forests

MDPI

Article

Diurnal Freeze-Thaw Cycles Modify Winter Soil Respiration in a Desert Shrub-Land Ecosystem

Peng Liu [1,2], Tianshan Zha [1,2,*], Xin Jia [1,2,3], Ben Wang [1,2], Xiaonan Guo [1,2], Yuqing Zhang [1,2], Bin Wu [1,2], Qiang Yang [1,2] and Heli Peltola [3]

1 Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University, Beijing 100083, China; spiritlover@126.com (P.L.); xinjia@bjfu.edu.cn (X.J.); benwang918@gmail.com (B.W.); littlepondGXN@163.com (X.G.); zhangyqbjfu@gmail.com (Y.Z.); wubin@bjfu.edu.cn (B.W.); yangq201310@163.com (Q.Y.)

2 Key Laboratory of State Forestry Administration on Soil and Water Conservation, Beijing Forestry University, Beijing 100083, China

3 School of Forest Sciences, Faculty of Science and Forestry, University of Eastern Finland, Joensuu 80101, Finland; heli.peltola@uef.fi

* Correspondence: tianshanzha@bjfu.edu.cn; Tel.: +86-10-6233-6608

Academic Editors: Brian D. Strahm and Timothy A. Martin
Received: 29 May 2016; Accepted: 26 July 2016; Published: 29 July 2016

Abstract: Winter soil respiration (R_s) is becoming a significant component of annual carbon budgets with more warming in winter than summer. However, little is known about the controlling mechanisms of winter R_s in dryland. We made continuous measurements of R_s in four microsites (non-crust (BS), lichen (LC), moss (MC), and a mixture of moss and lichen (ML)) in a desert shrub-land ecosystem northern China, to investigate the causes of R_s dynamics in winter. The mean winter R_s ranged from 0.10 to 0.17 μmol CO_2 $m^{-2} \cdot s^{-1}$ across microsites, with the highest value in BS. Winter Q_{10} (known as the increase in respiration rate per 10 °C increase in temperature) values (2.8–19) were much higher than those from the growing season (1.5). R_s and Q_{10} were greatly enhanced in freeze-thaw cycles compared to frozen days. Diurnal patterns of R_s between freeze-thaw and frozen days differed. Although the freeze-thaw period was relatively short, its cumulative R_s contributed significantly to winter R_s. The presence of biocrust might induce lower temperature, thus having fewer freeze-thaw cycles relative to bare soil, leading to the lower R_s for microsites with biocrusts. In conclusion, winter R_s in drylands was sensitive to soil temperature (T_s) and T_s-induced freeze-thaw cycles. The temperature impact on R_s varied among soil cover types. Winter R_s in drylands may become more important as the climate is continuously getting warmer.

Keywords: winter soil respiration; soil crust; frozen; freeze-thaw cycles; Q_{10}

1. Introduction

Dryland (arid and semiarid) areas cover more than one-third of the earth's surface, and are rapidly expanding under climate change and human activities [1]. Ecosystems in these areas store approximately 15% of total soil organic carbon (C) and play an important role in the global C budget [2]. However, they are particularly vulnerable to climate change [2]. In order to accurately predict global C cycling under a changing climate, it is necessary to know how dryland soil respiration (R_s), the primary path by which CO_2 fixed by plants returns to atmosphere [3], responds to variations in climate. Currently, the R_s of dryland ecosystems and its responses to environmental factors are studied to a much lesser extent compared to other ecosystems [4].

Recent studies reveal that winter R_s is an important component of annual R_s and significantly affects the regional C balance in cold biomes [5–7]. But little attention has been given to winter R_s

in drylands, and previous studies have concentrated on tundra and boreal forest ecosystems [7]. More pronounced warming in winter than in summer recently has been observed in dryland ecosystems, and this trend is expected to continue [8]. It was reported that winter R_s may be more sensitive to climate change because of its high temperature sensitivity at low temperatures [9,10]. Additionally, increases in air and soil temperatures during winter can lead to a shorter soil-freezing period, higher evaporative losses of soil moisture, and potentially alter the microbial community composition [11,12], which would significantly influence seasonal carbon processes such as soil respiration (R_s). However, the patterns, drivers and potential feedbacks of winter R_s in drylands remain unclear. This knowledge gap challenges our confidence in climate change and C budget estimates.

Freeze-thaw events, a significant characteristic of middle latitudes, occur frequently in Eurasian dryland ecosystems. Under a changing climate, there is growing concern about the effects of freeze-thaw events on R_s, as the increasing frequency of freeze-thaw events plays an important role in regulating the turnover rate of C [13]. Observations that freeze-thaw events cause additional losses of C from arable soils but may suppress soil C losses under natural vegetation [13,14] raise the question of the relevance of freeze-thaw events to R_s. Most studies on the effects of freeze-thaw cycles on R_s have been laboratory-based, and were conducted with arctic/arable soils. These studies did not compare thawing and frozen periods [14]. Freeze-thaw events are particularly important in cold dryland regions, because of the sparse cloud cover, and large diurnal amplitudes of solar irradiance and surface temperature [15]. However, no consensus exists concerning the effect of freeze-thaw events on R_s for drylands. A field study is needed that compares the impacts of frozen and freeze-thaw periods on R_s in drylands. Diurnal changes in SWC during freeze-thaw cycles may affect the diurnal patterns of R_s and help to explain the effects of freeze-thaw events on R_s.

