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Yonghui Wang and Huiying Liu contributed equally to this work.

Key Points:

- Four year continuous hourly monitoring of soil CO_2 flux (R_s) using automated system
- Non-growing-season cumulative R_s accounted for 11.8–13.2% of the annual total R_s
- Higher Q_{10} of thawed than frozen soil can trigger C loss in warmer winter

Supporting Information:

- Readme
- Table S1
- Table S2
- Table S3
- Figure S1
- Figure S2
- Figure S3
- Figure S4
- Figure S5

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Non-growing-season soil respiration is controlled by freezing and thawing processes in the summer monsoon-dominated Tibetan alpine grassland

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Abstract The Tibetan alpine grasslands, sharing many features with arctic tundra ecosystems, have a unique non-growing-season climate that is usually dry and without persistent snow cover. Pronounced winter warming recently observed in this ecosystem may significantly alter the non-growing-season carbon cycle processes such as soil respiration (R_s), but detailed measurements to assess the patterns, drivers of, and potential feedbacks on R_s have not been made yet. We conducted a 4 year study on R_s using a unique R_s measuring system, composed of an automated soil CO_2 flux sampling system and a custom-made container, to facilitate measurements in this extreme environment. We found that in the nongrowing season, (1) cumulative R_s was 82–89 g C m^{-2}, accounting for 11.8–13.2% of the annual total R_s; (2) surface soil freezing controlled the diurnal pattern of R_s and bulk soil freezing induced lower reference respiration rate (R_0) and temperature sensitivity (Q_{10}) than those in the growing season (0.40–0.53 versus 0.84–1.32 µmol CO_2 m^{-2} s^{-1} for R_0 and 2.5–2.9 versus 2.9–5.6 for Q_{10}); and (3) the intraannual variation in cumulative R_s was controlled by accumulated surface soil temperature. We found that in the summer monsoon-dominated Tibetan alpine grassland, surface soil freezing, bulk soil freezing, and accumulated surface soil temperature are the day-, season-, and year-scale drivers of the non-growing-season R_s, respectively. Our results suggest that warmer winters can trigger carbon loss from this ecosystem because of higher Q_{10} of thawed than frozen soils.

1. Introduction

Non-growing-season soil respiration (R_s) is an essential component of the global carbon cycling [*Fahnestock et al.*, 1998; *Monson et al.*, 2006a], and thus, it is crucial to thoroughly understand how it feedbacks to climate change [*Belshe et al.*, 2013; *Brooks et al.*, 2004; *Campbell et al.*, 2005]. Alpine and arctic tundra ecosystems are vulnerable and sensitive to climate change because of their large soil carbon storage, high soil carbon density [*McGuire et al.*, 2009; *Yang et al.*, 2008], and vast area of permafrost [*Koven et al.*, 2011]. In these ecosystems, the decomposition of soil organic carbon during the nongrowing season can occur at a high rate [*Monson et al.*, 2006b] due to soil microbes that maintain their activities at extremely low temperature [*Panikov et al.*, 2006]. Thus, the non-growing-season R_s can contribute significantly to annual carbon budgets [*Liptzin et al.*, 2009]. For instance, in heath tundra ecosystems, non-growing-season cumulative R_s ranges from 103 to 176 g C m^{-2}, accounting for 14–40% of the annual total R_s [*Elberling*, 2007; *Larsen et al.*, 2007; *Morgner et al.*, 2010]. In sedge and tussock tundra ecosystems, non-growing-season cumulative R_s ranges from 10 to 68 g C m^{-2}, contributing to 17–30% of the annual total R_s [*Fahnestock et al.*, 1999; *Morgner et al.*, 2010; *Oechel et al.*, 1997; *Sullivan et al.*, 2008; *Welker et al.*, 2004]. *Grogan and Chapin* [1999] used soda lime to measure respiration in acidic tussock tundra in Alaska and reported an extremely large value, 189 g C m^{-2}, contributing up to 52% of the annual total R_s.

The drivers of the day-, season-, and year-scale variations of the non-growing-season R_s have been shown to be different from those of the growing-season R_s. On the day scale, both distinct [*Elberling and Brandt*, 2003;

Kato et al., 2004; *Seok et al.*, 2009] and indistinct diurnal patterns [*Mariko et al.*, 2000; *Mo et al.*, 2005; *Zimov et al.*, 1996] have been observed. However, the drivers of the non-growing-season diurnal patterns of R_s have not been studied sufficiently, and only in one study in heath tundra of northeastern Greenland, it has been reported that the diurnal pattern of R_s during fast soil thawing period was partly influenced by soil thawing [*Elberling and Brandt*, 2003]. On the season scale, non-growing-season R_s is primarily due to microbial decomposition of soil organic carbon and tends to have a higher-temperature sensitivity (Q_{10}) than the growing-season R_s. This higher Q_{10} can be due to either fast substrate utilization of the unique soil microbial communities in snow-covered soils [*McMahon et al.*, 2011; *Monson et al.*, 2006b] or indirect controls of temperature on diffusion of extracellular enzymes and substrates through effects on physical factors [*Mikan et al.*, 2002]. Finally, on the year scale, the interannual variation of the non-growing-season cumulative R_s has been found to be regulated by snow depth in seasonal snow-covered ecosystems [*Monson et al.*, 2006b; *Nobrega and Grogan*, 2007]. These studies indicate that the non-growing-season R_s is sensitive to changes in climate, especially the temperature, and the duration and depth of snow cover, highlighting the importance of systematic investigation of the non-growing-season R_s.

The Tibetan alpine grassland is as vulnerable and sensitive to climate warming as the arctic tundra and may release a large amount of CO_2 to atmosphere when facing rising temperature [*Belshe et al.*, 2013; *Koven et al.*, 2011; *McGuire et al.*, 2009; *Tan et al.*, 2010; *Xu et al.*, 2010]. Alpine grassland of the Tibetan Plateau and arctic tundra share many similar features, such as a long nongrowing season, large soil carbon storage, high carbon density [*McGuire et al.*, 2009; *Shi et al.*, 2012; *Yang et al.*, 2008], and large area of permafrost [*Cheng*, 2005; *Cheng and Wu*, 2007; *Dörfer et al.*, 2013; *Koven et al.*, 2011]. Recent studies have shown that the Tibetan Plateau acts as a carbon sink, e.g., the net ecosystem CO_2 exchanges of alpine shrubland ecosystem and alpine meadow ecosystem were ~ -70 g C m^{-2} yr^{-1} (ranged from -58.5 to -75.5 g C m^{-2} yr^{-1}) and ~ -120.9 g C m^{-2} yr^{-1} (ranged from -78.5 to -192.5 g C m^{-2} yr^{-1}), respectively [*Kato et al.*, 2006; *Zhao et al.*, 2006]. Our previous study has reported that across the grasslands of the plateau, peak growing-season soil respiration is well predicted by belowground biomass and soil moisture, but not soil temperature [*Geng et al.*, 2012], highlighting the need to further explore the effect of soil temperature. In addition, further investigations have reported that the mean R_s of the northeastern part of the plateau is 0.96 μmol CO_2 m^{-2} s^{-1} (1 g C m^{-2} d^{-1}) between December and February [*Cao et al.*, 2004], and the mean non-growing-season R_s is 0.74 μmol CO_2 m^{-2} s^{-1} in a cropland ecosystem located in the southern part of the plateau [*Shi et al.*, 2006], indicating a large non-growing-season cumulative R_s (140–180 g C m^{-2}) on this plateau. These data suggest that carbon loss on this plateau during the nongrowing season cannot be overlooked, emphasizing its important role in global carbon cycling.

