Environmental Research Letters

LETTER

Responses of soil respiration to experimental warming in an alpine steppe on the Tibetan Plateau

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Keywords: climate warming, meta-analysis, carbon cycle, carbon-climate feedback, alpine ecosystem, arctic ecosystem

Supplementary material for this article is available online

Abstract

High-latitude and high-altitude ecosystems store large amounts of carbon (C) and play a vital role in the global C cycle. Soil respiration ($R_S$) in these ecosystems is believed to be extremely sensitive to climate warming and could potentially trigger positive C-climate feedback. However, this evidence is largely derived from wet ecosystems, with limited observations from dry ecosystems. Here, we explored the responses of $R_S$, autotrophic ($R_A$), and heterotrophic ($R_H$) respiration under experimental warming in a dry ecosystem, an alpine steppe on the Tibetan Plateau. We assessed the effects of soil temperature and moisture dynamics on $R_S$, $R_A$, and $R_H$ and performed a meta-analysis to examine whether the warming effects observed were similar to those reported in wet ecosystems, including Tibetan alpine meadow and arctic ecosystem. Experimental warming did not alter $R_S$, $R_A$, and $R_H$ in this alpine steppe, likely because decreased soil moisture constrained positive warming effects. In contrast, the meta-analysis revealed that $R_S$ exhibited a significant increase under experimental warming in both the Tibetan alpine meadow and arctic wet tundra. These results demonstrate that $R_S$ exhibits different responses to climate warming between dry and wet ecosystems, suggesting potential more complex C-climate feedback in cold regions.

1. Introduction

Soil respiration ($R_S$), the second largest C flux in terrestrial ecosystems, is an important regulator of atmospheric CO$_2$ concentrations (Bond-Lamberty and Thomson 2010, Melillo et al. 2017, Bond-Lamberty et al. 2018). The annual $R_S$ is 91 Pg C (1 Pg = 10$^{15}$ g), which is approximately ten times larger than the anthropogenic C release (Bond-Lamberty and Thomson 2010, Metcalfe et al. 2011, Hashimoto et al. 2015). Over the past decades, $R_S$ has exhibited an increasing trend because of continuous climate warming (Bond-Lamberty et al. 2018). Compared with other regions, temperature increase in high-altitude and high-latitude ecosystems is twice the rate of the global average (IPCC 2013). Considering the large C storage in these regions (Hugelius et al. 2014, Ding et al. 2016), the faster climate warming may induce large C loss from these cold ecosystems to the atmosphere through $R_S$ and trigger positive C-climate feedback (Schuur et al. 2015). $R_S$ generally consists of autotrophic respiration ($R_A$), produced by plant roots, and heterotrophic respiration ($R_H$) associated with soil organic matter (SOM) decomposition by soil microbes and fauna (Luo and Zhou 2006). Both components make near equal contribution to $R_S$ (Bond-Lamberty et al. 2018), but climate warming may cause distinct changes in $R_A$ and $R_H$ (Wang et al. 2014). More
importantly, increased $R_A$ may be balanced by plant production, but $R_H$ is not (Hicks Pries et al. 2013, 2015), which could then make these two components generate different contribution to the potential positive C-climate feedback. Therefore, a comprehensive understanding of the responses of $R_S$ and its autotrophic and heterotrophic parts to climate warming in cold regions is crucial for an accurate prediction of the direction and magnitude on feedbacks in the terrestrial C cycle.

