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 (Q_{10}) of soil respiration (R_s) 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 Q_{10} 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 Q_{10} of R_s, these two novel methods were combined with directly measured R_s for 6 years in two Tibetan alpine ecosystems. The results showed that, 1) confounded Q_{10} of R_s estimated from seasonal R_s-temperature relationship positively correlated with the seasonality of R_s, and 2) estimates of unconfounded Q_{10} of R_s 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 Q_{10} (≈ 2.4). These results support the convergence in the Q_{10} of R_s and imply a conserved R_s-temperature relationship. These findings indicate that the seasonality of R_s has to be eliminated from estimating the Q_{10} of R_s, otherwise the estimates should be questionable. They also indicate that seasonal Q_{10} and its responses to warming should not be directly used in carbon-climate models as they contain confounding effects.

1. Introduction

Soil respiration (R_s) 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 R_s-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 Q_{10} of R_s, a factor by which the rate of R_s 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., 2010; Todd-Brown et al., 2014). While some studies have shown a consistent Q_{10} of R_s in various types of ecosystems (Mahecha et al., 2010; Yvon-Durocher

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et al., 2012), other investigations have demonstrated a considerable variability of estimated Q_{10} of R_s (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 Q_{10} of R_s can be partly attributed to the methods used to estimate Q_{10}. Estimating Q_{10} from natural temperature gradients may contain the influences of non-temperature driven confounding factors that covary with temperature. For example, comparing R_s across seasons is commonly used for estimating Q_{10} of R_s (Davidson et al., 2006; Lloyd and Taylor, 1994; Suseela et al., 2012; Suseela and Dukes, 2013). However, seasonal changes in R_s 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 R_s rates in summer are attributable to both high temperature and high overall vegetation activities that provide substrates for R_s (Curiel Yuste et al., 2004; Högberg et al., 2001; Wang et al., 2010), evidenced by a positive correlation between Q_{10} of R_s 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 R_s and the estimated Q_{10} of R_s (Geng et al., 2012; Liu et al., 2016, 2009); summer drought can reduce R_s (Selsted et al., 2012) and counteract the influence of high temperature on R_s, masking the response of R_s to temperature. In summary, Q_{10} estimated from seasonal temperature gradients includes a suite of non-temperature driven confounding effects and thus does not truly reflect the responses of R_s to changing temperature. Given the high sensitivity of projected future climate to the Q_{10} of R_s (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 Q_{10} of R_s for an accurate prediction of how soil carbon flux will respond to climatic warming (Curiel Yuste et al., 2004; Mahecha et al., 2010; Wang et al., 2010).

Several recent studies attempted to estimate the unconfounded Q_{10} of R_s (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 Q_{10} of ER, assuming that non-temperature driven confounding effects remain constant in short term. They reported a convergent Q_{10} of ~1.4 across various types of ecosystems. Yvon-Durocher et al. (2012) employed a mixed-effects modeling approach to estimate unconfounded Q_{10} of R_s and found a consistent Q_{10} of about 2.4 for R_s 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 Q_{10} of R_s using eddy covariance data as in Mahecha et al. (2010) includes both the aboveground and belowground respirations. Also, Q_{10} estimated using air temperature instead of soil temperature may underestimate the true Q_{10} of R_s 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 R_s, soil temperature and the SSA has the potential to alleviate these shortcomings in Mahecha et al. (2010). Together, combining high-resolution measurements of soil R_s and temperature with multiple novel statistical approaches is a proper way to examine the robustness of the estimated Q_{10} of R_s and improve the current understanding of the temperature sensitivity of soil respiration.

In this study, multiple approaches were applied to estimate the Q_{10} of R_s based on continuous measurements of R_s 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 Q_{10} of R_s (Wang et al., 2014b), making it an ideal place to compare various methods of estimating the temperature dependence of R_s.

In this study, hourly R_s 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 Q_{10} of R_s. Specifically, the conventional regression method was used for estimating the Q_{10} of R_s from seasonal temperature changes; two novel methods, the SSA (Golyandina 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 Q_{10} of R_s. The non-temperature driven processes, such as the vegetation activity, contribute to the pronounced seasonality of R_s in the Tibetan alpine grasslands (Wang et al., 2014b), which can positively affect on the estimated Q_{10} of R_s (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 Q_{10} of R_s in the Tibetan alpine ecosystems. Furthermore, two novel methods that could eliminate the confounding effects were hypothesized to result in the Q_{10} of R_s consistent with the intrinsic Q_{10} of aerobic metabolic reactions at the subcellular level ($Q_{10} \approx 2.4$) (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 (R_s) 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 R_s of the mesic grassland and $n = 3$–5 for R_s in the meadow).

	Mesic grassland	Meadow
Mean annual precipitation (mm)	416.8 (350.6–501.3)*	416.8 (350.6–501.3)*
Mean air temperature (°C)	−1.08 (−22.70–14.99)*	−1.08 (−22.70–14.99)*
Mean soil temperature (°C)	2.45 (−10.68–15.41)	2.77 (−9.23–14.97)
Mean soil moisture (v/v)	29.6 ± 1.07	32.4 ± 1.78
Soil pH	7.85 ± 0.07	7.57 ± 0.18
Soil organic carbon (%)	7.82 ± 0.09	22.8 ± 0.56
Soil total nitrogen (%)	0.58 ± 0.03	1.72 ± 0.08
Above ground biomass (g m^{-2})	372.2 ± 22.5	310.8 ± 15.2
Annual cumulative R_s (g C m^{-2})	681.5 ± 24.7	574.5 ± 44.9
Growing-season cumulative R_s (g C m^{-2})	597.7 ± 24.0	487.5 ± 42.4

*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, 1995). The mesic grassland site is dominated by *Kobresia humilis* (C. A. Mey. ex Traut.) Serg., *Festuca ovina* L., *Elymus nutans* Griseb., *Poa pratensis* L., *Carex scabrirostris* Kük., *Scripus distigmaticus* (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). Detailed information on the mesic grassland site can be found in Wang et al. (2014b). The meadow study site is at the margin area of the Luanhaizi 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 CO_2 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, 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_REG}), the Singular Spectrum Analysis method (Q_{10_SSA}) (Golyandina and Korobeynikov, 2014; Mahecha et al., 2010), and the mixed-effects model (MEM) method (Q_{10_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 CO_2 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 (Curiel 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:

$$R_s = a \times (Q_{10})^{\frac{T}{10}}, \tag{1}$$

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:

$$ln(R_s) = a + ln(Q_{10}) \times \frac{T}{10}, \tag{2}$$

For the conventional regression approach, this linear regression between $ln(R_s)$ and T was directly used for estimating Q_{10_REG}, which includes the non-temperature driven confounding effects, based on the slope of the regression.

