Forest soil respiration and its heterotrophic and autotrophic components: Global patterns and responses to temperature and precipitation

Wang Wei*, Chen Weile, Wang Shaopeng

Department of Ecology, College of Urban and Environmental Sciences, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, Beijing 100871, China

ABSTRACT

Quantifying global patterns of forest soil respiration (SR), its components of heterotrophic respiration (HR) and belowground autotrophic respiration (AR), and their responses to temperature and precipitation are vital to accurately evaluate responses of the terrestrial carbon balance to future climate change. There is great uncertainty associated with responses of SR to climate change, concerning the differences in climatic controls and apparent Q_{10} (the factor by which respiration increases for a 10 °C increase in temperature) over HR and AR. Here, we examine available information on SR, HR, AR, the contribution of HR to SR (HR/SR), and Q_{10} of SR and its components from a diverse global database of forest ecosystems. The goals were to test how SR and its two components (AR and HR) respond to temperature and precipitation changes, and to test the differences in apparent Q_{10} between AR and HR. SR increased linearly with mean annual temperature (MAT), but responded non-linearly to mean annual precipitation (MAP) in naturally-regenerated forests. For every 1 °C increase in MAT, overall emissions from SR increased by 24.6 g C m^{-2} yr^{-1}. When MAP was less than 813 mm, every 100 mm increase in MAP led to a release of 75.3 g C m^{-2} yr^{-1}, but the increase rate declined to 20.3 g C m^{-2} yr^{-1} when MAP was greater than 813 mm. MAT explained less variation in AR than that in HR. The overall emissions in AR and HR for every 1 °C increase in MAT, increased by 12.9 and 16.1 g C m^{-2} yr^{-1}, respectively. The AR emissions for every 100 mm increase in MAP, increased by 44.5 g C m^{-2} yr^{-1} when MAP less than 1000 mm. However, above the threshold, AR emissions stayed relatively constant. HR increased linearly by 15.0 g C m^{-2} yr^{-1} with every 100 mm increased in MAP. The Q_{10} value of SR increased with increasing depth at which soil temperature was measured up to 10 cm and was negatively correlated with HR/SR. Our synthesis suggests AR and HR differ in their responses to temperature and precipitation change. We also emphasized the importance of information on soil temperature measurement depth when applying field estimation of Q_{10} values into current terrestrial ecosystem models. Q_{10} values derived from field SR measurements including AR, will likely overestimate the temperature response of HR on a future warmer earth.

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1. Introduction

Forest soil respiration (SR) is the primary pathway by which plant-fixed CO_2 is released back to the atmosphere (Högberg and Read, 2006; Gaumont-Guay et al., 2009), arising from the activity from roots and their associated mycorrhizal fungi (belowground autotrophic respiration, AR) and of heterotrophic respiration (HR) (Hanson et al., 2000; Subke et al., 2006). Because of large annual fluxes of carbon between forest ecosystems and the atmosphere (Bonan, 2008; Luyssaert et al., 2008), these ecosystems are likely to influence the global carbon balance in response to projected climate change (Dixon et al., 1994; Grace and Rayment, 2000; Savage et al., 2008). The net effect of climate change on an ecosystem carbon budget depends on the impact of changes in climatic parameters on photosynthesis and respiration (Schulze et al., 2000; Campbell et al., 2007). While our knowledge of the assimilatory component of the carbon balance (photosynthesis) and its response to climate change is well known (Mellilo et al., 1993; Litton and Giardina, 2008), there are considerable gaps in our understanding of the responses of SR to climate change (Trumbore, 2006; Davidson et al., 2006).

Mean annual temperature (MAT) is predicted to rise by 1.8–4.0 °C, and precipitation frequency and intensity are predicted to change at both regional and global scales over the next century (IPCC, 2007). At the global scale, SR is linearly correlated with MAT and mean annual precipitation (MAP) (Raich and Schlesinger, 1992; Schimel et al., 2001; Raich et al., 2002; Schuur, 2003). However,

most ecological processes respond non-linearly to environmental changes (Briske et al., 2006; Sasaki et al., 2008). For example, Luyssaert et al. (2007) found that canopy photosynthesis (gross primary production; GPP) initially increased linearly with MAP, but the response saturated at 1500 mm MAP. SR has been found to be strongly related to aboveground plant processes (Högberg et al., 2001) and thus may respond non-linearly to climate change. Furthermore, AR and HR may respond differently to changing temperature and moisture (Boone et al., 1998). However, little is known about the general pattern of SR and its two components for global forests.