Biocrusts, a key biotic component of dryland ecosystems, can exert important impacts on regional C processes such as R_s [4]. For instance, biocrusts were reported to affect R_s by constraining microsite factors, such as T_s and SWC [16]. But these reports were explored mostly during the growing season [3]. We have little knowledge about the influence of biocrusts on soil temperature and moisture during winter. Several studies reported that biocrusts may also affect soil physical processes and properties at low temperatures [17–19]. Therefore, the biocrusts potentially affect winter R_s through the effects of soil physical processes.

Our research here addressed the question: can biocrusts affect freeze-thaw processes of R_s in dryland? We hypothesized that the effects of soil cover types, including biocrusts, on winter R_s in a desert shrub-land are both direct and indirect through an influence on freeze-thaw cycles. To test the hypotheses, we took in-situ measurements of winter R_s from March 2013 to February 2014 at the southern edge of Mu Us desert, northern China. Measurements were made at four microsites including four different soil cover types: bare soil, lichen crust, moss crust and mixed lichen and moss. Our objectives were: (1) to compare differences in winter R_s across four microsites with contrasting soil cover types during fully frozen and freeze-thaw periods and (2) to investigate the main environmental controls on winter R_s during fully frozen and freeze-thaw periods and evaluate differences in these controls across the four microsites.

2. Materials and Methods

2.1. Site Description

The study area was located at the Yanchi Research Station (37°42′31″ N, 107°13′45″ E, 1530 m a.s.l.) at the southern edge of the Mu Us desert in the transition between the arid and semi-arid climatic zones in Ningxia province, northern China. The climate is characterized by a semiarid continental monsoonal climate, with a relative long and cold winter (late-November to February). The mean annual temperature (1954–2004) is 8 °C. The dominant vegetation is *Artemisia ordosica*, with sparse *Hedysarum mongolicum*. The soil surface of the inter-canopy is mostly covered by lichen and moss crusts. Soil organic carbon is 1.27 ± 0.14 (%), total nitrogen content is 0.06 ± 0.01 (%) and pH is 8.42 ± 1.4.

In winter, snow accumulation is typically less than 30 cm in depth and two weeks in length. The soils are predominantly sandy and have a bulk density of 1.54 g·cm^{-3} in the upper 10 cm.

2.2. Field Measurements

We selected the four most frequent soil cover types (hereafter called microsites) at the study site: bare soil (BS) and three biocrusts: >75% lichen cover (LC), >75% moss cover (MC), and mixed lichen and moss cover (ML, with >75% combined). Each of the microsites had two quadrats (replicates), located in the interplant space, which was ~45 cm away from nearby plants. BS was a microsite located on the top of a small sand dune where sand was not yet fixed.

Soil respiration rates were continuously measured in situ from March 2013 to February 2014 using an automated soil respiration system (LI-8100A equipped with an LI-8150 multiplexer and LI-104 chambers, LI-COR, Inc., Lincoln, NE, USA). In June 2012, eight PVC collars, 20.3 cm in diameter and 10 cm in height, were permanently inserted in individual quadrats to ~6 cm depth below the soil surface. The collars extended about 4 cm above the bare soil surface, but 3 cm above the biocrust surface because the biocrusts were about 1 cm thick. An opaque chamber (model LI-104, LI-COR, Lincoln, NE, USA) was set on each collar. The measurement time for each chamber was 3 min and 15 s, including a 30-s pre-purge, a 45-s post-purge, and a 2-min observation period. The measurement interval for each chamber was 1 h.

Hourly soil temperature (T_s) and soil water content (SWC) at 10 cm depth were measured simultaneously within 20 cm outside of each chamber using the 8150–203 soil temperature sensor and ECH2O soil moisture sensor (LI-COR, Lincoln, NE, USA), respectively. Winter lasted for less than four months from late November through February, during which daily mean soil temperature at 10 cm depth remained below 0.5 °C.

2.3. Data Processing and Analysis

Hourly mean R_s for each microsite was computed as the mean of the two chambers (replicates). Winter was partitioned into days when the soil remained frozen and days with freeze-thaw events. The freeze-thaw events were defined based on changes in soil temperature and water content using the following criteria: freezing occurred when daily maximum T_s fell below 0 °C and SWC declined, and thawing occurred when daily maximum T_s rose above 0 °C and SWC increased to values similar to those prior to freezing. A complete freeze-thaw cycle includes both freezing and thawing events. Bin-averaged hourly data (using T_s increments of 0.2 °C) were used to examine the relationships between T_s and R_s for all microsites.

The Q_{10} function was applied to describe the relationship between R_s and T_s as:

$$R_s = R_{10} Q_{10}^{(T_s - 10)/10} \tag{1}$$

where Q_{10} is the temperature sensitivity of R_s. This Q_{10} function fit our data well (see results below).