To calculate Q_{10_SSA}, the daily mean R_s rates were first natural logarithm transformed. The time series of both ST5 and log-transformed R_s were then decomposed to subsignals with different frequencies (Fig. 1d–g) using function *ssa* in the R package *Rssa* (Golyandina et al., 2013; Golyandina and Korobeynikov, 2014). According to Mahecha et al. (2010), a period length of 100 days was used as a cutoff for the high-frequency and the low-frequency bins. The high-frequency bin is a combination of all subsignals which have a period length of shorter than 100 days while the low-frequency bin contains all subsignals with a period longer than 100 days. Only the high-frequency bins of ST5 and log-transformed R_s were used to estimate the Q_{10_SSA} with eqn. (2) because low-frequency signals are assumed to contain the non-temperature driven confounding effects (Gu et al., 2008; Mahecha et al., 2010; Wang et al., 2010). Only results using 100 days as the cutoff for high- and low-frequency bins were presented, but using other thresholds for the high-frequency and the low-frequency bin has no effect on the estimated Q_{10_SSA} of R_s (Fig. S2). The seasonal variation in R_s was estimated as its seasonal amplitude, the difference between maximum and minimum values of low-frequency bin of R_s, and its effect on the estimated Q_{10_REG} was investigated using the Pearson correlation analysis.

The mixed-effects model approach was used to eliminate confounding effects and estimate Q_{10} (Q_{10_MEM}). As developed by Yvon-Durocher et al. (2012), the essential idea of the mixed model approach is that non-temperature driven confounding effects lead to a deviation in the intrinsic temperature sensitivity, and such deviation can be accounted for by random effects in the model. In the current study, the mixed-effects model used in Yvon-Durocher et al. (2012) was modified as:

$$ln(R_s) = (a + \varepsilon_a^S) + [ln(Q_{10}) + \varepsilon_Q^S] \times \frac{T}{10}, \tag{3}$$

where $ln(R_s)$ and $ln(Q_{10})$ is the natural logarithm of the daily mean R_s rate at temperature T and Q_{10}, respectively, ε_a^S is the random deviation in intercept (parameter a, representing R_s at 0 °C), ε_Q^S is the random deviation in the $ln(Q_{10})$ that accounts for the effects of non-temperature driven confounding factors (Yvon-Durocher et al., 2012). The linear mixed effect model specified in eqn. (3) was fitted using package *lme4* in R 3.0.1 software (Bates et al., 2015; R Core Team, 2013). This mixed model was applied to two datasets. For the global dataset of R_s (Bond-
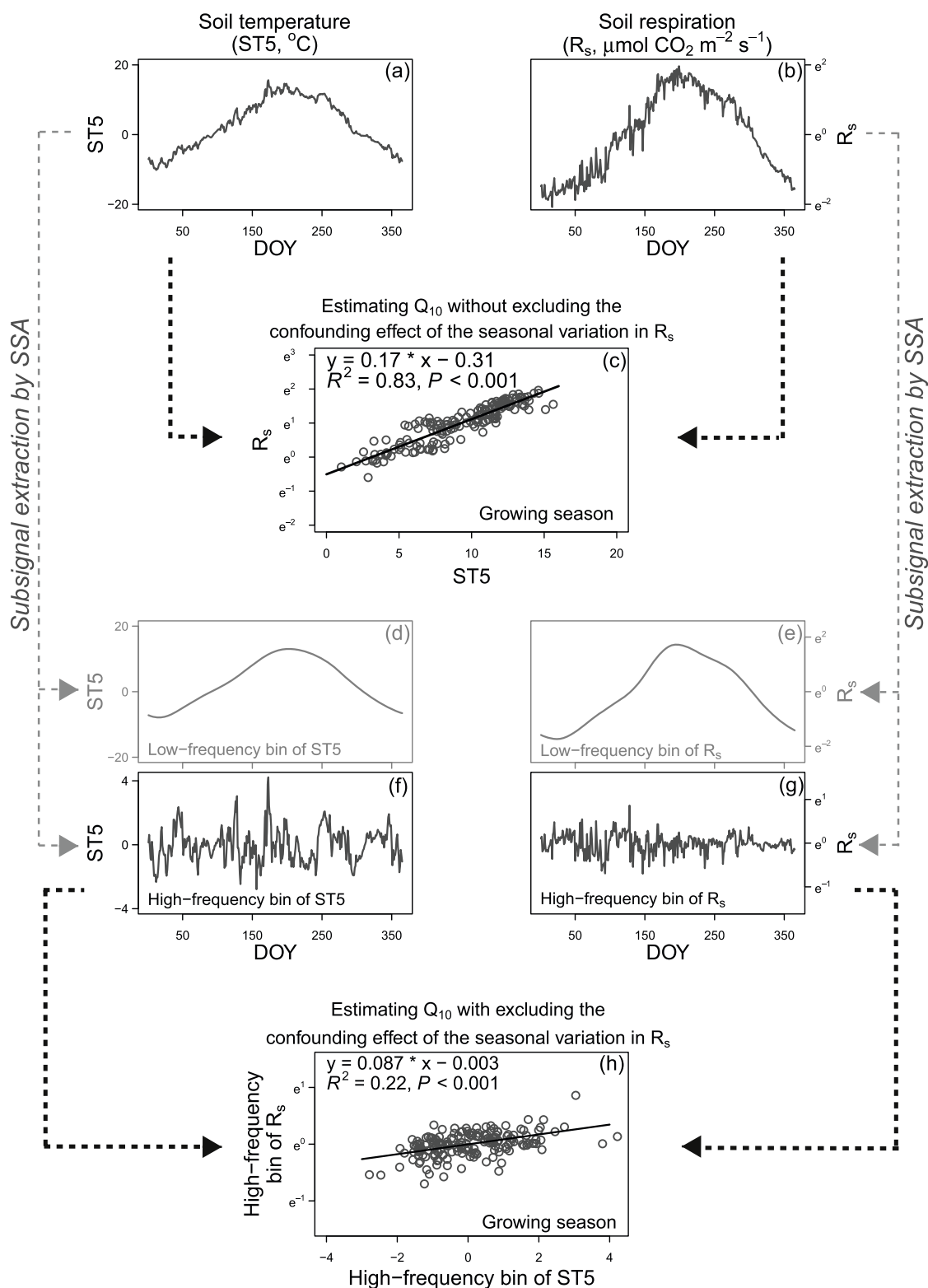
Fig. 1. Comparison of estimation protocols between conventional regression method (a–c) and Singular Spectrum Analysis (SSA) (d–h). In the conventional regression method, Q_{10} was estimated without excluding the seasonal variation in the soil respiration (R_s). In the SSA method, the seasonal variation 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 R_s and non-temperature driven factors of R_s contribute to the site-specified deviation in the estimated temperature sensitivity of R_s (Yvon-Durocher et al., 2012). For the R_s measured in the Tibetan alpine ecosystems, year of R_s 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 R_s (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-specified 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) ($F_{1, 21} = 0.90$, $P = 0.35$) and its interaction with estimation methods ($F_{2, 21} = 0.08$, $P = 0.92$) 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 R_s 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://datathief.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 R_s showed a pronounced seasonal pattern, with the lowest rate around January ($\sim 0.5 \, \mu mol \, CO_2 \, m^{-2} \, s^{-1}$), and the highest rate ($\sim 3.3 \, \mu mol \, CO_2 \, m^{-2} \, s^{-1}$) in late July or early August (Fig. 2). The annual cumulative R_s and the growing season cumulative R_s 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, R_s in the meadow also exhibited pronounced seasonal pattern, with minimum R_s of $\sim 0.5 \, \mu mol \, CO_2 \, m^{-2} \, s^{-1}$ in January and maximum R_s of $\sim 3.3 \, \mu mol \, CO_2 \, m^{-2} \, s^{-1}$ in mid-summer (Fig. 2). The annual cumulative R_s and the growing season cumulative R_s 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 R_s 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 R_s 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 R_s of the meadow in the Tibetan Plateau was not significantly differed 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 R_s was positively correlated with the amplitude of seasonal variation in R_s 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 R_s 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. 3b 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 R_s 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 R_s 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 R_s dataset (Bond-Lamberty and Thomson, 2010b) (one-way ANOVA, $F_{3, 69} = 0.94$, $P = 0.43$) (Figs. 5b and 6).