Another important uncertainty in predicting ecosystem carbon cycling within the context of climate change is the sensitivity of SR and its two components to temperature (Cox et al., 2000; Luo et al., 2001; Baath and Wallander, 2003; Reichstein et al., 2003; Davidson and Janssens, 2006). There are two measures for temperature sensitivity, including intrinsic temperature sensitivity and apparent temperature sensitivity (Davidson and Janssens, 2006). The former is the theoretic sensitivity determined by molecular structure, while the latter is the observed temperature sensitivity determined by both molecular structure and environmental constraints caused by heterogeneous soil properties. Hereafter, the temperature sensitivity in this study is stated for apparent temperature sensitivity. AR utilizes fresh photosynthates (Högberg et al., 2001), while HR derives from the mineralization of soil organic matter which is stored in large stocks (Fang et al., 2005; Knorr et al., 2005; Reichstein et al., 2005). However, most simulation models of regional and global carbon cycles use a single, fixed, Q_{10} coefficient (defined as the increase in respiration rate per $10\,^{\circ}C$ increase in temperature) to express this temperature sensitivity (Kirschbaum, 2006). Eventual differences in the temperature sensitivities of AR and HR may compromise modeling results of future soil C dynamics and atmospheric CO_2 concentrations (Zhou et al., 2009). Despite a growing body of information on SR (Hibbard et al., 2005; Bond-Lamberty and Thomson, 2010), the information on apparent Q_{10} of AR and HR is highly controversial (Boone et al., 1998; Epron et al., 1999; Giardina and Ryan, 2000; Rey et al., 2002; Baath and Wallander, 2003; Lavigne et al., 2003; Bhupinderpal-Singh et al., 2003; Schindlbacher et al., 2008).

In the past two decades, numerous studies on SR have been conducted across different forest types of the world, and some global databases have been established (Raich and Schlesinger, 1992; Hanson et al., 2000; Bond-Lamberty et al., 2004; Luyssaert et al., 2007; Bond-Lamberty and Thomson, 2010). However, information from these databases needs to be synthesized to address some of the remaining uncertainties. We assembled a new comprehensive global database, which included SR, HR, AR, HR/SR, and Q_{10} of SR, as well as ancillary site information, such as climate and vegetation types (Supplement Table 1). This new data set enabled us to test (1) how SR and its two components (AR and HR) respond to temperature and precipitation changes and (2) the differences in apparent Q_{10} between AR and HR.

2. Material and methods

We collected data related to forest SR, HR and AR from published databases such as the ones of Raich and Schlesinger (1992), Hanson et al. (2000), Bond-Lamberty et al. (2004), Lee et al. (2006), Subke et al. (2006), Luyssaert et al. (2007) and many published papers in English and Chinese, from additional studies of forest sites that were not included in these earlier syntheses (Supplement Table 1). For annual SR data, we only used estimates with one or more years of direct field measurements. We excluded data from forest sites that had been burned or fertilized and sites used for climate change experiments (increased temperature, precipitation, or CO_2 concentration). AR herein represents the combination of root respiration,

respiration of their mycorrhizal fungi, and respiration of rhizosphere microorganisms (Högberg and Read, 2006). HR or AR data derived mostly from the data set of Hanson et al. (2000), Bond-Lamberty et al. (2004) and Luyssaert et al. (2007), and the measurement methods are also described in Supplement Table 1.

We separated naturally-regenerated forests from plantations because no significant relationship was found between SR and MAT or MAP for plantations (Supplement Fig. 1; $P > 0.05$), unlike for naturally-regenerated sites. We therefore used information only from naturally-regenerated sites in the study of climatic control on SR. In naturally-regenerated forests, each study site was classified by four forest types: deciduous broadleaf forest (DBF), evergreen broadleaf forest (EBF), evergreen needleleaf forest (ENF) and needle and broadleaf mixed forest (MF).

MAT and MAP for each study site were extracted from literatures. A global climate database was used to estimate climate data for sites where original climate data were unavailable (Hijmans et al., 2005). Among all of climate data in our database, the observed vs. inferred values were 222 vs. 103 for MAT and 221 vs. 104 for MAP. In order to test the accuracy of inferred climate data using global climate database, we used the latitude and longitude information of the observed sites to infer their MAT and MAP. Through comparing the inferred values with the observed ones, we found that MAT could be simulated well, and MAP was slightly less than it's observed ones (Fig. 1). Sites from our data set span a wide gradient of forest types and climates (MAT: -5–$27\,^{\circ}C$; MAP: 270–4250 mm, Supplement Table 1).