Repeated measures ANOVA was used for testing the statistical significance of the difference among microsites. Daily mean data for each collar were used for repeated measures ANOVA. The datasets for ANOVA were firstly tested for assumptions of normality and homogeneity of variances, and were log-transformed. Datasets consisted of 4 microsites (bare surface (BS), lichen crust (LC), moss crust (MC), mixed crust of both moss and lichen (ML)); each microsite had two replicates (collars). The within-subject factor was time, and the between-subject factor was microsite. Multiple comparisons (LSD) were conducted between microsites if there was significant difference in microsites. The repeated measures ANOVA was performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA). Regression analyses were used to describe the relationships between soil respiration and the environmental variables. All the regression analyses were performed using Matlab 7.11 statistical software (R2010b, The Mathworks Inc., Natick, MA, USA). All statistical analyses were performed at a significance level of 0.05.

3. Results

3.1. Dynamics of Winter R_s and Corresponding Environmental Factors

Daily R_s showed significant fluctuations with a peak at the beginning of winter and a minimum in mid-winter (Figure 1a). Mean winter R_s values for the four surface cover types were 0.17 (BS), 0.16 (LC), 0.10 (MC) and 0.11 (ML) μmol CO_2 $m^{-2}{\cdot}s^{-1}$. Winter R_s was higher in BS and LC than in MC and ML microsites (Figure 1, Table 1, p = 0.053 and 0.044 for BS, and p = 0.045 and 0.038 for LC compared with MC and ML, respectively). Daily T_s changed dramatically over time with consistently higher values in BS than the other microsites (Figure 1, Table 1, p = 0.035, 0.046 and 0.024). Variation in hourly SWC clearly showed that freeze-thaw cycles occurred most frequently in December and January (Figure 1c). SWC was much higher in LC than in other microsites.

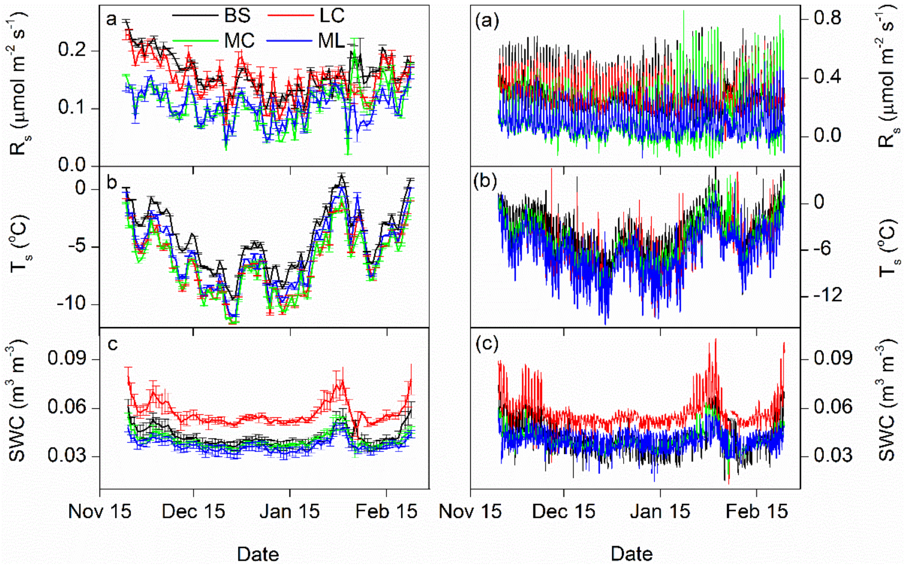

Figure 1. Seasonal variations in soil respiration (R_s), soil temperature (T_s) and soil water content (SWC) for four microsites including bare surface (BS), lichen crust (LC), moss crust (MC), and mixed crust of both moss and lichen (ML) in winter (from late November 2013 to February 2014). Data points in the left panels are daily means, and those in the right panels are hourly means.

Table 1. Winter soil respiration (R_s) and its contribution to annual total of R_s for four microsites including bare surface (BS), lichen crust (LC), moss crust (MC), and mixed crust of both moss and lichen (ML) [a].

Microsites	Mean Winter T_s (°C)	Mean Winter R_s (μmol·$m^{-2}{\cdot}s^{-1}$)	Mean Growing Season R_s (μmol·$m^{-2}{\cdot}s^{-1}$)	Winter R_s (g·C·m^{-2})	Annual R_s (g·C·m^{-2})	Winter R_s/Annual R_s (%)
BS	−4.22 m	0.17 m	0.92 m	15.3 m	259 m	5.90 m
LC	−6.20 n	0.16 m	0.92 m	14.4 m	258 m	5.60 m
MC	−6.44 n	0.10 n	0.91 m	10.0 n	251 m	4.00 m
ML	−5.49 n	0.11 n	0.59 n	10.1 n	169 n	6.00 m

[a] Letters (m and n) within a column represent significant difference between parameters (significance level α = 0.05).

BS had 32 diurnal freeze-thaw cycles in the study period, whereas LC, ML and MC had only 4, 12, and 8 diurnal freeze-thaw cycles, respectively, in the study period. Figure 2 shows the mean diurnal cycle for fully frozen and freeze-thaw periods. The peak R_s occurred from 12:00–14:00 and was greater in freeze-thaw periods than in fully frozen periods (Figure 2). Over diurnal cycles with freeze-thaw events, SWC drastically changed, with a change amplitude of 0.02 $m^3 \cdot m^{-3}$ and even 0.04 $m^3 \cdot m^{-3}$ (Figure 2b). Drastic diurnal changes in R_s occurred in accordance with freeze-thaw events.

