Short communication

Response of soil respiration to short-term experimental warming and precipitation pulses over the growing season in an alpine meadow on the Northern Tibet

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ABSTRACT

A warming and precipitation pulses experiment was conducted in an alpine meadow of Tibet over the growing season (June–September) in 2013. Soil respiration (R_s) was measured biweekly from early July to early September 2013. The effect of experimental warming on R_s varied with water availability. The effect of precipitation pulses on R_s depended on pulse sizes, antecedent precipitation and soil moisture conditions. Precipitation pulses increased the temperature sensitivity of R_s , which was not affected by experimental warming. Our findings suggest that water availability regulates the response of soil respiration to warming.

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The Tibetan Plateau is one of the most sensitive regions to climatic change and the alpine meadow on this Plateau is one of the most sensitive vegetation types (IPCC, 2013). For example, Fu et al., 2014b showed that the response of plant photosynthesis and biomass to climatic warming over the Tibetan Plateau was greater than that of the global average. Precipitation pulses and climatic warming can trigger series responses of soils and plants, such as ecosystem and soil respiration increases (Chen et al., 2008; Shi et al., 2006; Wu et al., 2011), soil microbial biomass and activity increases (Huxman et al., 2004; Lu et al., 2013), and plant photosynthesis and biomass increases (Fu et al., 2014b; Hao et al., 2010; Wu et al., 2011). Soil respiration (R_s) constitutes one of the largest carbon fluxes in terrestrial carbon cycle (Raich and Schlesinger, 1992; Rustad et al., 2001; Wu et al., 2011). Understanding the effects of warming and precipitation pulses on R_s is vital for predicting future changes of carbon cycle in alpine regions.

The main objectives of this study were to examine the effects of short-term experimental warming and precipitation pulses on R_s and the temperature sensitivity of R_s . Previous studies showed that precipitation pulses increased R_s and the warming effects on R_s

were regulated by water availability in arid and semi-arid ecosystems (Liu et al., 2009; Munson et al., 2010). Moreover, precipitation pulse significantly increased ecosystem respiration in an alpine meadow on the Northern Tibet (Shi et al., 2006). Thus, we hypothesized that water availability regulated the response of R_s to warming and precipitation pulses could increase R_s . The effects of precipitation pulses exhibited nonlinear increases with pulse sizes (Cable et al., 2008; Huxman et al., 2004; Sponseller, 2007). Our previous study demonstrated that the correlations between R_s and soil moisture varied with water availability in an alpine meadow of Tibet (Fu et al., 2010). Therefore, we also hypothesized that the response of R_s to precipitation pulses varied with initial soil moisture condition.

The study area (30°30'N, 91°04'E) is located at the Damxung Grassland Observation Station, Tibet Autonomous Region, China. Detailed descriptions of the climate, soil and vegetation conditions can be found in our previous studies (Fu et al., 2012; Yu et al., 2014). Briefly, annual mean air temperature is 1.3 °C. Annual mean rainfall is approximate 476.8 mm. The soil is classified as sandy loam, with organic matter of 0.3–11.2% and total nitrogen of 0.03–0.49%. The vegetation is *Kobresia*-dominated alpine meadow.

In this study, nine open-top chambers (OTCs) were randomly set up in the experimental area (25 m × 50 m) in June 2013 to increase the temperature in warming treatments by trapping solar energy (Marion et al., 1997). The bottom and top diameters and the height of the OTCs were 1.45, 1.00 and 0.40 m, respectively

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(Fu et al., 2013). There was one unwarmed plot in the vicinity of each OTC. The nine warmed and unwarmed plots were assigned randomly for three levels of precipitation pulses. Precipitation pulses were provided with hand sprinklers on June 27, July 6, July 24, August 5, August 20 and September 4, 2013. Considering a 5 mm increase of precipitation may offset experimental warming-induced soil drying and daily maximum total precipitation of approximate 20 mm in the experimental area, the three precipitation levels were 0, 5 and 20 mm on each day of water addition. That is, the increases were about 0, 6 and 25% for the three levels of water addition over the whole growing season (June–September). There were a total of 18 experimental plots and six treatments: control (C; unwarmed plot+0% precipitation level), warm (W; warmed plot+0% precipitation level), increased precipitation at a low level (LP; unwarmed plot+6% precipitation level), warm plus increased precipitation at a low level (W+LP; warmed plot+6% precipitation level), increased precipitation at a high level (HP; unwarmed plot+25% precipitation level) and warm plus increased precipitation at a high level (W+HP; warmed plot+25% precipitation level).