When available, Q_{10} of SR was summarized from every paper, as well as from Peng et al. (2009) (Chinese Q_{10} data set) and Hashimoto (2005) (Japanese Q_{10} data set). It is worth pointing out that the temperature sensitivity reported in the studies we use for our analysis is the apparent temperature sensitivity. The methods used to determine Q_{10} of SR are critical, with larger values occurring in laboratory incubation studies than in soil warming experiments or in field observations (Gu et al., 2004). To avoid method-induced bias, we only selected Q_{10} data from *in situ* field studies calculated by the van't Hoff equation ($SR = a \times e^{\beta T}$; $Q_{10} = e^{10\beta}$) (Van't Hoff, 1898), which provides a measure of apparent temperature sensitivity (Reichstein et al., 2003; Davidson and Janssens, 2006; Kirschbaum, 2006).

Within these constraints, we obtained 321 data sets from 174 publications available for analysis. Of these, 294 data sets from 161 publications contained the estimates for annual SR, 124 data sets contained AR (or HR) estimates from 69 publications, 185 data sets contained Q_{10} of SR from 69 publications and 13 data sets contained Q_{10} of HR and AR from 8 publications (Supplement Table 1). Geographic distribution of the sites contained in the database is shown in Fig. 2.

In order to test whether measurement depth of soil temperature influences the estimation of Q_{10} values, we compared Q_{10} values calculated by the soil temperature at five different depths (ST_0 (soil surface temperature), ST_5 (soil temperature at 5 cm), ST_{10} (soil temperature at 10 cm), ST_{15} (soil temperature at 15 cm), and ST_{20} (soil temperature at 20 cm)) for the same site. Paired t-test was used to compare the Q_{10} values among different measurement depths. In addition, we tested the role of forest types on Q_{10} at 5 cm soil depth because most studies reported Q_{10} values calculated from ST_5, to remove the effect of measurement depth bias. One-way ANOVA was used to evaluate whether Q_{10} values significantly differed among forest types.

To characterize the responses of SR, AR, and HR to climate change, we analyzed the data using a bent-cable form of a piecewise-regression model (Toms and Lesperance, 2003), to identify critical thresholds for climate changes. The piecewise-regression is a "broken-stick" model, where two or more lines are joined at
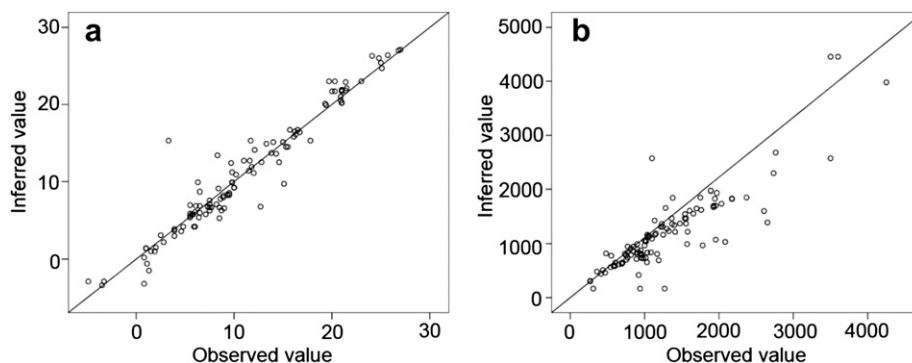
Fig. 1. Comparison of MAT (a) and MAP (b) between observed values and inferred ones from global climate database. Linear regression equations between observed and inferred values were $Y = 1.02\,X - 0.216$ for MAT ($R^2 = 0.94$, $P < 0.001$) and $Y = 0.886\,X + 49.7$ ($R^2 = 0.77$, $P < 0.001$). MAT = Mean Annual Temperature; MAP = Mean Annual Precipitation.

unknown point(s), called breakpoint(s), representing the threshold (s) (Toms and Lesperance, 2003). When the slopes before and after the breakpoint were significantly different, piecewise-regression models were used; otherwise, a simple linear regression model was adopted. Generally, the piecewise-regression method attempts to detect one or more potential breakpoints and fits linear trends before and after each breakpoint. The optimal solutions for the model are the breakpoints and phase slopes that minimize the residual sum of squares. In our calculations, restriction was made because our data points clustered in the median of MAT or MAP, so we assumed that only one breakpoint existed in each series, to avoid breakpoints occurring at the ends of the regression curve.