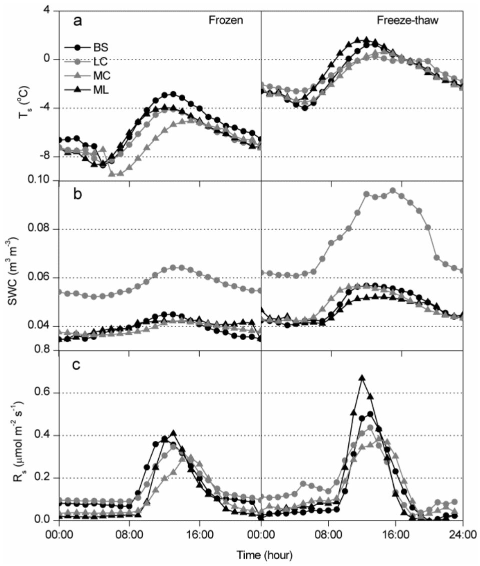

Figure 2. Mean diurnal cycle in soil temperature (T_s, **a**), soil water content (SWC, **b**) and soil respiration (R_s, **c**) during days when the soil remained frozen (left panels) and days with freeze-thaw cycles (right panels), for four microsites including bare soil (BS), lichen crust (LC), moss crust (MC), and mixed crust of both moss and lichen (ML).

3.2. Controlling Factors on Soil Respiration

Winter R_s was positively related to T_s, following an exponential (Q_{10}) relationship regardless of soil cover type or soil water status (Figure 3). During freeze-thaw cycles at all four microsites, a discontinuity was observed in the R_s–T_s relationship at T_s near 0 °C. The Q_{10} values were thus much higher for freeze-thaw periods than frozen periods regardless of microsite type (Figure 3). When calculated on the basis of the whole winter dataset, the Q_{10} values were 6.1 (R^2 = 0.83), 2.8 (R^2 = 0.55), 7.2 (R^2 = 0.68), and 19 (R^2 = 0.76) for BS, LC, MC, and ML, respectively (Figure 4).

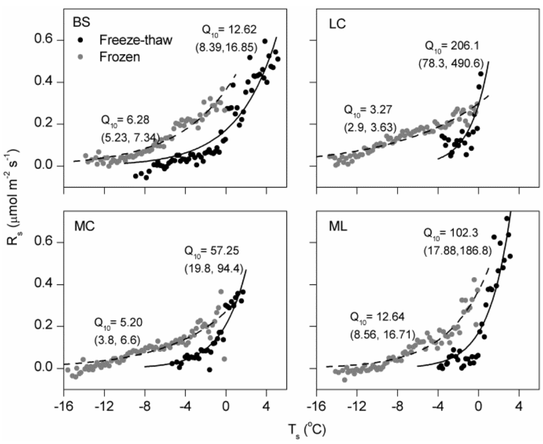

Figure 3. Soil respiration (R_s) as a function of soil temperature (T_s) during days with soil freeze-thaw cycles and days where the soil remains frozen, at four microsites including bare surface (BS), lichen crust (LC), moss crust (MC), and mixed crust of both moss and lichen (ML). Data points are bin-averaged hourly data using a T_s increment of 0.2 °C. The solid and dashed lines are fitted curves using the Q_{10} model (Equation (1)) for freeze-thaw and frozen periods, respectively. Values in parentheses are the 95% confidential interval (CI) derived from the Q_{10} function.

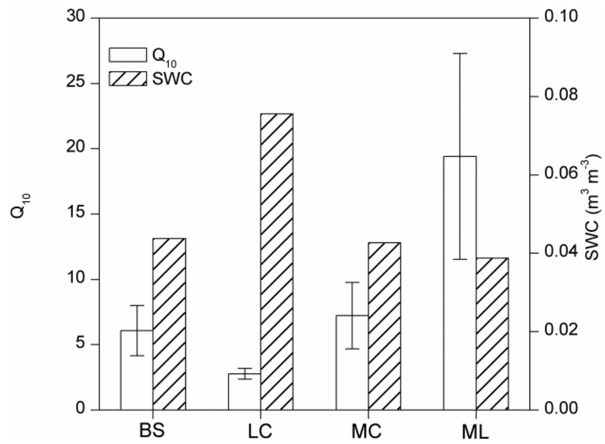

Figure 4. Q_{10} values calculated from the whole winter with corresponding mean SWC values for four microsites including bare surface (BS), lichen crust (LC), moss crust (MC), and mixed crust of both moss and lichen (ML). Error bars are the 95% confident intervals (CIs) derived from the Q_{10} function.

The diurnal dynamics of R_s in the relationship with T_s showed different patterns between freeze-thaw periods and frozen periods (Figures 5 and 6). During freeze-thaw periods, R_s dropped sharply as T_s decreased from above-zero °C to below-zero °C and as SWC dropped in response to soil freezing. But there was an increasing trend of R_s as T_s continued to decrease (Figure 5). During fully frozen periods (Figure 6), however, the response of R_s to T_s was clearly exponential when the temperature remained below zero, well fitting Equation (1).

