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Patterns and controls of soil respiration and its temperature sensitivity in grassland ecosystems across China

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Abstract. Soil respiration (Rs), a key process in the terrestrial carbon cycle, is very sensitive to climate change. In this study, we synthesized 54 measurements of annual Rs and 171 estimates of Q_{10} value (the temperature sensitivity of soil respiration) in grasslands across China. We quantitatively analyzed their spatial patterns and controlling factors in five grassland types, including temperate typical steppe, temperate meadow steppe, temperate desert steppe, alpine grassland, and warm-tropical grassland. Results showed that the mean (± SE) annual Rs was 582.0 ± 57.9 g C m^{-2} yr^{-1} across Chinese grasslands. Annual Rs significantly differed among grassland types, and positively correlated with mean annual temperature, mean annual precipitation, soil organic carbon content and aboveground biomass, but negatively correlated with latitude and soil pH ($P <$ 0.05). Among these factors, mean annual precipitation was the primary factor controlling the spatial variation of annual Rs in Chinese grasslands. The mean contributions of growing season Rs and heterotrophic respiration to annual Rs were 78.7% and 72.8%, respectively. Moreover, the mean (± SE) of Q_{10} across Chinese grasslands was 2.60 ± 0.08, ranging from 1.03 to 8.13, and varied largely within and among grassland types, and among soil temperature measurement depths. Generally, the seasonal variation of soil respiration in Chinese grasslands cannot be well explained by soil temperature using the van’t Hoff equation. Longitude and altitude were the dominant driving factors and accounted for 26.0% of the variation in Q_{10} derived by soil temperature at the depth of 5 cm. Overall, our findings advance our understanding of the spatial variation and environmental control of soil respiration and Q_{10} across Chinese grasslands, and also improve our ability to predict soil carbon efflux under climate change on the regional scale.

Keywords: Soil respiration, Soil carbon emission; Temperature sensitivity; Grassland ecosystem; Q_{10}

1 Introduction

Soil respiration (Rs) represents carbon dioxide (CO_2) efflux from the soil surface, including autotrophic/root respiration, and heterotrophic/microbial respiration associated with soil organic matter and litter decomposition (Boone et al., 1998; Kuzyakov, 2006; Schindlbacher et al., 2009). As one of the largest fluxes in the global carbon cycle, Rs plays an important role in regulating ecosystem carbon cycling, carbon-climate feedback, and climate change (Raich and Schlesinger, 1992; Davidson et al., 2002; Luo and Zhou, 2006; Bond-Lamberty and Thomson, 2010). The temperature sensitivity of Rs (Q_{10}), the factor by which Rs is multiplied when temperature increases by 10 ℃, is a key parameter to evaluate the feedback intensity between soil carbon efflux and climate warming (Reichstein et al., 2005; Davidson and Janssens, 2006). Knowledge on patterns and controls of Rs and Q_{10} variation on the large scale is crucial for better understanding and modeling soil carbon cycle in a warmer world (Peng et al., 2009; Wang et al., 2010).

Temperature and precipitation are commonly believed to be the most important climatic factors controlling Rs on the large scale, as suggested by a number of studies (Raich and Schlesinger, 1992; Raich and Potter, 1995; Chen et al., 2014; Hursh et al., 2017). As the indirect factors, altitude and latitude can also affect Rs by affecting climatic factors (Song et al., 2014). Soil properties, such as soil organic carbon (SOC), soil total nitrogen (STN) and soil pH, can also affect Rs in that they can directly or indirectly affect substrate quality and quantity, which strongly control soil microbial activity and heterotrophic respiration (Ryan and Law, 2005; Chen et al., 2010a, 2014; Song et al., 2014). Additionally, biotic factors including decomposer microbes and plant can directly influence soil respiration via heterotrophic and autotrophic respiration, respectively (Ryan and Law, 2005; Bahn et al., 2010). Previous studies have shown that Rs increased with total, aboveground and belowground net/gross primary production, aboveground biomass (AGB) and belowground biomass (BGB), leaf area index (Raich and Schlesinger, 1992; Hibbard et al., 2005; Bahn et al., 2008; Chen at al., 2014; Zhao et al. 2017).

Similarly, the temperature sensitivity of Rs is also largely regulated by both biotic and abiotic factors. Several studies have showed that climatic factors had strong controls on the spatial variation of Q_{10}, and Q_{10} generally decreased with mean annual temperature (MAT) and mean annual precipitation (MAP) (Raich and Schlesinger, 1992; Kirschbaum, 2000; Peng et al., 2009; Song et al., 2014). In terms of geographical variables, latitude and altitude can also indirectly influence Q_{10} via controlling MAT and MAP (Song et al., 2014; Xu et al., 2015). In addition to climatic and geographical variables, Q_{10} could be affected by other factors, such as plant biomass, soil pH, SOC and STN, which can directly influence microbial activity, substrate availability and nutrient supply (Zhou et al., 2009; Song et al. 2014; Zhao et al., 2017).

Grasslands in China cover 29–41% of its total land area (Shen et al., 2016) and have significant effects on regional climate and carbon cycle (Ni, 2002). As known to all, grasslands are widely distributed throughout China, and the different climate gradients and landforms in China support a number of grassland types, including tropical, warm, temperate, and alpine grassland, etc. (Chen et al., 2002; Shen et al., 2016). Specifically, the temperate arid and semi-arid grasslands in Inner Mongolia, and the alpine meadow and steppe in Qinghai-Tibet Plateau comprise the main body of temperate and alpine grasslands, respectively (Shen et al., 2016). In the past two decades, a large number of case studies on Rs have been widely conducted in grasslands across China. However, few have been included in global Rs and Q_{10} syntheses (Raich and Schlesinger, 1992; Wang et al., 2010; Bond-Lamberty and Thomson, 2010; Chen et al., 2014; Hursh et al., 2017), largely because most studies were published in Chinese journals. Given that diverse grassland types, especially alpine grasslands distributed in China, Rs and Q_{10} may vary among grassland types due to the differences in abiotic and biotic factors, and the patterns of Rs and Q_{10} across Chinese grasslands may differ from global terrestrial ecosystems and grasslands. However, how the spatial variation of Rs and Q_{10} varies with abiotic and biotic factors across Chinese grasslands and their differences among grassland types still remain poorly understood.

