Convergence in temperature sensitivity of soil respiration: Evidence from the Tibetan alpine grasslands

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ABSTRACT

Recent studies proposed a convergence in the temperature sensitivity (Q10) of soil respiration (Rs) after eliminating confounding effects using novel approaches such as Singular Spectrum Analysis (SSA) or the mixed-effects model (MEM) method. However, SSA has only been applied to eddy covariance data for estimating the Q10 with air temperature, which may result in underestimations in responses of below-ground carbon cycling processes to climate warming in coupled climate-carbon models; MEM remains untested for its suitability in single-site studies. To examine the unconfounded Q10 of Rs, these two novel methods were combined with directly measured Rs for 6 years in two Tibetan alpine ecosystems. The results showed that, 1) confounded Q10s of Rs estimated from seasonal Rs-temperature relationship positively correlated with the seasonality of Rs, and 2) estimates of unconfounded Q10s of Rs using SSA (mean = 2.4, 95% confidence interval [CI]: 2.1–2.7) and MEM (mean = 3.2, 95% CI: 2.3–4.2) were consistent with the theoretical subcellular-level Q10 (≈ 2.4). These results support the convergence in the Q10 of Rs and imply a conserved Rs-temperature relationship. These findings indicate that the seasonality of Rs has to be eliminated from estimating the Q10 of Rs, otherwise the estimates should be questionable. They also indicate that seasonal Q10s and its responses to warming should not be directly used in carbon-climate models as they contain confounding effects.

1. Introduction

Soil respiration (Rs) is a critical component of terrestrial ecosystems carbon cycle (Davidson and Janssens, 2006; Giardina et al., 2014; Luo, 2007). It is predicted to be stimulated by the pronounced global warming based on the universally observed positive Rs-temperature relationship, creating a positive feedback between climatic warming and soil respiration (Bond-Lamberty and Thomson, 2010a; Lloyd and Taylor, 1994; Yvon-Durocher et al., 2012). However, large uncertainty remains in the predicted strength of such positive feedback. The Q10 of Rs, a factor by which the rate of Rs is multiplied when temperature rises by 10 °C (Davidson and Janssens, 2006; Lloyd and Taylor, 1994), is one of the crucial parameters to reduce such uncertainty (Exbrayat et al., 2014; Jones et al., 2003; Knorr et al., 2005; Tan et al., 2016; Todd-Brown et al., 2014). While some studies have shown a consistent Q10 of Rs in various types of ecosystems (Mahecha et al., 2010; Yvon-Durocher et al., 2012), large uncertainty remains. 1 These authors contributed equally to this work.

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et al., 2012), other investigations have demonstrated a considerable variability of estimated Q10 of Rs (Peng et al., 2009; Wang et al., 2014a). Reconciling such a discrepancy becomes a critical task for a reliable prediction of climate-carbon feedback in the future.

The variability in observed Q10 of Rs can be partly attributed to the methods used to estimate Q10. Estimating Q10 from natural temperature gradients may contain the influences of non-temperature driven confounding factors that covary with temperature. For example, comparing Rs across seasons is commonly used for estimating Q10 of Rs (Davidson et al., 2006; Lloyd and Taylor, 1994; Suseela et al., 2012; Suseela and Duikes, 2013). However, seasonal changes in Rs are driven by both temperature and non-temperature driven processes, such as vegetation activity (Curiel Yuste et al., 2004; Wang et al., 2010), litter inputs (Gu et al., 2008), and soil water content (Reichstein et al., 2005; Xu and Baldocchi, 2004). For example, high Rs rates in summer are attributable to both high temperature and high overall vegetation activities that provide substrates for Rs (Curiel Yuste et al., 2004; Högberg et al., 2001; Wang et al., 2010), evidenced by a positive correlation between Q10 of Rs and the amplitudes of seasonal variations in vegetation activities (Curiel Yuste et al., 2004; Wang et al., 2010). Soil water content could also influence both Rs and the estimated Q10 of Rs (Geng et al., 2012; Liu et al., 2016, 2009); summer drought can reduce Rs (Selsted et al., 2012) and counteract the influence of high temperature on Rs, masking the response of Rs to temperature. In summary, Q10 estimated from seasonal temperature gradients includes a suite of non-temperature driven confounding effects and thus does not truly reflect the responses of Rs to changing temperature. Given the high sensitivity of projected future climate to the Q10 of Rs (Randerson et al., 2009; Tan et al., 2010; Todd-Brown et al., 2013), it is imperative to eliminate the non-temperature driven confounding effects when estimating the Q10 of Rs for an accurate prediction of how soil carbon flux will respond to climatic warming (Curiel Yuste et al., 2004; Mahecha et al., 2016; Wang et al., 2010).