Methods of estimating Q_{10} significantly influenced the estimated Q_{10} of R_s (ANOVA, $F_{2, 23} = 6.97$, $P = 0.004$, 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 R_s and combining two different estimating methods (SSA and MEM). The main conclusions are: 1) seasonal Q_{10} of R_s was positively correlated with the seasonality of R_s indicating it can be confounded by seasonal variations in the non-temperature driven factors of R_s 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 R_s (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 ($Q_{10} \approx 2.4$) (Gilooly 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 R_s.
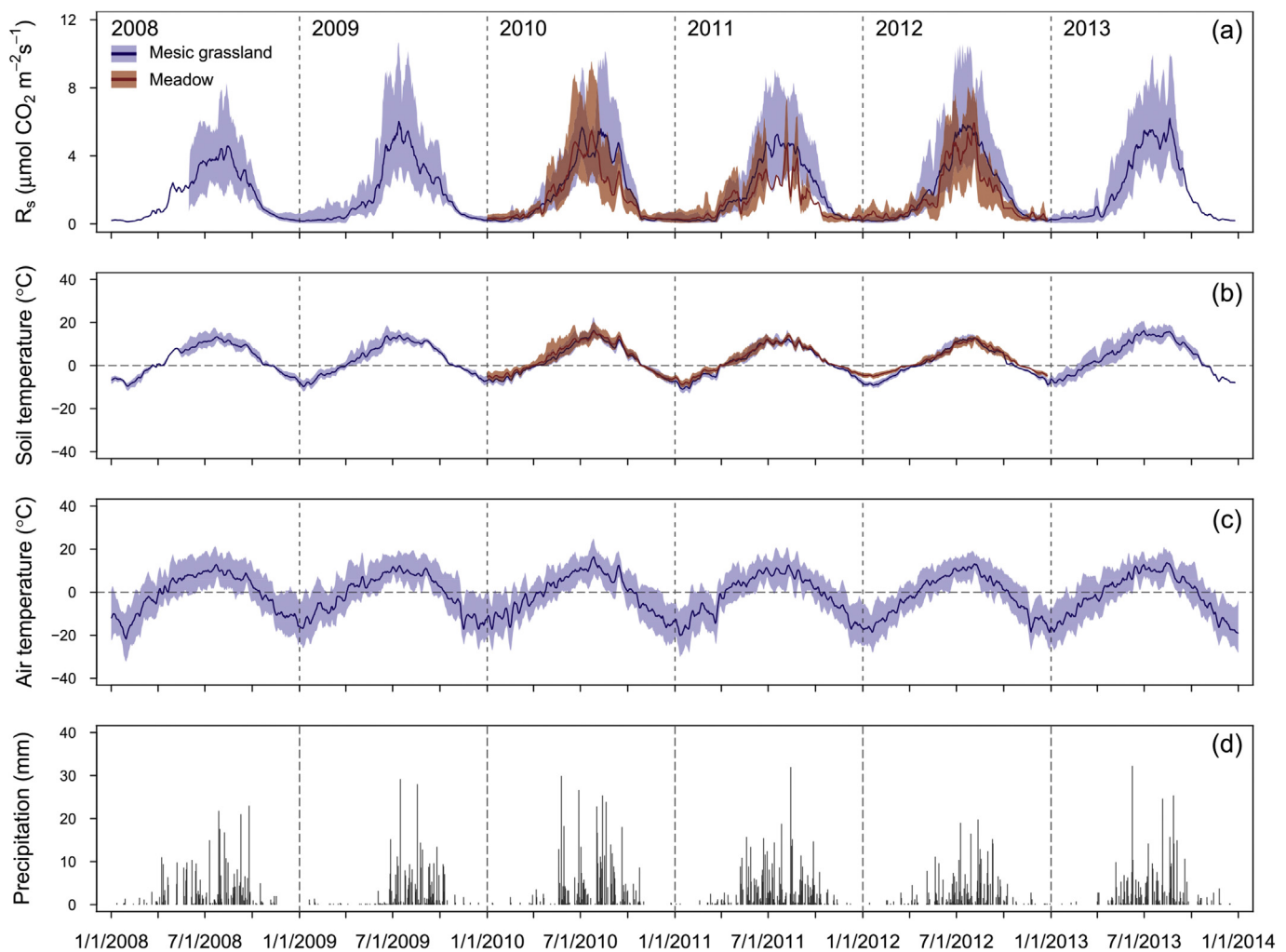
Fig. 2. Seasonal and annual variations of (a) soil respiration (R$_s$); (b) soil temperature; (c) air temperature; and (d) precipitation of the two study sites. Colored lines represent smoothed (7-days running mean) time series of R$_s$ and temperatures (soil temperature and air temperature). Time series (R$_s$, soil temperature and air temperature) also shown as a colored area between smoothed (7-days running mean) daily maximum and smoothed (7-days running mean) daily minimum values.

4.1. Convergence in the unconfounded Q$_{10}$ of respirations

The estimated Q$_{10}$ of R$_s$ 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$_{10}$ of R$_s$ or ER. For example, Yvon-Durocher et al. (2012) estimated the unconfounded Q$_{10}$ of R$_s$ and ER for diverse ecosystems and found that the unconfounded Q$_{10}$ of R$_s$ was 2.4 (95% CI: 2.0–2.5) for the global average, and the unconfounded Q$_{10}$ 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$_{10}$ of ER was 2.5 (95% CI: 1.5–4.1) at Hengill catchment in Iceland.

Although the unconfounded Q$_{10}$ in the current study is consistent with several previous reports, studies that showed lower Q$_{10}$ 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$_{10}$ of R$_s$ (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$_{10}$ of R$_s$ based on air temperature is lower than that based on soil temperature (Graf et al., 2011; Phillips et al., 2011). Furthermore, soil surface CO$_2$ 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 R$_s$

(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$_{10}$ in the current study is also higher than Q$_{10}$ estimated based on the longer time scale (Bond-Lamberty and Thomson, 2010a). Such bias may reflect the different drivers of R$_s$ 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$_{10}$ of photosynthesis is ∼1.5) (Yvon-Durocher et al., 2012), offering a plausible explanation for the lower Q$_{10}$ of R$_s$ estimated based on annual cumulative respiration.