In this study, we synthesized all the available data relating to Rs and Q_{10} in grasslands across China. Our main objectives were to: (1) analyze the spatial patterns of Rs and Q_{10} across various grassland ecosystems in China; (2) compare the differences in Rs and Q_{10} among grassland types; (3) identify how abiotic and biotic factors drive Rs and Q_{10} among sites on the regional scale, including geographic variables, climatic factors, soil properties and biotic factors; and (4) compare the Rs and Q_{10} in Chinese grasslands with those from previous syntheses on the global and regional scale.

2 Materials and Methods

2.1. Data collection

Peer-reviewed journal articles and published theses (including available online) before 1 December, 2017 were searched using Web of Science and China National Knowledge Infrastructure (CNKI, available online: http://epub.cnki.net) with the following search term combinations: (soil respiration OR soil CO_2 flux OR soil CO_2 efflux OR soil CO_2 emission OR soil carbon flux OR soil carbon efflux OR soil carbon emission) AND (grassland OR steppe OR meadow OR grass). Additional searches with the same keywords were conducted on ScienceDirect (Elsevier Ltd., Amsterdam, Nederland), Springer Link (Springer International Publishing AG, Berlin, Germany), and Wiley Online Library (John Wiley & Sons Ltd., Hoboken, USA). Furthermore, previous global and regional syntheses on the similar topic were also screened to check Chinese grassland data, such as Peng et al. (2009), Wang and Fang (2009), Bond-Lamberty and Thomson (2010), Wang et al. (2010) and Chen at al. (2010, 2014).

To ensure data consistency and accuracy, the following six criteria were applied to select appropriate studies: (1) experimental studies were conducted in the field; (2) experiments with the treatments of nitrogen (fertilizer) addition, increased or decreased precipitation, elevated CO_2, simulated acid rain, clipping, and grazing were removed; (3) the study must contain soil respiration or Q_{10} with a clear record of grassland type and experimental duration; (4) the investigation time for measuring Rs was not less than twelve months so that the annual Rs can be obtained, and modeled annual Rs based on the relationships between Rs rate and temperature were not included; (5) the investigation time for estimating Q_{10} value was not less than four months; and (6) Q_{10} values were calculated by the van't Hoff equation (Van's Hoff, 1898).

$$SR = \alpha \times \exp(\beta \times T) \qquad (1)$$

where SR is the measured soil respiration rate, T is the measured soil temperature at the given depth, and coefficient α and β are fitted parameters. The Q_{10} values were calculated as:

$$Q_{10} = \alpha \times \exp(\beta \times T) \qquad (2)$$

Several studies measured Rs and its temperature sensitivity at different years, and then these Rs and Q_{10} values were averaged across years. In this case, only the highest R^2 was extracted if more than one coefficient of determination (R^2) values of Q_{10} were available in the same study. In addition, the annual Q_{10} value was selected in our database if the growing season, non-growing season, and annual Q_{10} values were available. Within these constraints, 54 measurements of annul Rs rate and 171 estimates of Q_{10} value were obtained from 108 published experimental studies across Chinese grasslands (Table S1). Our database contained 14 variables associated with Rs, including annual Rs, growing and non-growing season Rs and their proportions to annual Rs, the proportion of autotrophic and heterotrophic respiration to annual Rs, and the Q_{10} of Rs. The Q_{10} values were divided into five types based on the soil temperature at different depths (ST0, soil surface temperature; ST5, soil temperature at 5 cm; ST10, soil temperature at 10 cm; ST15, soil temperature at 15 cm; and ST20, soil temperature at 20 cm) for the same site. In one study, the Q_{10} was derived by soil temperature at the depth of 6 cm, and then it was treated as $Q_{10\text{-ST5}}$ because of little difference in soil temperature between 5 cm and 6 cm.

In most of publications, the Rs, Q_{10} and its R^2 of the model were presented, and they were incorporated into our database directly. The Rs, Q_{10} and R^2 values were recalculated according to the available information if these values were not directly provided in some publications. The growing season, non-growing season and annual Rs were obtained by interpolating measured Rs rate between respective sampling dates for each seasonal measurement period of the year, and then computing the sum to obtain the corresponding values (Frank and Dugas, 2001; Sims and Bradford, 2001) as follows:

$$CSR = \Sigma\,(\Delta t_k \times F_{m,k}) \qquad (3)$$

where CSR is cumulative soil respiration during the season, Δt_k ($= t_k - t_{k-1}$) is the time interval between each field measurement within the season, and $F_{m,k}$ is the average Rs rate over the interval $t_k - t_{k-1}$.

In addition, for each study site, we also recorded other supporting information from the original publications, including grassland type, geographic variables (longitude, latitude and altitude), climatic factors (MAT and MAP), soil properties (soil pH, SOC and STN), and biotic factors (microbial biomass carbon (MBC), AGB and BGB). Missing climatic information were obtained using NASA Surface meteorology and Solar Energy-Location, and the other missing information were obtained from the related references according to the study site and described experiment design. Several studies provided the soil organic matter content, which was converted to SOC by multiplying a constant of 0.58. Given that BGB were measured in different soil depths, only BGB measured in 0−40 and 0−50 cm soil depths were selected because roots were mainly distributed in 0−50 cm and there were minor difference between 0−40 and 0−50 cm. The distributions of selected experimental sites were showed in Fig. 1.