Previous studies have explored the responses of $R_S$ and its components to experimental warming in different biomes (Zhou et al. 2007, Dorrepaal et al. 2009, Hicks Pries et al. 2015, Melillo et al. 2017). By integrating these site-level studies, meta-analyses have been performed to obtain comprehensive response tendencies on a global scale (Rustad et al. 2001, Wang et al. 2014, Carey et al. 2016). These meta-analyses revealed that experimental warming stimulated $R_S$ below a threshold of 25°C (Carey et al. 2016), and also enhanced $R_A$, but had little impact on $R_H$ (Wang et al. 2014). Although responses of $R_S$ and its components under climate warming are better understood, their attention has mainly focused on temperate and tropical ecosystems (Wang et al. 2014, Carey et al. 2016). Actually, climate warming is expected to result in a more drastic $R_S$ change in cold regions compared with temperate and tropical regions (Jahn et al. 2010). However, current studies on warming effects on $R_S$ in high-latitude and high-altitude ecosystems are mainly derived from wet ecosystems, such as wet tundra in arctic regions (Oberbauer et al. 2007, Dorrepaal et al. 2009, Hicks Pries et al. 2015, Natali et al. 2015) and alpine meadow on the Tibetan Plateau (Lin et al. 2011, Shi et al. 2012, Fu et al. 2013, Xue et al. 2015), with limited evidence from dry ecosystems. Compared with wet ecosystems, warming effects on $R_S$ in the dry ecosystems may be regulated by soil water availability due to its limitation on root and microbial growth and activity (Sheik et al. 2011, Suseela and Dukes 2013). Thus, whether warming effects on $R_S$ in cold and dry ecosystems are similar to those in cold and wet ecosystems require further investigation.

The purpose of our study was to explore the mechanisms by which $R_S$ and its components respond to experimental warming in cold and dry ecosystems, and whether these differ from those in wet ecosystems. Specifically, based on a warming experiment in a Tibetan alpine steppe (a typical cold and dry ecosystem), we conducted a three-year field measurement on $R_S$, $R_H$, and $R_A$. We then investigated how changes in soil moisture regulated warming effects on $R_S$ and its components, and performed a meta-analysis to examine whether the finding in our dry alpine steppe differed from that in those cold and wet ecosystems including Tibetan alpine meadow and arctic tundra.

2. Materials and methods

2.1. Field experiment in Tibetan alpine steppe

2.1.1. Experimental site and design

The field experiment was conducted in a typical alpine steppe in Gangca county, Qinghai Province, China (37°30’ N, 100°25’ E, elevation 3290 m). The mean annual temperature and precipitation at the study site are 0.08°C and 387 mm, respectively. This experiment site has experienced continuous climate warming over the past three decades, with a mean rate of 0.04°C per year (Li et al. 2019). Dominant plant species of the study site include Stipa purpurea as well as Carex stenophylloides, and the related soil type is Haplic Calcisol (Li et al. 2019, Zhang et al. 2019).

In May 2013, an enclosure in the study area was established to avoid disturbance from grazing and human activities. The field manipulation contained 10 blocks, with two plots within every block assigned to control and warming treatments. Hexagonal open-top chambers (OTC) were applied to achieve passive warming (Li et al. 2019). The size of OTCs was 80 cm along for the top edge, 120 cm along for the bottom edge, and 50 cm height. The transparent material was made of clear acrylic sheeting 2 mm thick and light transmission of over 92%. The OTCs were set out all year round in the field. From May 2014, soil temperature and moisture were monitored simultaneously at a depth of 5 cm in each plot using EM50 data collectors (Decagon, Washington, DC, USA) at 30 min intervals.

2.1.2. Soil respiration measurements

To explore the response of $R_S$ and its components to experimental warming, $R_S$, $R_H$, and $R_A$ fluxes were measured based on the deep-collar method used in previous studies (Dorrepaal et al. 2009, Hasselquist et al. 2012, Suseela and Dukes 2013, Peng et al. 2017a). Specifically, $R_S$ and $R_H$ were measured from 09:00 am to 12:00 pm (local time) every 10 days during the growing seasons of 2014–2016, using a detector of LI-8100 soil CO$_2$ flux chamber (LI-COR, Lincoln, Nebraska, USA). In each plot, $R_S$ measurements were taken using a PVC collar (20 cm in diameter and 5 cm tall) installed 3 cm into the soil. Meanwhile, $R_H$ measurements were taken using a PVC collar (20 cm in diameter and 62 cm tall) which was installed 60 cm into the soil to exclude roots. To eliminate aboveground respiration, small living plants in collars were weeded at least one day before each measurement. $R_A$ was got from calculating the difference between $R_S$ and $R_H$.

