Patterns 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 temperature, soil moisture, soil organic carbon content and aboveground biomass, but negatively correlated with soil pH ($p < 0.05$). Among these factors, mean annual precipitation was the primary factor controlling the variations of annual Rs among grassland types. Based on the overall data across Chinese grasslands, the Q_{10} values ranged from 1.03 to 8.13, with a mean (± SE) of 2.60 ± 0.08. Moreover, the Q_{10} values varied largely within and among grassland types and soil temperature measurement depths. Among grassland types, the highest Q_{10} derived by soil temperature at the depth of 5 cm occurred in alpine grasslands. In addition, the seasonal variation of soil respiration in Chinese grasslands generally cannot be well explained by soil temperature using the van't Hoff equation. Overall, our findings suggest that the combined factors of soil temperature and moisture would better predict soil respiration in arid and semi-arid regions, highlight the importance of precipitation in controlling soil respiration in grasslands, and imply that alpine grasslands in China might release more carbon dioxide to the atmosphere under climate warming.

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 at a 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 at 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). 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 roots (together with associated mycorrhizal fungi) 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), belowground biomass (BGB), and leaf area index (Raich and Schlesinger, 1992; Hibbard et al., 2005; Bahn et al., 2008; Chen at al., 2014; Zhao et al. 2017).

As the response of Rs to temperature is controlled by temperature effects on autotrophic respiration from roots and heterotrophic respiration from SOC decomposition, the temperature sensitivity of Rs should be regulated by plant-related biotic variables and soil-related environmental variables. Several studies have shown 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 addition to climatic variables, the spatial variation of Q_{10} could be affected by seasonality of plant activity. Previous studies suggested that plant growth plays an important role in the seasonal variation of Rs, and thereby the seasonal dynamic changes in plant activity affect seasonal Q_{10} (Yuste et al., 2004; Wang et al., 2010). Furthermore, Q_{10} is also affected by soil properties, such as soil temperature, soil moisture, soil pH, SOC and STN, which can directly influence root and microbial activities, 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). In China, grasslands are widely distributed throughout the country, 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 the 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 at 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 at 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, warming, 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:

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

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_Q^2 (coefficient of determination for calculating Q_{10} using Eq. (1)) was extracted if more than one R_Q^2 were available in the same study. In addition, the Q_{10} values were estimated by Rs measured at different plant growth stages, and they were further categorized into three types according to the Rs measurement period, including growing season Q_{10}, non-growing season Q_{10} and annual Q_{10}. If these three types of Q_{10} were all available, only the annual Q_{10} was selected in our database. 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, Q_{10} values of Rs and their corresponding R_Q^2. Here, the growing season was from May to October, and the non-growing season was from November to April in the next year. The Q_{10} values were divided into five soil depths with different soil temperature (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_Q^2 of the model were presented, and they were incorporated into our database directly. The Rs, Q_{10} and R_Q^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 and latitude), climatic factors (MAT and MAP), soil properties (soil temperature, soil moisture, soil pH, SOC and STN), and biotic factors (microbial biomass carbon (MBC), AGB and BGB). Missing climatic information was obtained using NASA Surface meteorology and Solar Energy-Location, and the other missing information was 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 conversion factor of 0.50 (Pribyl 2010). In case of gravimetrical soil moisture being provided, it was converted to volumetric soil moisture according to soil bulk density. 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 shown 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 grassland types 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, measuring periods or measuring methods. 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, and between autotrophic respiration and heterotrophic respiration. The reason for using paired-samples *t*-test was that these two corresponding variables were interconnected as they were from the same study sites. In addition, we used two statistical methods to explore the differences for Q_{10} among measurement depths. The paired-samples *t*-test was used to compare Q_{10} among different measurement depths from same sites, whereas the ANOVA was used to compare Q_{10} among different measurement depths from all sites. Compared with ANOVA, the advantages of paired-samples *t*-test was that it avoided the effects of unequal spatial distribution of samples from different depths on Q_{10} and only compared the effects of measurement depth. 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 multiple linear regression analyses were also performed to identify the comprehensive effects of environmental variables (including MAT, MAP, soil temperature and moisture as they had relatively enough sample sizes) 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, soil temperature, soil moisture, SOC, and AGB across all grasslands in China, but decreased with 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 MAT, MAP, soil temperature, soil moisture, SOC, soil pH, and AGB accounted for 22.4%, 31.3%, 20.9%, 32.0%, 29.6%, 20.6%, and 36.1% of the spatial variation of annual Rs, respectively (Fig. 2).