We measured soil temperature (T_s) at a depth of 5 cm and soil moisture (SM) at a depth of 10 cm for all treatments during the entire study period. We measured R_s using a CO_2 flux system with a

survey chamber of 20 cm in diameter (LI-8100, LI-COR Biosciences, Lincoln, NE, USA) (Fu et al., 2014a) after the application of water addition on July 6, July 24, August 5, August 20 and September 4, 2013. The SM in the experimental area was in a range from $0.04 \text{ m}^3 \text{ m}^{-3}$ to $0.30 \text{ m}^3 \text{ m}^{-3}$ over the growing season. The SM values on the five measuring occasions (Fig. 1) covered the moisture range and were divided into three ranges (i.e., $<0.10 \text{ m}^3 \text{ m}^{-3}$, between 0.10 and $0.20 \text{ m}^3 \text{ m}^{-3}$, and $>0.20 \text{ m}^3 \text{ m}^{-3}$). Our previous study showed that the dependence of R_s on SM changed with the three SM ranges (Fu et al., 2010). These results implied that the five measuring occasions can reflect the relationship between initial SM and the pulse effects on R_s . Before the measurement of R_s , polyvinyl chloride (PVC) collars (diameter, 20 cm; height, 5 cm) were inserted approximately 2–3 cm into the soil for all plots. The insertion of PVC collars into soil can create airtight seals between the LI-8100 survey chamber and the soil.

For a specific measuring date, repeated-measures ANOVA was used to estimate the main and interactive effects of measuring time, experimental warming and precipitation pulses on R_s , T_s and SM, respectively (Table 1). Student–Newman–Keuls multiple comparisons were performed among the three precipitation pulses, before which repeated-measures ANOVA with experimental warming and precipitation pulses as between-subject and with

Fig. 1. Daily variation in soil respiration (R_s), soil temperature (T_s) and soil moisture (SM) on (a–c) July 6; (d–f) July 24; (g–i) August 5–6; (j–l) August 20–21 and (m–o) September 4–5. C: unwarmed plot+0% precipitation level; W: warmed plot+0% precipitation level; LP: unwarmed plot+6% precipitation level; W+LP: warmed plot+6% precipitation level; HP: unwarmed plot+25% precipitation level; W+HP: warmed plot+25% precipitation level.

Table 1

Repeated-measures ANOVA for the main and interactive effects of measuring time (T), experimental warming (W) and precipitation pulses (PP) on soil respiration (R_s), soil temperature (T_s) and soil water content (SM) ($n = 3$).

Date		W	PP	T	W × PP	W × T	PP × T	W × PP × T
July 6	R_s	1.14	1.16	11.2 ^c	0.49	1.00	0.19	0.52
	T_s	16.3 ^b	17.2 ^c	470 ^c	2.01	0.04	2.48	0.65
	SM	4394 ^c	8246 ^c	78 ^c	173 ^c	113 ^c	362 ^c	131 ^c
July 24	R_s	0.33	0.05	3.0 ^a	0.13	0.49	0.93	0.68
	T_s	4.50	2.74	76.2 ^c	10.5 ^b	0.19	0.12	0.16
	SM	3918 ^c	2021 ^c	337 ^c	2990 ^c	4.6 ^c	2.8 ^a	25.6 ^c
August 5–6	R_s	1.63	30.1 ^c	152 ^c	3.73	1.60	13.8 ^c	1.64
	T_s	154 ^c	264 ^c	839 ^c	10.4 ^b	1.48	2.77	0.89
	SM	487 ^c	13742 ^c	1864 ^c	8.4 ^c	506 ^c	456 ^c	24.4 ^c
August 20–21	R_s	27.7 ^c	144 ^c	35.1 ^c	8.6 ^b	1.22	7.4 ^c	0.47
	T_s	1013 ^c	1520 ^c	847 ^c	155 ^c	2.46	4.1 ^a	2.77
	SM	6588 ^c	20016 ^c	52.1 ^c	69.9 ^c	1.19	8.3 ^b	6.6 ^a
September 4–5	R_s	0.31	0.24	14.6 ^b	0.86	2.08	1.21	0.81
	T_s	23.7 ^c	11.2 ^b	491 ^c	6.4 ^a	1.43	6.5 ^a	2.48
	SM	15723 ^c	3172 ^c	994 ^c	2109 ^c	97.4 ^c	70.9 ^c	21.6 ^c

^a Mean significant at 0.05 level.