The results of this study add to the wealth of evidence suggesting that the cellular level Q$_{10}$ of respiration (mean Q$_{10}$ 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$_{10}$ 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$_{10}$ of respiration varied in a small range (from 2.1 to 2.5) for oceanic planktonic communities in different studies (López-Urrutia et al., 2006; Regaudie-de-Gioux and Duarte, 2012). These reported Q$_{10}$ estimates of respiratory processes
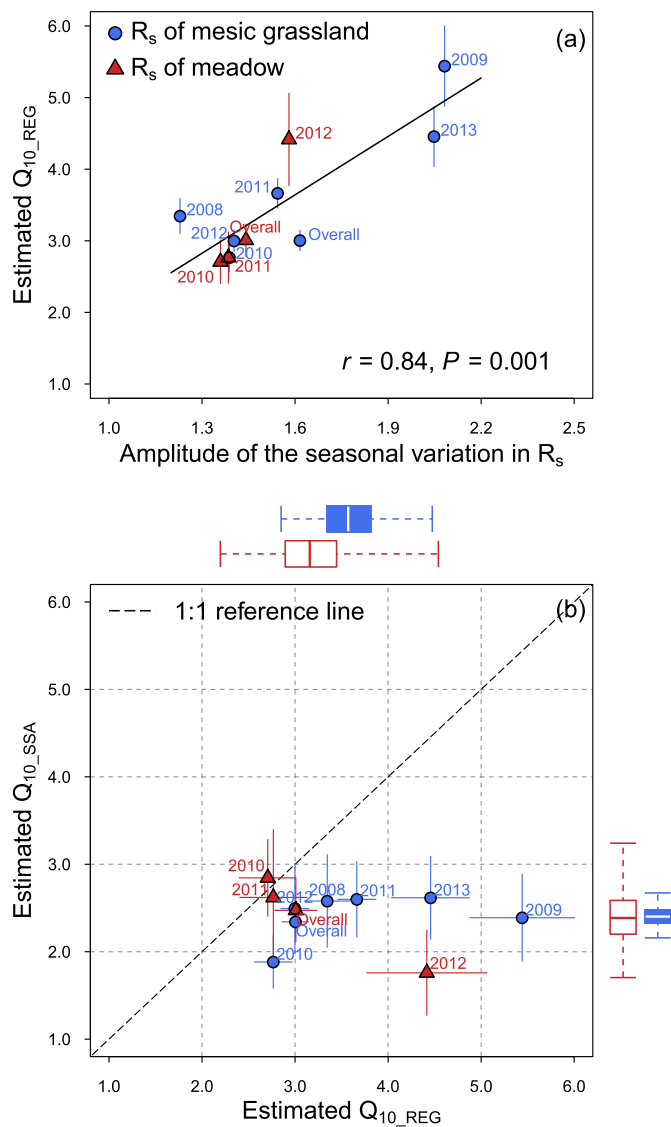
Fig. 4. Comparison of estimated Q_{10_REG} of soil respiration (R_s) between the Tibetan alpine grasslands and a published global dataset of Q_{10_REG} (Wang et al., 2010). Result of the one-way analysis of variance (one-way ANOVA) has shown in the figure. Different letters (a, b and c) represent significant difference of estimates (post hoc *t*-test, $P < 0.05$). Vertical bars represent the 95% confidence interval of the estimated Q_{10_REG}. Dashed horizontal line represents the subcellular-level Q_{10} of aerobic metabolic reactions ($Q_{10} \approx 2.4$).

the current study also potentially support the view that the convergent Q_{10} across diverse scales and taxonomic groups implies a conservative nature of the biochemical basis for respiration processes (Enquist et al., 2003; Gillooly et al., 2001; Yvon-Durocher et al., 2012).

4.2. Confounding effect of the seasonal variation in R_s on the seasonal Q_{10}

The current study showed that Q_{10} of R_s 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 R_s, which are consistent with previous reports (Curiel 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 R_s in the Tibetan alpine ecosystems than in many other ecosystems is potentially caused by the coincidence between substrate availability of R_s 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 R_s (Wang et al., 2014b). Theoretical work suggests that substrate availability that covaries with temperature could significantly amplify the estimated Q_{10} of respiration (Anderson-Teixeira et al., 2008). Thus, it is plausible that the dependence of the substrate availability of R_s on the seasonal variation in temperature in the Tibetan alpine ecosystems may be responsible for the higher seasonal Q_{10} of R_s than the global average.

The confounding effect of the seasonal variation in R_s on the seasonal Q_{10} also suggests that the seasonal Q_{10} cannot precisely reflect the effects of experimental warming on the temperature sensitivity of R_s. Firstly, experimental warming can asymmetrically affect on the non-growing-season R_s and growing-season R_s (Suseela and Dukes, 2013) or result in a prolonged growing season (Reyes-Fox et al., 2014), suggesting that the responses of seasonal Q_{10} of R_s to experimental warming can be confounded by the shifted seasonality of R_s. 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 R_s (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 R_s to rising temperature (Wang et al., 2014a; Carey et al., 2016). These indicate that the responses of the seasonal Q_{10} to experimental warming cannot purely reflect a difference in temperature

Fig. 3. The Pearson correlation analysis between the estimated Q_{10_REG} and the amplitude of the seasonal variation in soil respiration (R_s) (a) and comparison between estimated Q_{10_REG} and estimated Q_{10_SSA} (b). The Q_{10_REG} was estimated without excluding the confounding effect of the seasonal variation in R_s, while the Q_{10_SSA} was estimated with excluding this confounding effect. Vertical bars in Fig. 3a are the 95% confidence interval (CI) of estimated Q_{10_REG}. Horizontal bars and vertical bars in Fig. 3b are the 95% CI of estimated Q_{10_REG} and estimated Q_{10_SSA}, respectively. The 95% CI (dashed line), 50% CI (central box) and mean (solid line in the central box) of estimated Q_{10_REG} and estimated Q_{10_SSA} were shown as box plots (blue boxes for R_s of the mesic grassland and red boxes for R_s of the meadow) in the top side and the right side of Fig. 3b, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

from the cellular level to the community level are also consistent with the unconfounded ecosystem-level Q_{10} of R_s in this study.