The climate of the Tibetan Plateau is unique in comparison with other alpine and tundra ecosystems, because it is dominated by a monsoon. Specifically, in winter, the plateau is a source of cool air, with a higher atmosphere pressure than the surrounding areas. Therefore, the atmosphere current flows out of the plateau, and the climate is usually cold and dry. In summer, this plateau is a source of warm air with a lower atmosphere pressure than the surroundings, and thus the moist air moves toward the plateau, which creates a warm and humid climate [*Tang and Reiter*, 1984]. The nongrowing season of this plateau receives $<$ 15% of the annual precipitation and thus has no persistent snowpack [*Tian et al.*, 2003; *Zhang et al.*, 1995], in contrast to other tundra and alpine ecosystems where the nongrowing season receives 50–80% of the annual precipitation, and the depth of snowpack is usually $>$ 100 cm [*Brooks et al.*, 2004; *Liptzin et al.*, 2009; *Morgner et al.*, 2010]. Thorough understanding of the patterns of and drivers for non-growing-season R_s and evaluating its potential feedbacks to climate warming in Tibetan alpine grassland are urgently needed as the permafrost area in this ecosystem has been shrinking during the past several decades due to rapid increases in annual and winter temperature [*Cheng and Wu*, 2007; *Piao et al.*, 2010; *Wu and Zhang*, 2010; *You et al.*, 2010; *Zhang et al.*, 2013]. Although the importance of the non-growing-season R_s of the Tibetan alpine grassland has been recognized [*Cao et al.*, 2004; *Shi et al.*, 2006], the low time resolution (once per month) and short-term (1–2 years) measurements of previous studies, along with the complex relationships between drivers of non-growing-season R_s, limit our ability to accurately model its trend and potential responses to climate warming.

We conducted a 4 year study on R_s in alpine grasslands of the Tibetan Plateau. This is the first attempt to measure hourly R_s and heterotrophic respiration (R_h) throughout the year in a long-term experiment, made possible by

Table 1. Climate Characteristics of the Study Site[a]

	2009	2010	2011	2012
	Overall			
Annual mean air temperature (°C)	−0.81 (−23.60 – 14.20)	−0.83 (−22.58 – 17.31)	−1.46 (−23.38 – 14.63)	−1.82 (−21.96 – 14.34)
Annual mean ST_0 (°C)	4.25 (−15.66 – 17.48)	4.07 (−15.74 – 22.71)	2.48 (−18.02 – 20.40)	3.37 (−23.92 – 23.14)
Annual mean ST_5 (°C)	2.81 (−10.16 – 15.62)	2.38 (−8.50 – 16.92)	1.79 (−11.35 – 13.61)	1.12 (−10.65 – 13.77)
Annual precipitation (mm)	350.6	480.8	501.3	367.3
	Nongrowing Season			
Length (day)	175	193	182	189
Mean air temperature (°C)	−8.97 (−23.60 – 1.42)	−8.19 (−22.58 – 2.40)	−9.47 (−23.38 – 3.08)	−9.81 (−21.96 – 1.96)
Mean ST_0 (°C)	−4.62 (−15.66 – 7.99)	−4.76 (−15.74 – 7.38)	−5.61 (−18.02 – 5.99)	−4.58 (−23.92 – 7.34)
Mean ST_5 (°C)	−3.58 (−10.16 – 5.12)	−3.35 (−8.50 – 4.46)	−4.03 (−11.35 – 5.33)	−4.15 (−10.65 – 3.50)
Precipitation (snowfall, mm)	19.4	34.5	39.9	27.4
Number of days with surface soil freezing (day)	142	170	158	154
Number of days with daily maximum ST_0 > 0°C (day)	170	184	172	163
Number of days of snow recorded (day)	30	21	20	34
	Growing Season			
Length (day)	190	172	183	177
Mean air temperature (°C)	6.70 (−2.93 – 14.20)	7.43 (−4.03 – 17.31)	6.51 (−2.70 – 14.63)	6.71 (−1.54 – 14.34)
Mean ST_0 (°C)	12.28 (4.79 – 17.48)	13.84 (4.06 – 22.71)	11.29 (4.60 – 20.40)	11.85 (2.03 – 23.14)
Mean ST_5 (°C)	8.70 (−0.11 – 15.62)	8.82 (0.10 – 16.92)	7.57 (−0.97 – 13.61)	7.45 (−0.23 – 13.77)
Precipitation (rainfall, mm)	331.2	446.3	461.4	339.9

[a]ST_0: surface soil temperature; ST_5: soil temperature at 5 cm depth. Values in brackets are the ranges of the daily mean temperature.

employing a unique R_s measurement system. More specifically, a custom-made container, which maintained the internal temperature above 5°C, was used to protect our instruments from the extremely low temperature of the nongrowing season. During the nongrowing season in the Tibetan Plateau, the bulk soil is usually frozen, while the daily range of surface soil temperature is large and the daily maximum surface soil temperature is usually > 0°C due to the absence of persistent snowpack. Therefore, we first hypothesized that on the Tibetan Plateau, the non-growing-season cumulative R_s is large but its annual contribution is lower than those in the seasonal snow-covered ecosystems due to the lack of insulation by snowpack. We also hypothesized that the day-, season-, and year-scale processes of the non-growing-season R_s are driven by the daily surface soil freezing-thawing process (surface soil freezing), the seasonal change of bulk soil frozen-thawed condition (bulk soil freezing), and the accumulated soil temperature, respectively.

2. Materials and Methods

2.1. Study Site

Our study site is at the Haibei Alpine Grassland Ecosystem Research Station (Haibei Station, 101°12′E, 37°30′N, 3200 m above sea level), located in the northeastern part of the Tibetan Plateau, China. This area, dominated by alpine grassland, has a continental monsoon climate, with a long nongrowing season and a short growing season [*Zhao and Zhou*, 1999]. From 2009 to 2012, the mean annual air temperature ranged from −0.81 to −1.82°C and the annual precipitation from 350.6 to 501.3 mm (Table 1). Generally, the nongrowing season starts in late October and ends in mid-April. Though the nongrowing season is as long as 180 days, it receives only 6–8% of the annual precipitation; this period is usually characterized as dry, cold, and with no persistent snowpack (Table 1). The soil developed is Mat-Gryic Cambisol [*Chinese Soil Taxonomy Research Group*, 1995]. Soil organic carbon content and bulk density at 0–10 cm and 10–20 cm depth were 63 and 36 g kg^{-1} soil and 0.82 and 0.98 g cm^{-3}, respectively (L. Lin, unpublished data, 2013). The pH value of the 0–10 cm soil was 6.4 [*Jing et al*., 2013].

The plant community is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa pratensis*, *Carex scabrirostris*, *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontop odiumnanum*, *Blvsmus sinocompressus*, *Potentilla nivea,* and *Dasiphora fruticosa*, and the aboveground net primary production was about 350 g m^{-2} yr^{-1} (300–450 g m^{-2} yr^{-1}) from 2006 to 2010 [*Wang et al*., 2012]. Detailed information on our study site and the experimental platform can be found in previously published papers [*Kimball et al*., 2008; *Luo et al*., 2010].