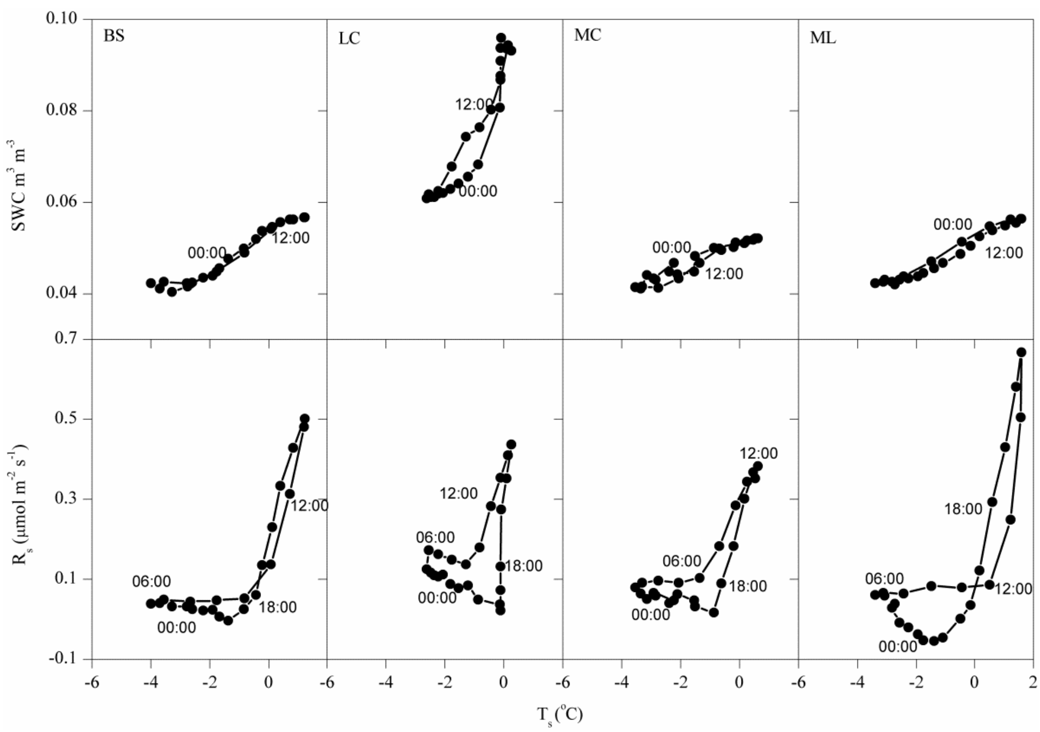

Figure 5. Mean diurnal soil respiration (R_s) and soil water content (SWC) in relationship to soil temperature (T_s) on days with freeze-thaw cycles, for four microsites including bare surface (BS), lichen crust (LC), moss crust (MC), and mixed crust of both moss and lichen (ML).

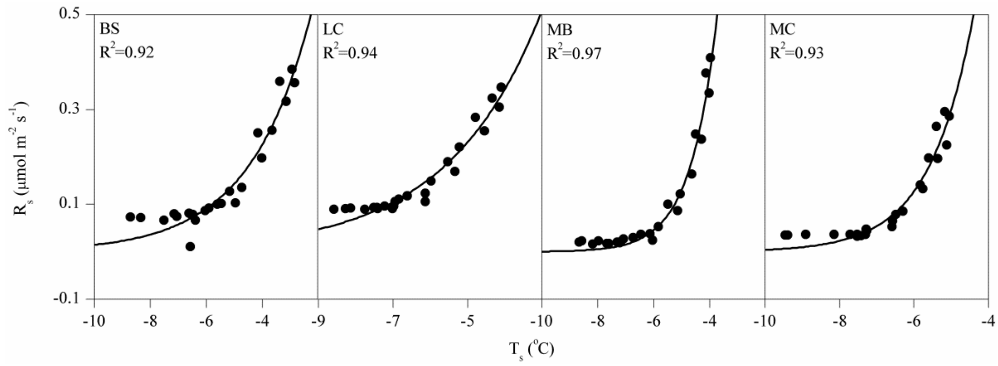

Figure 6. Mean diurnal soil respiration (R_S) in relationship to soil temperature (T_S) on days where the soil remained frozen, for four microsites including bare surface (BS), lichen crust (LC), moss crust (MC), and mixed crust of both moss and lichen (ML).

3.3. Contribution of Winter R_s to Annual R_s

Annual R_s for ML (169 g·C·m^{-2}) was much lower than the other three microsites (251 to 258 g·C·m^{-2}) (Table 1). Total winter R_s was higher for BS (15.3 g·C·m^{-2}) and LC (14.4 g·C·m^{-2}) and lower for MC (10.0 g·C·m^{-2}) and ML (10.1 g·C·m^{-2}). The relative contribution of winter R_s to annual R_s ranged from 4% to 6% (Table 1). Fully-frozen periods contributed more to cumulative winter R_s than freeze-thaw periods (Figure 7).