The universality of unconfounded Q_{10} 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 tricarboxylicacid cycle (Morowitz et al., 2000). Temperature is a crucial factor in regulating the biochemical reactions according to the kinetic theory of metabolism (Davidson and Janssens, 2006; Raven and Geider, 1988; Vetter, 1995). Thus, results of
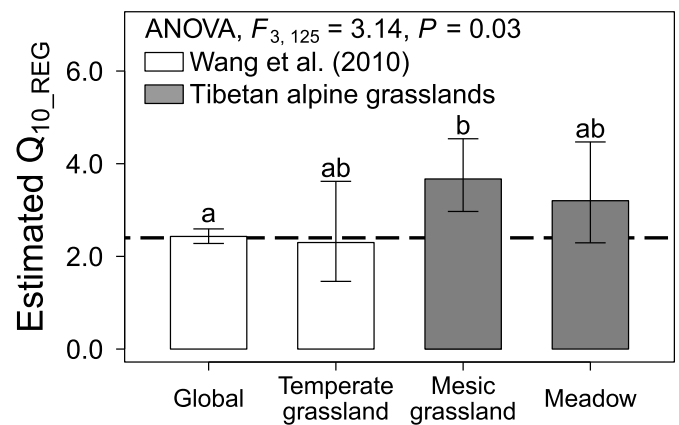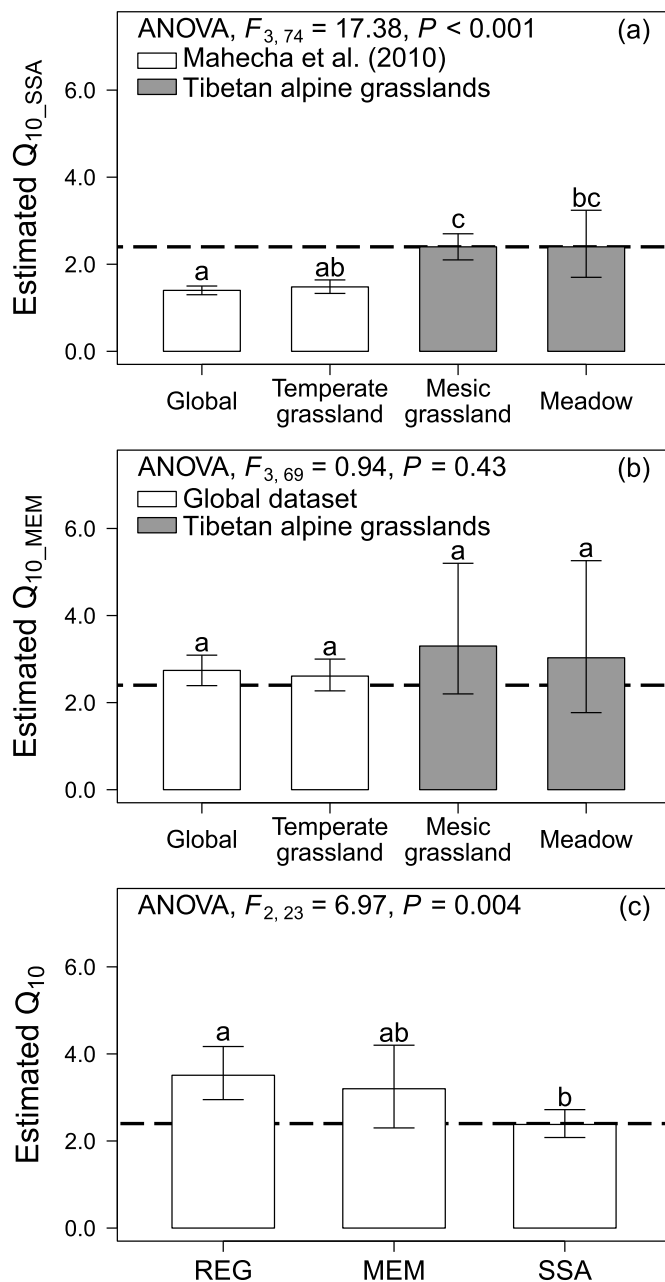
Fig. 5. Comparisons of estimated Q_{10} between different ecosystems and different methods. (a) Comparison of the Q_{10} estimated with Singular Spectrum Analysis (Q_{10_SSA}) for the Tibetan alpine ecosystems (mesic grassland and meadow) and from a previous report (Mahecha et al., 2010) (global and temperate grassland). (b) Comparison of the estimated Q_{10} using the mixed-effects model (Q_{10_MEM}) for the Tibetan alpine ecosystems (mesic grassland and meadow) and from a global dataset (global and temperate grassland) (Bond-Lamberty and Thomson, 2010b). (c) Comparison of the Q_{10} estimated using conventional regression method (REG), the mixed-effects model (MEM) method and the Singular Spectrum Analysis (SSA) for the Tibetan alpine grasslands. Result of the one-way analysis of variance (one-way ANOVA) was showed in each subfigure. Different letters (a, b and c) represent significant difference of estimates (post hoc *t*-test, $P < 0.05$). Vertical bars represent the 95% confidence interval of the estimated Q_{10}. Dashed horizontal line represents the subcellular-level Q_{10} of aerobic metabolic reactions ($Q_{10} \approx 2.4$).

sensitivity of R_s, but also differences in seasonality of R_s and other confounding factors, therefore, directly including its responses to rising temperature into carbon-climate models may result in questionable results.

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 R_s are both important in determining the net influence of warming on R_s. For instance, a recent study showed that the global annual R_s 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 R_s to warming. For example, single-site experimental warming studies have shown that the stimulations of warming on the R_s 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 R_s 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 R_s to warming. A precise prediction of the response of R_s 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.

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.
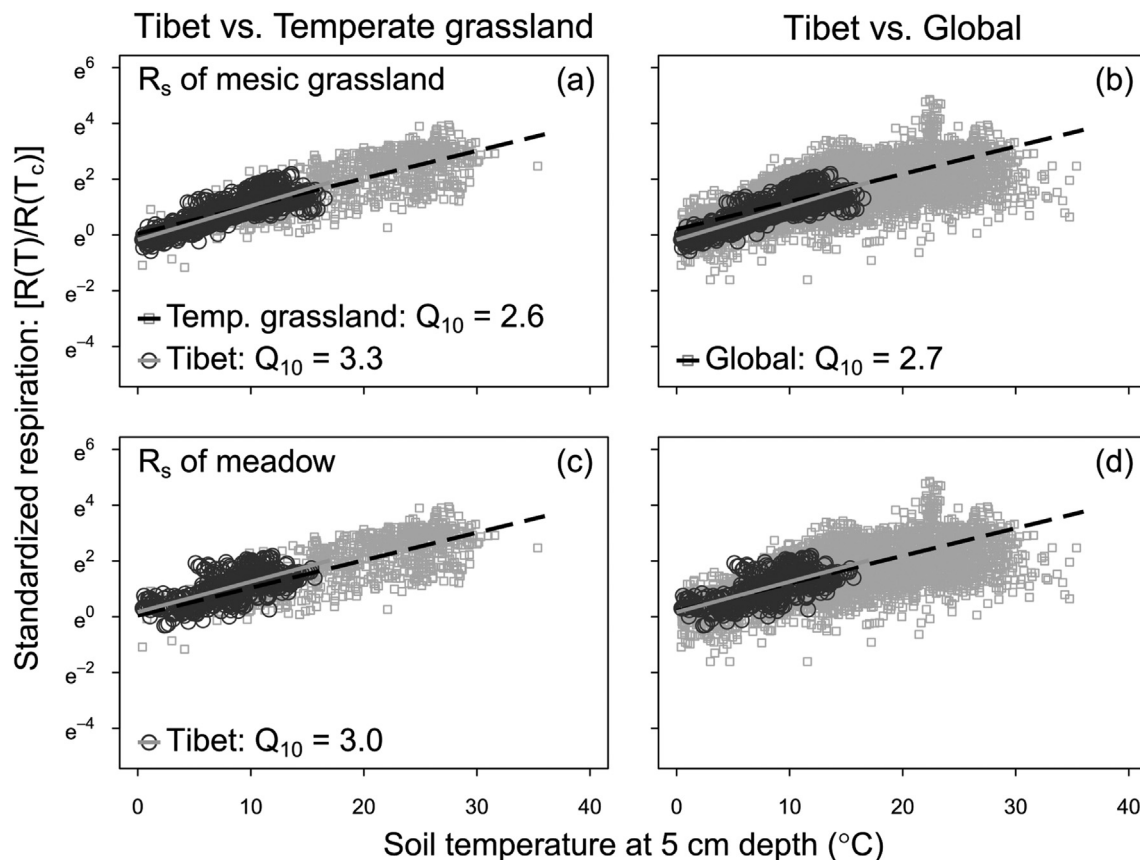
Tibet vs. Temperate grassland

