7 mm, respectively; 80% of the precipitation falls during the growing season (from May to September). The soil types in the study region belong to alpine meadow soil (Li et al., 2011). Alpine meadow is the dominant vegetation type in this region, followed by swamp meadow. The vegetation of alpine meadow mainly consists of *Kobresia pygmaea* (C. B. Clarke), *K. humilis* (C. A. Meyerex Trautvetter), *Sergievskaja, Kobresia capillifolia* (Decaisne) (C. B. Clarke), *Kobresia myosuroides* (Villars) Foiri, *Kobresia graminifolia* (C. B. Clarke), *Carex atrofusca Schkuhrsub* sp. (minor (Boott) T. Koyama), and *Carex scabriostris* (Kukenthal). The swamp meadow is dominated by *Kobresia tibetica* Maximowicz, *Stipa aliena* Keng and *Festuca* spp. (Li et al., 2011).

2.2. Experimental design

Warming was achieved using open top chambers (OTCs) in alpine meadow and swamp meadow (Marion et al., 1997). Two different heights of OTCs were constructed to create different warming levels (Li et al., 2011; Yang et al., 2015). Chambers of 40-cm height with a basal area of 0.98 m^2 were used to create a moderate level of warming, approximately 2.4 °C, and chambers of 80-cm height with a basal area of 2.01 m^2 were used for a high level of warming, approximately 5.3 °C (Table S1). The experiment was conducted with a random block design in the alpine meadow and swamp meadow. Three blocks, with one no-warming (NW) plot, one moderate-warming (MW) plot and one high-warming (HW) plot in each block, were installed in June 2008 in each meadow. Air temperature measurements at 15 cm above the ground were recorded every 10 min by a Decagon ECT sensor fitted with a radiation shield; soil temperature and soil moisture at 5, 20 and 40 cm depths were measured in each treatment at both meadow types using Decagon 5TM and EC-TM sensors with Em50G data acquisitor (Decagon Devices, Pullman, Washington, USA).

2.3. Ecosystem respiration measurement

In this study, all measurements were taken in 2013 after 6 years of experimental warming. ER was measured both in the growing season and the non-growing season. The growing season was usually from late May to mid-September and the non-growing season was from late September to May in this study site (Zhang et al., 2015). ER was measured three times each month from April to October and once each month from November to March using the LI-8100a portable CO$_2$ flux system equipped with a CO$_2$ flux chamber (LI-COR Inc., Lincoln, NE, USA) (Qin et al., 2015). One polyvinyl chloride collar (20.3 cm in diameter and 5 cm in height) was inserted into each plot for ER measurements. Living plants inside the collar were measured carefully to avoid disturbance. All of the collars were left in place until the end of the study. ER was measured between 9:00 and 11:30 a.m. local time to represent the daily average flux based on diurnal measurements (data not shown). Soil temperature and moisture at 5 cm were measured at the same time as the ER measurements near the collar.