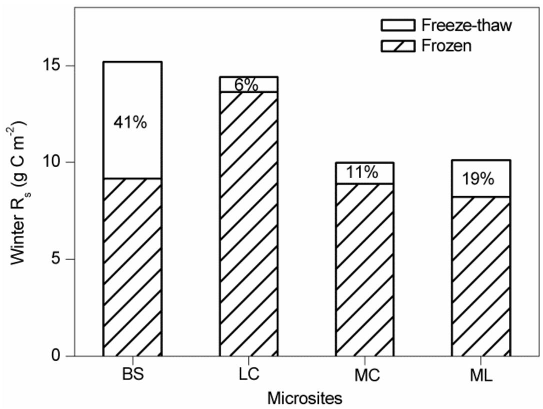

Figure 7. Total winter soil respiration (R_S) and its separation into days with soil freeze-thaw cycles and days with frozen soils, for four microsites including bare soil (BS), lichen crust (LC), moss crust (MC), and mixed crust of both moss and lichen (ML). The value within the bar is the percentage contribution of the freeze-thaw days to winter R_S.

4. Discussion

4.1. Magnitude of Winter R_s and Its Q_{10}

Although recent studies have demonstrated that winter R_s represents a considerable part of annual R_s in some ecosystems [5,6], winter R_s and Q_{10} values are still rarely reported in drylands. In our study area for semiarid shrubland, mean winter R_s ranged from 0.10 to 0.17 μmol CO_2 m^{-2}·s^{-1}, being consistent with results for a forest-steppe area of North China (0.15–0.26 μmol·m^{-2}·s^{-1}) [18]. At our site, winter R_s was approximately estimated to be 11%–17% of growing-season R_S. However, several studies have reported higher values. Average winter R_s was 0.52–0.80 μmol·m^{-2}·s^{-1} within five different types of land use on the semiarid Loess Plateau of China [6], and 0.67 μmol·m^{-2}·s^{-1} in a mixed conifer forest in Washington State, USA [5]. The shallow snow depth (<30 cm) and short snow duration (two weeks) in our study area led to low winter T_s, thus causing low winter R_S. Our estimated contribution of winter R_s to annual R_s was 4%–6% among different microsites, consistent with the values of 3.5% to 7.3% reported in a forest steppe ecotone northeast China [20]. We should caution that our estimate of total winter soil respiration is based on two replicates for each biocrust. Further research is suggested to include more replicates representing spatial heterogeneity sufficiently for more accurate estimate. Q_{10} derived for the whole winter varied from 2.8 to 19 among microsites with an average value of 8.9, much higher than the growing-season value of 1.5 [3]. High Q_{10} values in winter have been reported previously. For example, Shi et al. [21] reported increased Q_{10} in two forests in the dormant season (4.0) relative to the growing season (1.0) in the Loess Plateau of China, a semiarid ecosystem. Unlike the growing-season R_s, which originates from both the auto- and heterotrophic components, winter R_s mostly originates from the heterotrophic component. Seasonal variations in the composition of the soil microbial community may lead to higher Q_{10} in winter. According to Monson et al. [22], microbes collected during summer were not capable of growing below 4 °C; those collected under the snowpack grew exponentially at 0 °C, and their growth rates increased rapidly with increasing temperature. Furthermore, the reduction in liquid water with soil freezing may invoke a physical limitation to substrate diffusion and render R_s more sensitive to temperature [23]. Whatever the underlying mechanism, the high performance (R^2 = 0.55–0.83) of the Q_{10} model with our observations, along with the high Q_{10} indicated that the potential magnitude of winter R_s may be increased with global warming.

4.2. Effects of Freeze-Thaw Cycles on R_s

R_s values were sensitive to temperature changes during freeze-thaw cycles. The striking results in Figures 3 and 5 showed a large increase in R_s as the soil warmed to and increased above 0 °C, with higher temperature sensitivity during freeze-thaw than frozen periods (Figure 3). This is in agreement with a previous study in Qinghai-Tibet Plateau showing higher Q_{10} (5.7–9.4) during the initial thaw and freeze period than winter Q_{10} (2.68–2.97) [24]. The diurnal patterns also showed increased R_s (the maximum value) in freeze-thaw cycles than in the fully frozen period. These variations may mainly result from changes in SWC. Microbial activity under low temperatures relies strongly on the availability of free water [25]. So even minor changes in T_s around 0 °C that induce thawing may relieve the physical limitation to substrate diffusion, when coupled with the higher temperatures during freeze-thaw events, leading to increased R_s and Q_{10} relative to periods that are fully frozen. Although freeze-thaw cycles occupy only a short portion of winter, cumulative R_s during these cycles contributes significantly to winter R_s (Figure 7), and this contribution may increase under climate change.

Many studies have observed a sustained release of CO_2 throughout the winter. Our investigation showed that R_s of completely frozen soils remained above zero to at least T_s of −8 °C, indicating that the microbial community still remains active below 0 °C. The CO_2 emission under laboratory conditions of frozen soils from northern regions has been found to remain positive and measurable at −16 °C [26]. Winter CO_2 production has also been observed in field studies [24]. But the mechanism for soil CO_2 efflux in the cold season (winter) is not absolutely clear. One possible explanation is that microbes are cold-adapted and more sensitive to T_s in winter. Over diurnal cycles (Figures 2 and 5), R_s followed changes in T_s and increased rapidly from very low levels. This may indicate that microbes respond rapidly to minor changes in T_s, e.g., within several hours. Our measurement of T_s was at 10 cm depth, which in winter may be warmer than shallower depths. So even under frozen conditions, R_s is responsive to the diurnal cycle in T_s, while microbial responses occur within several hours, thus leading to pulsed R_s.