2.2. Data analysis

In this study, grasslands were divided into five groups, including temperate typical steppe, temperate meadow steppe, temperate desert steppe, alpine grassland, and warm-tropical grassland. If grassland type was not provided directly, it was determined according to the dominant plant species reported in selected publications and the Classification of Grassland Ecosystem in China (Chen et al., 2002). Detailed statistical parameters for the five grasslands were presented in Table S2.

One-way analysis of variance (ANOVA) was used to examine whether annual Rs and Q_{10} values differed among grassland types or soil temperature measurement depths. In case of homogeneity of variances, the least significant differences (LSD) test was applied; otherwise, the Dunnett T3 test was applied. Paired-samples *t*-test was performed to compare the differences between growing season and non-growing season Rs, between autotrophic respiration and heterotrophic respiration, and the Q_{10} values among different measurement depths. The univariate regression analysis was used to identify the relationships between annual Rs, Q_{10}, and a given biotic or abiotic factor mentioned above, except for MBC because of its limited sample size. The stepwise linear regression analyses were also performed to identify the comprehensive effects of environmental variables (including latitude, altitude, MAT, and MAP as they were in one-to-one correspondence) on annual Rs, and Q_{10} derived by ST5 and ST10. Correlations among these factors were calculated with the Pearson correlation coefficients. All statistical analyses were performed using the software IBM SPSS Statistics 20.0 (IBM Corporation, New York, USA).

3 Results

3.1 Soil respiration and its controlling factors

3.1.1. Patterns of annual soil respiration across Chinese grasslands

The annual Rs ranged from 122.9 to 2407.1 g C m^{-2} yr^{-1}, with the total mean (± SE) of 582.0 ± 57.9 g C m^{-2} yr^{-1}. There were significant differences in annual Rs between grassland types ($p < 0.001$), with the highest annual Rs in the warm-tropical grassland and the lowest annual Rs in the temperate desert steppe (Table 1). The proportions of growing season or non-growing season Rs varied slightly among different grassland types ($P > 0.05$), but the proportion of Rs in growing season was significantly higher than that in non-growing season ($p < 0.001$). Overall, growing season and non-growing season Rs consisted of 78.7% and 21.3% of the annual Rs, respectively, across all grasslands in China (Table 1). In addition, growing season Rs was significantly positively correlated with the annual Rs based on linear regression model ($r^2 = 0.923$, $p < 0.001$, Fig. S1). At the annual scale, the mean contribution of heterotrophic respiration to Rs was 72.8% across Chinese grasslands, which was significantly larger than that of autotrophic respiration with the mean of 27.2% ($p < 0.01$, Fig. S2).

3.1.2. Spatial controls of abiotic and biotic factors over soil respiration

In the univariate linear regressions, annual Rs significantly increased with MAT, MAP SOC, and AGB across all grasslands in China, but decreased with latitude, altitude, and soil pH ($p < 0.05$, Fig. 2). In contrast, annual Rs did not correlate well with STN and BGB ($p > 0.05$). The single factor of latitude, MAT, MAP, SOC, soil pH, and AGB accounted for 25.7%, 22.4%, 31.3%, 30.2%, 20.6%, and 36.1% of the spatial variation of annual Rs, respectively (Fig. 2). In addition, only the variable of MAP was selected in the analysis of stepwise linear regression, indicating that MAP was the primary factor controlling the spatial variation of annual Rs in Chinese grasslands.

3.2 Temperature sensitivity of soil respiration and its controlling factors

3.2.1 Distributions of Q_{10} values and its coefficient of determination

Most of the Q_{10} values (83.0%) were distributed between 1.5 and 3.8. However, the distributions of Q_{10} values derived by the five temperature types were different (Fig. 3a-e). The largest relative frequency for $Q_{10\text{-ST5}}$ and $Q_{10\text{-ST10}}$ values was within the range of 1.5 to 3.0 (68.5%) and 1.5 to 3.5 (83.1%), respectively, while that of $Q_{10\text{-ST0}}$ was mainly within 1.0–2.0 (88.2%, Fig. 3). In addition, the distribution of $Q_{10\text{-ST15}}$ and $Q_{10\text{-ST20}}$ were relatively uniform (Fig. 3d and e).

Similarly, the distributions of R^2 for Q_{10} derived by the five temperature types also differed from each other (Fig. 3f-g). The R^2 values for $Q_{10\text{-ST5}}$ and $Q_{10\text{-ST10}}$ were mainly distributed in 0.6–0.9 and 0.5–0.7, respectively, while those for $Q_{10\text{-ST15}}$ and $Q_{10\text{-ST20}}$ were mainly distributed in 0.3–0.6. The R^2 value for $Q_{10\text{-ST0}}$ was distributed uniformly (Fig. 3f). Overall, only 35.6% R^2 values for Q_{10} were within the range of 0.7–1.0.

3.2.2 Patterns of Q_{10} values across Chinese grasslands

Across all grasslands, the overall Q_{10} values ranged largely from 1.03 to 8.13, with the mean (± SE) of 2.60 ± 0.08. Specifically, the mean (± SE) of Q_{10} values derived by ST0, ST5, ST10, ST15, and ST20 was 1.65 ± 0.08, 2.80 ± 0.14, 2.56 ± 0.12, 2.64 ± 0.33, and 2.81 ± 0.31, respectively (Fig.3 a-e). Paired *t*-test demonstrated that Q_{10} significantly differed between two adjacent depths in the top 15 cm soil ($P < 0.05$), whereas no difference occurred below 15 cm depth ($p > 0.05$; Fig. 4). Generally, the overall Q_{10} and paired Q_{10} increased with soil temperature measurement depth (Fig. 4; Fig. S3). In terms of grassland types, there were significant differences for Q_{10} derived by ST5 and ST10 among grassland types, respectively ($p < 0.05$, Fig. 4b and c). For Q_{10} derived by ST5, it was highest in alpine grassland, while for Q_{10} derived by ST10, the highest value was in warm-tropical grassland. In addition, Q_{10} values derived by ST0, ST15 and ST20 were not enough to meet the demand of statistical analysis, so their differences among grassland types were not examined.