2.1.3. Data analysis of the field measurements

Data from the field measurements were analysed using a repeated measures ANOVA to examine the effects of warming, sampling times and their interactions on $R_S$, $R_H$ and $R_A$. Paired $t$-tests were performed to determine the differences in seasonal average of soil temperature, moisture and $R_S$, $R_H$ and $R_A$ between warming and
control treatments. To explore the warming effects on temperature sensitivity of $R_S$ and its components, we fitted the relationships of $R_S$, $R_H$ and $R_A$ with soil temperature across the growing season using the following exponential equation (Hui and Luo 2004):

$$R = ae^{VT},$$

(1)

where $R$ is soil respiration rate (mol CO$_2$ m$^{-2}$ s$^{-1}$), $T$ is soil temperature at 5 cm (°C), $a$ and $b$ are constants. Here, $b$ was used to calculate the respiration quotient ($Q_{10}$), which characterized the respiration changes under an increase by 10 °C of soil temperature, described as the following equation (Zhou et al 2007):

$$Q_{10} = e^{10b}.$$  

(2)

To determine the treatment effects on $R_S$ and its components, linear regressions were performed to determine the relationships of response ratios (RR) of $R_S$, $R_H$ and $R_A$ with RR$s$ of soil temperature and moisture, where the RR$s$ were calculated as the ratios of variables between warming and control groups. Given that data obtained in different years were not independent in statistic, linear mixed-effects models were performed with fixed effects being explanatory variables and the random effect being experimental year (Li et al 2017, Peng et al 2017b). Three data points for $R_S$ and $R_H$ and two data points for $R_A$ were outliers based on Boxplot Procedures (figure S1 is available online at stacks.iop.org/ERL/14/094015/mmedia; Hoaglin and Iglewicz 1987, Sim et al 2005); therefore, these data points were excluded in the final model. All statistical analyses were conducted using R statistical software v3.4.0 (R Core Team 2018).

2.2. Meta-analysis of field experiments in Tibetan alpine meadow and arctic ecosystems

To explore how $R_S$ in cold regions responded to warming over a large scale, we synthesized published studies reporting warming effects on $R_S$ from the Tibetan alpine meadow and arctic ecosystems using Web of science (http://apps.webofknowledge.com/). To avoid publication bias, selected papers had to meet the following criteria: (i) in situ warming experiments were conducted using one of the three frequently used methods (e.g. OTCs, infrared heater and soil heating cable); (ii) $R_S$ was measured for at least one complete growing season; and (iii) the mean value, standard deviation (or standard error) and number of replicate were reported. Based on the above criteria, 11 observations were collected in the form of ‘control-warming’ pairs from seven studies in the Tibetan alpine meadow, and 23 observations were identified from 10 studies in the arctic and subarctic zones (table S1). The background information, including latitude, longitude, mean annual temperature, mean annual precipitation, experiment duration, and changes in soil temperature as well as moisture in the studies, was also recorded (table S1).