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 soil depths 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_Q^2 for Q_{10} derived by the five soil depths also differed from each other (Fig. 3f-g). The R_Q^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_Q^2 value for $Q_{10\text{-ST0}}$ was distributed uniformly (Fig. 3f). Overall, only 35.6% of R_Q^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 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 1.73 ± 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, $Q_{10\text{-ST5}}$ significantly positively correlated with SOC, AGB and BGB, whereas negatively correlated with soil temperature ($p < 0.05$, Fig. 5). In contrast, $Q_{10\text{-ST10}}$ significantly correlated with MAP, soil temperature and SOC ($p < 0.05$, Fig. 5). In addition, combined MAP and MAT, and combined soil temperature and soil moisture affected $Q_{10\text{-ST5}}$, and jointly accounted for 22.1% and 13.9% of the spatial variation of $Q_{10\text{-ST5}}$ across Chinese grasslands (Table S4).

4 Discussion

4.1 Spatial patterns and controlling factors of annual soil respiration

4.1.1 Annual soil respiration among grassland types

In arid and semi-arid ecosystems, such as grassland and desert, MAP might play a key role in controlling carbon cycling. Our results also suggested that MAP had significant controls on mean annual Rs among various grassland types in China ($p < 0.01$, Fig S4). The significant difference in mean annual Rs might be mainly attributed to the differences in AGB, BGB and microbial activity induced by precipitation across various grassland types. Previous studies suggested that grasslands with higher MBC had larger heterotrophic respiration (Colman and Schimel, 2013; Ding et al., 2016). Meanwhile, a regional study demonstrated that microbial biomass increased with MAP in grasslands (Chen et al., 2016b), which was also found in this study (Table S3). Altogether, these suggested that the regions with high MAP would have larger heterotrophic respiration. Additionally, a previous study demonstrated that both AGB and BGB increased with MAP across Chinese grasslands (not including warm-tropical grasslands) (Ma et al., 2014). In this case, autotrophic respiration would be higher in the grasslands with high plant biomass. Collectively, the grasslands with high MAP would have relatively higher Rs rate.

4.1.2 Controls of environmental factors on annual Rs

Across Chinese grasslands, annual Rs was strongly related to MAT, MAP, soil temperature and soil moisture, which was consistent with previous results obtained from global terrestrial ecosystems (Raich and Schlesinger, 1992; Raich and Potter 1995; Chen at al., 2014; Hursh et al. 2017), global grasslands (Wang and Fang, 2009), and Chinese forests (Song et al., 2014; Xu et al., 2015). Compared with MAT and soil temperature, MAP and soil moisture explained more spatial variations of annual Rs, suggesting that these two factors are more important in predicting Rs in arid and semi-arid ecosystems under climate change.

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 from microbial decomposition of soil organic carbon is ultimately 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 at 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) at local scales, while annual Rs did not correlate well with STN in this study. Given that SOC and STN are closely associated with one another (Table S3), the insignificant correlation of Rs with STN might be due to the fact that soil total nitrogen might not well represent nitrogen availability for plants and microbes. Therefore, how STN influence Rs across Chinese grasslands at regional scale should be further studied.