3.2.3 Spatial controls of environmental factors over Q_{10}

The relationships of $Q_{10\text{-ST5}}$ and $Q_{10\text{-ST10}}$ with abiotic and biotic factors were presented in Fig. 5. Among these abiotic and biotic factors, $Q_{10\text{-ST5}}$ correlated well with latitude, altitude, SOC, AGB and BGB ($P < 0.05$, Fig. 5). In contrast, $Q_{10\text{-ST10}}$ significantly correlated with MAP and SOC ($P < 0.05$, Fig. 5). In addition, only three factors including altitude, MAP and MAT were selected in the analysis of stepwise linear regression, indicating that they interactively affected $Q_{10\text{-ST5}}$, and accounted for 26.0% of the spatial variation of $Q_{10\text{-ST5}}$ across Chinese grasslands (Table S3).

4 Discussion

4.1 Spatial patterns and controlling factors of annual soil respiration

4.1.1 Annual soil respiration among grassland types

Significant differences among the five grasslands suggested grassland type had significant influence on annual Rs ($p < 0.001$, Table 1), which might be mainly attributed to the differences in AGB, BGB and microbial activity across various grassland types. Previous incubation experiments showed microbial respiration positively correlated with microbial biomass (Colman and Schimel, 2013; Ding et al., 2016), indicating grasslands with higher MBC would have larger heterotrophic respiration. Meanwhile, regional study suggested that microbial biomass was closely increased with MAP in grasslands (Chen et al., 2016b), which was also found in this study. Altogether, these suggested that the regions with high MAP would have larger heterotrophic respiration. Additionally, previous study demonstrated that both AGB and BGB increased with MAP across Chinese grasslands (not including warm-tropical grasslands) (Ma et al., 2014). Therefore, autotrophic respiration would be higher in the grasslands with high biomass. Collectively, the grasslands with high MAP would have relatively higher Rs rate. Our results also showed this trend that mean annual Rs in each of the four grassland types increased significantly with MAP ($p < 0.01$, Fig S4).

4.1.2 Controls of environmental factors on annual Rs

Across Chinese grasslands, annual Rs were strongly related to latitude, MAT and MAP, which were consistent with previous results obtained from global terrestrial ecosystems (Raich and Schlesinger, 1992; Raich and Potter 1995; Chen at al., 2014), global grasslands (Wang and Fang, 2009), and Chinese forests (Song et al., 2014; Xu et al., 2015). As a key factor controlling climate conditions on the regional and global scale, latitude could significantly influence Rs by affecting climatic variables (Song et al., 2014). Our study showed that MAT and MAP decreased closely with latitude ($p < 0.001$, Table S3), indicating that latitude is an indirect factor affecting annual Rs on the large scale.

In addition, spatial variations of annual Rs were also controlled by soil properties, such as SOC and soil pH. The relationships between annual Rs and SOC as well as pH were also observed in global, regional and local terrestrial ecosystems (Chen et al., 2010b, 2014; Song et al., 2014; Xu et al., 2016). Since Rs involves the process of converting organic carbon into inorganic carbon, the soil CO_2 emission is untimely determined by the supply of C substrate (Wan et al., 2007). Additionally, soil pH can directly regulate the activities of microbes and C-acquiring enzymes (Turner, 2010). In neutral and alkaline soils, microbial biomass tended to decrease with soil pH (Ding et al., 2016). Therefore, this led to a negative correlation between Rs and soil pH in Chinese grasslands because most of grasslands in China are distributed in neutral and alkaline soils. Further, Chen et al. (2010b) demonstrated that annual Rs significantly increased with soil total nitrogen on the global scale. Meanwhile, some case studies revealed the similar relationship between growing season Rs and soil total nitrogen among different grassland types and vegetation communities (Chen et al., 2010a; Wang et al., 2015; Xu et al., 2016) on the local scale, while annual Rs did not correlate well with STN in this study. Altogether, these results suggested that the effect of soil total nitrogen on Rs depended on plant growth period, vegetation type, and spatial scale. Therefore, how STN influence Rs across Chinese grasslands on the regional scale should be further studied.

Furthermore, as the source of autotrophic respiration, BGB can directly influence Rs, which has been observed in ecosystems on global and local scale (Chen at al., 2010a, 2014). However, no significant correlation between BGB and Rs was observed in the present study, which might be attributed to the limited sample size (n = 20) and the uncertainty in measuring BGB (due to inconsistent or insufficient sampling depth). In grassland ecosystems, BGB generally increased with AGB (Ma et al., 2014), and this relationship was also observed in this study ($p < 0.10$, Fig. S5). Therefore, given the significant correlation between AGB and Rs in Chinese grasslands (Fig. 2), BGB may also have the potential to control annual Rs across Chinese grasslands, although this should be further investigated based on accurate quantification of BGB and Rs across a large number of sites.