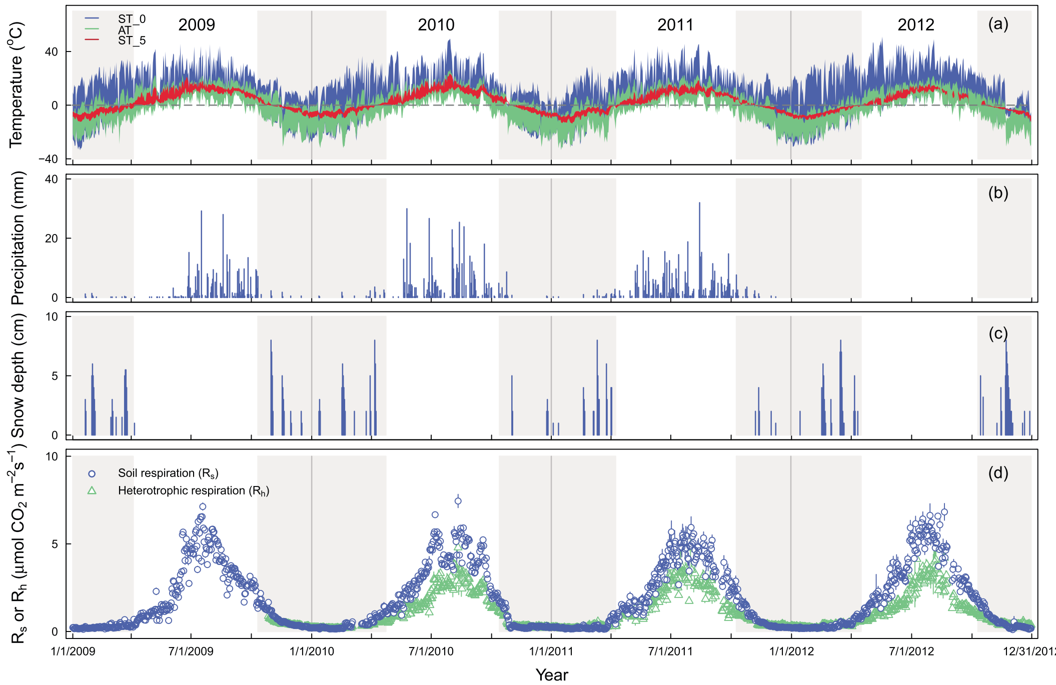

Figure 1. Seasonal and annual variation of (a) air temperature (AT), surface soil temperature (ST_0), and soil temperature at 5 cm depth (ST_5); (b) precipitation; (c) snow depth; and (d) soil respiration rate (R_s) and heterotrophic respiration rate (R_h). Shading periods represent the nongrowing season. Vertical bars represent the standard error of the means (n = 3–4 for R_s and n = 2 for R_h).

2.2. Measurements of Soil Respiration, Heterotrophic Respiration, Air Temperature, and Soil Temperature

A square study site (27 m side length) was separated into four rows of 3 m width. Each row was then further separated into four 3 m diameter circular areas (3 m interval), and one of them was randomly selected as sampling plot; thus, there were four plots to measure R_s and R_h (Figure S1 in the supporting information). In each plot, a polyvinyl chloride collar (20 cm diameter and 10 cm height) was installed to a soil depth of 3 cm and a deep collar (20 cm diameter and 65 cm height) was installed to a soil depth of 60 cm to exclude plant roots and organic matter inputs (> 90% of the belowground biomass is distributed in the top 20 cm of soil). The shallow and deep collars were used to measure R_s and R_h, respectively. The effect of dead roots on R_h was large in the first growing season after the insertion of deep collar, but it subsided in the following year (Figure S2). To avoid the effects of dead roots on R_h, only the R_h data from January 2010 to December 2012 were included in our analyses.

We had four replicates (from January to October 2009) or three replicates (from November 2009 to December 2012) for R_s and two replicates for R_h (from October 2009 to December 2012) for the hourly data (Figure 1) automatically measured using the LI-8150 Multiplexer composed of a LI-8100 Automated Soil CO_2 Flux System and five LI-8100-104 long-term chambers (Li-Cor Inc., Lincoln, NE, USA). As the non-growing-season temperature is extremely low, the instruments were placed in a custom-made container (60 cm long, 70 cm wide, and 70 cm high; power by AC220V) to protect them from extremely low temperature and ensure their normal operation. The internal temperature of this container was controlled by a heating system composed of a Toky-AI208 temperature controller (Toky Electrical Co., Ltd., Zhongshan, Guangdong, China), a temperature sensor, and heating cable embedded in the internal surface of the container. The heating system maintained the internal temperature of the container above 5°C.

We also added one more replicate for R_s and two more replicates for R_h measured manually at an interval of 5–7 days using the LI-8100 Automated Soil CO_2 Flux System with LI-8100-103 short-term chamber from November 2009 to the end of 2012. The manual measurements were carried out at different plots but at the same time as the measurements of automated CO_2 analyzer. The means of manually measured R_s (or R_h) and those of automatically measured R_s (or R_h) were calculated separately. Subsequently, the slopes of regression line between these two groups of means were compared to a 1:1 line using standardized major axis estimation in the R package *smatr* [*R Core Team*, 2012]. The slopes did not differ significantly from 1 ($P > 0.05$, Figure S3), indicating that our plots selected adequately sampled the extant spatial variation. Thus, although only the hourly data from long-term measurements (three to four replicates for R_s and two replicates for R_h) were used to investigate the day-, season-, and year-scale variations of the non-growing-season R_s (or R_h), our results should be reliable.

Data on soil temperature and moisture at 5 cm depth (ST_5 and SM_5) were automatically collected at an interval of 1 h through Decagon EC-5 Soil Moisture Sensors (Decagon Devices Inc., Pullman, WA, USA) and LI-8150-203 soil temperature probes attached to long-term chambers. We also collected hourly data on air temperature (AT) and bare-surface soil temperature (ST_0), as well as daily precipitation (rainfall and snowfall) from a weather station located near our study site (< 50 m).

2.3. Definition of the Nongrowing Season, the Surface Soil Freezing, and the Bulk Soil Freezing

The definition of the nongrowing season in this study follows that of previous phenological studies [*Körner and Paulsen*, 2004; *Piao et al.*, 2007; *Tanja et al.*, 2003], meta-analysis of winter ecosystem respiration [*Wang et al.*, 2011], and carbon flux research in boreal black spruce forest of Canada [*Bergeron et al.*, 2007]. The first day that the 7 day smoothed daily mean AT remained < 0°C for at least five consecutive days was defined as the start of the nongrowing season. Similarly, the first day that the 7 day smoothed daily mean AT remained > 0°C for at least five consecutive days was defined as the onset of the growing season.

In the nongrowing season, the daily maximum ST_0 was frequently higher than 0°C (Figure 1), although the bulk soil was frozen. Surface soil freezing and bulk soil freezing are different and should not be confused. The former occurs at the day scale, regulating daily variation; the latter occurs at the season scale and regulates seasonal variation. Thus, referenced to *Konestabo et al.* [2007] and *Zhu et al.* [2012], a day was identified as having a surface soil freezing when it matched the following conditions: (1) daily minimum ST_0 below 0°C for at least 3 h and (2) daily maximum ST_0 above 0°C for at least 3 h. The definition of bulk soil freezing was based on the 7 day smoothed daily minimum or maximum ST_5 (ST_5_{min} or ST_5_{max}). Bulk soil is considered thawed when daily ST_5_{min} remains > 0°C for at least five consecutive days; it is considered frozen when daily ST_5_{max} remains < 0°C for at least five consecutive days [*Guo et al.*, 2011].

2.4. Statistical Analysis

The hourly R_s and R_h rates were used to calculate the daily mean respiration rates, seasonal mean respiration rates, cumulative respiration, contribution of the non-growing-season R_s to annual total R_s, and the contribution of seasonal variation in R_h to R_s. Nonlinear regression approach with a four-parameter Gaussian function was employed to investigate the seasonal variations in diurnal patterns of R_s, because this function performed better than the quadratic function, sinusoidal function, and three-parameter Gaussian function (Table S1). This function is as follows:

$$R_{s\cdot\mathrm{Hour}} = a + b \times e^{\left[-0.5 \times \left(\frac{\mathrm{BST_{hour}} - c}{d}\right)^2\right]} \tag{1}$$

where $R_{s\cdot\mathrm{Hour}}$ is the simulated hourly R_s rate and $\mathrm{BST_{hour}}$ is the Beijing Standard Time (BST, UTC + 08). The parameters *a*, *b*, *c*, and *d* represent four characteristics of the diurnal curve: *a*, the daily minimum R_s rate; *b*, the amplitude; *c*, the time R_s rate reaches its peak value; and *d*, the width of peak (Figure 3a). The paired samples *t* test was used to identify the differences of parameters between the nongrowing season and the growing season.