Estimates of cumulative ER were obtained by interpolating the daily

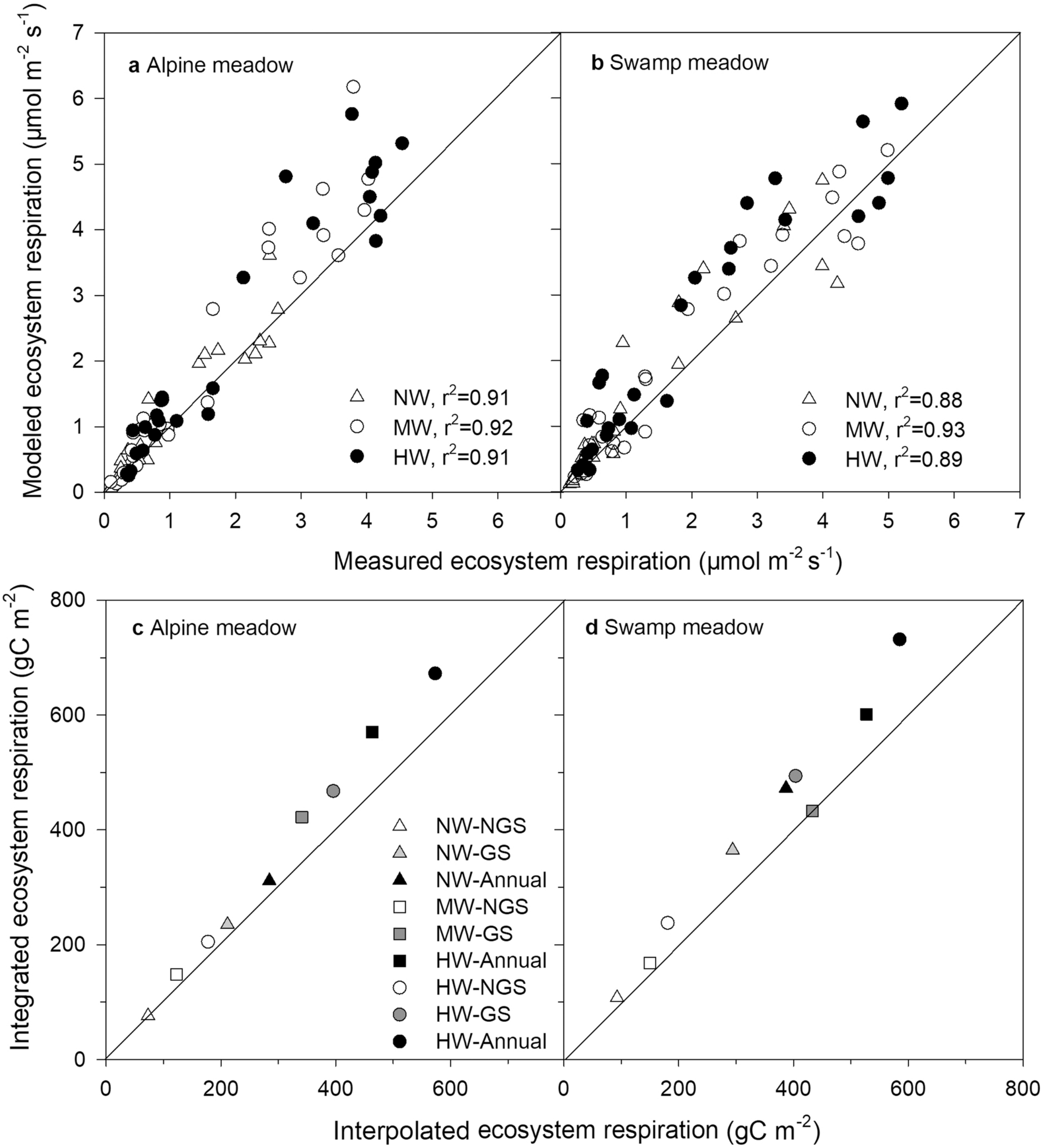

Fig. 3. Measured vs. modeled ecosystem respiration (a, b) and interpolated vs. integrated annual, growing season (GS), non-growing season (NGS) ER emission (c, d) of alpine meadow and swamp meadow in no warming (NW), moderate warming (MW) and high warming (HW) treatments. The solid line is the 1:1 line.

average ER between sampling dates and computing the sum of the products of the average ER and the time between respective sampling dates for each measurement period as follows (Zhang et al., 2015):

$$ER = \sum_{k=1}^{n-1} ERm,\, k\Delta t_k \tag{1}$$

where $\Delta t_k = t_{k+1}\text{-}t_k$ is the number of days between each measurement, *ER* is the total ER, and *ERm, k* is the average ER over the interval $t_{k+1}\text{-}t_k$ measured by the LI-8100a. Additionally, cumulative ER was computed by integrating the soil temperature response function (Eq. (3)) and the continual soil temperature data at 5 cm.

Warming effects were defined as percentages by the Eq. (2):

$$\%\text{effect} = ((\text{warming-control})/\text{control})*100 \tag{2}$$

2.4. Dependence of ER on soil temperature

The temperature sensitivity of ER (Q_{10}) was calculated as follows (Zhang et al., 2015):

$$ER = ae^{bST} \tag{3}$$

$$Q_{10} = e^{10b} \tag{4}$$

where *ER* and *ST* are ecosystem respiration and soil temperature at 5 cm depth, respectively, and *a* and *b* are constant coefficients.