4.2 Spatial patterns and controlling factors of Q_{10} values

4.2.1 R^2 for Q_{10} in Chinese grasslands

In this study, only 37.3% of R^2 for Q_{10} was larger than 0.7, indicating that most of the seasonal variation of Rs rate cannot be well explained by soil temperature using the van't Hoff equation (Eq. 2). Compared with the results obtained from Chinese forests (Xu et al., 2015), the van't Hoff equation (Eq. 2) was not very suitable to describe the relationships between Rs rate and soil temperature in most of Chinese grasslands. This might be associated with the difference in soil moisture between these two ecosystems because besides temperature, soil moisture may strongly influence the apparent Q_{10} (Subke and Bahn, 2010). Previous studies have suggested that in humid and semi-humid regions the effect of soil moisture on Rs is weak, whereas in arid and semi-arid regions, Rs is significantly influenced by soil moisture (Jia et al., 2006; Li et al., 2011; Wang et al., 2014a, 2014b). Moreover, some studies showed that soil moisture and temperature had an interactive effect on the seasonal variations of Rs rate (Davidson et al., 1998; Jia et al., 2006; Wang et al., 2014b; Liu et al., 2016), indicating that the two-variable equations could better explain the variation in Rs than single variable of temperature. Our results also showed that, in general, R^2 for Q_{10} closely increased with MAP ($P < 0.05$, Fig. S6), indicating that the R^2 for Q_{10} tended to be larger in the regions with abundant precipitation. Collectively, for ecosystems (e.g., grassland and desert) in arid and semi-arid regions, Rs could be better estimated by the combined factors of soil temperature and moisture. By comparison, 46.6% of R^2 for $Q_{10\text{-ST5}}$ was distributed in 0.7–1.0, which was higher than those derived by soil temperature at other depths, suggesting that the seasonal variation of Rs can be better explained by soil temperature at the depth of 5 cm across Chinese grasslands.

4.2.2 Q_{10} among soil depths and grassland types

In Chinese grasslands, the estimated Q_{10} generally increased with soil temperature measurement depth, which was consistent with previous synthesis study about Chinese ecosystems (Peng et al., 2009). The differences for Q_{10} among measurement depths might be due to the seasonal amplitudes of temperature at different soil depths (Pavelka et al., 2007; Graf et al., 2008).

In terms of grassland types, the highest $Q_{10\text{-ST5}}$ was in the alpine grassland and the lowest in the temperate desert steppe and typical steppe (Fig. 4). This difference could be associated with soil properties and climatic conditions. For example, it is well known that the alpine grasslands are usually distributed in high altitude regions (above 3000 m), where the climate is relatively colder and SOC is relatively higher (Table S2). However, the temperate desert steppes and typical steppes are mainly distributed in north China, with relatively high MAT and low MAP that may lead to low Q_{10}. Moreover, as shown in Fig. 4, the highest $Q_{10\text{-ST10}}$ occurred in warm-tropical grassland, which might be associated with the abundant substrate supply in this grassland type because high substrate availability can enhance apparent Q_{10} of soil respiration (Davidson et al., 2006; Zhu and Cheng, 2011).

4.2.3 Controls of environmental factors on Q_{10}

Generally, the Q_{10} derived by either ST5 or ST10 did not correlate well with climatic factors, which was inconsistent with previous results on the global and regional scale (Chen and Tian, 2005; Peng at al., 2009; Wang et al., 2010; Song et al., 2014; Xu et al., 2015). This suggested that the single factor of temperature or precipitation could not critically control the variations of Q_{10} in Chinese grasslands, which are mainly distributed in arid and semiarid regions. In addition, the negative correlation between latitude and $Q_{10\text{-ST5}}$ in Chinese grasslands was not in line with Chinese forests, in which positive correlation was observed (Song et al., 2014; Xu et al., 2015). The difference might be that alpine grasslands in China were mainly distributed in regions with low latitude but high altitude. Previous studies and the present result indicated that Q_{10} tended to be higher at high altitude regions (Song et al., 2014; Xu et al., 2015).

Additionally, the positive relationships of $Q_{10\text{-ST5}}$ with SOC, AGB and BGB indicated that soil properties and plant biomass can also profoundly influence the spatial variation of Q_{10}. Previous studies suggested higher plant biomass and SOC can lead to more substrate supply for soil respiration and then result in higher Q_{10} values, because apparent Q_{10} increased with increasing substrate availability (Gershenson et al., 2009; Zhao et al., 2017).

The extremely low R^2 value for the relationship of Q_{10} with abiotic factors suggested that the spatial variation of Q_{10} in Chinese grasslands cannot be well explained by a single factor. Therefore, the variation of Q_{10} in Chinese grasslands should be controlled by multiple factors due to the complex and diverse environments among grasslands on the large scale. Stepwise linear regression analysis also demonstrated that latitude, MAP and MAT had the comprehensive effects on the spatial variation of $Q_{10\text{-ST5}}$. Additionally, both univariate and multiple regression analyses demonstrated that generally there were no significant relationships between $Q_{10\text{-ST10}}$ and abiotic and biotic factors, indicating that the $Q_{10\text{-ST10}}$ did not have clear spatial pattern. Therefore, the variation of $Q_{10\text{-ST10}}$ might be controlled by other factors, and should be further studied.

4.3 Comparisons of Rs and Q_{10} between Chinese grasslands and the global ecosystems

4.3.1 Comparisons of annual Rs

The annual Rs varied largely within and among the grassland types across China (Table 1), with the mean value of 582.0 g C m^{-2} yr^{-1}, which was much lower than that in global terrestrial ecosystems (Table 2). Similarly, the mean annual Rs rate in Chinese grasslands was also much lower than that in Chinese forests. For these global results, the main biomes in their dataset were forests, which had relatively higher Rs than grasslands. Therefore, this would lead to the differences between Chinese grasslands, and Chinese forests and global terrestrial ecosystems (Table 2). Compared with global grasslands, our result was much lower or higher than the results obtained from Chen et al. (2010b, 2014) and Wang and Fang (2009), but approximately consistent with Hursh et al. (2017). In general, the mean annual Rs rate across Chinese grasslands was between the lowest and highest Rs across global grasslands.