The Q_{10} function was employed in investigating the dependence of R_s (or R_h) on temperature as follows:

$$\ln R_{s\cdot\mathrm{Day}} = m + n \times T \quad \text{or} \quad R_{s\cdot\mathrm{Day}} = e^m \times e^{n\times\mathrm{T}} \tag{2}$$

where $\ln R_{s\cdot\mathrm{Day}}$ or $R_{s\cdot\mathrm{Day}}$ are natural-log-transformed daily mean respiration rate ($\ln R_{s\cdot\mathrm{Day}}$ or $\ln R_{h\cdot\mathrm{Day}}$) or daily mean respiration rate (R_s or R_h) and *T* is the daily mean temperature. In this study, the natural-log-transformed respiration rate was used, as it can clearly display the seasonal variation of temperature dependence of R_s [*Elberling and Brandt*, 2003; *Tilston et al.*, 2010]. Parameters *m* and *n*, representing

Table 2. The Non-Growing-Season and the Growing-Season Mean Soil Respiration (R_s) Rate (1 μmol CO_2 m^{-2} s^{-1} = 12 μg C m^{-2} s^{-1}), Contribution of Heterotrophic Respiration (R_h), the Ratio of Non-Growing-Season R_h to the Growing-Season R_h (NG_R_h/GS_R_h), Cumulative R_s, and the Contribution of Non-Growing-Season R_s to Annual Total R_s[a]

	2009	2010	2011	2012
	Mean R_s Rate			
Nongrowing season (μmol CO_2 m^{-2} s^{-1})	0.49 (0.02)	0.44 (0.02)	0.43 (0.07)	0.45 (0.06)
Growing season (μmol CO_2 m^{-2} s^{-1})	2.97 (0.04)	3.41 (0.06)	3.22 (0.27)	3.45 (0.26)
	Contribution of R_h			
Nongrowing season (%)	—	91.8 (9.1)	98.1 (11.9)	88.1 (4.2)
Growing season (%)	—	58.5 (0.7)	59.6 (4.5)	51.2 (5.0)
NG_R_h/GS_R_h (%)	—	22.4 (0.9)	22.1 (0.8)	23.9 (0.3)
	Cumulative R_s			
Nongrowing season (g C m^{-2})	89 (4)	87 (5)	82 (13)	88 (12)
Growing season (g C m^{-2})	584 (9)	609 (10)	612 (51)	633 (48)
Non-growing-season contribution (%)	13.2 (0.5)	12.5 (0.4)	11.8 (1.1)	12.2 (0.9)

[a]Values in brackets are the standard error of the means (n = 3–4 for R_s and n = 2 for R_h).

intercept and slope, respectively, were used to calculate the reference respiration rate (R_0, simulated R_s rate at 0°C) and temperature sensitivity (Q_{10}) with the following functions:

$$R_0 = e^m \tag{3}$$

$$Q_{10} = e^{(10 \times n)} \tag{4}$$

A large body of work has shown that enzyme-catalyzed reactions can occur below 0°C [*Monson et al.*, 2006b; *Panikov et al.*, 2006], while in frozen soil, extremely slow diffusion of extracellular enzymes and substrates and/or intracellular desiccation can significantly influence temperature dependence of R_s [*Davidson and Janssens*, 2006; *Mikan et al.*, 2002]. Thus, piecewise linear regression (PLR) was used to explore whether there is a breakpoint in the functional relationship between respiration and temperature. In this analysis, the breakpoint was defined as the temperature where the residual standard error of the PLR model reached its minimum value. The ordinary linear regression (OLR) and PLR models were compared using an F test. Only when the PLR model performed better than the OLR model was the breakpoint considered significant [*Toms and Lesperance*, 2003]. The intercept and slope parameters were employed to calculate the R_0 and Q_{10} before and after the breakpoint using equations (3) and (4). Analysis of covariance (ANCOVA) was conducted to investigate the difference of R_0 (or Q_{10}) between the nongrowing season and the growing season.

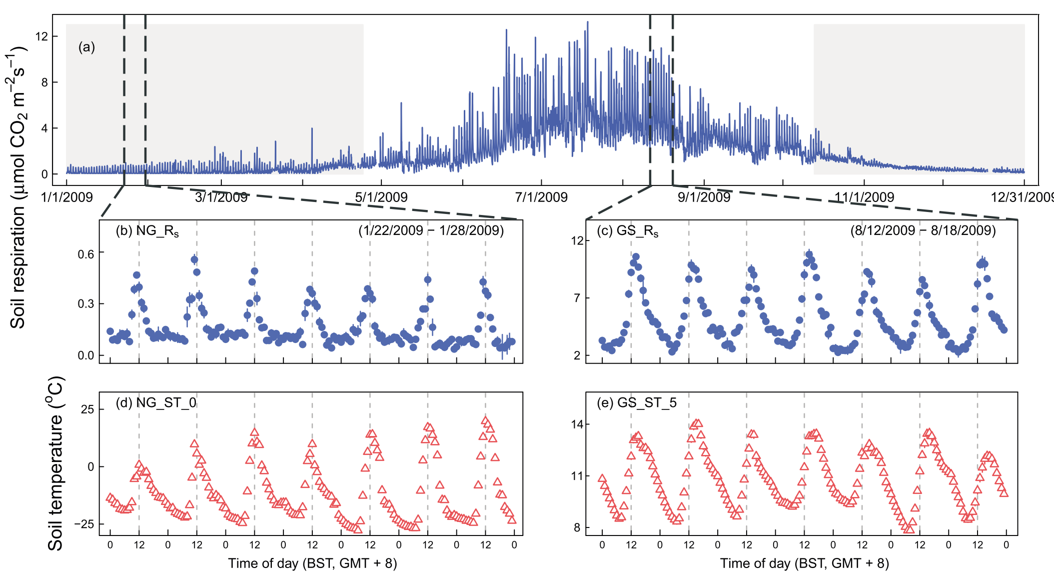

Figure 2. Comparisons of (a) diurnal patterns of (b) the non-growing-season soil respiration (NG_R_s), (c) the growing-season soil respiration (GS_R_s), (d) the non-growing-season surface soil temperature (NG_ST_0), and (e) the growing-season soil temperature at 5 cm depth (GS_ST_5). Vertical bars represent the standard error of the means (n = 3–4).