2.5. Vegetation sampling

Aboveground biomass was collected from three subplots within each plot by clipping vegetation above the soil surface in mid-August

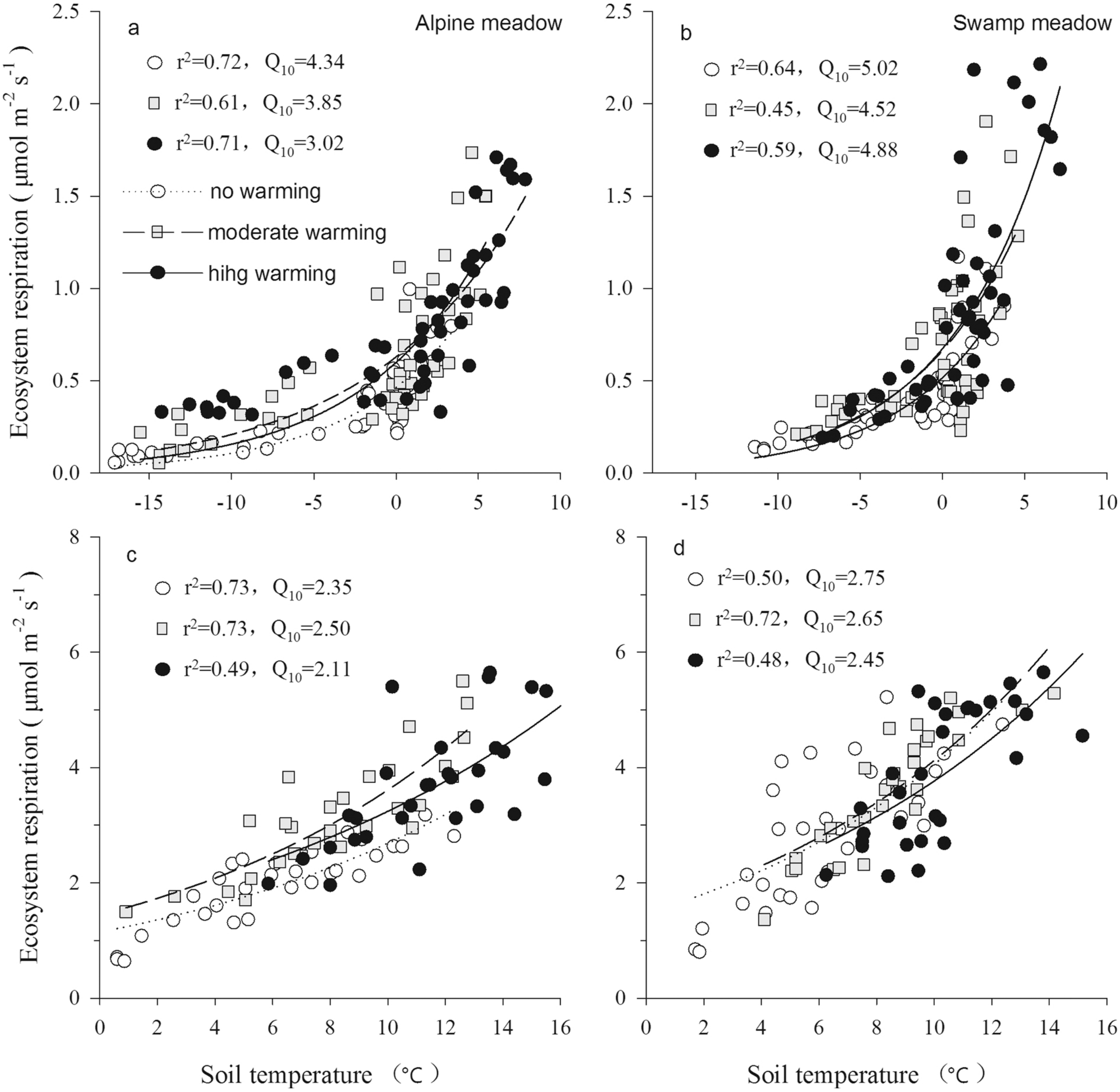

Fig. 4. Exponential relationship between ecosystem respiration and soil temperature at 5 cm in the non-growing season (a and b) and the growing season (c and d) in alpine meadow and swamp meadow.

