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Authors: Fei, Peng, Manhou, Xu, Quangang, You, Xuhui, Zhou, Tao, Wang, et al.

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

Peng Fei[1]
Xu Manhou[1,2]
You Quangang[1,2]
Zhou Xuhui[3]
Wang Tao[1] *and*
Xue Xian[1,4]

[1]Key Laboratory of Desert and Desertification, Chinese Academy of Sciences, Cold and Arid Regions Environmental and Engineering Research Institute, Chinese Academy of Sciences, West Donggang Road, Lanzhou 730000, China
[2]Graduate school of Chinese Academy of Sciences, Yuquanlu, No. 19A Yuquan Road, Beijing 100049, China
[3]Tiantong National Field Observation Station for Forest Ecosystem, School of Ecological and Environmental Sciences, East China Normal University, 500 Dong Chuan Road, Shanghai 200062, China
[4]Corresponding author: xianxue@lzb.ac.cn

Abstract

Soil water content (SWC) regulation on the responses of soil respiration (R_s), autotrophic respiration (R_a), and heterotrophic respiration (R_h) 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 R_s and its components (R_a and R_h) to warming. Infrared heaters were used to simulate climatic warming. Soil respiration was measured inside surface collars (2–3 cm deep) and R_h was measured inside deep collars (50 cm deep), which excludes root respiration. Autotrophic respiration was calculated by subtracting R_h from R_s. Warming increased the average R_s and R_h by 9.9% and 12.7% but had no significant effect on R_a. Interaction between warming and SWC had significant effect on R_s and its components. Soil respiration and R_a 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.

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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 (R_s), 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 R_s could significantly aggravate or mitigate the buildup of CO_2 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 (R_a) from plant roots and their symbionts, and heterotrophic respiration (R_h) from litter and soil organic C decomposition (Hanson et al., 2000), which have different implications for ecosystem C balance. In general R_a consumes photosynthate recently fixed by the canopy, hence it has little impact on annual net ecosystem C balance (Hogberg et al., 2001), whereas R_h 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 R_a and R_h 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 R_a and R_h bring about diverse response of R_s to climatic warming. Most studies show significant increase in R_s (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 R_a resulted from soil water stress, or because soil drying inhibited R_h 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 (Pacific 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 CO_2, whereas anoxic decomposition produces both CH_4 and CO_2 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 1.8 Gg 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 R_s and its components to warming in alpine meadow are different from those in Arctic tundra in sites with different soil water content (SWC).

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Materials and Methods

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 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 moorcroftii*, 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 cryosols in World Reference Base taxonomy) with a mattic epipedon 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, Kalglo 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_h. 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 R_h after three months of deep collar insertion. The R_a value was calculated as the difference between R_s and R_h, 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 CO_2 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_h, R_a, 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_h, and the calculated R_a were averaged. Mean R_s, R_a, and R_h 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.