Tibet vs. Global

Fig. 6. Linear relationship between standardized soil respiration (R_s) ($R_s(T)/R_s(T_c)$, $T_c = 0\,°C$) and temperature. The solid lines represent the fitted regression lines for soil respiration (R_s, a-b) of the mesic grassland and R_s (c–d) of the meadow. The dashed lines represent the fitted regression lines for R_s of the temperate grasslands (a, c) and R_s of a published global dataset (b, d) (Bond-Lamberty and Thomson, 2010b).

References

Anderson-Teixeira, K.J., Vitousek, P.M., Brown, J.H., 2008. Amplified temperature dependence in ecosystems developing on the lava flows of Mauna Loa, Hawai'i. Proceedings of the National Academy of Sciences 105, 228–233. http://dx.doi.org/10.1073/pnas.0710214104.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67, 1–48. http://dx.doi.org/10.18637/jss.v067.i01.

Bond-Lamberty, B., Thomson, A., 2010a. Temperature-associated increases in the global soil respiration record. Nature 464, 579–582. http://dx.doi.org/10.1038/nature08930.

Bond-Lamberty, B., Thomson, A., 2010b. A global database of soil respiration data. Biogeosciences 7, 1915–1926. http://dx.doi.org/10.5194/bg-7-1915-2010.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789. http://dx.doi.org/10.1890/03-9000.

Carey, Joanna C., Tang, J., Templer, P.H., Kroeger, K.D., Crowther, T.W., Burton, A.J., Dukes, J.S., Emmett, B., Frey, S.D., Heskel, M.A., Jiang, L., Machmuller, M.B., Mohan, J., Panetta, A.M., Reich, P.B., Reinsch, S., Wang, X., Allison, S.D., Bamminger, C., Bridgham, S., Collins, S.L., de Dato, G., Eddy, W.C., Enquist, B.J., Estiarte, M., Harte, J., Henderson, A., Johnson, B.R., Larsen, K.S., Luo, Y., Marhan, S., Melillo, J.M., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Rastetter, E., Reinmann, A.B., Reynolds, L.L., Schmidt, I.K., Shaver, G.R., Strong, A.L., Suseela, V., Tietema, A., 2016. Temperature response of soil respiration largely unaltered with experimental warming. Proceedings of the National Academy of Sciences 113, 13797. http://dx.doi.org/10.1073/pnas.1605365113.

Chinese Soil Taxonomy Research Group, 1995. Chinese Soil Taxonomy. Science Press, Beijing, China.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grünwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T., Valentini, R., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437, 529–533. http://dx.doi.org/10.1038/nature03972.

Curiel Yuste, J., Janssens, I.A., Carrara, A., Ceulemans, R., 2004. Annual Q10 of soil respiration reflects plant phenological patterns as well as temperature sensitivity. Global Change Biology 10, 161–169. http://dx.doi.org/10.1111/j.1529-8817.2003.00727.x.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440, 165–173. http://dx.doi.org/10.1038/nature04514.

Davidson, E.A., Janssens, I.A., Luo, Y., 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q10. Global Change Biology 12, 154–164. http://dx.doi.org/10.1111/j.1365-2486.2005.01065.x.

Enquist, B.J., Economo, E.P., Huxman, T.E., Allen, A.P., Ignace, D.D., Gillooly, J.F., 2003. Scaling metabolism from organisms to ecosystems. Nature 423, 639–642. http://dx.doi.org/10.1038/nature01671.

Exbrayat, J.-F., Pitman, A., Abramowitz, G., 2014. Disentangling residence time and temperature sensitivity of microbial decomposition in a global soil carbon model. Biogeosciences 11, 6999–7008. http://dx.doi.org/10.5194/bg-11-6999-2014.

Geng, Y., Wang, Y., Yang, K., Wang, S., Zeng, H., Baumann, F., Kuehn, P., Scholten, T., He, J.-S., 2012. Soil respiration in Tibetan alpine grasslands: belowground biomass and soil moisture, but not soil temperature, best explain the large-scale patterns. PLoS One 7, e34968. http://dx.doi.org/10.1371/journal.pone.0034968.

Giardina, C.P., Litton, C.M., Crow, S.E., Asner, G.P., 2014. Warming-related increases in soil CO2 efflux are explained by increased below-ground carbon flux. Nature Climate Change 4, 822–827. http://dx.doi.org/10.1038/NCLIMATE2322.

Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M., Charnov, E.L., 2001. Effects of size and temperature on metabolic rate. Science 293, 2248–2251. http://dx.doi.org/10.1126/science.1061967.

Golyandina, N., Korobeynikov, A., 2014. Basic Singular Spectrum Analysis and forecasting with R. Computational Statistics & Data Analysis 71, 934–954. http://dx.doi.org/10.1016/j.csda.2013.04.009.

Golyandina, N., Korobeynikov, A., Shlemov, A., Usevich, K., 2013. Multivariate and 2D extensions of Singular Spectrum Analysis with the Rssa package. Journal of Statistical Software 67, 1–78. http://dx.doi.org/10.18637/jss.v067.i02.

Graf, A., Weihermüller, L., Huisman, J.A., Herbst, M., Vereecken, H., 2011. Comment on "Global convergence in the temperature sensitivity of respiration at ecosystem level". Science 331http://dx.doi.org/10.1126/science.1196948. 1265–1265.

Gu, L.H., Hanson, P.J., Mac Post, W., Liu, Q., 2008. A novel approach for identifying the true temperature sensitivity from soil respiration measurements. Global Biogeochemical Cycles 22, GB4009. http://dx.doi.org/10.1029/2007gb003164.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A., Ekblad, A., Högberg, M., Nyberg, G., Ottosson-Löfvenius, M., Read, D., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–792. http://dx.doi.org/10.1038/35081058.

Jones, C.D., Cox, P., Huntingford, C., 2003. Uncertainty in climate–carbon–cycle projections associated with the sensitivity of soil respiration to temperature. Tellus B 55, 642–648. http://dx.doi.org/10.1034/j.1600-0889.2003.01440.x.

Knorr, W., Prentice, I.C., House, J.I., Holland, E.A., 2005. Long-term sensitivity of soil

carbon turnover to warming. Nature 433, 298–301. http://dx.doi.org/10.1038/nature03226.

Kuzyakov, Y., Gavrichkova, O., 2010. Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. Global Change Biology 16, 3386–3406. http://dx.doi.org/10.1111/j.1365-2486.2010.02179.x.