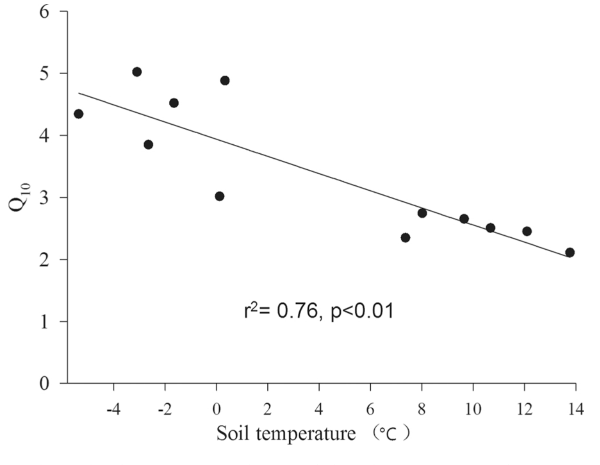

Fig. 5. Relationship between seasonal Q_{10} and the relative average soil temperature at 5 cm based on all treatments.

2013. Root biomass was collected by soil cores (5 cm in diameter) from the same subplot at a depth of 40 cm. Soil cores were washed to separate roots from the soil. All biomass samples were dried for 48 h at 60 °C before weighing. The aboveground and belowground biomass for each experimental plot was averaged from the three subplots.

2.6. Statistical analysis

A repeated ANOVA was used for statistical analysis; warming and vegetation types were the main factors and the sampling date was the within-subject factor including interactions on ER. A two-way ANOVA was used for multi-comparison with factors of warming and vegetation type-dependent variables for total ER emission, aboveground biomass and belowground biomass. Regression analysis was performed between ER and soil temperature, soil moisture, aboveground biomass and duration of thaw days. All statistical analyses were at a significance level of 0.05 and were completed using SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

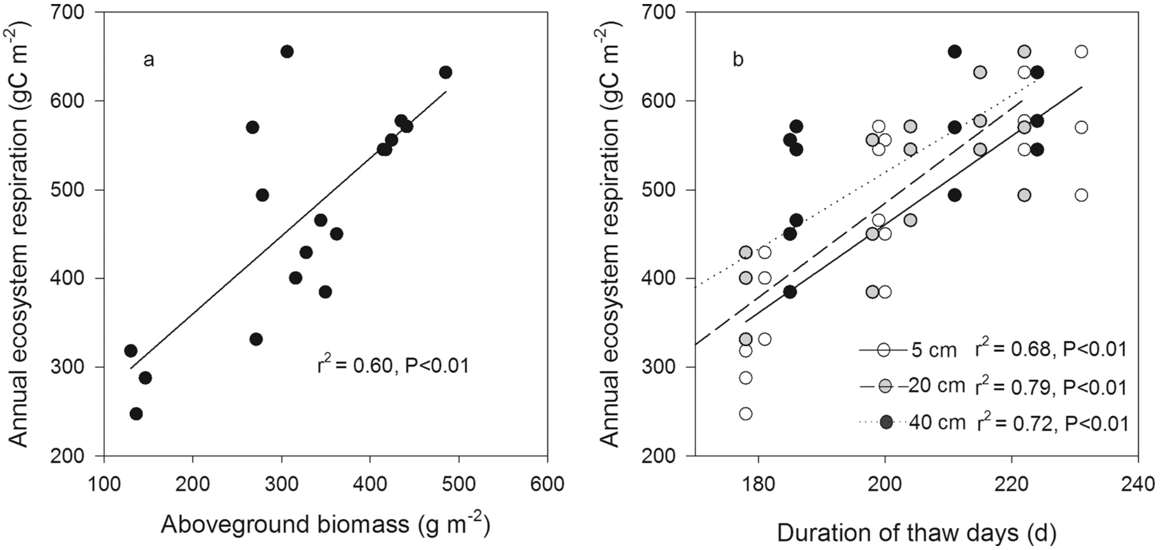

Fig. 6. Linear correlation between ecosystem respiration and aboveground biomass (a) and duration of thaw days (b) at 5, 20 and 40 cm depth of soil. The duration of thaw days was ranging from the first 7 consecutive days with average daily soil temperature at 5 cm above 0 °C to the first 7 consecutive days with average daily soil temperature below 0 °C.