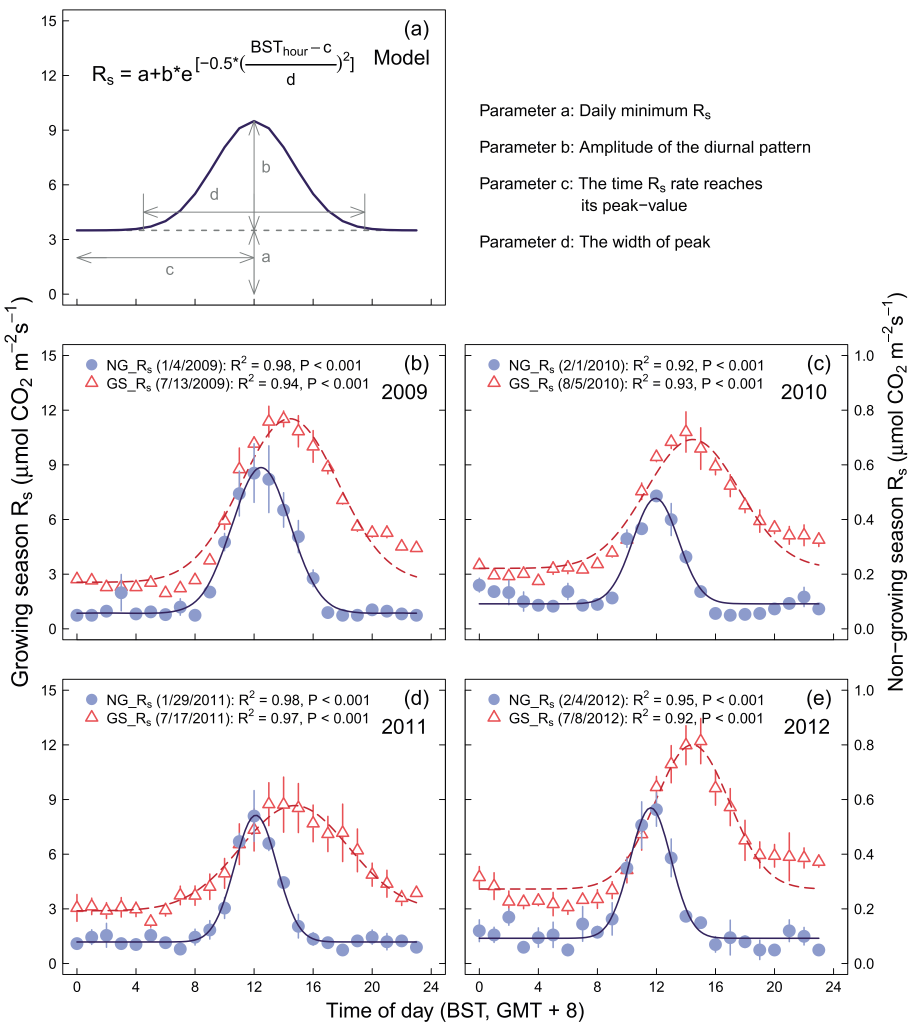

Figure 3. Comparisons of observed and simulated R_s diurnal patterns. (a) The four-parameter Gaussian function. (b–e) Observed (triangles and circles) and simulated (dashed and solid lines) R_s diurnal patterns of the nongrowing season (NG_R_s) and the growing season (GS_R_s). Vertical bars represent the standard error of the means (n = 3–4).

The Q_{10} function was also used to determine the functional relationship between the daily cumulative R_s and the daily accumulated ST_0 (ST_0 > 0°C) in the nongrowing season. Here the daily accumulated ST_0 was calculated based on hourly ST_0 data and defined as the sum of ST_0 when it is higher than 0°C. The daily cumulative R_s is the sum of hourly measured R_s, which was averaged across replicated collars (n = 3–4).

All statistical analyses were performed, and graphs were prepared using R 2.15.1 software [*R Core Team*, 2012]. Differences were considered to be significant when the *P* value was ≤ 0.05.

3. Results

3.1. Climate Characteristics of the Study Site

From 2009 to 2012, the non-growing-season precipitation varied from 19.4 to 39.9 mm, contributing to only 6–8% of the annual total. There was no persistent snowpack in the nongrowing seasons; the number of days of snow recorded was only 20–34 days. The number of daily maximum ST_0 higher than 0°C was 163–184 days, and the number of days with surface soil freezing was 142–170 days in the nongrowing seasons (Figure 1 and Table 1).

3.2. Quantity and Source of the Non-Growing-Season R_s

From 2009 to 2012, R_s showed a clear seasonal pattern, with averages of 0.43–0.49 μmol CO_2 m^{-2} s^{-1} in the nongrowing season and 2.97–3.45 μmol CO_2 m^{-2} s^{-1} in the growing season (Figure 1 and Table 2).

Table 3. Comparisons of Diurnal Pattern Parameters Between the Nongrowing Season and the Growing Season[a]

	2009	2010	2011	2012
		Daily Minimum R_s (Parameter a)		
Nongrowing season	0.36 (0.03) b	0.36 (0.02) b	0.38 (0.06) b	0.26 (0.03) b
Growing season	2.16 (0.02) a	2.62 (0.03) a	2.49 (0.17) a	2.67 (0.15) a
		Amplitude of the Diurnal Pattern (Parameter b)		
Nongrowing season	0.50 (0.05) b	0.29 (0.05) b	0.24 (0.06) b	0.20 (0.03) b
Growing season	2.82 (0.06) a	2.63 (0.17) a	2.77 (0.38) a	3.08 (0.33) a
		The Time R_s Rate Reaches Its Peak Value (Parameter c)		
Nongrowing season	12.48 (0.21) b	13.33 (0.27) a	12.98 (0.17) b	12.65 (0.20) b
Growing season	14.23 (0.14) a	14.11 (0.07) a	13.94 (0.15) a	14.06 (0.10) a
		The Width of Peak (Parameter d)		
Nongrowing season	2.03 (0.11) b	2.62 (0.31) a	1.99 (0.10) b	2.46 (0.30) a
Growing season	2.79 (0.05) a	2.91 (0.09) a	2.61 (0.04) a	2.43 (0.05) a

[a]Values in brackets are the standard error of the means ($n = 3$–4). Letters (a and b) within a column represent significant difference between parameters (paired t test, $P < 0.05$).

The non-growing-season cumulative R_s ranged from 82 to 89 g C m^{-2}, contributing to 11.8–13.2% of the annual cumulative R_s (Table 2). The interannual variation of both the non-growing-season cumulative R_s (coefficient of variation (CV) = 3.6% across 4 years) and its contribution to annual total R_s (CV = 5.5% across 4 years) was small. R_h was the major component of R_s, contributing to 88.1–98.1% of the non-growing-season R_s and 51.2–59.6% of the growing-season R_s (Table 2). The soil organic carbon decomposed in the nongrowing season was 22.1–23.9% of that during the growing season (Table 2).

3.3. Diurnal Pattern of R_s in the Non-Growing-Season

Across the 4 years, R_s displayed clear diurnal patterns (Figures 2a–2c), and the four-parameter Gaussian function explained > 90% of its variation (Figures 3b–3e). Further analysis showed that the daily minimum R_s rates (parameter a) and amplitudes (parameter b) of the non-growing-season diurnal curves were significantly lower than their growing-season counterparts (paired t test, $P < 0.05$, Table 3), and the diurnal curves of the nongrowing season had significantly earlier peaks than those of the growing season (paired t test, $P < 0.05$, Table 3), although this trend was not significant in 2010 (paired t test, $P > 0.05$, Table 3).

The peak time of R_s diurnal pattern was consistent with that of ST_0 in the nongrowing season (Figures 2b and 2d), while in the growing season, it had a similar peak time with that of ST_5 (Figures 2c and 2e). The explanatory power of ST_0 and ST_5 in predicting the R_s in the nongrowing and the growing seasons was compared. In the nongrowing season, the explanatory power of ST_0 (13.1–25.2%) was equal to or larger than that of ST_5 (9.8–26.0%, Table 4). In the growing season, however, ST_5 (66.5–80.9%) was a better predictor of R_s than ST_0 (35.2–53.8%, Table 4).