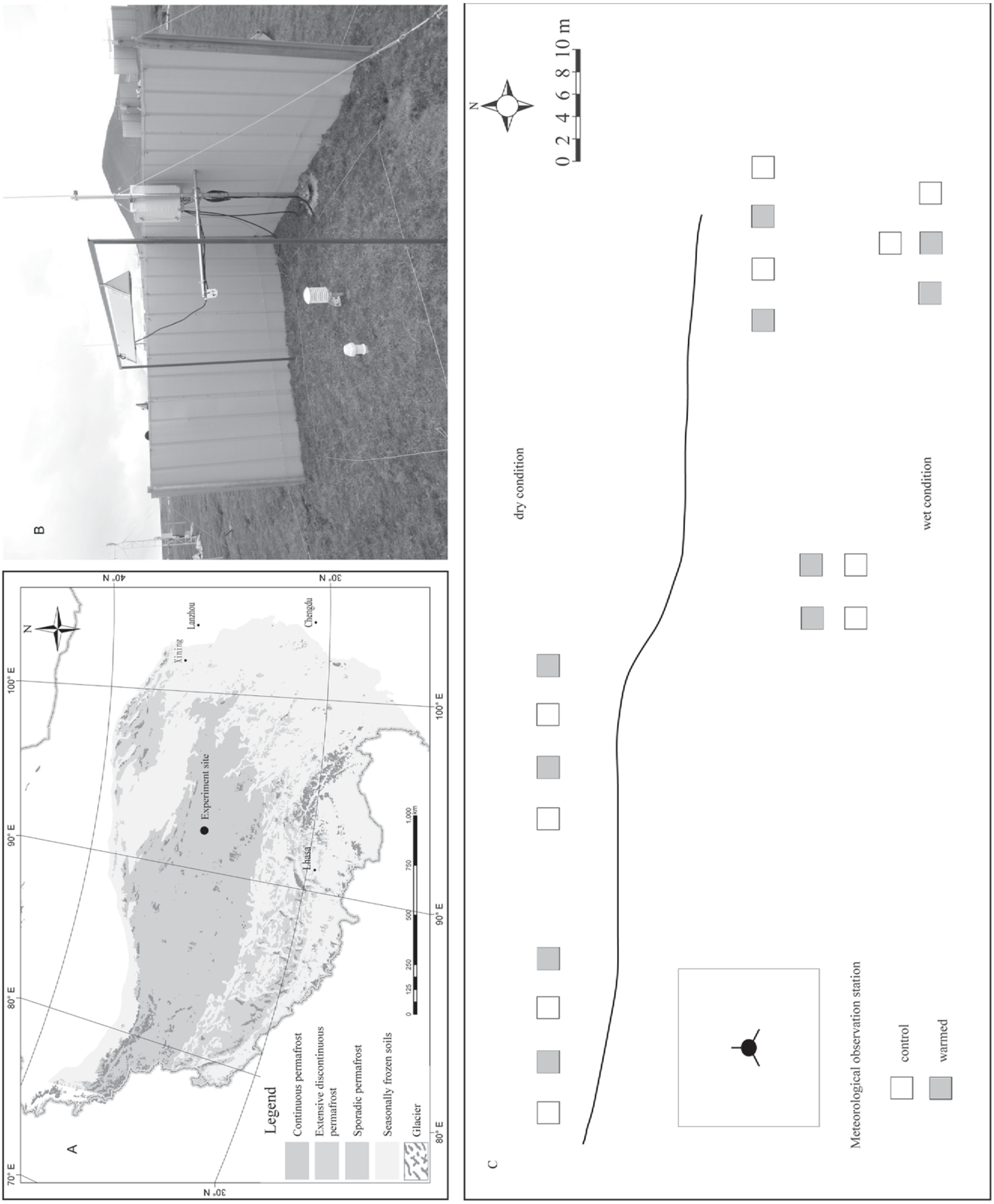

FIGURE 1. (A) Location, (B) warming equipment installation, and (C)plots distribution of the experimental site.

TABLE 1

Soil pH, $CaCO_3$ (g kg^{-2}), soil organic carbon (SOC, g kg^{-2}), total nitrogen (TN, g kg^{-2}), inorganic nitrogen (IN, mg kg^{-2}), and bulk density (BD, g cm^{-3}) in the 0–20 cm, and plant coverage (Cov., %) and height (H, cm) in the dry and wet conditions

	Soil properties						Plant feature	
	pH	$CaCO_3$	SOC	TN	IN	BD	Cov.	H
Dry	8.84 ± 0.01	5.81 ± 0.23	4.91 ± 0.22	0.44 ± 0.01	8.99 ± 0.38	1.25 ± 0.03	65 ± 5%	6.03 ± 0.64
Wet	8.33 ± 0.03	6.26 ± 0.16	10.48 ± 0.95	0.88 ± 0.07	10.63 ± 0.44	1.00 ± 0.05	90 ± 3%	6.78 ± 1.12

Notes: Soil properties were obtained by analyzing soil samples collected in September 2011. Plant height and coverage were also measured in September 2011.

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_s and R_a 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_a 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_a but had no effect on R_h (Fig. 5; Table 2). Both R_s and R_a decreased in dry but increased in wet condition. On average R_s and R_a 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 increase 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