Across Chinese grassland types, the proportions of Rs in growing season ranged from 76.2–86.8%, which were 2.2–5.6 times higher than those in non-growing season. As a whole, heterotrophic respiration contributed 72.8% of the annual Rs, 2.7 times of autotrophic respiration, which was close to that of global terrestrial ecosystems and grasslands (Wang and Fang, 2009; Chen et al., 2014) and Chinese forests (Song et al., 2014). Generally, our findings and previous studies suggested that Rs during growing season and heterotrophic respiration was an important part of the annual Rs, respectively, and should be given enough attention.

4.3.2 Comparisons of Q_{10}

The overall mean Q_{10} of 2.60 derived by soil temperature at all measurement depths was similar to global terrestrial ecosystems with 2.40 and 2.54 (Raich and Schlesinger, 1992; Lenton and Huntingford, 2003). The Q_{10} derived by ST5 varied from 1.39 to 8.13, with the mean of 2.80, which was higher than that of global and Chinese terrestrial ecosystems, Chinese forests, especially higher than that of global grasslands (Table 2). The difference may be partly due to the distribution of grasslands in China and the grassland types. Chinese grasslands are mainly distributed in the high latitude (temperate grassland) and high altitude (Qinghai-Tibet Plateau alpine grassland) regions, and Q_{10} takes relatively higher values in cold regions than in warm regions (Chen and Tian, 2005; Wang et al., 2010). In addition, in this study, averaged $Q_{10\text{-ST5}}$ was highest in alpine grassland with the mean of 3.30. However, there were no alpine grasslands in the global database. Collectively, this may lead to higher Q_{10} value in Chinese grasslands. In terms of Q_{10} derived by ST10, the mean value for Chinese grasslands was close to Chinese terrestrial ecosystems, but much lower than the global ecosystems (Table 2).

4.4 Uncertainties

In order to ensure data consistency and minimize the error, only field experiments in accordance with the six aforementioned criteria were selected. However, the inter-annual variation in Rs and Q_{10} might be very large for grassland at one site, which was associated with the variations in annual precipitation and mean temperature between two adjacent years (Peng et al., 2014; Wang et al., 2016). Therefore, the inter-annual variation of Rs would impact the accuracy of the results. Additionally, three methods including static closed chamber, dynamic closed chamber, and alkali absorption were widely applied to measure Rs in the selected experiments, and previous studies have suggested that measurement methods affected the results of Rs rate and Q_{10} value (Bekku et al., 1997; Yim et al., 2002; Peng et al., 2009). However, in this study, there were no significant differences for $Q_{10\text{-ST5}}$ and $Q_{10\text{-ST10}}$ among the three measurement methods (Fig. S7). Given that only one sample of annual Rs was measured by alkali absorption, therefore the effects of measurement methods on Rs could be neglected. Including the data measured by the AA method in our synthesis does not meaningfully change the results of Rs and Q_{10}.

In this study, the selected experiments were mainly conducted in temperate and alpine grasslands, so the limited data obtained from desert, tropical and subtropical grasslands might lead to some uncertainties in these ecosystems. Moreover, grassland management practices such as land use/cover change, intensity and pattern of livestock grazing, and fencing can have significant effect on soil carbon emission (Chen at al., 2013; Zhang et al., 2015b; Chen et al., 2015; Chen at al., 2016a). In the past three decades, several ecological projects relating to grassland have been implemented in China, and have observably increased the grassland area and altered the land cover (Zhang et al., 2015a). To some extent, these changes can also impact our findings.

5 Conclusion

Chinese grasslands cover vast area, have high spatial heterogeneity, and include various grassland types. By synthesizing all the available data relating to Rs and Q_{10}, we analyzed their spatial patterns and driving factors in grasslands across China. Our results showed that Rs and its temperature sensitivity varied largely within and among grassland types, with the mean annual Rs and Q_{10} of 582.0 g C m^{-2} yr^{-1} and 2.60, respectively. MAT, MAP, and SOC all significantly positively affected annual Rs, whereas both latitude and soil pH negatively affected annual Rs. The Rs during growing season and heterotrophic respiration were the major component of annual Rs, contributing 78.7% and 72.8% of the annual Rs, respectively. The altitude, MAP and MAT were the dominant factors and accounted for 26.0% of the variation of $Q_{10\text{-ST5}}$ across Chinese grasslands. These findings should advance our understanding of the spatial variation and environmental control of soil respiration and Q_{10} across Chinese grasslands, and also improve our ability to predict soil carbon efflux under climate change on the regional scale.

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Table 1 The annual soil respiration (Rs) and the proportions of growing season, non-growing season Rs to annual Rs in different grassland ecosystems across China.

Grassland types	*N*	Annual Rs (g C m^{-2} yr^{-1})			Rs proportion (%)	
		Mean ± SE	Min.	Max.	Growing season	Non-growing season
Temperate typical steppe	16	371.3 ±94.8 a	122.9	1670.0	79.6 ±2.9 a	20.4 ±2.9 a
Temperate meadow steppe	6	442.1 ±83.4 a	218.8	784.7	86.8 ±2.7 a	13.2 ±2.7 a
Alpine grassland	20	581.5 ±62.3 a	246.3	1161.1	77.3 ±2.5 a	22.7 ±2.5 a
Warm-tropical grassland	12	933.6 ±161.8 b	428.8	2407.1	76.2 ±2.5 a	23.8 ±2.5 a
Total	54	582.0 ±57.9	122.9	2407.1	78.7 ±1.5 A	21.3 ±1.5 B

There was no sample for temperate desert steppe, so the data was not presented in this table. The different lowercase letters in each column indicate the significant difference at $P = 0.05$, and different uppercase letters indicate the significant difference between growing and non-growing season at $P = 0.001$. *N*: number of samples.