To evaluate warming effects on $R_S$, the RR was calculated as described by Hedges et al (1999):

$$RR = \ln(X_i / X_c) = \ln(X_i) - \ln(X_c),$$

(3)

where $X_i$ and $X_c$ are the mean values of control and treatment groups, respectively. Moreover, variance ($V_i$) of individual studies was calculated based on sample size and standard deviation:

$$V_i = \frac{S_i^2}{n_i} + \frac{S_c^2}{n_c},$$

(4)

where $n_i$ and $n_c$ and $s_i$ and $s_c$ are the sample size and standard deviation for treatment and control groups, respectively. Due to the limited number of data points, the overall mean RR$s$ and the corresponding 95% confidence intervals (CI) were calculated using resampling methods (e.g. bootstrapping; Adams et al 1997). If the 95% CI did not overlap with 1, treatment effects on $R_S$ were considered significant. To further explore whether the mean effect size was different between the Tibetan alpine meadow and arctic ecosystems, total heterogeneity ($Q_t$) was partitioned into within-group heterogeneity ($Q_{w}$) and between-group heterogeneity ($Q_{b}$). The significant $Q_b$ implies that the RR$s$ differ between the two ecosystems (Hedges et al 1999). All above analyses were conducted using MetaWin 2.1 software (Rosenberg et al 1997).

3. Results

3.1. Warming effects on $R_S$ and the regulating factors in our field study

During the growing seasons of 2014–2016, warming treatments significantly increased soil temperature in this alpine steppe by 1.4, 1.6, and 2.0 °C, respectively, while the corresponding soil moisture significantly decreased by 2.5, 3.4, and 2.7%, respectively (figure S2). Experimental warming had no significant effects on $R_S$, $R_H$, and $R_A$ at the seasonal scale (table 1), although $R_S$ and its components exhibited seasonal pattern (figure 1). Similarly, there were no significant changes in seasonal means of the three parameters ($R_S$, $R_H$, and $R_A$) between warmed and control plots (figure 1 inserts). However, warming significantly reduced the $Q_{10}$ of the three parameters during the three growing seasons, except for that of $R_A$ in 2016 (figures 2(d), (b), (l)).

The insignificant responses of $R_S$, $R_H$, and $R_A$ in this alpine steppe were likely associated with the lowered soil moisture (figure S2), particularly for $R_S$ and $R_H$. Consistent with the above results of insignificant warming-induced changes in $R_S$, $R_H$, and $R_A$ no obvious relationships were observed between RR$s$ of $R_S$ and its components and RR of soil temperature across the three years ($R_S$: $r^2 = 0.02$, $P = 0.23$; $R_H$: $r^2 = 0.02$, $P = 0.32$; $R_A$: $r^2 = 0.06$, $P = 0.07$; figures 3(a), (c), (e)). However, results from the linear mixed-effects models showed that RR$s$ of $R_S$ and $R_H$ were positively correlated with the RR of soil moisture ($R_S$: $r^2 = 0.27$, $P < 0.001$; $R_H$: $r^2 = 0.30$, $P < 0.001$; figures 3(b), (d)), although it had little effects on $R_A$ ($r^2 = 0.05$, $P = 0.11$; figure 3(f)).
3.2. Responses of $R_S$ in Tibetan alpine meadow and arctic ecosystems

Meta-analysis revealed that the mean $R_S$ exhibited a significantly positive response under experimental warming in both Tibetan alpine meadow and arctic ecosystems. Specifically, in the Tibetan alpine meadow, a significant $R_S$ response was observed in seven out of 11 individual observations, accounting for 64% of the total. The mean RR of $R_S$ was 1.13 and the corresponding 95% bootstrap CI ranged from 1.04 to 1.23 (figure 4(a)). In arctic ecosystems, a significant $R_S$ response to warming was observed in 16 out of 23 study sites, accounting for 70% of the total. The mean effect size of $R_S$ was 1.23 and the corresponding 95% CI ranged from 1.14 to 1.34 (figure 4(b)).

Qb test indicated that no significant warming effects on $R_S$ occurred between the two ecosystems ($P = 0.09$).