Furthermore, as the source of autotrophic respiration, BGB can directly influence Rs, which has been observed in ecosystems at 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 ($n = 6$) 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_Q^2 for Q_{10} in Chinese grasslands

In this study, only 37.3% of R_Q^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 the single variable of temperature. Our results also showed that, in general, R_Q^2 for Q_{10} closely increased with MAP and soil moisture ($p < 0.05$, Fig. S6), indicating that the R_Q^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_Q^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 than the other grassland types (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 at global and regional scales (Chen and Tian, 2005; Peng at al., 2009; Wang et al., 2010; Song et al., 2014; Xu et al., 2015). However, we found that Q_{10} derived by soil temperature at the depth of 5 and 10 cm decreased closely with increasing soil temperature, partly supporting the idea that Q_{10} tends to be higher in colder regions. 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 climatic variables suggested that the single factor of temperature, precipitation or soil moisture poorly control the spatial variations of Q_{10} in Chinese grasslands. Therefore, the variation of Q_{10} in Chinese grasslands should be controlled by multiple factors due to the complex and diverse environments among grasslands at large scale. Multiple linear regression analyses also showed that combined MAT and MAP, and combined soil temperature and moisture could better explain the variations of Q_{10} derived by ST5 (Table S4), indicating their integrative effects on the spatial variation of $Q_{10\text{-ST5}}$. Additionally, both univariate and multiple regression analyses demonstrated that there were no significant relationships between $Q_{10\text{-ST10}}$ and abiotic and biotic factors (not shown), indicating that the $Q_{10\text{-ST10}}$ might not have clear spatial pattern or its variation might be controlled by other factors.

In addition to the environment variables discussed above, seasonality of plant activity could also affect the spatial variation of Q_{10} at large scale. Plant activity can directly affect Rs via controlling root respiration, and can indirectly affect SOC decomposition by microbes via regulating rhizosphere priming effect (see Wang et al., 2010). In this study, the dataset covered various climatic regions, and accordingly seasonal amplitudes of plant activity among grassland types were also different. A previous global synthesis using NDVI (normalized difference vegetation index) as an indicator of plant activity demonstrated that seasonal amplitude of plant activity dominated the variation of seasonal Q_{10} among different sites (Wang et al., 2010). Therefore, the seasonal amplitude of plant activity might be an important factor explaining the spatial variation of Q_{10} across Chinese grasslands, 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 those in global terrestrial ecosystems and in Chinese forests (Table 2). For these results, the main biomes in their dataset were forests, which had relatively high precipitation and net primary productivity (Hursh et al., 2017), leading to relatively higher Rs than grasslands (Table S2). 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). These differences might be associated with data sources and distributions of case study sites. In general, the mean annual Rs rate across Chinese grasslands was within the lowest and highest Rs across global grasslands.

Across Chinese grasslands, the proportions of Rs during growing season ranged from 76.2–86.8%, which were 2.2–5.6 times higher than those during non-growing season. Microbial activity and plant growth is constrained by temperature and precipitation during non-growing season, leading to lower decomposition of soil organic carbon and root respiration. In addition, 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). Previous studies suggested that the proportions of heterotrophic respiration to total Rs varied with ecosystem types and depended on the magnitude of total Rs (Subke et al., 2006). However, the limited samples ($n = 7$) limited our comparisons among these grassland types. Generally, our findings and previous studies suggested that both Rs during growing season and heterotrophic respiration were an important part of the annual Rs in Chinese grasslands, 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 2.40 and 2.54 in global terrestrial ecosystems (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, and particularly 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, implying that grasslands in alpine regions may release more carbon dioxide under climate warming. 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 inter-annual variations in annual precipitation and mean temperature (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 generally no significant differences for Rs, $Q_{10\text{-ST5}}$ 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, the effects of measurement methods on Rs could be neglected. Therefore, including data measured by the alkali absorption method in our synthesis does not meaningfully change the results of Rs and Q_{10}.