^b Mean significant at 0.01 level.

^c Mean significant at 0.001 level.

measuring time as within-subject were conducted. For each treatment, a stepwise multiple regression analysis was used to analyze the relationships between R_s and T_s and SM (Table 2), before which natural-logarithm transformations were made for R_s and SM. We analyzed the sensitivity of R_s to temperature for each treatment using all measurement data according to:

$$R_s = ae^{bT_s}, \quad (1)$$

where a is the intercept of R_s when T_s is 0 °C, and b reflects the temperature sensitivity of R_s . The b values were used to calculate the respiration quotient (Q_{10})

$$Q_{10} = e^{10b} \quad (2)$$

One-way ANOVA was used to test the main and interactive effects of experimental warming and precipitation pulses on the temperature sensitivity of R_s . In addition, we also analyzed the simple linear relationship between R_s and SM. All statistical tests were produced with the SPSS software (version 16.0; SPSS Inc., Chicago, IL, USA).

Regardless of precipitation pulses, experimental warming significantly increased average R_s by 29.6% ($0.41 \mu\text{mol m}^{-2} \text{s}^{-1}$) on August 20 and 21, but had negligible effects on average R_s for the other measuring dates (Table 1, Fig. 1). However, non-significant differences were found between the C and W treatment for all the five measuring dates. Average R_s of the W + LP treatment was 34.3% ($0.48 \mu\text{mol m}^{-2} \text{s}^{-1}$, $p < 0.01$) greater than that of the LP treatment, while that of the W + HP treatment was 38.4% ($0.76 \mu\text{mol m}^{-2} \text{s}^{-1}$, $p < 0.01$) higher than that of the HP treatment on August 20–21 (Fig. 1j). These results implied that the significant warming effect on R_s was mainly due to the significant changes under water addition conditions. Moreover, these findings also suggested that warming effects on R_s differed with water availability (Lellei-Kovács et al., 2008; Liu et al., 2009). Experimental warming significantly increased T_s by 1.36, 0.41, 1.24, 1.89 and 1.12 °C on July 6, July 24, August 5–6, August 20–21 and September 4–5, respectively (Table 1, Fig. 1). In contrast, experimental warming significantly decreased SM by 0.03, 0.02, 0.003, 0.02 and $0.04 \text{ m}^3 \text{m}^{-3}$ on July 6, July 24, August 5–6, August 20–21 and September 4–5, respectively (Table 1, Fig. 1). Specifically, experimental-warming-induced soil

Table 2

Stepwise multiple regression analyses between soil respiration (R_s) and soil temperature (T_s) and soil moisture (SM), showing changes in the regression coefficient, significance probability (p), coefficient of determination (R^2) and partial correlation coefficient. Natural logarithm transformations were made for R_s and SM prior to regression analysis. C: unwarmed plot + 0% precipitation level; W: warmed plot + 0% precipitation level; LP: unwarmed plot + 6% precipitation level; W + LP: warmed plot + 6% precipitation level; HP: unwarmed plot + 25% precipitation level; W + HP: warmed plot + 25% precipitation level.