Table 2 The comparisons of annual soil respiration and Q_{10} between Chinese grasslands and other syntheses.

Scope	Annual Rs (g C m^{-2} yr^{-1})	$Q_{10\text{-ST5}}$	$Q_{10\text{-ST10}}$	Reference source
Global terrestrial ecosystems	910.0 (657)			Chen at al., 2010
	870.0 (1195)			Chen at al., 2014
	791.2 (1741)			Hursh et al., 2017
		2.40 (77)	3.10 (46)	Wang et al., 2010
Global grasslands	448.9 (46)	2.13 (41)		Wang and Fang, 2009
	745.0 (179)			Chen at al., 2010
	840.0 (113)			Chen at al., 2014
	599.1 (163)			Hursh et al., 2017
Chinese terrestrial ecosystems		2.03 (64)	2.61 (33)	Peng et al., 2009
Chinese forests	919.7 (139)	2.46 (107)		Song et al., 2014
		2.51 (145)		Xu et al., 2015
Chinese grasslands	582.0 (54)	2.80 (73)	2.56 (59)	This study

The numbers in parentheses represent the number of samples.

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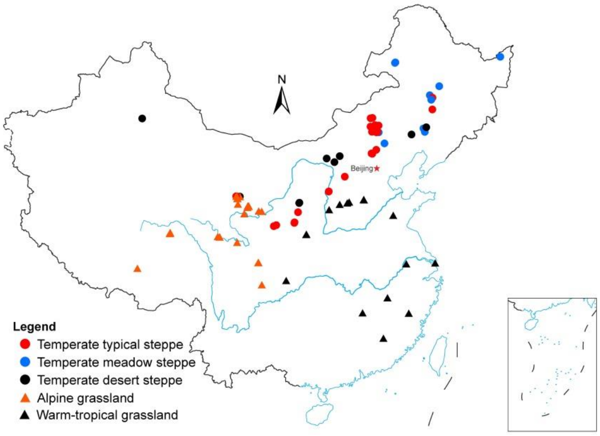

Figure 1. The site location of soil respiration studies selected in this study across Chinese grasslands.

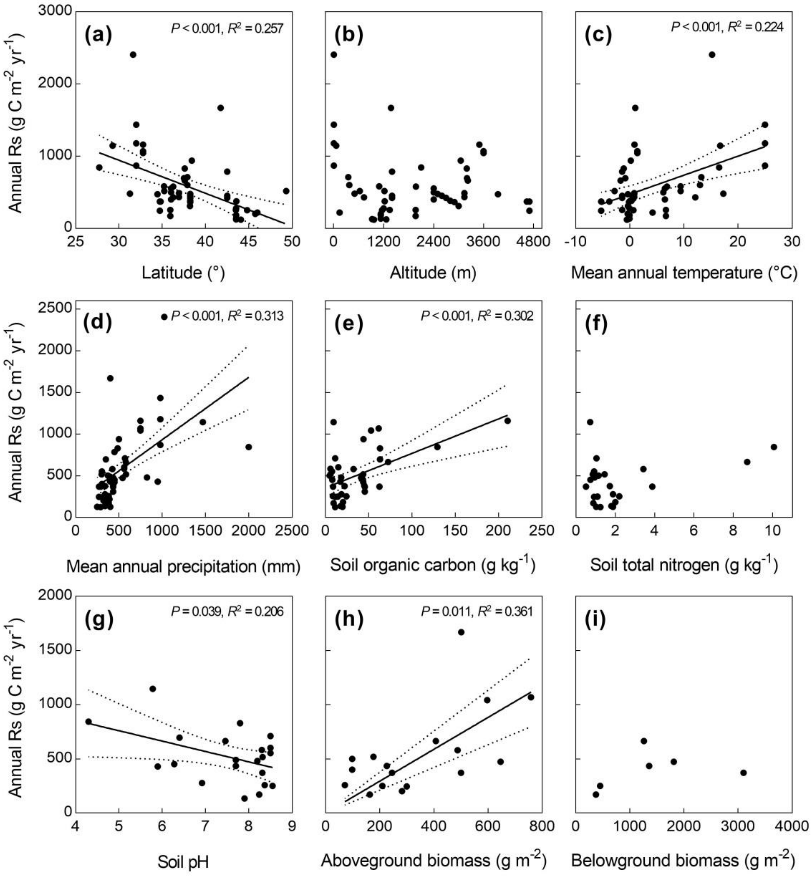

Figure 2. Relationships of annual soil respiration (Rs) with abiotic and biotic factors. The dash lines represent the 95% confidence interval.