Several recent studies attempted to estimate the unconfounded Q10 of Rs (or ecosystem respiration, ER) using novel approaches. For example, Mahecha et al. (2010) applied Singular Spectrum Analysis (SSA) with eddy covariance data to estimate the Q10 of ER, assuming that non-temperature driven confounding effects remain constant in short term. They reported a convergent Q10 of ~1.4 across various types of ecosystems. Yvon-Durocher et al. (2012) employed a mixed-effects modeling approach to estimate unconfounded Q10 of Rs and found a consistent Q10 of about 2.4 for Rs and ER. Although these novel approaches eliminated the non-temperature driven confounding effects to a large extent, several limitations remain in these approaches. For instance, the mixed-model approach assumes that the non-temperature driven confounding effects are random across sites and are zero on average. Such an assumption may be suitable for a meta-analysis but may not apply to single-site studies, which remains to be tested. Estimating Q10 of Rs using eddy covariance data as in Mahecha et al. (2010) includes both the aboveground and belowground respirations. Also, Q10 estimated using air temperature instead of soil temperature may underestimate the true Q10 of Rs because soils typically experience less temperature fluctuation compared to the corresponding air temperature (Graf et al., 2011; Xu and Qi, 2001). Using direct measurements of Rs, soil temperature and the SSA has the potential to alleviate these shortcomings in Mahecha et al. (2010). Together, combining high-resolution measurements of soil Rs and temperature with multiple novel statistical approaches is a proper way to examine the robustness of the estimated Q10 of Rs and improve the current understanding of the temperature sensitivity of soil respiration.

In this study, multiple approaches were applied to estimate the Q10 of Rs based on continuous measurements of Rs and temperature in alpine grasslands in Tibetan Plateau. The alpine grassland ecosystem in this region provides an ideal model system to investigate this problem. On the one hand, the large soil carbon storage in this region (Shi et al., 2012; Yang et al., 2008) could exhibit strong feedback to the warming climate (Zhuang et al., 2010). On the other hand, the pronounced seasonality of vegetation could confound the estimated Q10 of Rs (Wang et al., 2014b), making it an ideal place to compare various methods of estimating the temperature dependence of Rs.

In this study, hourly Rs was automatically measured in a mesic grassland ecosystem (6-years) and a meadow ecosystem (3-years) in the Tibetan Plateau. Three methods were employed to estimate the Q10 of Rs. Specifically, the conventional regression method was used for estimating the Q10 of Rs from seasonal temperature changes; two novel methods, the SSA (Golyandin and Korobeynikov, 2014; Mahecha et al., 2010) and the mixed-effects model (MEM) method (Yvon-Durocher et al., 2012), were employed to eliminate temperature independent confounding factors and estimate the intrinsic Q10 of Rs. The non-temperature driven processes, such as the vegetation activity, contribute to the pronounced seasonality of Rs in the Tibetan alpine grasslands (Wang et al., 2014b), which can positively affect on the estimated Q10 of Rs (Curiel Yuste et al., 2004; Mahecha et al., 2010; Wang et al., 2010). Thus, the regression method that does not account for these confounding effects was hypothesized to give rise to a higher Q10 of Rs in the Tibetan alpine ecosystems. Furthermore, two novel methods that could eliminate the confounding effects were hypothesized to result in the Q10 of Rs consistent with the intrinsic Q10 of aerobic metabolic reactions at the subcellular level (Q10 = 2.4) (Gillooly et al., 2001; Raven and Geider, 1988; Vetter, 1995; Yvon-Durocher et al., 2012).

2. Materials and methods

2.1. Site description

This study was performed at the Haibei Alpine Grassland Ecosystem Research Station (Haibei Station, 101°12’E, 37°30’N, 3200 m a.s.l.), located in the northeastern part of the Tibetan Plateau, China. This area has a continental monsoon climate, with a short growing season (Wang et al., 2014b). From 2008 to 2013, the mean annual air temperature was ~1.08°C (ranging from ~1.82 to ~0.81°C). The mean annual precipitation was 416.8 mm (ranging from 350.6 to 501.3 mm) (Table 1), and ~90% of the precipitation was concentrated in the growing season from May to September (Wang et al., 2014b).