Furthermore, Q_{10} values measured during three periods, including growing season, non-growing season and the whole year, were selected as long as the investigation time was longer than four months. The seasonal dynamics of plant growth and microbial activity may influence autotrophic and heterotrophic respiration, thus the Q_{10} of Rs. Our results showed that measurement period did not significantly affect $Q_{10\text{-ST10}}$, but significantly affected $Q_{10\text{-ST5}}$ (Fig. S7). In terms of $Q_{10\text{-ST5}}$, the significant differences between annual Q_{10} and non-growing season Q_{10} across all sites was mainly caused by alpine grasslands, in which annual Q_{10} was much higher than non-growing season Q_{10} (Fig. S7). Likely, the seasonal amplitude of plant activity at annual scale is much greater than that at non-growing season scale in alpine regions. Therefore, the different investigation time and measurement period for estimating Q_{10} would inevitably affect the accuracy of results.

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 annual Rs and Q_{10} varied greatly within and among grassland types. Across Chinese grasslands the mean annual Rs and Q_{10} were 582.0 g C m^{-2} yr^{-1} and 2.60, respectively. MAT, MAP, soil temperature, soil moisture, SOC and AGB all significantly positively affected annual Rs, whereas soil pH negatively affected annual Rs. Among these environmental factors, MAP played an important role in controlling Rs variations across Chinese grasslands. Moreover, the combined factors of MAP and MAT accounted for 22.1% of the variation of $Q_{10\text{-ST5}}$ across Chinese grasslands. The $Q_{10\text{-ST5}}$ in Chinese grasslands was much higher than that in global ecosystems, mainly attributed to the higher Q_{10} value in alpine grasslands. These findings together advance our understanding of the spatial variation and environmental control of Rs and Q_{10} across Chinese grasslands, and also improve our ability to predict soil carbon efflux under climate change at regional scale. However, the few experiments measuring soil and microbial variables, Rs and Q_{10} at annual scale, especially measuring autotrophic and heterotrophic respiration separately, limit our in-depth knowledge on the key drivers of Rs and Q_{10} in grasslands across China. Therefore, more field measurements are strongly needed to verify the relationships found here and reveal how environmental variables fundamentally control Rs and its temperature sensitivity in relatively arid grassland ecosystem.

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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. There was no sample for annual Rs in temperate desert steppe, so the data were 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* represents the number of samples.

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

Table 2 Comparisons of annual soil respiration and Q_{10} between Chinese grasslands and other syntheses. The numbers in parentheses represent the number of samples.

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

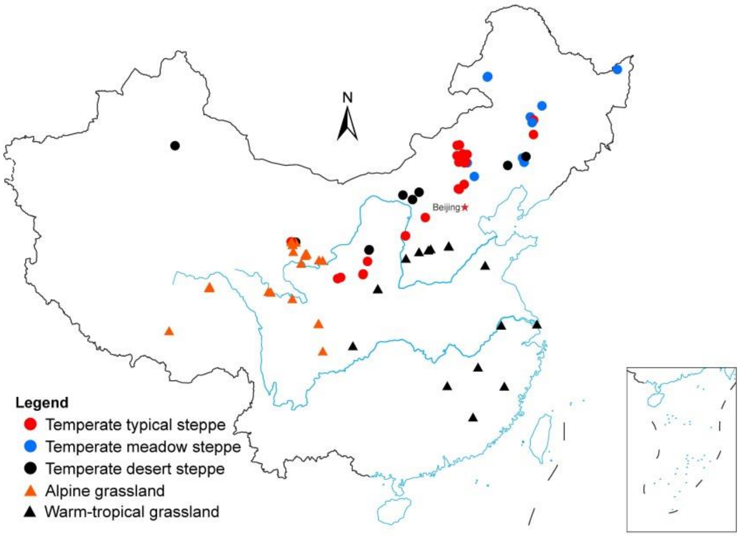

Figure 1. The site location of soil respiration studies selected in this study across Chinese grasslands.