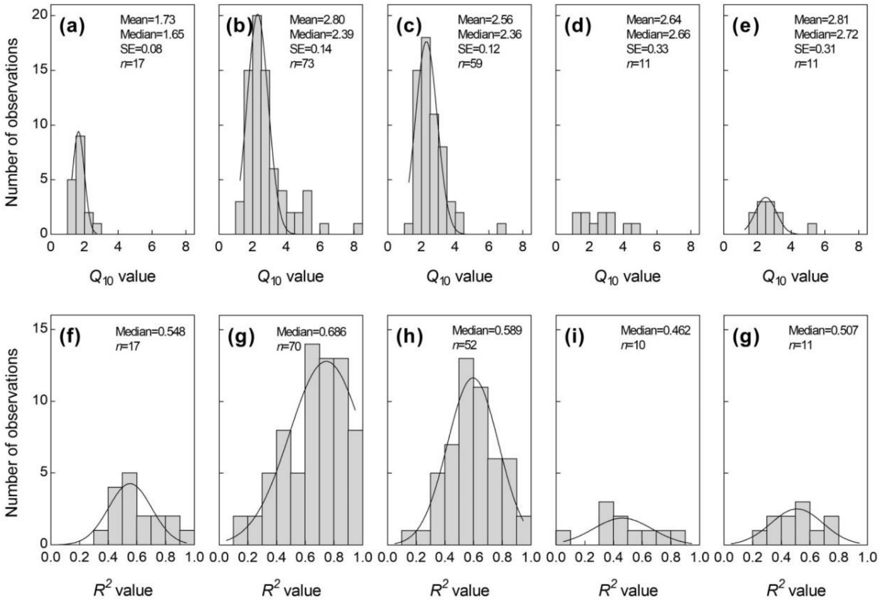

Figure 3. Histogram plots for Q_{10} values (a-e) and its coefficient of determination (R^2) for Q_{10} (f-j) across Chinese grasslands. (a) and (f): soil surface temperature; (b) and (g): soil temperature at the depth of 5 cm; (c) and (h): soil temperature at the depth of 10 cm; (d) and (i): soil temperature at the depth of 15 cm; (e) and (j): soil temperature at the depth of 20 cm. *n* represents the number of samples.

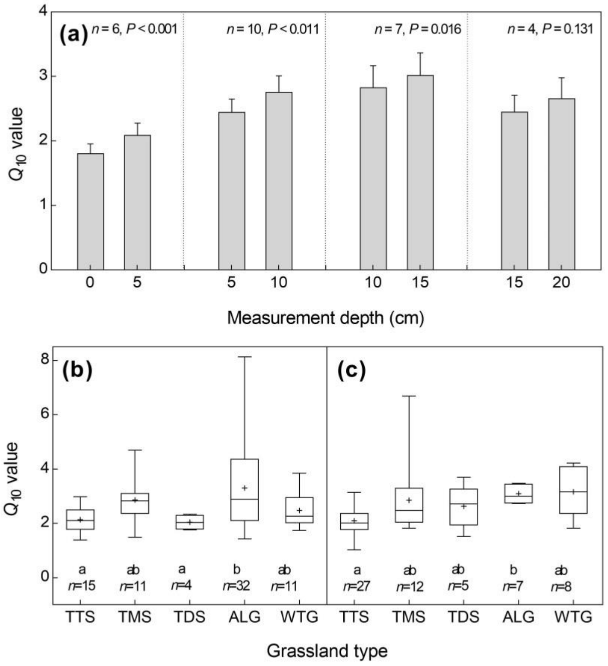

Figure 4. Comparisons Q_{10} values among soil temperature measurement depths (a) and among grassland types (b, c). (a) Q_{10} values derived by soil temperature at the depth of 0, 5, 10, 15, and 20 cm, respectively. (b) Q_{10} values derived by soil temperature at the depth of 5 cm. (c) Q_{10} values derived by soil temperature at the depth of 10 cm. TTS, TMS, TDS, ALG, and WTG represent temperate typical steppe, temperate meadow steppe, temperate desert steppe, alpine grassland, and warm-tropical grassland, respectively. In the box plot, the "+" represent mean values, horizontal lines inside box represent medians, box ends represent the 25th and the 75th quartiles, vertical lines represent 2.5th and 97.5th percentiles, hollow circles represent outliers, and *n* represents the number of samples. Error bars represent standard errors. Different lowercase letters indicate significant differences among soil depths or grassland types at $P = 0.05$.

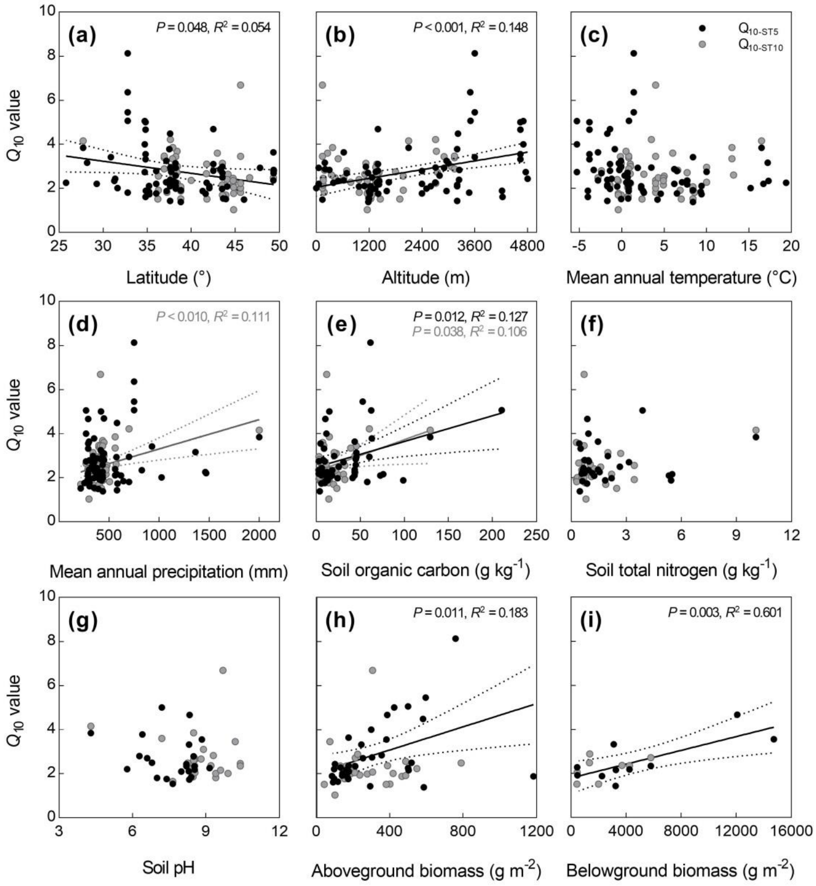

Figure 5. Relationships of the Q_{10} derived by soil temperature at the depth of 5 cm with abiotic and biotic factors.