4. Discussion

Our results showed that $R_S$ and its components exhibited insignificant responses to experimental warming in the Tibetan alpine steppe (figure 1). Generally, climate warming should increase $R_S$ in cold

| Effect | 2014 | 2015 | 2016 |
|--------|------|------|------|
| $R_S$  |      |      |      |
| W      | 2.08 | 3.7  | 3.16 |
| D      | 82.39| 70.09| 78.09|
| W × D  | 5.62 | 9.24 | 3.99 |
| $R_H$  |      |      |      |
| W      | 4.25 | 2.2  | 0.45 |
| D      | 42.42| 34.23| 54.76|
| W × D  | 3.31 | 3.66 | 5.01 |
| $R_A$  |      |      |      |
| W      | <0.001| 1.01 | 1.93 |
| D      | 25.43| 22.84| 3.58 |
| W × D  | 4.37 | 3.81 | 0.7  |

Note: Values in bold denote statistically significance.
regions due to the alleviated temperature limitation (Schuur et al 2015). Yet reductions in soil moisture which accompany warming can also affect Rs responses (Carey et al 2016). In our field study, the warming-induced changes in Rs were significantly related to changes in soil moisture (figure 3(b)). Although slight decline in soil moisture can still increase growth and activity of soil organisms, and thus stimulate RA, severe soil drying would depress RH (figure 3(d)), eventually leading to unchanged RH. However, the non-significant RA response cannot be explained by the changes in soil temperature or moisture (figures 3(e), (f)), indicating that other factors may regulate this process, and the potential mechanisms require further investigation. Altogether, the unchanged RH and RA resulted in a non-significant Rs response to experimental warming in this alpine steppe.

Although investigating RH and RA can provide a mechanical understanding of the Rs response to warming (Bond-Lamberty et al 2018), the root exclusion method, which has been widely used for distinguishing RH and RA (Dorrepaal et al 2009, Hasselquist et al 2012, Suseela and Dukes 2013, Peng et al 2017a), may create some artifacts. Deep collar installation could temporarily stimulate RH due to the decomposition of dead roots. Considering that this transient increase was reported to last for approximately five months (Zhou et al 2007), we started the respiration measurements one year after collars were installed to minimize this limitation. Live root exclusion in deep collars also affected the presence of root exudates, which would in turn affect RH. Despite these inevitable uncertainties, we found that the ratio of RH to Rs was between 57% and 72% during the experimental period, within the previously reported range (25%–90%) for global grasslands (Subke et al 2006), indicating that the method is feasible to partition RH and RA in our experiment.

In contrast to the observations in the dry alpine steppe, our results also revealed that experimental warming significantly increased Rs in the Tibetan alpine meadow and arctic ecosystems (figure 4). The different responses of Rs to warming among various ecosystems may be caused by the following three aspects. First, regional differences in environmental factors, including temperature and water availability, may have led to different Rs responses. It has been reported that mean annual temperature in the Tibetan alpine steppe (0.80 °C) was higher than those in the Tibetan alpine meadow (0.15 °C, Chen et al 2019). Moreover, background information of synthesized studies indicated that the sites in Tibetan alpine meadow had a higher temperature range than those in arctic ecosystems (table S1). This temperature difference may have led to lower Rs response levels to experimental warming in our field experiment, since Rs in cold regions often show higher temperature sensitivity (Carey et al 2016, Hursh et al 2017). In addition, soil moisture in the Tibetan alpine steppe (10.9%) was...
lower than the Tibetan alpine meadow (22.3%, Chen et al. 2019), and the soil moisture in arctic tundra were likely to remain unchanged under experimental warming (table S1). Consequently, Rs in the Tibetan alpine meadow and arctic tundra are not severely impacted by the limited water supply, and may be stimulated by experimental warming.