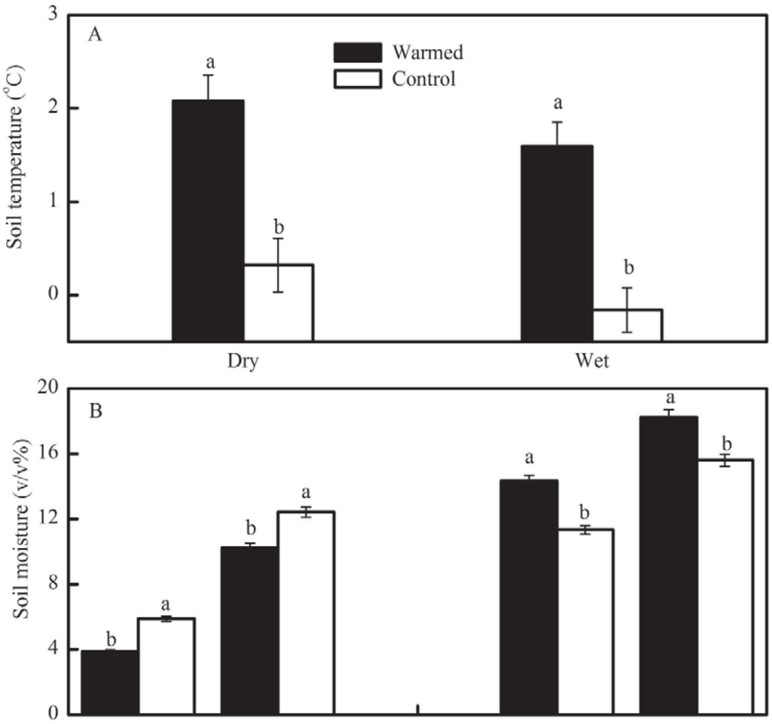

FIGURE 2. (A) Mean soil temperature (°C, 5 cm) and (B) soil moisture (v/v%, 0–10 and 60–100 cmb) from 1 October 2010 to 18 July 2013 in dry and wet conditions. Different labels above columns represent significant difference between control and warming. ($P < 0.05$).