Liang, N., Inoue, G., Fujinuma, Y., 2003. A multichannel automated chamber system for continuous measurement of forest soil CO_2 efflux. Tree Physiology 23, 825–832. http://dx.doi.org/10.1093/treephys/23.12.825.

Liu, L., Wang, X., Lajeunesse, M.J., Miao, G., Piao, S., Wan, S., Wu, Y., Wang, Z., Yang, S., Li, P., Deng, M., 2016. A cross-biome synthesis of soil respiration and its determinants under simulated precipitation changes. Global Change Biology 22, 1394–1405. http://dx.doi.org/10.1111/gcb.13156.

Liu, W.X., Zhang, Z., Wan, S.Q., 2009. Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. Global Change Biology 15, 184–195. http://dx.doi.org/10.1111/j.1365-2486.2008.01728.x.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Functional Ecology 8, 315–323. http://dx.doi.org/10.2307/2389824.

López-Urrutia, Á., San Martin, E., Harris, R.P., Irigoien, X., 2006. Scaling the metabolic balance of the oceans. Proceedings of the National Academy of Sciences 103, 8739–8744. http://dx.doi.org/10.1073/pnas.0601137103.

Luo, Y.Q., 2007. Terrestrial carbon-cycle feedback to climate warming. Annual Review of Ecology Evolution and Systematics 38, 683–712. http://dx.doi.org/10.1146/annurev.ecolsys.38.091206.095808.

Luo, Y.Q., Wan, S.Q., Hui, D.F., Wallace, L.L., 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413, 622–625. http://dx.doi.org/10.1038/35098065.

Mahecha, M.D., Reichstein, M., Carvalhais, N., Lasslop, G., Lange, H., Seneviratne, S.I., Vargas, R., Ammann, C., Arain, M.A., Cescatti, A., Janssens, I.A., Migliavacca, M., Montagnani, L., Richardson, A.D., 2010. Global convergence in the temperature sensitivity of respiration at ecosystem level. Science 329, 838–840. http://dx.doi.org/10.1126/science.1189587.

Melillo, J.M., Steudler, P.A., Aber, J.D., Newkirk, K., Lux, H., Bowles, F.P., Catricala, C., Magill, A., Ahrens, T., Morrisseau, S., 2002. Soil warming and carbon-cycle feedbacks to the climate system. Science 298, 2173–2176. http://dx.doi.org/10.1126/science.1074153.

Morowitz, H.J., Kostelnik, J.D., Yang, J., Cody, G.D., 2000. The origin of intermediary metabolism. Proceedings of the National Academy of Sciences 97, 7704–7708. http://dx.doi.org/10.1073/pnas.110153997.

Pavelka, M., Acosta, M., Marek, M.V., Kutsch, W., Janous, D., 2007. Dependence of the Q_{10} values on the depth of the soil temperature measuring point. Plant and Soil 292, 171–179. http://dx.doi.org/10.1007/s11104-007-9213-9.

Peng, S.S., Piao, S.L., Wang, T., Sun, J.Y., Shen, Z.H., 2009. Temperature sensitivity of soil respiration in different ecosystems in China. Soil Biology and Biochemistry 41, 1008–1014. http://dx.doi.org/10.1016/j.soilbio.2008.10.023.

Perkins, D.M., Yvon-Durocher, G., Demars, B.O.L., Reiss, J., Pichler, D.E., Friberg, N., Trimmer, M., Woodward, G., 2012. Consistent temperature dependence of respiration across ecosystems contrasting in thermal history. Global Change Biology 18, 1300–1311. http://dx.doi.org/10.1111/j.1365-2486.2011.02597.x.

Phillips, C.L., Nickerson, N., Risk, D., Bond, B.J., 2011. Interpreting diel hysteresis between soil respiration and temperature. Global Change Biology 17, 515–527. http://dx.doi.org/10.1111/j.1365-2486.2010.02250.x.

R Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Randerson, J.T., Hoffman, F.M., Thornton, P.E., Mahowald, N.M., Lindsay, K., Lee, Y., Nevison, C.D., Doney, S.C., Bonan, G., Stöckli, R., Covey, C., Running, S.W., Fung, I.Y., 2009. Systematic assessment of terrestrial biogeochemistry in coupled climate–carbon models. Global Change Biology 15, 2462–2484. http://dx.doi.org/10.1111/j.1365-2486.2009.01912.x.

Raven, J.A., Geider, R.J., 1988. Temperature and algal growth. New Phytologist 110, 441–461. http://dx.doi.org/10.1111/j.1469-8137.1988.tb00282.x.

Regaudie-de-Gioux, A., Duarte, C.M., 2012. Temperature dependence of planktonic metabolism in the ocean. Global Biogeochemical Cycles 26, GB1015. http://dx.doi.org/10.1029/2010GB003907.

Reichstein, M., Beer, C., 2008. Soil respiration across scales: the importance of a model-data integration framework for data interpretation. Journal of Plant Nutrition and Soil Science 171, 344–354. http://dx.doi.org/10.1002/jpln.200700075.

Reichstein, M., Falge, E., Baldocchi, D., Papale, D., Aubinet, M., Berbigier, P., Bernhofer, C., Buchmann, N., Gilmanov, T., Granier, A., Grünwald, T., Havránková, K., Ilvesniemi, H., Janous, D., Knohl, A., Laurila, T., Lohila, A., Loustau, D., Matteucci, G., Meyers, T., Miglietta, F., Ourcival, J.M., Pumpanen, J., Rambal, S., Rotenberg, E., Sanz, M., Tenhunen, J., Seufert, G., Vaccari, F., Vesala, T., Yakir, D., Valentini, R., 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Global Change Biology 11, 1424–1439. http://dx.doi.org/10.1111/j.1365-2486.2005.001002.x.

Reyes-Fox, M., Steltzer, H., Trlica, M., McMaster, G.S., Andales, A.A., LeCain, D.R., Morgan, J.A., 2014. Elevated CO_2 further lengthens growing season under warming conditions. Nature 510, 259–262. http://dx.doi.org/10.1038/nature13207.

Savage, K., Davidson, E.A., Tang, J., 2013. Diel patterns of autotrophic and heterotrophic respiration among phenological stages. Global Change Biology 19, 1151–1159. http://dx.doi.org/10.1111/gcb.12108.

Selsted, M.B., van der Linden, L., Ibrom, A., Michelsen, A., Larsen, K.S., Pedersen, J.K., Mikkelsen, T.N., Pilegaard, K., Beier, C., Ambus, P., 2012. Soil respiration is stimulated by elevated CO_2 and reduced by summer drought: three years of measurements in a multifactor ecosystem manipulation experiment in a temperate heathland (CLIMAITE). Global Change Biology 18, 1216–1230. http://dx.doi.org/10.1111/j.1365-2486.2011.02634.x.

Shi, Y., Baumann, F., Ma, Y., Song, C., Kühn, P., Scholten, T., He, J.-S., 2012. Organic and inorganic carbon in the topsoil of the Mongolian and Tibetan grasslands: pattern, control and implications. Biogeosciences 9, 2287–2299. http://dx.doi.org/10.5194/bg-9-2287-2012.