Treatment		Coefficient	R^2	Partial correlation	p
C	Constant	1.28			<0.001
	T_s	0.04	0.20	0.56	<0.001
	SM	0.87	0.36	0.73	<0.001
W	Constant	0.79			<0.001
	T_s	0.04	0.29	0.63	<0.001
	SM	0.62	0.28	0.73	<0.001
LP	Constant	0.09			0.619
	T_s	0.05	0.34	0.66	<0.001
	SM	0.35	0.11	0.40	<0.001
W + LP	Constant	−0.06			0.759
	T_s	0.06	0.37	0.67	<0.001
	SM	0.3	0.09	0.37	<0.001
HP	Constant	0.03			0.895
	T_s	0.07	0.52	0.76	<0.001
	SM	0.43	0.06	0.34	<0.001
W + HP	Constant	−0.28			0.21
	T_s	0.08	0.52	0.74	<0.001
	SM	0.27	0.03	0.23	<0.05

drying can dampen the positive effect of warming on R_s (Lellei-Kovács et al., 2008; Liu et al., 2009), which in turn resulted in non-significant warming effects on R_s under the condition of natural precipitation. In other words, soil moisture regulated the response of R_s to warming (Table 2).

Regardless of experimental warming, average R_s was increased by 35.7% ($0.47 \mu\text{mol m}^{-2} \text{s}^{-1}$) and 52.1% ($0.68 \mu\text{mol m}^{-2} \text{s}^{-1}$), and by 119.4% ($0.90 \mu\text{mol m}^{-2} \text{s}^{-1}$) and 214.5% ($1.61 \mu\text{mol m}^{-2} \text{s}^{-1}$) under the low and high sizes of the pulse on August 5–6 and August 20–21, respectively, but non-significant differences were found for the other measuring dates (Table 1, Fig. 1). Average T_s was significantly decreased by 0.73 and 2.71 °C, and by 1.17 and 3.91 °C under the low and high sizes of the pulse on August 5–6 and August 20–21, respectively (Table 1, Fig. 1h and k). The high size of the pulse significantly decreased T_s by 1.75 and 0.77 °C on July 6 and September 4–5, respectively, while the low size of the pulse had little effects on T_s (Table 1, Fig. 1b and n). In addition, average T_s tended to be decreased by 0.45 and 0.51 °C under the low and high sizes of the pulse on July 24, respectively (Table 1, Fig. 1e). In contrast, average SM was significantly increased by 0.002 and $0.05 \text{ m}^3 \text{m}^{-3}$, by 0.02 and $0.02 \text{ m}^3 \text{m}^{-3}$, by 0.01 and $0.03 \text{ m}^3 \text{m}^{-3}$, by 0.01 and $0.05 \text{ m}^3 \text{m}^{-3}$, and by 0.02 and $0.03 \text{ m}^3 \text{m}^{-3}$ under the low and high sizes of the pulse on July 6, July 24, August 5–6, August 20–21 and September 4–5, respectively (Table 1, Fig. 1).

There were non-significant interactive effects of precipitation pulses and measuring time on July 6, July 24 and September 4–5, indicating that no pulse effects on R_s were found on the three measuring dates. The antecedent SM values were higher than $0.20 \text{ m}^3 \text{m}^{-3}$ on July 24 and September 4–5, but less than $0.10 \text{ m}^3 \text{m}^{-3}$ on July 6. Precipitation lasted continuously two days and 13 days prior to the pulse on July 6 and September 4–5. In contrast, precipitation pulse effects on R_s lasted approximately 6–7 h and 9–10 h under the low and high size of the pulse, respectively, on August 5–6. Precipitation pulse effects on R_s lasted approximately 15–16 h under the low size of the pulse on August 20–21. Under the high size of the pulse on August 20–21,

Fig. 2. Relationships between soil respiration (R_s) and soil temperature (T_s) and soil moisture ($\text{m}^3 \text{ m}^{-3}$) in (a, b) the unwarmed plot + 0% precipitation level (C); (c, d) warmed plot + 0% precipitation level (W); (e, f) unwarmed plot + 6% precipitation level (LP); (g, h) warmed plot + 6% precipitation level (W + LP); (i, j) unwarmed plot + 25% precipitation level (HP); (k, l) warmed plot + 25% precipitation level (W + HP).

precipitation pulse effects on R_s may exceed 24 h. The antecedent SM values were within $0.10\text{--}0.15 \text{ m}^3 \text{ m}^{-3}$ and less than $0.10 \text{ m}^3 \text{ m}^{-3}$ on August 5–6, August 20–21, respectively. Non-precipitation

lasted continuously seven and eight days prior to the pulse on August 5–6 and August 20–21. Our finding that the precipitation pulse significantly increased R_s after continuous drought was in

line with previous studies which were conducted in arid and semi-arid ecosystems (Cable et al., 2008; Chen et al., 2008; Huxman et al., 2004; Sponseller, 2007).