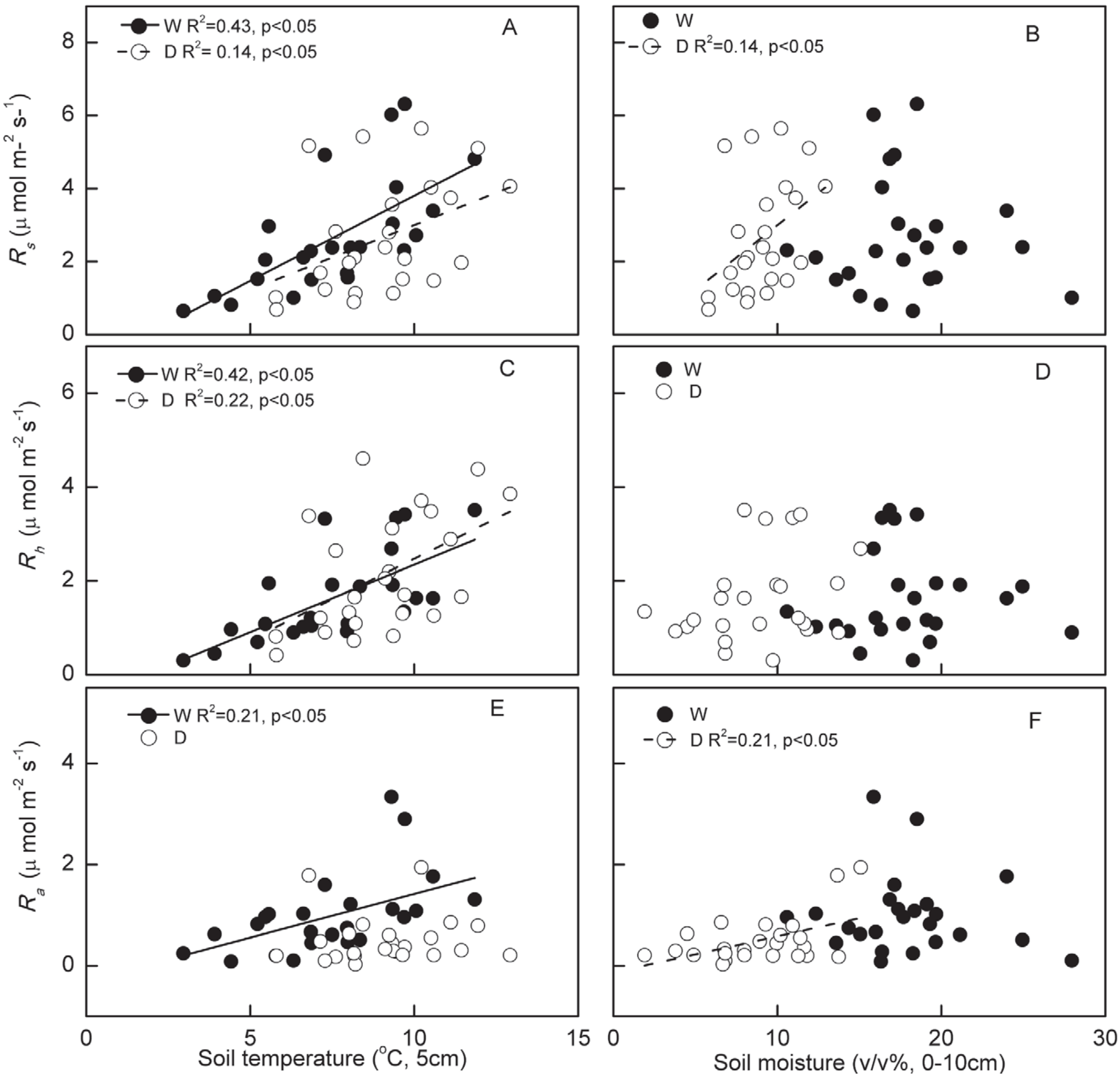

FIGURE 3. Relationship of soil respiration (R_s μ mol m^{-2} s^{-1}) and its components (R_a and R_h) with soil temperature (°C, 5 cm) and soil moisture (v/v%, 10 cm) in wet (filled circles and solid lines) and dry conditions (open circles and dashed lines).

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). R_s and R_h were more sensitive to AGB than was R_a (Fig. 7).

Discussion

RESPONSES OF R_S AND ITS COMPONENTS TO WARMING

In most field experiments, warming manipulation increases R_s (Rustad et al., 2001; Wu et al., 2011), but the negative warming effect on R_s is also reported (Saleska et al., 1999). We found that warming effects on R_s depend on SWC, which was stimulated in wet but suppressed in dry condition (Fig. 5). The opposite respons-