3.4. Temperature Dependence of R_s and R_h in the Non-Growing-Season

The PLR approach demonstrated that a breakpoint around 0°C exists in the functional relationship between ln$R_{s\text{-Day}}$ and ST_5 (Figure 4). Given that the freezing point of water is 0°C (neglecting salinity effects), 0°C was

Table 4. Correlations Between Soil Respiration (R_s) and Soil Temperature During the Nongrowing Season and the Growing Season[a]

	2009	2010	2011	2012
		Nongrowing Season (Frozen Soil)		
R_s versus ST_0	0.224 (0.079) a	0.131 (0.003) a	0.252 (0.070) a	0.200 (0.053) a
R_s versus ST_5	0.165 (0.095) b	0.098 (0.008) b	0.260 (0.120) a	0.189 (0.103) a
		Growing Season (Thawed Soil)		
R_s versus ST_0	0.352 (0.038) b	0.359 (0.029) b	0.526 (0.040) b	0.538 (0.041) b
R_s versus ST_5	0.666 (0.034) a	0.724 (0.030) a	0.809 (0.019) a	0.665 (0.037) a

[a]Values in brackets are the standard error of the means ($n = 3$–4). Letters (a and b) within a column represent significant difference between explanation powers (R^2) of surface soil temperature (ST_0) and soil temperature at 5 cm depth (ST_5) on R_s (paired t test, $P < 0.05$).

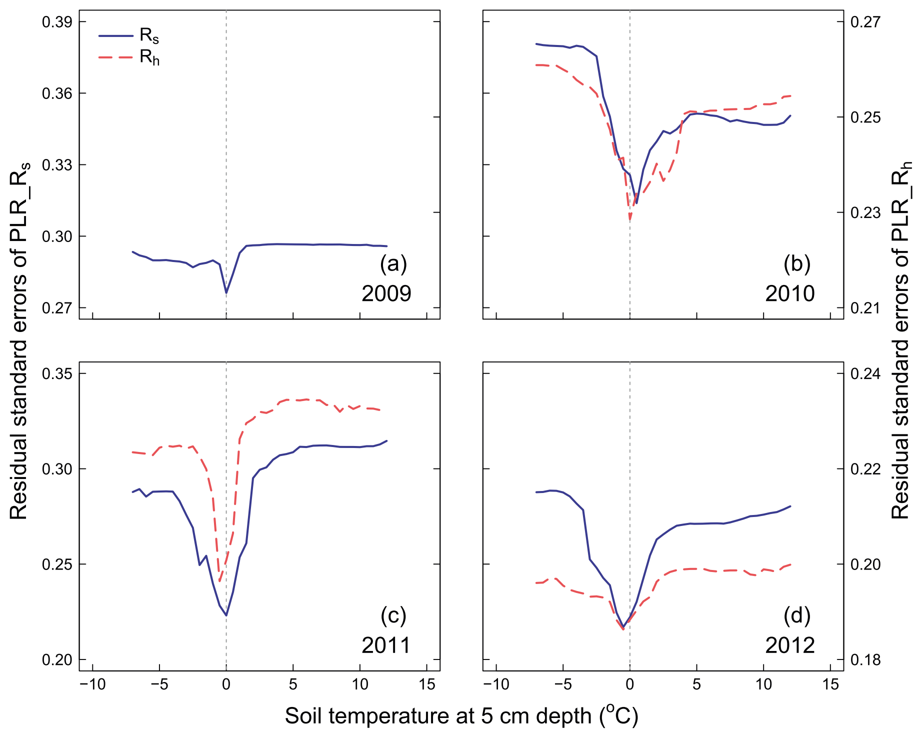

Figure 4. Residual standard errors (RSE) of piecewise linear regression model (PLR). Blue (solid) lines represent RSE of PLR model when it was used to analyze the relationship between R_s and ST_5 (PLR_R_s); red (dashed) lines represent RSE of PLR model when it was used to analyze the relationship between R_h and ST_5 (PLR_R_h).

chosen as the breakpoint of the ln$R_{s\text{-Day}}$ versus ST_5 relationship. Further analyses showed that for both R_s and R_h, PLR models performed significantly better than OLR models (Table S2).

Therefore, we calculated the R_0 and Q_{10} of R_s and R_h under two different environmental conditions: the non-growing-season frozen soil and the growing-season thawed soil. The ANCOVA showed that in the former, either the R_0 or Q_{10} of R_s was not significantly different from their R_h counterparts ($P > 0.05$, Table 5).

Table 5. Differences of Reference Respiration Rate (R_0) and Temperature Sensitivity (Q_{10}) Between the Nongrowing Season and the Growing Season[a]

	2009	2010	2011	2012
		Nongrowing season (frozen soil)		
		Reference Respiration Rate (R_0, μmol CO_2 m^{-2} s^{-1})		
R_s	0.46 (0.03) B	0.40 (0.03) aB	0.44 (0.09) aB	0.53 (0.08) aB
R_h	––	0.38 (0.02) aB	0.44 (0.02) aB	0.47 (0.03) aB
		Temperature Sensitivity (Q_{10})		
R_s	2.89 (0.13) B	2.48 (0.10) aB	2.77 (0.11) aB	2.60 (0.13) aB
R_h	––	2.48 (0.06) aB	2.51 (0.17) aB	2.60 (0.16) aB
		Growing season (thawed soil)		
		Reference Respiration Rate (R_0, μmol CO_2 m^{-2} s^{-1})		
R_s	0.84 (0.03) A	1.21 (0.03) aA	1.09 (0.02) aA	1.32 (0.05) aA
R_h	––	0.73 (0.05) bA	0.75 (0.01) bA	0.69 (0.03) bA
		Temperature Sensitivity (Q_{10})		
R_s	5.58 (0.13) A	2.89 (0.10) aA	3.60 (0.12) aA	3.06 (0.13) aA
R_h	––	2.77 (0.11) aA	3.28 (0.19) aA	3.08 (0.17) aA

[a]Values in brackets are the standard error of the means ($n = 3$–4 for R_s and $n = 2$ for R_h). Letters in lowercase (a and b) within a column indicate a significant difference of R_0 (or Q_{10}) between soil respiration (R_s) and heterotrophic respiration (R_h) in the same season (ANCOVA, $P < 0.05$). Letters in uppercase (A and B) within a column indicate a significant seasonal difference of R_0 (or Q_{10}) (ANCOVA, $P < 0.05$).

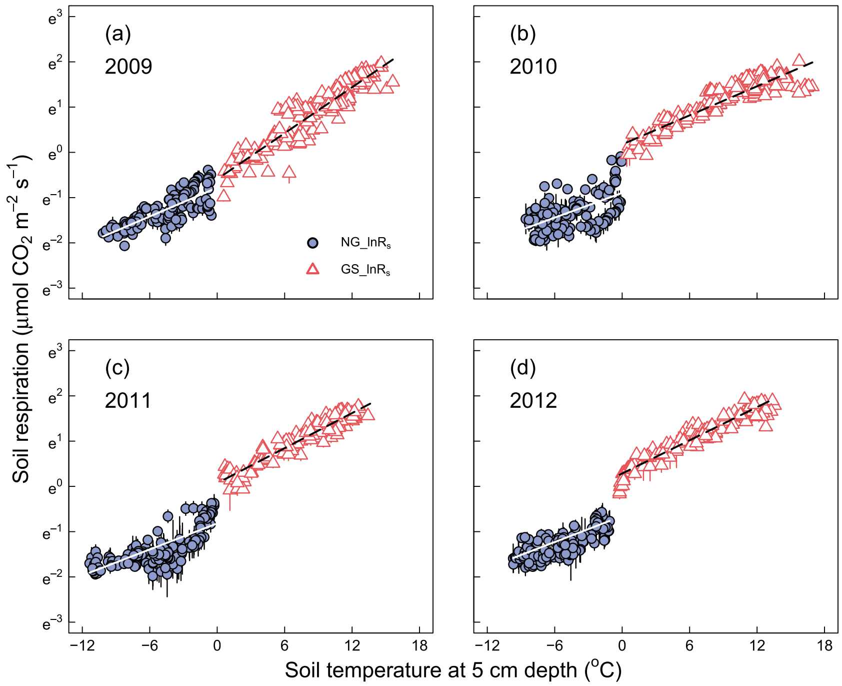

Figure 5. Difference of R_s temperature dependence between the nongrowing season (frozen soil, NG_R_s) and the growing season (thawed soil, GS_R_s). Vertical bars represent the standard error of the means ($n = 3$–4).