Second, SOC differences across regions may contribute to different patterns of Rs under warming. SOC density (C amount per area) within the 1 m depth was reported as 4.5 kg C m$^{-2}$ in the Tibetan alpine steppe, lower than 9.0 kg C m$^{-2}$ in the Tibetan alpine meadow (Yang et al. 2008, Ding et al. 2016) and 34.8 kg m$^{-2}$ in arctic tundra (Ping et al. 2008). It has been suggested that the responses of Rs to climate warming are directly related to SOC stock, with larger SOC triggering stronger Rs response (Crowther et al. 2016). Consequently, elevated temperature may lead to higher Rs levels in the Tibetan alpine meadow and arctic ecosystems than in the Tibetan alpine steppe. In addition, SOC quality is another important factor controlling Rs response. Laboratory incubation experiments have shown that SOM is highly decomposable in both Tibetan alpine meadow and arctic tundra (Schadel et al. 2014, Treat et al. 2014, Chen et al. 2016a), which may contribute to more sensitive Rs changes under climate warming in these regions (Eberwein et al. 2015).

Third, differences in plant and microbial growth may cause the heterogeneity in Rs response among various regions. Previous research revealed that the average aboveground biomass in the Tibetan alpine steppe was 50.1 g m$^{-2}$ (Yang et al. 2009), while that in the Tibetan alpine meadow and arctic tundra was 90.8 and 315.4 g m$^{-2}$, respectively (Yang et al. 2009, Howard et al. 2012). The higher aboveground biomass may be responsible for larger Rs fluxes in the Tibetan alpine meadow and arctic ecosystems. In addition to plants, soil microorganisms are also of great importance in determining the response of Rs to warming (Allison et al. 2010, Wieder et al. 2013). Soil microbial biomass in the Tibetan alpine steppe was reported to be 13.5 mmol C kg$^{-1}$, lower than that in the Tibetan alpine meadow (33.5 mmol C kg$^{-1}$; Chen et al. 2016b) and arctic tundra (340.5 mmol C kg$^{-1}$; Xu et al. 2013). The lower soil microbial biomass indicates that soil microbes in the Tibetan alpine steppe may respire less

Figure 3. Relationships of the response ratios (RRs) of Rs, RH and Ra with the RR of soil temperature (ST) (a), (c), (e) and moisture (SM) (b), (d), (f). Hollow points are the outliers determined by Boxplot Procedures and excluded from the fittings. Insignificant relationships are shown with dashed lines in subfigures (a), (c), (e) and (f).
CO₂ under warming. Overall, the larger plant and microbial biomass may contribute to a significant warming-induced Rₘ increase in the Tibetan alpine meadow and arctic ecosystems.

In summary, our study demonstrated that changes to Rₘ under climate warming in the Tibetan alpine steppe were different from those reported in Tibetan alpine meadow and arctic ecosystems. Although warming significantly increased Rₘ in the Tibetan alpine meadow and arctic tundra, it exerted no significant effect on Rₘ in the Tibetan alpine steppe. This finding does not support the traditional view that climate warming would induce a significant increase in Rₘ in cold regions, suggesting that a more complex C-climate feedback mechanism exists in cold regions. Therefore, future evaluations on terrestrial C-feedback, even in warming-sensitive ecosystems, should call for a comprehensive consideration of the heterogeneous ecosystem responses and complex regulating mechanisms.

**Acknowledgments**

The data that support the findings of this study are available from the corresponding author upon reasonable request. We appreciate the editor and two anonymous reviewers for their critical comments on an early version of this manuscript. We thank Dr Tianfeng Han for his help in field measurements, and acknowledge the financial support from the National Natural Science Foundation of China (31825006 and 41877046), Key Research Program of Frontier Sciences, Chinese Academy of Sciences (QYZDB-SSWSMC049), and Chinese Academy of Sciences-Peking University Pioneer Cooperation Team.