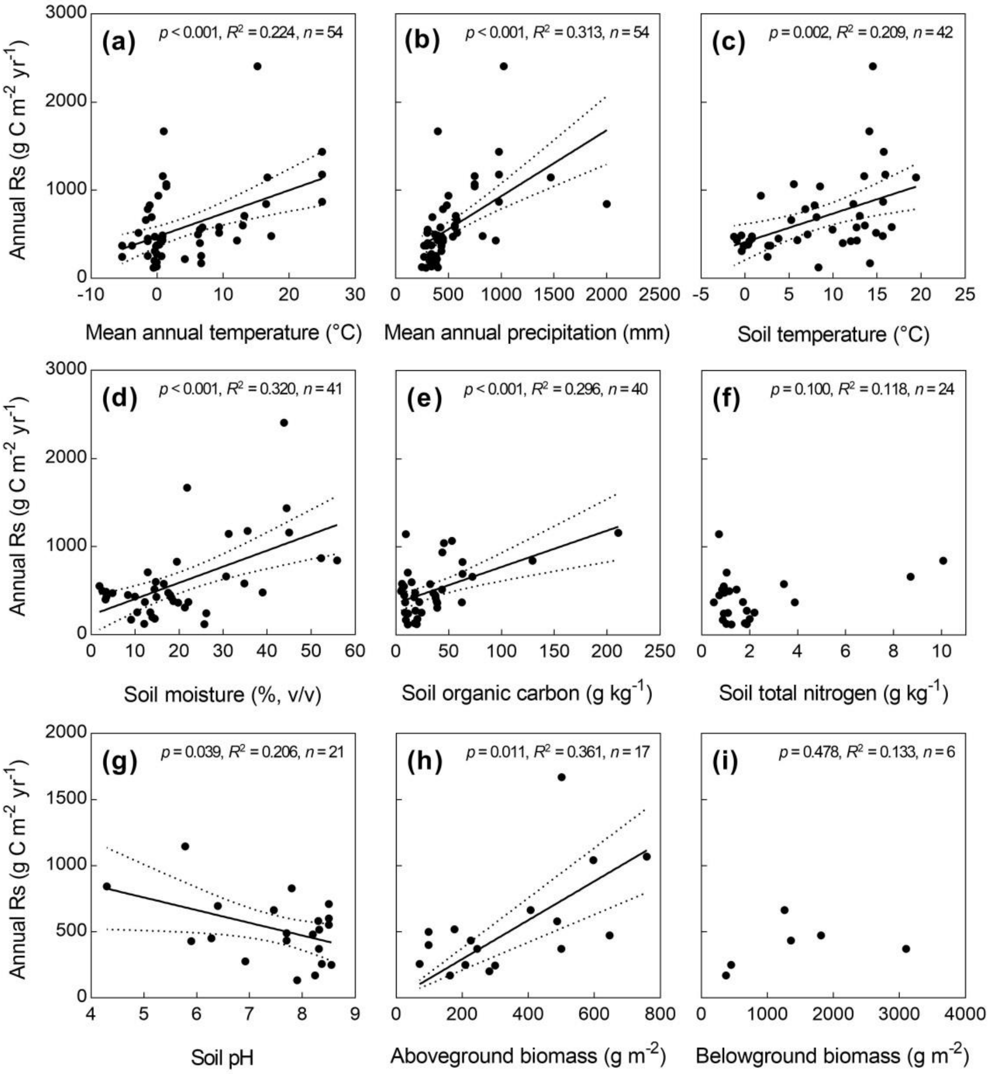

Figure 2. Relationships of annual soil respiration (Rs) with abiotic and biotic factors. The dash lines represent the 95% confidence interval. When *p* value was greater than 0.05, the regression lines were not drawn.