In the latter, R_s and R_h had a different R_0 ($P < 0.05$, Table 5) but a similar Q_{10} ($P > 0.05$, Table 5). R_s of the non-growing-season frozen soil had lower R_0 and Q_{10} than that of the growing-season thawed soil ($P < 0.05$, Figure 5 and Table 5). Similarly, R_h of the non-growing-season frozen soil had lower R_0 and Q_{10} than that of the growing-season thawed soil ($P < 0.05$, Table 5). These results indicate that when investigating year-round R_s, employing two Q_{10} functions with a breakpoint at 0°C would be better than just using a single Q_{10} function.

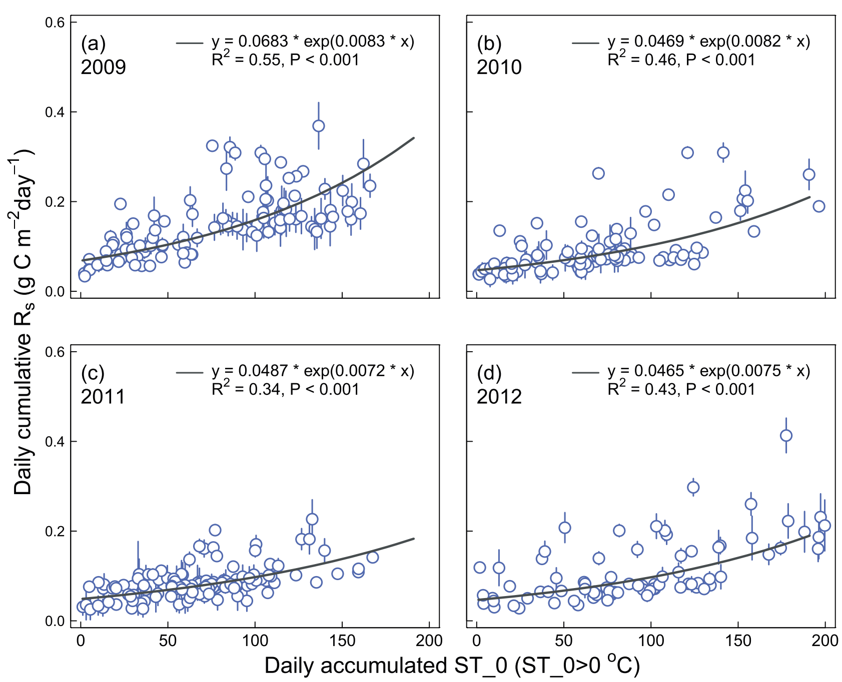

Figure 6. (a–d) The relationship between the daily cumulative R_s and the daily accumulated soil surface temperature (ST_0, ST_0 > 0°C) in the nongrowing season. Vertical bars represent the standard error of the means ($n = 3$–4).

3.5. Cumulative R_s in the Non-Gowing-Season

In the nongrowing season, the daily cumulative R_s exponentially increased with daily accumulated ST_0 (ST_0 > 0°C), explaining 34–55% of the intraannual variations (Figures 6a–6d). This result is also consistent with our deduction that the surface soil freezing drives the non-growing-season diurnal pattern of R_s.

4. Discussion

The non-growing-season R_s is an essential carbon cycling process in the Tibetan alpine grassland. The main conclusions of this study are the following: (1) the non-growing-season cumulative R_s is large, accounting for 11.8–13.2% of the annual total R_s, indicating that it plays a significant role in the global carbon cycling and (2) surface soil freezing, bulk soil freezing, and accumulated surface soil temperature are the day-, season-, and year-scale drivers of the non-growing-season R_s, respectively. Our results suggest that warmer winters can trigger carbon loss from the Tibetan alpine grassland because of higher-temperature sensitivity of thawed soils than frozen soils.

4.1. General Patterns of the Non-Growing-Season R_s

The large amount of carbon respired during the nongrowing season suggests that the non-growing-season R_s of the Tibetan alpine grassland leads to significant carbon loss and plays an important role in the global carbon cycle. R_h stemming from the microbial decomposition of soil organic matter was the dominant component of non-growing-season R_s; it accounted for one fifth of the growing-season R_h. These results imply that in the Tibetan alpine grassland, though there is no persistent snow cover in the nongrowing season and the soil temperature is low, soil microbes are still active and are the major biotic controller of the non-growing-season R_s. Therefore, the non-growing-season carbon processes must be taken into consideration when assessing the carbon sink/source function of the Tibetan alpine grassland; otherwise, the annual decomposition of soil organic carbon will be significantly underestimated.

The non-growing-season cumulative R_s (82–89 g C m^{-2}) and its contribution to annual total R_s (11.8–13.2%) of the Tibetan alpine grassland are lower than the R_s values (103 to 176 g C m^{-2}) and annual contributions (14–40%) reported for the heath tundra ecosystems [*Elberling*, 2007; *Larsen et al*., 2007; *Morgner et al*., 2010; *Sullivan et al*., 2010]. When compared to sedge and tussock tundra, which share many similarities with the Tibetan alpine grassland including the vegetation, the Tibetan alpine grassland has higher non-growing-season cumulative R_s. On the other hand, the annual contribution of the non-growing-season cumulative R_s to total R_s is lower than the reported range (17–30%) of the sedge and tussock tundra [*Fahnestock et al*., 1999; *Morgner et al*., 2010; *Oechel et al*., 1997; *Sullivan et al*., 2008; *Welker et al*., 2004]. Variation in estimated non-growing-season cumulative R_s among ecosystems is likely due to the differences in non-growing-season temperature [*Wang et al*., 2011], snow cover and its insulating effect [*Brooks et al*., 1997; *Nobrega and Grogan*, 2007; *Welker et al*., 2000], vegetation type [*Grogan and Jonasson*, 2006], substrate availability [*Brooks et al*., 2004], grazing intensity [*Chen et al*., 2013], and R_s measurement technique [*Grogan and Chapin*, 1999; *McDowell et al*., 2000].

The lower annual contribution of non-growing-season cumulative R_s to total R_s compared to that of sedge and tussock tundra is likely due to the unique non-growing-season climate of this plateau. More specifically, in the nongrowing season, the Tibetan alpine grassland receives only 6–8% of its annual precipitation and usually has no thick and persistent snowpack. In contrast, in tundra ecosystems, the nongrowing season receives 50–80% of annual precipitation via snowfall, and the non-growing-season snow depth is often > 50 cm [*Sullivan et al*., 2008] or even > 100 cm [*Brooks et al*., 2004; *Morgner et al*., 2010]. The duration and depth of snow cover can have a marked impact on soil temperature [*Campbell et al*., 2005], and manipulated deeper snowpack has been shown to induce higher non-growing-season R_s than ambient plots [*Morgner et al*., 2010; *Nobrega and Grogan*, 2007; *Schimel et al*., 2004].