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References

Adams D C, Gurevitch J and Rosenberg M S 1997 Resampling tests for meta-analysis of ecological data Ecology 78 1277–83
Allison S D, Wallenstein M D and Bradf ord M A 2010 Soil-carbon response to warming dependent on microbial physiology Nat. Geosci. 3 336–40
Bond-Lamberty B, Bailey V L, Chen M, Gough C M and Vargas R 2018 Globally rising soil heterotrophic respiration over recent decades Nature 560 80–3
Bond-Lamberty B and Thomson A 2010 Temperature-associated increases in the global soil respiration record Nature 464 579–82
Carey J C et al 2016 Temperature response of soil respiration largely unaltered with experimental warming Proc. Natl Acad. Sci. USA 113 13797–802
Chen L, Liang J, Qin S, Liu L, Fang K, Xu Y, Ding J, Li F, Luo Y and Yang Y 2016a Determinants of carbon release from the active layer and permafrost deposits on the Tibetan Plateau Nat. Commun. 7 13046
Chen Y et al 2016b Linking microbial C:N:P stoichiometry to microbial community and abiotic factors along a 5000 km grassland transect on the Tibetan Plateau Glob. Ecol. Biogeogr. 25 1416–27
Chen Y, Kou D, Li F, Ding J, Yang G, Kang K and Yang Y 2019 Linkage of plant and abiotic properties to the abundance and activity of N-cycling microbial communities in Tibetan permafrost-affected regions Plant Soil 434 453–66
Crowther T W et al 2016 Quantifying soil global carbon losses in response to warming Nature 540 104–8
Ding J et al 2016 The permafrost carbon inventory on the Tibetan Plateau: a new evaluation using deep sediment cores Glob. Change Biol. 22 6288–701
Dorropaal E, Toet S, van Logtestijn R S P, Swart E, van de Weg M J, Fu G, Shen Z, Zhang X, Yu C, Zhou Y, Li Y and Yang P 2013 Climate Change 2013: The Physical Science Basis. (Cambridge: Cambridge University Press)
Jahn M, Sachs T, Mansfeldt T and Oversch M 2010 Global climate change and its impacts on the terrestrial Arctic carbon cycle with special regards to ecosystem components and the greenhouse-gas balance J. Plant Nutr. Soil Sci. 173 627–43
Li F et al 2017 Warming effects on permafrost ecosystem carbon fluxes associated with plant nutrients Ecology 98 2851–9
Li F, Peng Y, Zhang D, Yang G, Fang K, Wang G, Wang J, Yu J, Zhou G and Yang Y 2019 Leaf area rather than photosynthetic rate determines the response of ecosystem productivity to experimental warming in an alpine steppe J. Geophys. Res. Biogeosci. 124 2277–87
Lin X et al 2011 Response of ecosystem respiration to warming and grazing during the growing seasons in the alpine meadow on the Tibetan Plateau Agric. Forest Meteorol. 151 792–802
Luo Y and Zhou X 2006 Soil Respiration and the Environment (New York: Academic) (https://doi.org/10.1016/B978-012088782-8.50012-7)
Melillo J M, Frey S D, DeAngelis K M, Werner W J, Bernard M J, Bowles F P, Pold G, Knorr MA and Grandy AS 2017 Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world Science 358 101–5
Metcalfe D B, Fisher R A and Wardle D A 2011 Plant communities as drivers of soil respiration: pathways, mechanisms, and significance for global change Biogeosciences 8 2047–61
Natali S M et al 2015 Permafrost thaw and soil moisture driving CO2 and CH4 release from upland tundra J. Geophys. Res. Biogeosci. 120 525–37
Oberbauer S F et al 2007 Tundra CO2 fluxes in response to experimental warming across latitudinal and moisture gradients Ecol. Monogr. 77 221–38
Peng Y et al 2017a Nonlinear response of soil respiration to increasing nitrogen additions in a Tibetan alpine steppe Environ. Res. Lett. 12 024018