This study was conducted in two sites, a mesic grassland site and a meadow site. The soils at the mesic grassland site and the meadow site are Mat-Cryic Cambisols and Fib-Orthic Histosols, respectively (Chinese Table 1 Average values of climate, soil, vegetation and soil respiration (Rs) characteristics of the two study sites. Values in brackets are the range of mean annual precipitation and the range of the daily mean temperature. Values following ± are the standard error of the means (n = 3–4 for Rs of the mesic grassland and n = 3–5 for Rs in the meadow).

<table>
<thead>
<tr>
<th></th>
<th>Mesic grassland</th>
<th>Meadow</th>
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<tbody>
<tr>
<td>Mean annual precipitation (mm)</td>
<td>416.8 (350.6–501.3)</td>
<td>416.8 (350.6–501.3)</td>
</tr>
<tr>
<td>Mean air temperature (°C)</td>
<td>1.08 (~22.70–14.99)</td>
<td>1.08 (~22.70–14.99)</td>
</tr>
<tr>
<td>Mean soil temperature (°C)</td>
<td>2.45 (~10.68–15.41)</td>
<td>2.77 (~9.23–14.97)</td>
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<tr>
<td>Mean soil moisture (%)</td>
<td>29.4 ± 1.07</td>
<td>32.4 ± 1.78</td>
</tr>
<tr>
<td>Soil pH</td>
<td>7.85 ± 0.07</td>
<td>7.57 ± 0.18</td>
</tr>
<tr>
<td>Soil organic carbon (%)</td>
<td>7.82 ± 0.09</td>
<td>22.8 ± 0.56</td>
</tr>
<tr>
<td>Soil total nitrogen (%)</td>
<td>0.58 ± 0.03</td>
<td>1.72 ± 0.08</td>
</tr>
<tr>
<td>Above ground biomass (g m⁻²)</td>
<td>372.2 ± 22.5</td>
<td>310.8 ± 15.2</td>
</tr>
<tr>
<td>Annual cumulative Rs (g C m⁻²)</td>
<td>681.5 ± 24.7</td>
<td>574.5 ± 44.9</td>
</tr>
<tr>
<td>Growing-season cumulative Rs (g C m⁻²)</td>
<td>597.7 ± 24.0</td>
<td>487.5 ± 42.4</td>
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* Denotes two sites shared the data of a same weather station as the distance between sites is small (~1.5 km).
Soil Taxonomy Research Group, (C. A. M. ex Tust.) Ser, Festuca ovina L., Elymus nutans Griseb., Poa pratensis L., Carex scabrirostris Kük., Scirpus distichus Kük. T. Tang et F. T. Wang, Gentiana straminea Maxim., Gentiana farreri Balf. f. and Potentilla nivea L. (Wang et al., 2012, 2014b), and the mean aboveground net primary productivity is 372.2 g m\(^{-2}\) year\(^{-1}\) (Table 1). The meadow study site is at the margin area of the Luanhaizai wetland, located about 1.5 km from the mesic grassland study site. The plant community of this site is dominated by Kobresia tibetica Maxim., Blysmus sinocompressus T. Tang et F. T. Wang and Carex atrofusca Schkuhr subsp. minor (Boott) T. Koyama, and the mean aboveground net primary productivity is 310.8 g m\(^{-2}\) year\(^{-1}\) (Table 1).

2.2. Measurements of soil respiration and soil temperature

Hourly \(R_s\) was automatically measured with 3–4 replicates at the mesic grassland site from June of 2008 to October of 2012 and 3 replicates at the meadow site from January 2010 to June 2011 using two sets of LI-8150 Multiplexer Automated Soil CO2 Flux System (Li-Cor Inc., Lincoln, NE, USA). In each site, 3–4 sampling plots were randomly selected with a polyvinyl chloride collar (20 cm diameter and 10 cm height) installed to a soil depth of 3 cm in each plot. The above-ground plants inside the collar were clipped to exclude aboveground respiration inside the chamber, but the respiration of roots of the neighboring plants can still contribute to the \(R_s\) by growing into soils beneath the collar. From August, 2011 to the end of 2012, the hourly \(R_s\) in the meadow was measured with a new custom designed multichannel automated chamber system (Liang et al., 2003), consisting of a datalogger (CR1000, Campbell Scientific, Utah, USA) and an Infrared Gas Analyzer (Li-Cor 840, Li-Cor, Lincoln, NE, USA). After switching to the new measurement system, 2 additional sampling plots were established, resulting in a total of 5 plots for hourly \(R_s\) measurements in the meadow site. To ensure consistency between equipment, the \(R_s\) measured with multichannel automated chamber system was calibrated to \(R_s\) measured with LI-8150 based on the linear relationship between them (Fig. S1).