3. Results

3.1. Climatic and biomass variables

Warming increased the annual mean air temperature by 2.08 and 2.73 °C for MW and by 4.91 and 5.67 °C for HW in alpine meadow and swamp meadow, respectively (Table S1). The annual mean surface soil temperature (5 cm) was raised by 2.88 and 1.49 °C for MW and 5.75 and 3.61 °C for HW in alpine meadow and swamp meadow, respectively (Table S1 and Fig. S1a, b). Soil moisture at 5 cm was 0.03 (MW) and 0.02 $m^3 m^{-3}$ (HW) lower in alpine meadow and 0.05 $m^3 m^{-3}$ (MW and HW) higher in swamp meadow compared to the NW (Fig. S1c, d). Warming accelerated the permafrost thawing and delayed the freezing time of the active layer; the duration of thaw days increased 22 (MW) and 53 (HW) days in alpine meadow, and 18 (MW) and 41 (HW) days in swamp meadow at 5 cm soil depth (Fig. S2).

Warming significantly increased aboveground biomass (AGB) in both meadows with an increase of 175.2% (MW) and 106.5% (HW) in alpine meadow and 31.1% (MW) and 46.2% (HW) in swamp meadow, respectively ($P < 0.05$, Table 1). The AGB of MW was significantly higher than HW in alpine meadow ($P < 0.05$) but was slightly lower than that of HW in swamp meadow ($P = 0.12$). Warming significantly increased belowground biomass (BGB) in alpine meadow ($P < 0.05$), but there was no difference in swamp meadow ($P > 0.05$, Table 1). Generally, the magnitude of the response varied between the two meadows; both the AGB and BGB were more responsive to warming in alpine meadow than in swamp meadow.

3.2. Warming effect on ER

ER showed large seasonal changes associated with surface soil temperature (Figs. 1 and S1), which was lowest because of permafrost frozen in mid-winter, increased in late April due to permafrost thaw, reached the maximum at the peak of plant growth (August) and subsequently decreased with plant senescence in September. In natural conditions, the annual average ER in alpine meadow (0.72 μmol $m^{-2} s^{-1}$) was significantly lower than that in swamp meadow (0.94 μmol $m^{-2} s^{-1}$) ($P < 0.05$, Fig. 1).

In general, ER was significantly affected by warming, grassland type, sampling dates and their interaction ($P < 0.05$, Table 2). Both MW and HW significantly stimulated ER across the year, but the ER increases differed in strength between the two meadows and warming levels (Figs. 1 and 2). The same amplitude of warming led to a greater increase of ER in alpine meadow than in swamp meadow, and the HW had a stronger effect on ER compared with MW ($P < 0.05$, Fig. 2a). The interpolated annual ER emission of MW and HW increased by 62.2% and 101.3% in alpine meadow and 36.6% and 52.0% in swamp meadow, respectively (Fig. 2b). When the data were divided into different seasons, we found that the warming-induced increase in ER was significantly higher in the non-growing season than in the growing season ($P < 0.05$, Fig. 2b), with the exception of MW in alpine meadow. Non-growing season ER contributed approximately 25% to annual ER emission in natural conditions, whereas warming tended to increase the contribution of non-growing season ER to annual emissions with significant increases in HW in both meadows ($P < 0.05$, Figs. 2 a and S3). The modeled ER matched the measured values well (r^2:0.88–0.93, Fig. 3a, b), and the integrated annual and non-growing season ER values were higher than interpolated values in all treatments (Fig. 3c, d).

3.3. Factors affecting C fluxes

ER showed a positive exponential increase with soil temperature (5 cm) both in the non-growing season and the growing season (Fig. 4); soil temperature explained 44.5%–73.2% of the temporal variation across all treatments. The temperature sensitivity of ER (Q_{10}) in the non-growing season was 4.34 and 5.02 in alpine meadow and swamp meadow in control treatments, and decreased with warming (Fig. 4a and b). The growing season Q_{10} (2.11–2.75) was lower compared with non-growing season (Fig. 4c and d). The Q_{10} values were negative correlated with soil temperature (r^2: 0.76) (Fig. 5). Aboveground biomass and duration of thaw days explained 59.6% and 67.5%–78.8% of annual ER emissions for pooled plots, respectively ($P < 0.05$, Fig. 6). ER of warming treatments showed a negative linear relationship (r^2: 0.18–0.30, $P < 0.05$) to soil moisture in swamp meadow during the growing season (Fig. S4b).