Suseela, V., Conant, R.T., Wallenstein, M.D., Dukes, J.S., 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. Global Change Biology 18, 336–348. http://dx.doi.org/10.1111/j.1365-2486.2011.02516.x.

Suseela, V., Dukes, J.S., 2013. The responses of soil and rhizosphere respiration to simulated climatic changes vary by season. Ecology 94, 403–413. http://dx.doi.org/10.1890/12-0150.1.

Tan, K., Ciais, P., Piao, S.L., Wu, X.P., Tang, Y.H., Vuichard, N., Liang, S., Fang, J.Y., 2010. Application of the ORCHIDEE global vegetation model to evaluate biomass and soil carbon stocks of Qinghai-Tibetan grasslands. Global Biogeochemical Cycles 24, GB1013. http://dx.doi.org/10.1029/2009GB003530.

Tang, J., Baldocchi, D.D., Xu, L., 2005. Tree photosynthesis modulates soil respiration on a diurnal time scale. Global Change Biology 11, 1298–1304. http://dx.doi.org/10.1111/j.1365-2486.2005.00978.x.

Todd-Brown, K.E.O., Randerson, J.T., Hopkins, F., Arora, V., Hajima, T., Jones, C., Shevliakova, E., Tjiputra, J., Volodin, E., Wu, T., Zhang, Q., Allison, S.D., 2014. Changes in soil organic carbon storage predicted by Earth system models during the 21st century. Biogeosciences 11, 18969–19004. http://dx.doi.org/10.5194/bg-11-2341-2014.

Todd-Brown, K.E.O., Randerson, J.T., Post, W.M., Hoffman, F.M., Tarnocai, C., Schuur, E.A.G., Allison, S.D., 2013. Causes of variation in soil carbon simulations from CMIP5 Earth system models and comparison with observations. Biogeosciences 10, 1717–1736. http://dx.doi.org/10.5194/bg-10-1717-2013.

Vargas, R., Baldocchi, D.D., Bahn, M., Hanson, P.J., Hosman, K.P., Kulmala, L., Pumpanen, J., Yang, B., 2011. On the multi-temporal correlation between photosynthesis and soil CO_2 efflux: reconciling lags and observations. New Phytologist 191, 1006–1017. http://dx.doi.org/10.1111/j.1469-8137.2011.03771.x.

Vargas, R., Detto, M., Baldocchi, D.D., Allen, M.F., 2010. Multiscale analysis of temporal variability of soil CO_2 production as influenced by weather and vegetation. Global Change Biology 16, 1589–1605. http://dx.doi.org/10.1111/j.1365-2486.2009.02131.x.

Vetter, R., 1995. Ecophysiological studies on citrate-synthase:(I) enzyme regulation of selected crustaceans with regard to temperature adaptation. Journal of Comparative Physiology B 165, 46–55. http://dx.doi.org/10.1007/BF00264685.

Wan, S., Norby, R.J., Ledford, J., Weltzin, J.F., 2007. Responses of soil respiration to elevated CO_2, air warming, and changing soil water availability in a model old-field grassland. Global Change Biology 13, 2411–2424. http://dx.doi.org/10.1111/j.1365-2486.2007.01433.x.

Wang, S.P., Duan, J.C., Xu, G.P., Wang, Y.F., Zhang, Z.H., Rui, Y.C., Luo, C.Y., Xu, B., Zhu, X.X., Chang, X.F., Cui, X.Y., Niu, H.S., Zhao, X.Q., Wang, W.Y., 2012. Effects of warming and grazing on soil N availability, species composition, and ANPP in an alpine meadow. Ecology 93, 2365–2376. http://dx.doi.org/10.1890/11-1408.1.

Wang, X., Liu, L., Piao, S., Janssens, I.A., Tang, J., Liu, W., Chi, Y., Wang, J., Xu, S., 2014a. Soil respiration under climate warming: differential response of heterotrophic and autotrophic respiration. Global Change Biology 20, 3229–3237. http://dx.doi.org/10.1111/gcb.12620.

Wang, X.H., Piao, S.L., Ciais, P., Janssens, I.A., Reichstein, M., Peng, S.S., Wang, T., 2010. Are ecological gradients in seasonal Q_{10} of soil respiration explained by climate or by vegetation seasonality? Soil Biology and Biochemistry 42, 1728–1734. http://dx.doi.org/10.1016/j.soilbio.2010.06.008.

Wang, Y., Liu, H., Chung, H., Yu, L., Mi, Z., Geng, Y., Jing, X., Wang, S., Zeng, H., Cao, G., Zhao, X., He, J.-S., 2014b. Non-growing-season soil respiration is controlled by freezing and thawing processes in the summer-monsoon-dominated Tibetan alpine grassland. Global Biogeochemical Cycles 28, 1081–1095. http://dx.doi.org/10.1002/2013gb004760.

Xu, L.K., Baldocchi, D.D., 2004. Seasonal variation in carbon dioxide exchange over a Mediterranean annual grassland in California. Agricultural and Forest Meteorology 123, 79–96. http://dx.doi.org/10.1016/j.agrformet.2003.10.004.

Xu, M., Qi, Y., 2001. Spatial and seasonal variations of Q_{10} determined by soil respiration measurements at a Sierra Nevadan forest. Global Biogeochemical Cycles 15, 687–696. http://dx.doi.org/10.1029/2000GB001365.

Xu, X., Shi, Z., Li, D., Zhou, X., Sherry, R.A., Luo, Y., 2015. Plant community structure regulates responses of prairie soil respiration to decadal experimental warming. Global Change Biology 21, 3846–3853. http://dx.doi.org/10.1111/gcb.12940.

Yang, Y.H., Fang, J.Y., Tang, Y.H., Ji, C.J., Zheng, C.Y., He, J.S., Zhu, B., 2008. Storage, patterns and controls of soil organic carbon in the Tibetan grasslands. Global Change Biology 14, 1592–1599. http://dx.doi.org/10.1111/j.1365-2486.2008.01591.x.

Yu, L., Wang, H., Wang, G., Song, W., Huang, Y., Li, S.-G., Liang, N., Tang, Y., He, J.-S., 2013. A comparison of methane emission measurements using eddy covariance and manual and automated chamber-based techniques in Tibetan Plateau alpine wetland. Environmental Pollution 181, 81–90. http://dx.doi.org/10.1016/j.envpol.2013.06.018.

Yvon-Durocher, G., Caffrey, J.M., Cescatti, A., Dossena, M., del Giorgio, P., Gasol, J.M., Montoya, J.M., Pumpanen, J., Staehr, P.A., Trimmer, M., Woodward, G., Allen, A.P., 2012. Reconciling the temperature dependence of respiration across timescales and ecosystem types. Nature 487, 472–476. http://dx.doi.org/10.1038/nature11205.

Zhuang, Q., He, J., Lu, Y., Ji, L., Xiao, J., Luo, T., 2010. Carbon dynamics of terrestrial ecosystems on the Tibetan Plateau during the 20th century: an analysis with a process-based biogeochemical model. Global Ecology and Biogeography 19, 649–662. http://dx.doi.org/10.1111/j.1466-8238.2010.00559.x.