Soil temperature at 5 cm depth (ST5) was simultaneously measured with the \(R_s\) using either LI-8150-203 soil temperature probes attached to automated chambers (from June of 2008 to October of 2012 in the mesic grassland and from January 2010 to June 2011 in the meadow) or type T thermocouple connected to the datalogger (CR1000, Campbell Scientific, Utah, USA) (from early August 2011 to the end of 2012 in the meadow). The ST5 was chosen to estimate the \(Q_{10}\) of \(R_s\) based on the following two considerations. Firstly, ST5 has been found to have the highest explanatory power on the \(R_s\) (Phillips et al., 2011; Reichstein and Beer, 2008), making it suitable to estimate the temperature response of \(R_s\). Secondly, 40–50% of the belowground biomass is distributed in the top 10 cm of soil in this region, indicating a higher biological activity in the top 10 cm soil layer than that in the deep soil layers. Detailed information on the \(R_s\) measurement protocol of the mesic grassland site can be found in Wang et al. (2014b); details about the custom designed multichannel automated chamber system can be found in Liang et al. (2003) and Yu et al. (2013).

2.3. Statistical analysis

The daily mean \(R_s\) and ST5 was used to estimate the \(Q_{10}\) of \(R_s\) with three approaches: the conventional regression method (\(Q_{10,\text{REG}}\)), the Singular Spectrum Analysis method (\(Q_{10,\text{SSA}}\)) (Golyandina and Korobeynikov, 2014; Mahecha et al., 2010), and the mixed-effects model (MEM) method (\(Q_{10,\text{MEM}}\)) (Yvon-Durocher et al., 2012). These analyses were based on three considerations. First, the daily mean \(R_s\) calculated from the hourly measurements of \(R_s\) was used for analyses because the diel variation in below-ground transmission of photosynthetic products is known to significantly drive the diel variation of \(R_s\) (Savage et al., 2013; Tang et al., 2005) and soil surface flux often lags from temperature changes by several hours as a result of vertical heat and CO2 transport (Phillips et al., 2011). Second, only growing season \(R_s\) was used to estimate the \(Q_{10}\) of \(R_s\) because \(R_s\) in the growing season contributes 90% of the total annual \(R_s\) flux, and the flux measurements during the non-growing season are regulated primarily by the physical thawing-freezing of the soil (Wang et al., 2014b). Third, the daily \(R_s\) data were averaged across all plots within a site, allowing for a comparison of \(Q_{10}\) of \(R_s\) in the current study with previous studies (Curie Yuste et al., 2004; Luo et al., 2001; Suseela et al., 2012; Suseela and Dukes, 2013) and the global dataset of \(R_s\), which only reported cross-plot averaged \(R_s\) data (Bond-Lamberty and Thomson, 2010b).

The temperature dependence of soil respiration can be described with a \(Q_{10}\) formulation:

\[
R_s = a \times (Q_{10})^{\frac{T}{10}},
\]

where \(a\) is a normalization constant representing respiration rate at 0 °C and \(T\) is soil temperature. This equation (eqn. (1)) can be linearized by taking the logarithm of both sides as:

\[
\ln(R_s) = a + \ln(Q_{10}) \times \frac{T}{10}.
\]
Fig. 1. Comparison of estimation protocols between conventional regression method (a–c) and Singular Spectrum Analysis (SSA) (d–h). In the conventional regression method, $Q_{10}$ was estimated without excluding the seasonal variation in the soil respiration ($R_s$). In the SSA method, the seasonal variation in $R_s$ was excluded and the $Q_{10}$ was estimated using high-frequency bins of $R_s$ and soil temperature at 5 cm depth (ST5).
Lamberty and Thomson, 2010b), the study site was set as a random factor in the mixed-effects model, assuming that site-specific seasonal co-variation in Rs and non-temperature driven factors of Rs contribute to the site-specific deviation in the estimated temperature sensitivity of Rs (Yvon-Durocher et al., 2012). For the Rs measured in the Tibetan alpine ecosystems, year of Rs measurements for each study site was treated as a random factor to account for the effects of interannual fluctuations in non-temperature confounding factors, such as precipitation, soil moisture and vegetation activity on the Q_{10} estimates. For example, fluctuation in precipitation can result in the variation in the seasonality of Rs (Suseela et al., 2012; Suseela and Dukes, 2013) or indirectly affect it via influencing vegetation activity (Ciais et al., 2005), and thus contribute to the year-specific deviation in estimated Q_{10}.