Specifically, our finding that precipitation pulse effects on R_s varied with measuring date may be attributed to different antecedent soil moisture and precipitation conditions (Cable et al., 2008; Huxman et al., 2004). The pulse-induced magnitude and duration of the increase in R_s depended on pulse size (Chen et al., 2008; Sponseller, 2007), and initial soil moisture and precipitation conditions (Cable et al., 2008; Huxman et al., 2004). That is, the wet initial water conditions reduced or even masked the response of R_s to the pulse, while the dry initial water conditions strengthened the responses of R_s to the pulse. Similarly, the sensitivity of R_s to soil moisture was more responsive in dry conditions (Liu et al., 2009; Wu et al., 2011). In addition, larger pulses caused greater respiration rates and durations, whereas the magnitudes and durations increased nonlinearly with pulse sizes (Cable et al., 2008; Huxman et al., 2004; Sponseller, 2007). The nonlinear increases probably resulted from the following reasons. First, a greater decline in soil temperature was found in this study when there was more extra precipitation. Second, soil microbial activity was limited by carbon and nitrogen availability at a short-term timescale (Sponseller, 2007). Third, the process rates in deeper soil layer were greatly decreased (Sponseller, 2007). Fourth, higher initial water availability dampened or even masked the pulse effect (Cable et al., 2008).

Soil respiration significantly increased with T_s for all the six treatments, whereas it only had a positive relationship with SM for the C and W treatments (Fig. 2). Soil temperature explains the most variation of R_s for the HP and W+HP treatments, the second most variation for the LP and W+LP treatments and the least variation for the C and W treatments (Fig. 2). Soil moisture explained more variation of R_s than T_s for the C treatment, while T_s explained more variation for all the other five treatments in the multiple regression equations (Table 2). In addition, the partial correlation coefficient between R_s and SM was greater than that between R_s and T_s for the C and W treatment, while the partial correlation coefficient between R_s and T_s was greater for the other four treatments (Table 2).

The net effects of experimental warming and precipitation pulses on R_s were determined by the relative strengths of the positive and negative effects on T_s and SM due to treatments (Lellei-Kovács et al., 2008; Munson et al., 2010; Zhou et al., 2006). Experimental warming and precipitation pulses altered the relative importance of soil temperature and moisture in controlling the variation of R_s (Table 2).

Experimental warming and its interaction with precipitation pulses had little effect on Q_{10} ($F=3.92$, $p=0.07$ for warming; $F=0.68$, $p=0.52$ for the interaction). In contrast, Q_{10} increased significantly with precipitation pulses ($F=61.66$, $p<0.001$). In detail, there were no significant differences in Q_{10} between C and W treatments, between LP and W+LP treatments and between HP and W+HP treatments. However, Q_{10} was largest for HP and W+HP, mid-range for LP and W+LP, and least for C and W.

Across all the 18 plots, Q_{10} was positively correlated with SM ($R=0.71$, $p<0.001$), but negatively correlated with T_s ($R=-0.63$, $p<0.01$), indicating that the temperature sensitivity of R_s was more closely related to SM than T_s .

Previous studies showed that experimental warming reduces the temperature sensitivity of R_s (Luo et al., 2001; Zhou et al., 2006). However, our findings indicate that warming did not affect the temperature sensitivity of R_s partly owing to the experimental-warming-induced drying of the soil (Xu et al., 2010). Values of Q_{10} of W+HP and W+LP were significantly greater than that of C. The findings show that warming increased the temperature sensitivity of R_s when warming-induced soil drying was not limited.

Additionally, precipitation pulses increased the temperature sensitivity of R_s , which was in line with the results of previous studies (McCulley et al., 2007). Therefore, water availability regulated the temperature sensitivity of R_s .

In summary, precipitation pulses increased the temperature sensitivity of soil respiration, whereas experimental warming did not significantly affect the temperature sensitivity. The effects of experimental warming and precipitation pulses on soil respiration differed with water availability.

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