The relatively short nongrowing season and high growing-season R_s of the Tibetan alpine grassland than arctic tundra may also lead to lower contribution of the non-growing-season cumulative R_s. Though the non-growing-season length is ~ 180 days on the Tibetan Plateau, it is relatively shorter than that of the tundra ecosystems which can be ~ 240 days [*Belshe et al*., 2013; *Fahnestock et al*., 1999; *Grogan and Jonasson*, 2006; *Oechel et al*., 1997]. In addition, the growing-season cumulative R_s of our study site was as high as 584–633 g C m^{-2}, which is 3–8 times higher than that of tundra ecosystems (82–200 g C m^{-2}) [*Elberling*, 2007; *Grogan and Chapin*, 1999]; this explains the lower annual contribution of the non-growing-season R_s in the Tibetan alpine grassland than the arctic tundra ecosystems.

4.2. The Day-, Season-, and Year-Scale Drivers of the Non-Growing-Season R_s

We observed that the non-growing-season R_s had a lower daily minimum R_s rate and amplitude and an earlier peak than those of the growing season. Two factors may explain this seasonal variation of diurnal pattern. Autotrophic respiration (R_a) of plant roots is the major component of the growing-season R_s that accounts for 40.4–48.8% of the growing-season R_s, but it accounts for only 1.9–11.9% of the non-growing-season R_s. In the nongrowing season, the interruption of the belowground transmission of plant photosynthate lowers R_a and consequently induces a lower daily minimum R_s rate and a lower amplitude [*Högberg et al.*, 2001; *Kuzyakov*, 2006; *Tang et al.*, 2005].

Our study shows that the drivers of diurnal pattern of R_s are different between the growing and nongrowing seasons. In the growing season, soil temperature (ST_5) is the most important driver of diurnal pattern of R_s, while temperature-induced surface soil freezing, a unique characteristic of the non-growing-season soil of this plateau, drives the non-growing-season diurnal pattern of R_s. Surface soil freezing-thawing process is regulated by the climate properties of the Tibetan Plateau in nongrowing season, i.e., high solar radiation, no polar night, and no thermal insulation of snow cover. In the night, surface soil temperature drops quickly to < 0°C due to the heat exchange between soil and atmosphere; in the day, solar radiation warms the surface soil directly and induces thawing of surface soil [*Bristow and Campbell*, 1984; *Pan et al.*, 2013]. The CO_2 production continues in frozen soil at night because soil microbes can maintain their activities at extremely low temperature [*Panikov et al.*, 2006], but the CO_2 produced is trapped by frozen ground [*Elberling and Brandt*, 2003]. In the day, rising temperatures and thawing of surface soil allow CO_2 to be released, inducing a pulse in CO_2 emission [*Matzner and Borken*, 2008]. Because surface soil temperature rises faster than the soil temperature at 5 cm depth during the daytime, this results in an earlier peak time than that of the growing season.

Bulk soil freezing is an important regulator of the season-scale variation in temperature dependence of R_s, and both the R_0 and Q_{10} of the non-growing-season R_s were lower than their growing-season counterparts. The relatively lower Q_{10} in the nongrowing season is not consistent with a previous study conducted in a seasonal snow-covered alpine coniferous forest in Rocky Mountains, USA. In that study, the maximum snow depth was ~ 120 cm and the R_s showed a significantly higher Q_{10} under snowpack due to soil microbial communities of fast substrate utilization [*Monson et al.*, 2006b]. Thin and patchy snow cover in the Tibetan Plateau and differences in soil water content may explain these apparent inconsistencies. More specifically, under thin snow cover, soil microbes had a lower activity than under thick snow cover, due to the absence of insulation effects [*Brooks et al.*, 1998; *Brooks and Williams*, 1999]. In addition, in a laboratory soil incubation study, Q_{10} increased with higher soil water content when soil temperature was < 0°C [*Elberling and Brandt*, 2003]. Thus, the low precipitation and drought during the nongrowing season in the Tibetan alpine grassland may explain the lower non-growing-season Q_{10} than the seasonal snow-covered ecosystems. On the other hand, not considering the breakpoint of the functional relationship between R_s and soil temperature may account for the inconsistent reports. When the changes of R_0 around the breakpoint are not included in models, it may lead to overestimation of the non-growing-season Q_{10}.

Our study shows that using two Q_{10} functions with a breakpoint of 0°C is superior to using a single Q_{10} function when investigating year-round temperature dependence of R_s (or R_h), but the Q_{10} function employed in current analyses cannot mechanistically explain why R_0 and Q_{10} vary between seasons and why an observed breakpoint exists. Here we emphasize the effects of bulk soil freezing on unfrozen water content and substrate supply for soil microorganisms. In a field study, it was shown that fluid water is depleted when soil water freezes under temperature lower than 0°C; unfrozen water content exponentially decreases with soil temperature when soil temperature is < 0°C [*Schimel et al.*, 2006]. Recently, another study showed that in frozen soil, unfrozen water content was highly dependent on temperature, especially between −2 and 0°C, and strongly affects substrate supply, soil microbial activity, and temperature dependence of the non-growing-season R_s [*Tucker*, 2014]. Laboratory soil incubation studies have shown that the soil CO_2 production was negatively correlated with unfrozen water content at −4°C [*Öquist et al.*, 2009] and the temperature dependence of R_h at subzero temperature was moderated by unfrozen water content [Tilston et al., 2010], indicating that soil microbial activity in frozen soil is controlled by water availability. In addition, extremely cold temperature will limit the substrate supply for soil microorganisms. The non-growing-season R_s is almost entirely from microbial decomposition, which is a temperature-dependent biological process. In this process, activation energy is one of the dominant abiotic factors according to the Arrhenius kinetic theory, while activation energy is directly related to the molecular structure of substrates. Less reactive and more recalcitrant substrates, which are complex molecules and have higher activation energy, should have higher-temperature sensitivity than the labile substrates [*Davidson and Janssens*, 2006]. Under freezing temperature, decomposition of recalcitrant substrates is limited due to low activation energy supply, resulting in lower R_0 and Q_{10} in the nongrowing season. Therefore, a single Q_{10} model cannot adequately represent the year-round temperature dependence of R_s.

In the current study, we found that the amount of soil organic carbon decomposed during the nongrowing season contributed a considerable proportion (about one fifth of that in the growing season), which are directly driven by surface soil temperature. Considering that the Tibetan Plateau has been experiencing a larger-than-average trend of warming and the cold months have been facing even faster rate of warming than the growing season during the last decades [*Piao et al.*, 2010; *You et al.*, 2010; *Zhang et al.*, 2013], our study suggests that the warming climate will cause an increase in the non-growing-season soil CO_2 emission.

4.3. Implications

The Tibetan Plateau is one of the most sensitive and vulnerable regions to global warming; it has the largest permafrost coverage in the low-middle latitudes, but the speed of permafrost loss over this plateau has been rapid in the last decades [*Cheng*, 2005; *Cheng and Wu*, 2007; *Nan et al.*, 2005; *Wu and Zhang*, 2010]. Recent studies reported that the permafrost soils may positively feedback to climate warming, because of the increased decomposition rates of soil carbon with rising temperature [*Belshe et al.*, 2013; *Dörfer et al.*, 2013; *Koven et al.*, 2011]. In our study, both R_0 and Q_{10} of thawed soil were higher than those of the frozen soil, and the thawed soil had the potential to release significantly more CO_2 into the atmosphere than the frozen soil (Table S3 and Figure S4). Although our study site does not contain permafrost, these results are relevant to permafrost thawing because this site is located in the transitional zone from permafrost to seasonally frozen soil in the northeastern region of the Tibetan Plateau (Figure S5). Considering that this plateau acts as carbon sink [*Kato et al.*, 2006; *Zhao et al.*, 2006], our results suggest that degradation of permafrost area can trigger carbon loss from this plateau, weaken the carbon sink function, or even shift the Tibetan alpine grassland from a net carbon sink to a source.

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