The Q_{10} estimated with the three methods outlined above were compared using analysis of variance (ANOVA). The first ANOVA model included the main effects of grasslands and estimation methods and their interaction, and showed that the main effect of the type of grassland (i.e. mesic grassland and meadow) (F_{1, 21} = 9.09, P = 0.35) and its interaction with estimation methods (F_{3, 21} = 0.08, P = 0.92) on estimated Q_{10} were non-significant. Then, the type of grassland was treated as a blocking factor in the model, and the post hoc t-test was used to compare the pairwise differences in estimated Q_{10} among the three methods. The Q_{10} of Rs was log-transformed to conform to the assumption of normality and homogeneity of error variance.

The Q_{10} estimated from the current datasets was compared to the estimates based on global scale datasets. For comparison of Q_{10, REG}, Q_{10, REG} estimates in this study were compared to a published global dataset of Q_{10, REG} (only the Q_{10, REG} estimated with ST5 was included) (Wang et al., 2010). For comparison of Q_{10, MEM}, the mixed-effects model based on Q_{10} formulation (eqn. (3)) was applied to the current datasets and a global compilation of soil respiration (Bond-Lamberty and Thomson, 2010b). For comparison of Q_{10, SSA} previous published Q_{10, SSA} from Mahecha et al. (2010) was extracted using “Data Thief” software (http://datatheif.org). The one-way ANOVA was used to compare estimated Q_{10} between the current datasets and the global datasets, and pairwise differences were tested with post hoc t-test.

All statistical analyses were performed, and graphs were prepared using R 3.0.1 (R Core Team, 2013). Differences were considered significant when the P value was ≤0.05.

3. Results

3.1. Seasonal patterns of soil respiration

In the mesic grassland, the Rs showed a pronounced seasonal pattern, with the lowest rate around January (~0.5 μmol CO_2 m^{-2} s^{-1}), and the highest rate (~3.3 μmol CO_2 m^{-2} s^{-1}) in late July or early August (Fig. 2). The annual cumulative Rs and the growing season cumulative Rs during the study period were estimated to be 681.5 g C m^{-2} and 597.7 g C m^{-2}, respectively (Table 1). Similarly, Rs in the meadow also exhibited pronounced seasonal pattern, within minimum of ~0.5 μmol CO_2 m^{-2} s^{-1} in January and maximum of ~3.3 μmol CO_2 m^{-2} s^{-1} in mid-summer (Fig. 2). The annual cumulative Rs and the growing season cumulative Rs during the study period were 574.5 g C m^{-2} and 487.5 g C m^{-2}, respectively (Table 1).

3.2. Estimated seasonal Q_{10}

Mean Q_{10, REG} of Rs in the Tibetan alpine grasslands was 3.8 (95% confidence interval (CI): 2.8–4.5) for the mesic grassland and 3.3 (95% CI: 2.2–4.5) for the meadow. The overall mean Q_{10, REG} over the two sites was 3.6 (95% CI: 3.0–4.4) (Figs. S3–S4, Fig. 3b). Compared to a previously published Q_{10, REG} dataset (Wang et al., 2010), the Q_{10, REG} of Rs of the mesic grassland in the Tibetan Plateau found in this study was significantly higher than the mean Q_{10, REG} worldwide (mean = 2.4, 95% CI: 2.3–2.6) (t-test, t-value = 3.64, degree of freedom (DF) = 5.97, P = 0.01), but was not significantly different from the Q_{10, REG} in temperate grasslands (mean = 2.3, 95% CI: 1.5–3.6) (t-test, t-value = 1.83, DF = 5.72, P = 0.12) (Fig. 4). Additionally, the estimated Q_{10, REG} of Rs of the meadow in the Tibetan Plateau was not significantly different from either the global average Q_{10, REG} (t-test, t-value = 1.59, DF = 2.15, P = 0.24) or the temperate grassland (t-test, t-value = 1.15, DF = 5.99, P = 0.29) (Fig. 4). Pearson correlation analysis showed that the estimated Q_{10, REG} of Rs was positively correlated with the amplitude of seasonal variation in Rs in the Tibetan alpine grasslands (r = 0.84, P = 0.001) (Fig. 3a).