4. Discussion

4.1. Warming effect on ER

In natural conditions, the interpolated annual ER was 284–387 gC m^{-2}, which is in agreement with the 195–377 gC m^{-2} in three (dry, mesic and wet site) Canadian High Arctic ecosystems (Welker et al., 2004), but higher than the two representative tundra ecosystems (heath and wet sedge, 173–269 gC m^{-2}) in northern Alaska

(Euskirchen et al., 2012). Warming significantly increased the growing season ER, by 29–87% in the present study, similar to the results in other alpine meadows (17%–59%) (Hu et al., 2016; Qin et al., 2015) and Arctic tundra (48%–64%) (Dorrepaal et al., 2009; Fouche et al., 2014), whereas some studies have also reported negative (Zong et al., 2013) or null (Lin et al., 2011) effects on ER. Moreover, ER was higher in HW than that in MW in both meadows, which suggests that the ER was increased with temperature increase.

ER primarily consists of autotrophic respiration from plants and heterotrophic respiration from soil microorganisms, both of which respond equally strongly to warming and thawing permafrost (Dorrepaal et al., 2009; Hicks Pries et al., 2013). First, warming may increase the ecosystem autotrophic respiration by enhancing plant production (Jansson et al., 2008) because ER was positively correlated with aboveground biomass (Ganjurjav et al., 2014). In the present study, warming significantly extended the growing season (author's unpublished data) and increased the aboveground biomass (Table 1). We found a positive relationship between ER and aboveground biomass (Fig. 6a), suggesting that a large part of the ER increase was derived from the warming-induced increase in aboveground biomass. Similar results were also found in Tibetan (Jiang et al., 2013), Antarctic (Zhu et al., 2014) and Arctic (Natali et al., 2011) tundra ecosystems.

Second, warming may increase heterotrophic respiration by stimulating the thawing of permafrost, which may enhance the soil microbial activities and the decomposition of previously frozen soil (Dorrepaal et al., 2009; Natali et al., 2014; Schuur et al. 2009). In the present study, temperature remained above 0 °C at 5 cm depth for approximately 18–53 days and at 20 cm depth for approximately 26–56 days longer under warming treatment than under control treatment in the two meadows (Fig. S2). Therefore, more soil carbon is subject to decomposition in the warming treatment due to the strong microbial activity increases at temperatures above the freezing point (Monson et al., 2006). A previous study has shown that warming significantly stimulated heterotrophic respiration near our study site (Peng et al., 2015). Trucco et al. (2012) indicated that sites with more permafrost degradation had greater ER compared with sites with the least degradation. Consistent with these findings, we found that ER increased as the duration of thaw days increased as a result of warming (Fig. 6b).

In contrast to other studies in alpine tundra and steppe ecosystems (Gill, 2014; Luo et al., 2001; Zhou et al., 2016), the warming effects on ER did not decline (acclimation) after 6 years compared with our second year measurements (Bai et al., 2011). Similar results were also found in other boreal and subarctic ecosystems (Dorrepaal et al., 2009; Vogel et al., 2014). Generally, adaptation to warming is thought to result from the reduction of soil C supply and changes of microbial community (Bradford et al., 2008). We cannot verify this because we lack data on soil process response to warming in the study year. However, a previous study in this region has shown that both short-term (2-year) and long-term (10-year) warming did not significantly affect soil organic carbon, microbial biomass C and enzyme activities (Wang et al., 2014a). The continuous increase in the present study may be attributed to the significant increase of plant growth (Xu et al., 2015) and litter input (Yang et al., 2015). Warming could promote litter accumulation (Yang et al., 2015), which significantly increased soil CO_2 efflux over several years due to greater labile plant-derived carbon input into the soil (Sayer et al., 2011). Additionally, a possible reason for the continuous increase may be the warm-induced permafrost degradation at our study site, which may increase the old carbon emission (Schuur et al. 2009). For example, warming of 1 °C increased ER by 52–60% of which 69% originated from old C of active layer (25–50 cm) over 8 years (Dorrepaal et al., 2009). However, Bond-Lamberty and Thomson (2010) indicated that the belowground respiration increase could be driven by higher C input to soil rather than decomposing old C. Therefore, further study for determining the source of ER in response to warming is needed to verify the underlying mechanisms.