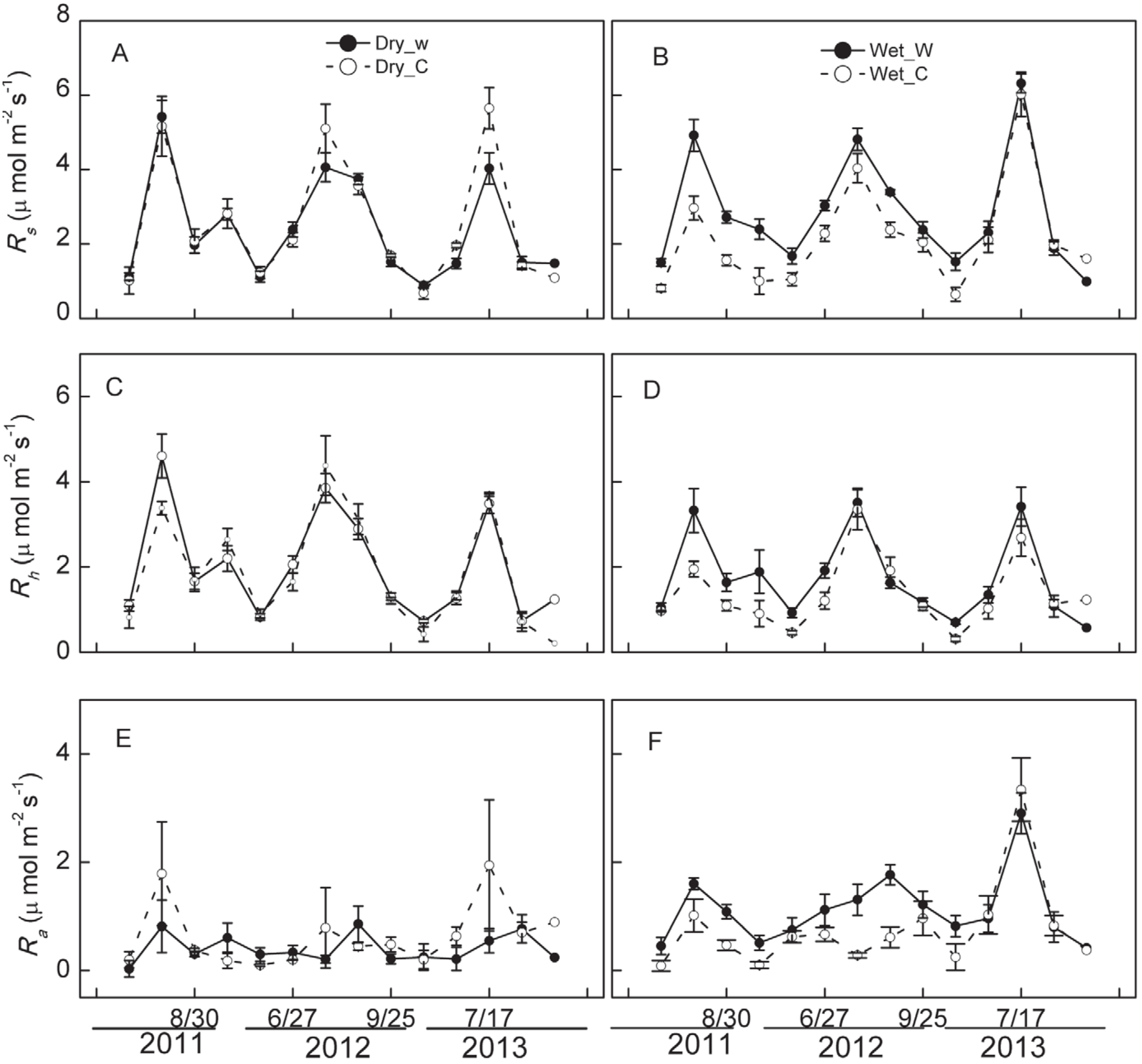

FIGURE 4. Seasonal dynamic of soil respiration (R_s) and its components (R_a and R_h) in control and warming plots in dry and wet conditions. Data are averaged from replicates, $n = 14$. Dates are given in the form m/dd/yyyy.

TABLE 2

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_h and R_a), aboveground biomass (AGB), and root biomass (RB).

variance source	R_s	R_h	R_a	R_h/R_s	AGB	RB
SWC	0.006	0.85	3.9^	8.9**	0.4	3.3
W	5.3*	5.9*	0.5	0.4	0	0.1
W × SWC	12.9**	1.3	10.7**	4.7*	15.7*	2.6