3.3. Estimated unconfounded Q_{10}

Mean estimated Q_{10, SSA} of Rs was 2.4 in both the mesic grassland (95% CI: 2.1–2.7) and the meadow (95% CI: 1.7–3.2) and there was no significant difference between these two ecosystems (t-test, t-value = 0.02, DF = 2.45, P = 0.99) (Figs. 5b and 5a, Figs. S5–S6). The estimated Q_{10, SSA} was mostly lower than the Q_{10, REG}, as evidenced by most points below the 1:1 line in the Q_{10, SSA}-Q_{10, REG} plot (Fig. 3b). The estimated Q_{10, SSA} of the Tibetan alpine ecosystems was significantly higher than that reported by Mahecha et al. (2010) (ANOVA, F_{3, 74} = 17.38, P < 0.001) (Fig. 5a). Specifically, the Q_{10, SSA} of the mesic grassland in the Tibetan plateau was significantly higher than that of both the global average (mean = 1.4, 95% CI: 1.3–1.5) (t-test, t-value = 8.80, DF = 7.79, P < 0.001) and the temperate grassland (mean = 1.5, 95% CI: 1.3–1.6) (t-test, t-value = 6.04, DF = 11.44, P < 0.001) (Fig. 5a). The meadow in the Tibetan Plateau had a significantly higher Q_{10, SSA} of Rs than that of the worldwide (t-test, t-value = 4.18, DF = 2.21, P = 0.04), but no difference with the temperate grassland (t-test, t-value = 3.23, DF = 2.66, P = 0.06) (Fig. 5a).

The estimated Q_{10, MEM} of Rs was 3.3 (95% CI: 2.2–5.2) and 3.0 (95% CI: 1.8–5.2) for the mesic grassland and the meadow, respectively (Figs. 5b and 6). The Q_{10, MEM} found in the Tibetan alpine ecosystems was consistent with the Q_{10, MEM} of both temperate grassland (mean = 2.6, 95% CI: 2.3–3.0) and worldwide (mean = 2.7, 95% CI: 2.4–3.1) of a previously published global Rs dataset (Bond-Lamberty and Thomson, 2010b) (one-way ANOVA, F_{3, 65} = 0.94, P = 0.43) (Figs. Sb and 6).

Methods of estimating Q_{10} significantly influenced the estimated Q_{10} of Rs (ANOVA, F_{3, 32} = 6.97, P = 0.004, Fig. 5c). Specifically, Q_{10, SSA} was significantly lower than Q_{10, REG} (t-test, t-value = 3.53, DF = 15.07, P = 0.003), and the Q_{10, MEM} was not significantly different from either Q_{10, REG} (t-test, t-value = 0.49, DF = 12.08, P = 0.63) or Q_{10, SSA} (t-test, t-value = 1.62, DF = 10.62, P = 0.13).

4. Discussion

To our best knowledge, the current study is the first field test of the convergence hypothesis of Q_{10} (Mahecha et al., 2010; Yvon-Durocher et al., 2012) using long-term direct measurements of Rs and combining two different estimating methods (SSA and MEM). The main conclusions are: 1) seasonal Q_{10} of Rs was positively correlated with the seasonality of Rs indicating it can be confounded by seasonal variations in the non-temperature driven factors of Rs and directly including it in carbon-climate models should be questionable, and 2) the two methods produce similar estimates of the unconfounded Q_{10} of Rs (Q_{10} is 2.4 with a 95% CI: 2.1–2.7 and Q_{10} is 3.2 with a 95% CI: 2.3–4.2 for SSA and MEM, respectively) in the Tibetan alpine ecosystems, and the estimated values corresponded with the intrinsic Q_{10} of subcellular-level aerobic metabolic reactions (Q_{10} = 2.4) (Gillooly et al., 2001; Raven and Geider, 1988; Vetter, 1995; Yvon-Durocher et al., 2012), the global average and the temperate grasslands. This study provided additional evidence supporting the hypothesis of convergence in the Q_{10} of Rs.
4.1. Convergence in the unconfounded Q\textsubscript{10} of respirations

The estimated Q\textsubscript{10} of Rs in mesic grassland and meadow using methods that eliminate non-temperature driven confounding effects was similar, and were consistent with several previously reported unconfounded Q\textsubscript{10} of Rs or ER. For example, Yvon-Durocher et al. (2012) estimated the unconfounded Q\textsubscript{10} of Rs and ER for diverse ecosystems and found that the unconfounded Q\textsubscript{10} of Rs was 2.4 (95% CI: 2.0–2.5) for the global average, and the unconfounded Q\textsubscript{10} of ER was 2.3 (95% CI: 2.1–2.5) and 2.6 (95% CI: 2.2–2.9) for the forest ecosystems and the non-forest ecosystems, respectively. In addition, Perkins et al. (2012) showed that the unconfounded Q\textsubscript{10} of ER was 2.5 (95% CI: 1.5–4.1) at Hengill catchment in Iceland.