Besides, we also observed different patterns in R_s to T_s between frozen and freeze-thaw times at the diurnal scale (Figures 5 and 6). The increasing R_s followed the freezing process (i.e., decrease in T_s) at freeze-thaw times indicated the involvement of other process other than T_s. We assume that this phenomenon may be caused by the physical release of trapped CO_2 in the soil pores in freezing soils during the transition of moisture from the liquid to solid state.

4.3. Effects of Cover Types on R_s

Microsites with biocrusts (LC, MC, and ML) had lower winter R_s than bare soil (BS). The difference may be related to T_s. Yang et al. [17] reported that the presence of biocrusts changed the structure of surface soils, inducing lower T_s under biocrusts compared to bare land in the Mu Us Sand Land, which was more significant under cold and dry conditions. This result may help to explain the observed T_s differences between BS and biocrusts in our study. Lower temperature (Table 1) may lead to fewer freeze-thaw cycles (less than 15 days) in biocrusts, which might account for their lower mean winter R_s. Therefore, the cover types may affect winter R_s in drylands through the effects of freeze-thaw cycles (i.e., induce fewer freeze-thaw cycles). Because of the low number of replicates in our study (two replicates), the spatial heterogeneity may be a potential caveat. Although the autotrophic respiration was considered low in winter, the autotrophic respiration of the crust and roots might account for a certain portion of R_s in winter. Heterogeneous distribution of roots and biocrust may also contribute to the difference between BS and BSC microsites. Further studies will be needed to clarify the exact mechanism triggering the differential R_s between BS and biocrusts.

5. Conclusions

Winter R_s in a semiarid shrub-land ecosystem in northern China varied among microsites, ranging from 0.10 to 0.16 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Winter Q_{10} (2.8–19) was considerably higher than that measured in summer (1.5). When the winter was stratified into days with soil freeze-thaw events and days that remained fully frozen, different diurnal patterns of R_s were found that may be caused by the physical release of trapped CO_2 from soil pores. Different freeze-thaw cycles and Q_{10} values were observed among microsites. Lower T_s under biocrusts gave rise to fewer freeze-thaw cycles in biocrust microsites relative to BS. R_s and Q_{10} were greatly enhanced during freeze-thaw cycles compared to fully frozen periods. Further, given the future climate projections of warmer temperature and more frequent freeze-thaw cycles in terrestrial ecosystems, winter warming may have an important impact on R_s.

Acknowledgments: We acknowledge the support obtained from National Natural Science Foundation of China (NSFC) (31361130340, 31270755), Fundamental Research Funds for the Central Universities (2015ZCQ-SB-02) the Academy of Finland (proj. No. 14921), University of Eastern Finland and USCCC. This work is related to the ongoing Finnish-Chinese research collaboration project EXTREME, between Beijing Forestry University (BJFU) and University of Eastern Finland (UEF). We thank Mingyan Zhang and Yuan Li for their assistance with the field measurements and instrumentation maintenance.

Author Contributions: All authors made intellectual contributions to this research work. Tianshan Zha, Ben Wang conceived and designed the experiments, Qiang Yang and Xiaonan Guo performed the experiments, Peng Liu and Xin Jia analyzed the experimental data. Peng Liu wrote the paper. Together, all authors discussed and interpreted the results, and approved the final manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Asner, G.P.; Archer, S.; Hughes, R.F.; Ansley, R.J.; Wessman, C.A. Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937–1999. *Glob. Chang. Biol.* **2003**, *9*, 316–335. [CrossRef]
2. Li, S.G.; Asanuma, J.; Eugster, W.; Kotani, A.; Liu, J.J.; Urano, T.; Oikawa, T.; Davaa, G.; Oyunbaatar, D.; Sugita, M. Net ecosystem carbon dioxide exchange over grazed steppe in central Mongolia. *Glob. Chang. Biol.* **2005**, *11*, 1941–1955. [CrossRef]
3. Wang, B.; Zha, T.S.; Jia, X.; Wu, B.; Zhang, Y.Q.; Qin, S.G. Soil moisture modifies the response of soil respiration to temperature in a desert shrub ecosystem. *Biogeosciences* **2014**, *11*, 259–268. [CrossRef]
4. Castillo-Monroy, A.P.; Maestre, F.T.; Rey, A.; Soliveres, S.; García-Palacios, P. Biological soil crust microsites are the main contributor to soil respiration in a semiarid ecosystem. *Ecosystems* **2011**, *14*, 835–847. [CrossRef]
5. McDowell, N.G.; Marshall, J.D.; Hooker, T.D.; Musselman, R. Estimating CO_2 flux from snowpacks at three sites in the Rocky Mountains. *Tree Physiol.* **2000**, *20*, 745–753. [CrossRef] [PubMed]