Significance: ^, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$

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

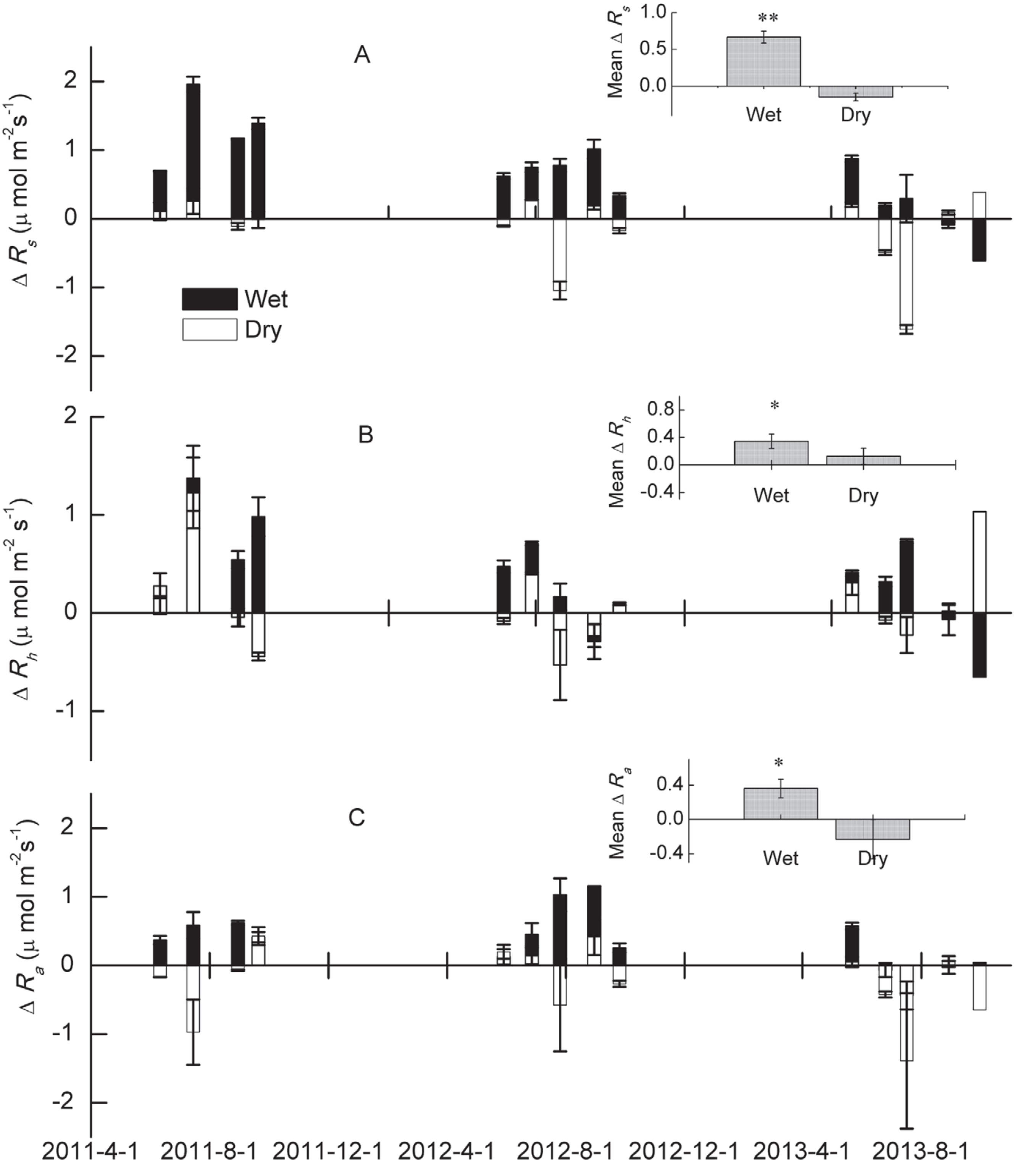

FIGURE 5. **Seasonal and average (inserted panels, mean ± SE, *n* = 13) warming effects on (A) soil respiration (R_s), (B) heterotrophic respiration (R_h), and (C) autotrophic respiration (R_a) in wet (dark columns) and dry (white columns) conditions. Asterisks denote significance between warming and control treatments (** $P < 0.01$; * $P < 0.05$).**

flowing surface water in the growing season in tundra ecosystem (Shaver et al., 1998). 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.