Although the unconfounded Q\textsubscript{10} in the current study is consistent with several previous reports, studies that showed lower Q\textsubscript{10} in the range of 1.4–1.5 also exist (Mahecha et al., 2010; Wang et al., 2010). The difference may result from using air temperature (Mahecha et al., 2010) rather than soil temperature to estimate the Q\textsubscript{10} of Rs (Graf et al., 2011; Peng et al., 2009). Soil buffers temperature variation and typically experience a smaller range of fluctuation compared to air temperature. As a result, estimated Q\textsubscript{10} of Rs based on air temperature is lower than that based on soil temperature (Graf et al., 2011; Phillips et al., 2011). Furthermore, soil surface CO\textsubscript{2} efflux typically lags behind changes in air temperature due to the vertical transport of heat and gas, and ST5 was often found to have the highest explanatory power on Rs (Pavelka et al., 2007; Phillips et al., 2011; Reichstein and Beer, 2008). These findings suggest that using ST5 as in the current study could be the most robust way to quantify temperature dependence of soil. The estimated Q\textsubscript{10} in the current study is also higher than Q\textsubscript{10} estimated based on the longer time scale (Bond-Lamberty and Thomson, 2010a). Such bias may reflect the different drivers of Rs at different temporal scales (Kuzyakov and Gavrichkova, 2010; Vargas et al., 2011, 2010; Yvon-Durocher et al., 2012). For example, annual cumulative respiration may be limited by available substrates fixed by photosynthesis. Consequently, the temperature dependence of annual respiration may reflect the temperature dependence of photosynthesis (Q\textsubscript{10} of photosynthesis is ~1.5) (Yvon-Durocher et al., 2012), offering a plausible explanation for the lower Q\textsubscript{10} of Rs estimated based on annual cumulative respiration.

The results of this study add to the wealth of evidence suggesting that the cellular level Q\textsubscript{10} of respiration (mean Q\textsubscript{10} of 2.4, ranging from 1.3 to 5.4) could be applicable to multiple higher ecological organizations (Brown et al., 2004; Raven and Geider, 1988; Vetter, 1995). For instance, the estimated unconfounded Q\textsubscript{10} of respiratory processes were 2.7 (95% CI: 2.0–3.8) and 2.3 (95% CI: 2.2–2.7) for unicellular aerobic microbes and plants, respectively (Gillooly et al., 2001). At the community level, the estimated unconfounded Q\textsubscript{10} of respiration varied in a small range (from 2.1 to 2.5) for oceanic planktonic communities in different studies (Lopez-Urrutia et al., 2006; Regaudie-de-Gioux and Duarte, 2012). These reported Q\textsubscript{10} estimates of respiratory processes.
from the cellular level to the community level are also consistent with the unconfounded ecosystem-level Q10 of Rs in this study.

The universality of unconfounded Q10 of respiratory processes for different levels and diverse ecosystem types may stem from the fundamental similarity of respiratory processes across diverse taxa of organisms and levels of ecological organization (Brown et al., 2004; Yvon-Durocher et al., 2012). Aerobic metabolism (respiration) of vast majority organisms is governed by a small number of biochemical reactions that form the basis of the tricarboxylic acid cycle (Morowitz et al., 2003; Gillooly et al., 2001; Yvon-Durocher et al., 2012). Theoretical work suggests that substrate availability that covaries with temperature could significantly amplify the estimated Q10 of respiration (Anderson-Teixeira et al., 2008). Thus, it is plausible that the dependence of the substrate availability of Rs on the seasonal variation in temperature in the Tibetan alpine ecosystems may be responsible for the higher seasonal Q10 of Rs than the global average.

The confounding effect of the seasonal variation in Rs on the seasonal Q10

The current study showed that Q10 of Rs estimated directly based on seasonal temperature gradient in the Tibetan alpine ecosystems is higher than the global-average and positively correlated with seasonal variation in Rs, which are consistent with previous reports (Curie-Yuste et al., 2004; Peng et al., 2009; Wang et al., 2010). A previous study in this region showed that higher amplitude of the seasonal variation in Rs in the Tibetan alpine ecosystems than in many other ecosystems is potentially caused by the coincidence between substrate availability of Rs and seasonal temperature variation, e.g. both the transition from the non-growing season to the growing season and the switching between the frozen and thawed soil covary with temperature and can affect on the substrate availability of Rs (Wang et al., 2014b). Theoretical work suggests that substrate availability that covaries with temperature could significantly amplify the estimated Q10 of respiration (Anderson-Teixeira et al., 2008). Thus, it is plausible that the dependence of the substrate availability of Rs on the seasonal variation in temperature in the Tibetan alpine ecosystems may be responsible for the higher seasonal Q10 of Rs than the global average.