6. Shi, W.Y.; Yan, M.J.; Zhang, J.G.; Guan, J.H.; Du, S. Soil CO_2 emissions from five different types of land use on the semiarid Loess Plateau of China, with emphasis on the contribution of winter soil respiration. *Atmos. Environ.* **2014**, *88*, 74–82. [CrossRef]
7. Morgner, E.; Elberling, B.; Strebel, D.; Cooper, E.J. The importance of winter in annual ecosystem respiration in the High Arctic: Effects of snow depth in two vegetation types. *Polar Res.* **2010**, *29*, 58–74. [CrossRef]
8. Piao, S.; Ciais, P.; Huang, Y.; Shen, Z.; Peng, S.; Li, J.; Zhou, L.; Liu, H.; Ma, Y.; Ding, Y. The impacts of climate change on water resources and agriculture in China. *Nature* **2010**, *467*, 43–51. [CrossRef] [PubMed]
9. Mikan, C.J.; Schimel, J.P.; Doyle, A.P. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biol. Biochem.* **2002**, *34*, 1785–1795. [CrossRef]
10. Tilston, E.; Sparrman, T.; Öquist, M. Unfrozen water content moderates temperature dependence of sub-zero microbial respiration. *Soil Biol. Biochem.* **2010**, *42*, 1396–1407. [CrossRef]
11. Aanderud, Z.T.; Jones, S.E.; Schoolmaster, D.R.; Fierer, N.; Lennon, J.T. Sensitivity of soil respiration and microbial communities to altered snowfall. *Soil Biol. Biochem.* **2013**, *57*, 217–227. [CrossRef]
12. Zhao, Z.M.; Zhao, C.Y.; Mu, Y.H.; Yu, S.; Li, J. Contributions of root respiration to total soil respiration before and after frost in *Populus euphratica* forests. *J. Plant Nutr. Soil Sci.* **2011**, *174*, 884–890. [CrossRef]
13. Kim, D.G.; Vargas, R.; Bond Lamberty, B.; Turetsky, M. Effects of soil rewetting and thawing on soil gas fluxes: A review of current literature and suggestions for future research. *Biogeosciences* **2012**, *9*, 2459–2483. [CrossRef]
14. Matzner, E.; Borken, W. Do freeze-thaw events enhance C and N losses from soils of different ecosystems? A review. *Eur. J. Soil Sci.* **2008**, *59*, 274–284. [CrossRef]
15. Li, F.; Zhao, J.; Zhao, C.; Zhang, X. Succession of potential vegetation in arid and semi-arid area of China. *Acta Ecol. Sin.* **2010**, *31*, 689–697.
16. Arevalo, C.; Bhatti, J.S.; Chang, S.X.; Jassal, R.S.; Sidders, D. Soil respiration in four different land use systems in north central Alberta, Canada. *J. Geophys. Res. Biogeosci.* **2010**, *115*. [CrossRef]
17. Yang, Y.S.; Bu, C.F.; Gao, G.X. Effect of biological soil crust on soil temperature in the Mu Us Sand Land. *Arid Zone Res.* **2012**, *29*, 352–359.
18. Johansen, J.R.; Ashley, J.; Rayburn, W.R. Effects of rangefire on soil algal crusts in semiarid shrub-steppe of the lower Columbia Basin and their subsequent recovery. *Great Basin Nat.* **1993**, *53*, 73–88.
19. Ma, Q.L.; Wang, J.H.; Zhu, S.J. Effects of precipitation, soil water content and soil crust on artificial *Halox-ylon ammodendron* forest. *Acta Ecol. Sin.* **2007**, *27*, 5057–5067. [CrossRef]
20. Wang, W.; Peng, S.; Wang, T.; Fang, J. Winter soil CO_2 efflux and its contribution to annual soil respiration in different ecosystems of a forest-steppe ecotone, north China. *Soil Biol. Biochem.* **2010**, *42*, 451–458. [CrossRef]
21. Shi, W.Y.; Zhang, J.G.; Yan, M.J.; Yamanaka, N.; Du, S. Seasonal and diurnal dynamics of soil respiration fluxes in two typical forests on the semiarid Loess Plateau of China: Temperature sensitivities of autotrophs and heterotrophs and analyses of integrated driving factors. *Soil Biol. Biochem.* **2012**, *52*, 99–107. [CrossRef]
22. Monson, R.K.; Lipson, D.L.; Burns, S.P.; Turnipseed, A.A.; Delany, A.C.; Williams, M.W.; Schmidt, S.K. Winter forest soil respiration controlled by climate and microbial community composition. *Nature* **2006**, *439*, 711–714. [CrossRef] [PubMed]
23. Brooks, P.D.; McKnight, D.; Elder, K. Carbon limitation of soil respiration under winter snowpacks: Potential feedbacks between growing season and winter carbon fluxes. *Glob. Chang. Biol.* **2005**, *11*, 231–238. [CrossRef]
24. Wang, Y.; Liu, H.; Chung, H.; Yu, L.; Mi, Z.; Geng, Y.; Jing, X.; Wang, S.; Zeng, H.; Cao, G. Non-growing season soil respiration is controlled by freezing and thawing processes in the summer monsoon-dominated Tibetan alpine grassland. *Glob. Biogeochem. Cycles* **2014**, *28*, 1081–1095. [CrossRef]
25. Osterkamp, T.; Romanovsky, V. Freezing of the active layer on the coastal plain of the Alaskan Arctic. *Permafr. Periglac. Process.* **1997**, *8*, 23–44. [CrossRef]
26. Panikov, N.S.; Dedysh, S. Cold season CH_4 and CO_2 emission from boreal peat bogs (West Siberia): Winter fluxes and thaw activation dynamics. *Glob. Biogeochem. Cycles* **2000**, *14*, 1071–1080. [CrossRef]