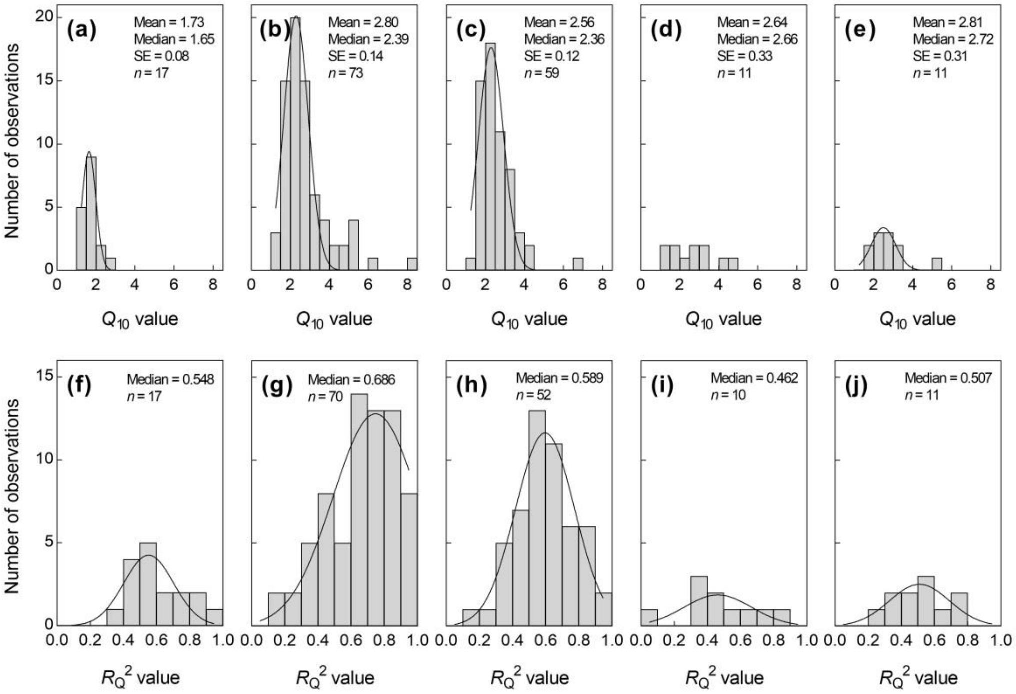

Figure 3. Histogram plots for Q_{10} values (a-e) and the coefficient of determination for Q_{10} (R_Q^2, f-j) across Chinese grasslands. (a) and (f): soil surface temperature; (b) and (g): soil temperature at the depth of 5 cm; (c) and (h): soil temperature at the depth of 10 cm; (d) and (i): soil temperature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

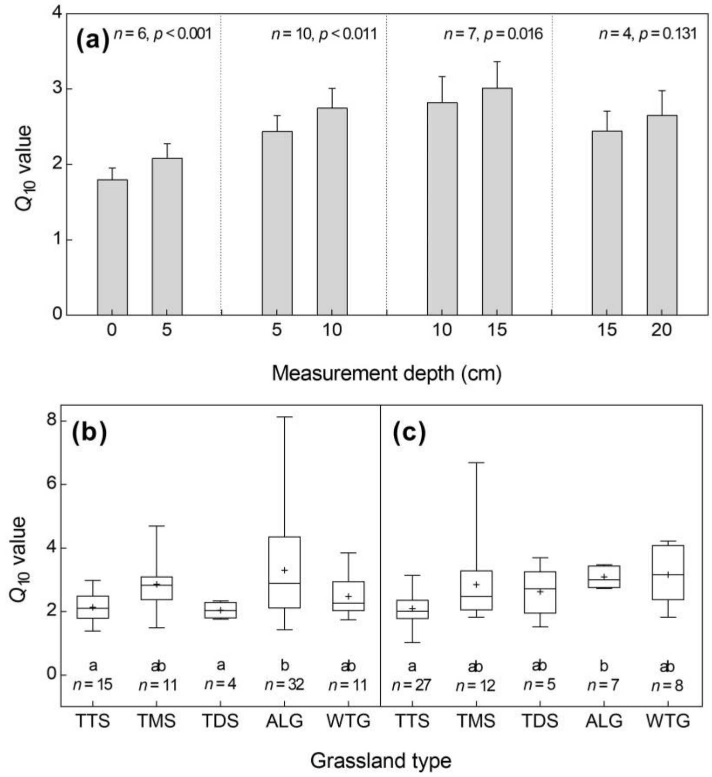

Figure 4. Comparisons of Q_{10} values among soil temperature measurement depths (a) and among grassland types (b, c). (a) Q_{10} values derived by soil temperature at the depth of 0, 5, 10, 15, and 20 cm, respectively. (b) Q_{10} values derived by soil temperature at the depth of 5 cm. (c) Q_{10} values 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. Error bars in (a) represent standard errors. In the box plot (b and c), 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. Different lowercase letters indicate significant differences among soil depths or grassland types at $p = 0.05$.