The confounding effect of the seasonal variation in Rs on the seasonal Q10 also suggests that the seasonal Q10 cannot precisely reflect the effects of experimental warming on the temperature sensitivity of Rs. Firstly, experimental warming can asymmetrically affect the non-growing season Rs and growing-season Rs (Suseela and Dukes, 2013) or result in a prolonged growing season (Reyes-Fox et al., 2014), suggesting that the responses of seasonal Q10 of Rs to experimental warming can be confounded by the shifted seasonality of Rs. In addition, experimental warming can indirectly affect the activities of plants and soil microbes via reducing the soil water availability (Liu et al., 2009; Luo, 2007; Suseela and Dukes, 2013; Wan et al., 2007). Soil water availability is a crucial factor in affecting the Rs (Liu et al., 2016, 2009), and recent investigations have also shown that experimental warming induced changes in soil water availability is essential in regulating the responses of Rs to rising temperature (Wang et al., 2014a; Carey et al., 2016). These indicate that the responses of the seasonal Q10 to experimental warming cannot purely reflect a difference in temperature.
4.3. Implications

The lower bound of the 95% CI of Q_{10,MEM} overlapped with the subcellular-level Q_{10} (≈ 2.4), indicating a marginally significant difference between them. This may result from limitations of the MEM method in estimating the unconfounded Q_{10} of respiratory processes. A critical assumption of the MEM method is that the site-specific confounding effects are 0 on average (Yvon-Durocher et al., 2012). This assumption may be suitable for datasets containing a large number of sites as these confounding effects may lead to higher temperature sensitivities at some sites but lower temperature sensitivities at other sites. However, this assumption may not be applicable to studies in a single location over time. For example, the two sites in the current study are located in the same climatic region and exhibited similar seasonality of vegetation activity, precipitation and temperature over the years, which may consistently lead to a higher estimate of temperature sensitivity. This may partially explain why the temperature sensitivity estimated from the mixed-effects model approach is higher than the SSA approach but lower than the regression approach. This result suggests that caution should be taken when applying the mixed-effects model approach in estimating Q_{10} for a single site study or a few sites constrained in the same region because this approach may not completely eliminate non-temperature driven confounding effects under such circumstances.

Temperature and non-temperature driven factors of Rₘ are both important in determining the net influence of warming on Rₘ. For instance, a recent study showed that the global annual Rₘ flux is significantly affected by the interaction of precipitation and temperature in the last 50 years (Bond-Lamberty and Thomson, 2010a). Substrate availability is also crucial in determining the long-term responses of Rₘ to warming. For example, single-site experimental warming studies have shown that the stimulations of warming on the Rₘ can decline with year due to the consumption of labile soil carbon pool (Melillo et al., 2002) or increase with year as the increased plant productivity and quantity of substrates inputting to soil microbes (Xu et al., 2015). The current investigation suggests that the effects of non-temperature factors contained in the seasonal variation in Rₘ can significantly amplify the estimated Q_{10} and thus have to be eliminated from the estimation of Q_{10} to accurately predict the response of Rₘ to warming. A precise prediction of the response of Rₘ to climate warming requires quantification of the pure temperature driven responses (Kuzyakov and Gavrichkova, 2010; Reichstein and Beer, 2008; Vargas et al., 2011, 2010). The current study demonstrated a feasible way to quantify such temperature response.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2018.04.005.
Fig. 6. Linear relationship between standardized soil respiration (Rs) and temperature. The solid lines represent the fitted regression lines for soil respiration (Rs) of the temperate grassland and Rs of the meadow. The dashed lines represent the fitted regression lines for Rs of the temperate grassland (a, b) and Rs of a published global dataset (c, d) (Bond-Lamberty and Thomson, 2010).

References


58
Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer,
Y. Wang et al.
Soil Biology and Biochemistry 122 (2018) 50–59
Regaudie-de-Gioux, A., Duarte, C.M., 2012. Temperature dependence of planktonic me-
Reichstein, M., Beer, C., 2008. Soil respiration across scales: the importance of a model-
Randerson, J.T., Ho
Magill, A., Ahrens, T., Morrisseau, S., 2002. Soil warming and carbon-cycle feedbacks
Luo, Y.Q., 2007. Systematic assessment of terrestrial biogeochemistry in coupled clima-
Mikkelsen, T.N., Pilegaard, K., Beier, C., Ambus, P., 2012. Soil respiration is stimu-