4.2. *Grassland type and season modify the ER response to warming*

We observed that warming led to a greater increase of ER in alpine meadow than in swamp meadow, which suggests that ER responses to warming differs in strength in different meadow types, with greater increases of Re under drier conditions compared with moist conditions. This was supported by Oberbauer et al. (2007), who reported that warming-induced increase in ER was greatest in dry conditions among many tundra ecosystems. Regardless of the temperature, higher soil moisture in the swamp meadow compared with alpine meadow (Fig. S1) may potentially suppress belowground respiration by limiting oxygen and nutrient availability (Schuur et al., 2015). We found that ER was negative correlated to soil moisture in swamp meadow during the growing season (Fig. S4b). Additionally, given that long-term warming-induced increase in ER is mainly due to plant-derived processes (Hicks Pries et al., 2015), a significant warming-induced increase in root biomass in alpine meadow compared with no change in swamp meadow would partly be a response to the higher increase of ER in alpine meadow because of root maintenance and growth respiration, as well as the aboveground biomass (Table 1). Moreover, although the air temperature was increased higher in swamp meadow than that in alpine meadow under the warming treatment, the soil temperature was increased less in swamp meadow compared with alpine meadow due to the moist soil conditions (Table S1), thereby resulting in stronger ER in alpine meadow.

The non-growing season CO_2 emission plays an important role in determining the annual C balance but has been poorly studied compared with the growing season due to the limitation of extreme environments (Trucco et al., 2012). The lack of snowpack at our study site made the measurement of non-growing season CO_2 efflux under warming treatments possible. CO_2 loss during the non-growing season accounted for approximately a quarter of the annual ER emission, showing that the non-growing season comprises a huge source of C to the atmosphere. Similar results have been reported in previous studies in this region (25%) (Zhang et al., 2015) and in tundra ecosystems in the Arctic (15–28%) (Merbold et al., 2012; Schuur et al., 2009).

In the present study, warming-induced increase in ER was higher in the non-growing season compared with growing season and resulted in an increase in the contribution of the non-growing season ER to annual emissions (Figs. 2 b and S3). This result suggests that warming effect on non-growing season ER was stronger than growing season ER. The higher increase of ER may be attributed to the higher temperature sensitivity of ER in the non-growing season compared with the growing season (Janssens and Pilegaard, 2003; Kato et al., 2005). We observed that Q_{10} was higher in the non-growing season compared with the growing season and decreased with increased temperature. This finding was supported by a previous study in this region, which indicated that Q_{10} was 2.1 above −1 °C and 15.3 below −1 °C (Kato et al., 2005). Strong responses of the non-growing season ER to warming were also found in the Alaskan tundra ecosystem (Natali et al., 2011), where the contribution of winter ER to annual ER increased from 28% in the control to 37% in the warming treatments and resulted a net C loss on an annual basis. The increased non-growing season ER due to climate warming could cause the permafrost ecosystem to change from its historical C sink to a C source (Webb et al., 2016). Therefore, the warming-induced increase in non-growing season CO_2 loss has an important effect on the C balance of permafrost ecosystems and should not be neglected.

5. Conclusions

ER was mainly affected by soil temperature, duration of thaw days and aboveground biomass. The temperature sensitivity coefficients of ER (Q_{10}) were negatively correlated with soil temperature. In addition, warming effects on ER were grassland types and season-dependent, with greater increase of ER in alpine meadow (dry conditions) than in swamp meadow (moist soil conditions) and greater increase in non-growing season than growing season, suggesting that soil moisture mediates the response of ER to climate warming. These different responses to warming within grassland types and seasons should be considered when estimating the annual carbon balance. We also found that the integrated cumulative ER were higher than interpolated values in all treatments. whereas both the integrated model and interpolated non-growing season ER were based on monthly collected data, more frequent non-growing season *in-situ* measures are needed to accurate evaluate the warming effects on ER by using models and interpolation method in the Tibetan permafrost region.

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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.2017.08.010.

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