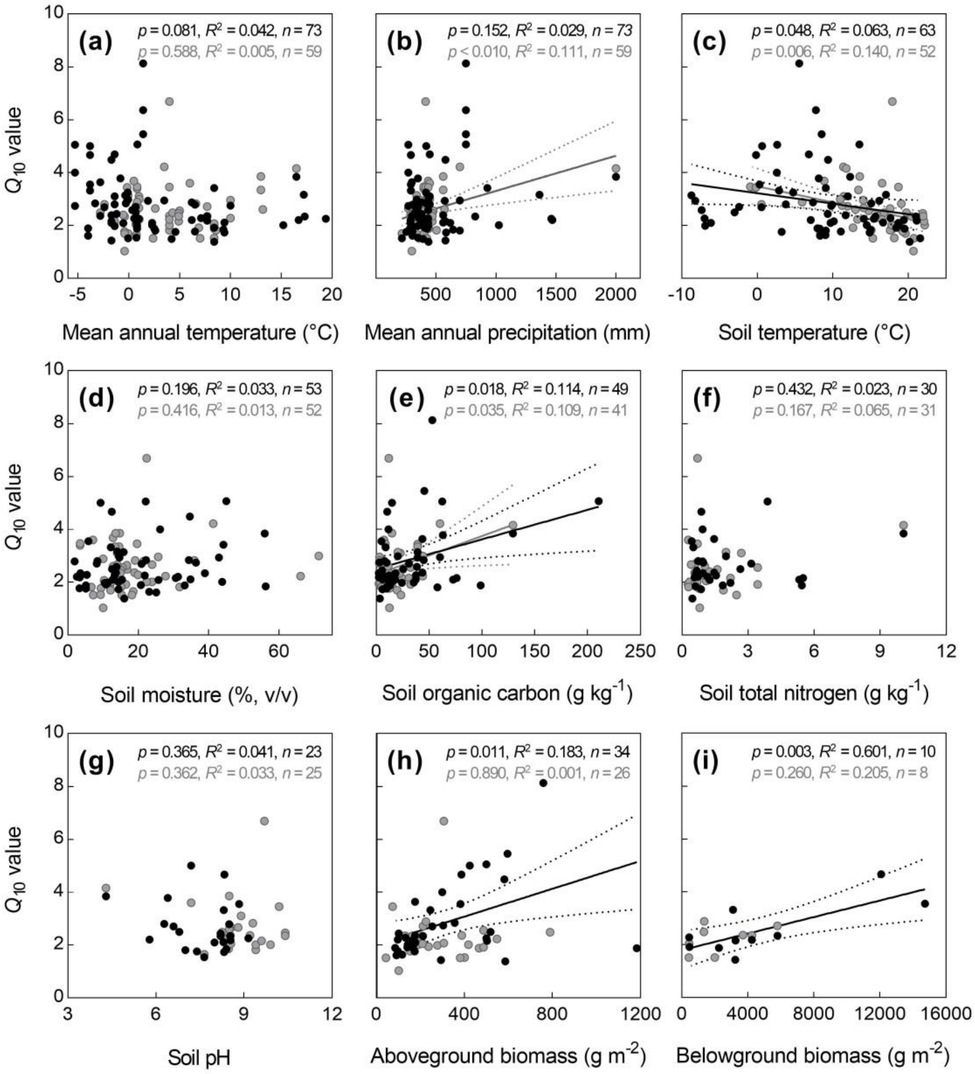

Figure 5. Relationships of temperature sensitivity of soil respiration (Q_{10}) with abiotic and biotic factors. The black and gray points represent Q_{10} derived by soil temperature at the depth of 5 and 10 cm, respectively, and the black and gray lines represent their corresponding relationships with environmental factors. When *p* value was greater than 0.05, the regression lines were not drawn.