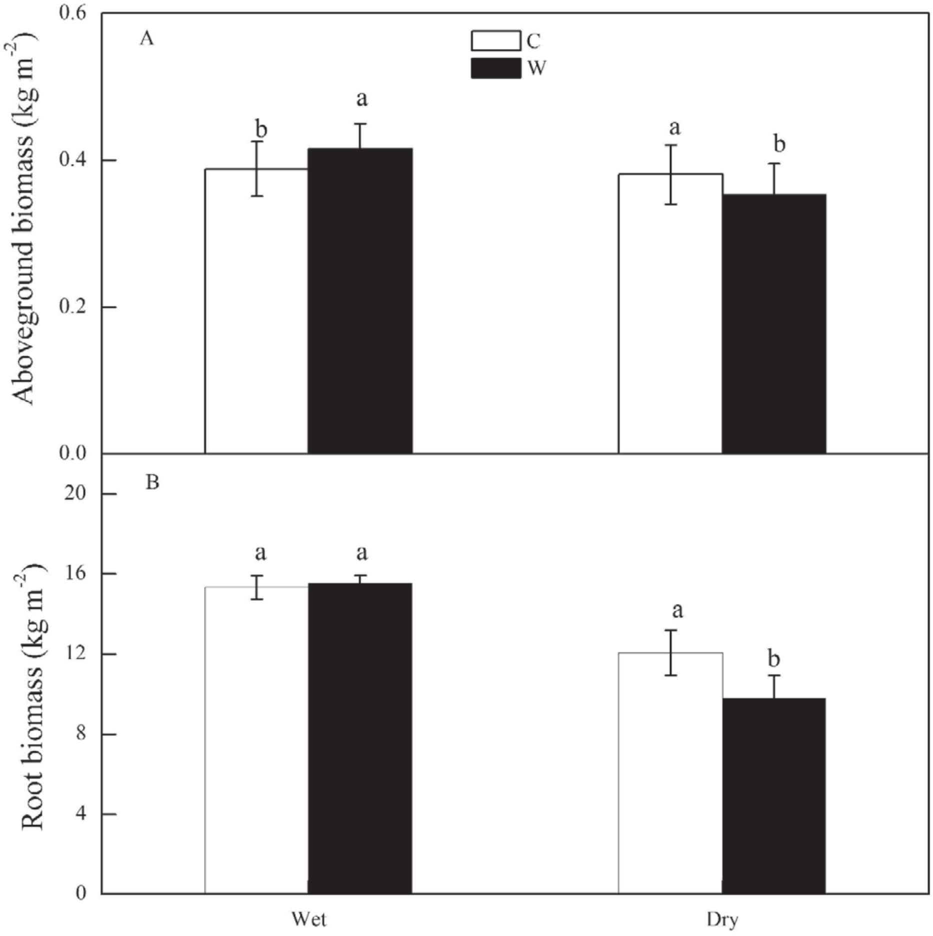

FIGURE 6. Warming effects on above-ground biomass (AGB) and root biomass (RB, 0–50 cm soil depth) in wet and dry conditions. Values are the average of four replicates in dry and six replicates in wet from May to September 2012. Different labels above columns indicate the significant difference at the *P* < 0.05 level.

Autotrophic respiration and R_h 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_h and soil temperature but no obvious relationship between SWC and R_h 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_h is affected by total detritus input or AGB (Bond-Lamberty et al., 2004), and R_a is determined by RB (Zhou et al., 2007) and temperature dependence of specific root respiration (Boone et al., 1998). Possible elevated

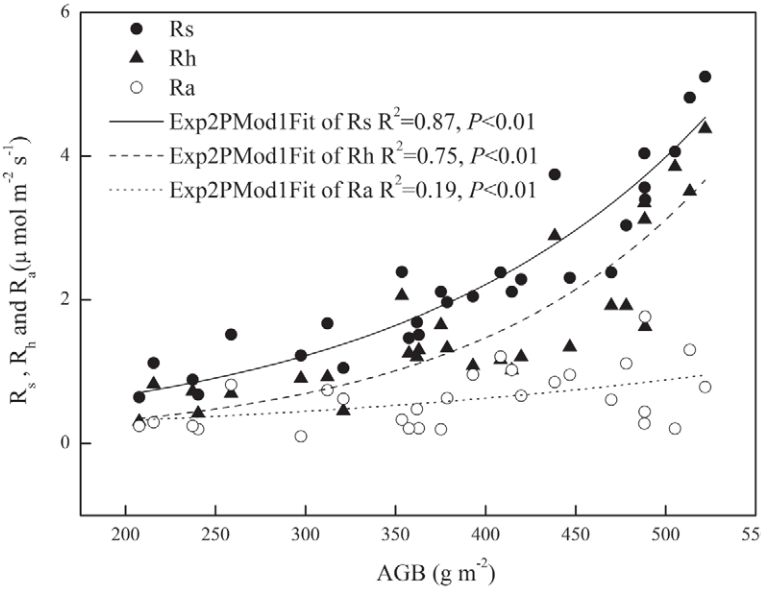

FIGURE 7. Relationship of soil respiration (R_s μ mol m^{-2} s^{-1}) and its components (R_a and R_h) with above-ground biomass (AGB) in all plots.

detritus input and the associated AGB increase in wet (Fig. 6, part A) therefore would be responsible for the R_h increase because of the positive relationship between AGB and R_h (Fig. 7). The effect of AGB decrease on R_h could be compensated by the increase in RB, thus resulting in non-significant change in R_h in dry condition. R_a 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_a through limitation on annual productivity (Li et al., 2013), root growth (Zhou et al., 2007), and specific R_a rate (Michele and Douglas, 2009). Non-significant change in RB under warming in dry condition suggests the change in specific R_a rate. We have no direct data on the specific R_a, but the species composition change in our study site (Xu et al., 2014) might change the RB quality, thus resulting in the specific R_a change under warming.

The response of R_a to warmer soil can affect ecosystem C allocation and the strength of positive feedback of soil CO_2 efflux to climate warming. Both R_h and R_a increased with larger relative increase in R_a in wet (53% vs. 33% in R_a and R_h), 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_h in dry than in wet conditions is similar to the result in an incubation study where Q_{10} of R_h 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_h 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_h in wet and dry in our study suggests that R_a has a large effect on apparent Q_{10} of R_s and indicates apparent Q_{10} obtained in field studies without exclusion of R_a 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_a) 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_a 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_a 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_a 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_a 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.

Acknowledgments

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