Peng Y, Li F, Zhou G, Fang K, Zhang D, Li C, Yang G, Wang G, Wang J and Yang Y 2017b Linkages of plant stoichiometry to ecosystem production and carbon fluxes with increasing nitrogen inputs in an alpine steppe Glob. Change Biol. 23 5249–59
Peng Y, Michaelson G J, Jorgenson M T, Kimble J M, Epstein H, Romanovsky V E and Walker D A 2008 High stocks of soil organic carbon in the North American Arctic region Nat. Geosci. 1 615–9
R Core Team 2018 R: A language and environment for statistical computing R Foundation for Statistical Computing (Vienna, Austria: R Foundation for Statistical Computing) (https://www.r-project.org/)
Rosenberg M S, Adams D C and Gurevitch J 1997 Meta-analysis: statistical software for meta-analysis with resampling tests (Sunderland, MA: Sinauer Associates)
Rustad L, Campbell J, Marion G, Norby R, Mitchell M, Hartley A, Cornelissen J, Gurevitch J and Giske N 2001 A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental warming Oecologia 126 543–62
Schadl C, Schuur E A, Bracho R, Elberling B, Knoblauch C, Lee H, Luo Y, Shaver G R and Turetsky M R 2014 Circumpolar assessment of permafrost C quality and its vulnerability over time using long-term incubation data Glob. Change Biol. 20 641–52
Schuur E A G et al 2015 Climate change and the permafrost carbon feedback Nature 520 171–9
Sheik C S, Beasley W H, Elshahed M S, Zhou X H, Luo Y Q and Krumholz L R 2011 Effect of warming and drought on grassland microbial communities ISME J. 5 1692–700
Shi F, Chen H, Chen H, Wu Y and Wu N 2012 The combined effects of warming and drying suppress CO2 and N2O emission rates in an alpine meadow of the eastern Tibetan Plateau Ecol. Res. 27 725–33
Sim C H, Gan F F and Chang T C 2005 Outlier labeling with boxplot procedures J. Am. Stat. Assoc. 100 642–52
Subke J A, Ingham I and Francesca Cotrufo M 2006 Trends and methodological impacts in soil CO2 efflux partitioning: a meta analytical review Glob. Change Biol. 12 921–43
Suseela V and Dukes J S 2013 The responses of soil and rhizosphere respiration to simulated climatic changes vary by season Ecology 94 403–13
Treat C C, Wollheim W M, Varner R K, Grandy A S, Talbot J and Frolking S 2014 Temperature and peat type control CO2 and CH4 production in Alaskan permafrost peats Glob. Change Biol. 20 2674–86
Wang X, Liu L, Piao S, Janssens I A, Tang J, Liu W, Chi Y, Wang J and Xu S 2014 Soil respiration under climate warming: differential response of heterotrophic and autotrophic respiration Glob. Change Biol. 20 3229–37
Wieder W R, Bonan G B and Allison S D 2013 Global soil carbon projections are improved by modelling microbial processes Nat. Clim. Change 3 909–12
Xu X, Thornton P E and Post W M 2013 A global analysis of soil microbial biomass carbon, nitrogen and phosphorus in terrestrial ecosystems Glob. Ecol. Biogeogr. 22 737–49
Xue X, Peng F, You Q, Xu M and Dong S 2015 Belowground carbon responses to experimental warming regulated by soil moisture change in an alpine ecosystem of the Qinghai–Tibet Plateau Ecol. Evol. 5 4063–78
Yang Y, Fang J, Tang Y, Ji C, Zheng C, He J and Zhu B 2008 Storage, patterns and controls of soil organic carbon in the Tibetan grasslands Glob. Change Biol. 14 1592–9
Yang Y, Fang J, Pan Y and Ji C 2009 Aboveground biomass in Tibetan grasslands J. Arid Environ. 73 91–5
Zhang D, Peng Y, Li F, Yang G, Wang J, Yu J, Zhou G and Yang Y 2019 Trait identity and functional diversity co-drive response of ecosystem productivity to nitrogen enrichment J. Ecol. 107 2402–14
Zhou X, Wan S and Luo Y 2007 Source components and interannual variability of soil CO2 efflux under experimental warming and clipping in a grassland ecosystem Glob. Change Biol. 13 761–75