To test the differences of apparent Q_{10} between AR and HR, the relationships between HR, AR, HR/SR and the magnitude of the warming response (Q_{10} of SR at 5 cm soil depth) were examined using linear regression. All statistical analyses were performed with a significance level of 0.05 with R software (version 2.4.1).

3. Results and discussions

3.1. SR and its climatic controls

Observed SR in naturally-regenerated forests ranged from 220 to 2560 g C m^{-2} yr^{-1}. These data derived mostly from boreal and temperate areas (Fig. 2), which were well represented. However, there were very few measurements from tropical area; the lack of measurements in this area represented a major deficiency in estimating global forest SR. Therefore, despite an abundance of SR data, global coverage is poor. Raich and Schlesinger (1992) reported that SR averaged 322, 662 and 1092 g C m^{-2} yr^{-1} for boreal, temperate and tropical forests, which were significantly lower than our estimates of 521, 900 and 1489 g C m^{-2} yr^{-1} for boreal, temperate and tropical forests, respectively. This discrepancy may be due to the method used. In earlier studies, SR was mainly measured by alkaline absorption method. This method was shown to underestimate

SR (Janssens et al., 2001; Kabwe et al., 2002). SR was higher in EBF (1189.4 ± 79.8 g C m^{-2} yr^{-1} (mean ± SE)), and lower in ENF (650.4 ± 37.4 g C m^{-2} yr^{-1} (mean ± SE)). Overall SR increased linearly with MAT (Fig. 3). For every 1 °C increase in MAT, overall emissions from SR increased by 24.6 g C m^{-2} yr^{-1}. This was similar to the mean increase rate for global vegetation (25.6 g m^{-2} year^{-1}) (Raich and Schlesinger, 1992) and higher than that of global grasslands (16.5 g m^{-2} year^{-1}) (Wang and Fang, 2009). Within four forest types, this linear positive relationship still existed (Fig. 4).

Unlike to MAT, SR responded non-linearly to MAP with a breakpoint of 813 mm (Fig. 5). Below the threshold, for every 100 mm increase in MAP, additional 75.3 g C m^{-2} yr^{-1} was released. However, once that threshold was exceeded, the increase rate declined to 20.3 g C m^{-2} yr^{-1} (Fig. 5). For global vegetation, Raich and Schlesinger (1992) reported that SR increased linearly with MAP, and showed that for every 100 mm increase in MAP, SR released additional 40 g C m^{-2} yr^{-1}. The different response of SR to MAP was mainly due to the difference in regression method used. The simple linear model used by Raich and Schlesinger (1992) is a special case of piecewise-regression model, in which the values for the two slopes are identical. When a simple linear regression was used through our results, SR released additional 27 g C m^{-2} yr^{-1} for every 100 mm increase in MAP. Our estimate was below to that of global vegetation (Raich and Schlesinger, 1992).

Fig. 2. Geographic distribution of the sites contained in the database.
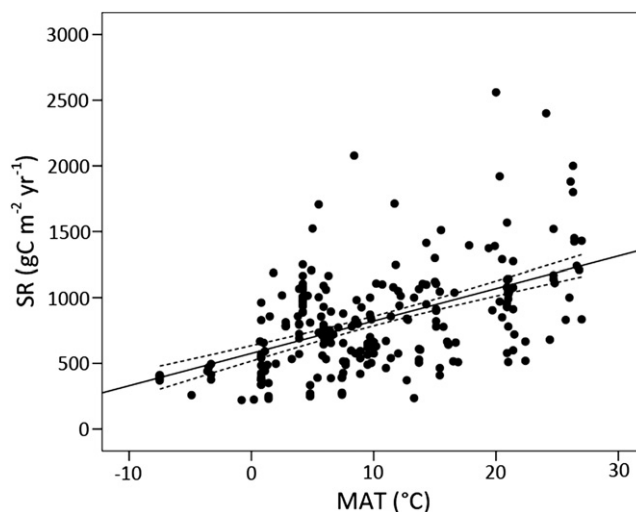

Fig. 3. SR correlates linearly with MAT in naturally-regenerated forests ($Y = 576 + 24.6\,X$; $R^2 = 0.26$, $P < 0.001$). SR = Soil Respiration. MAT = Mean Annual Temperature. Dash lines showed 95% confidence intervals.
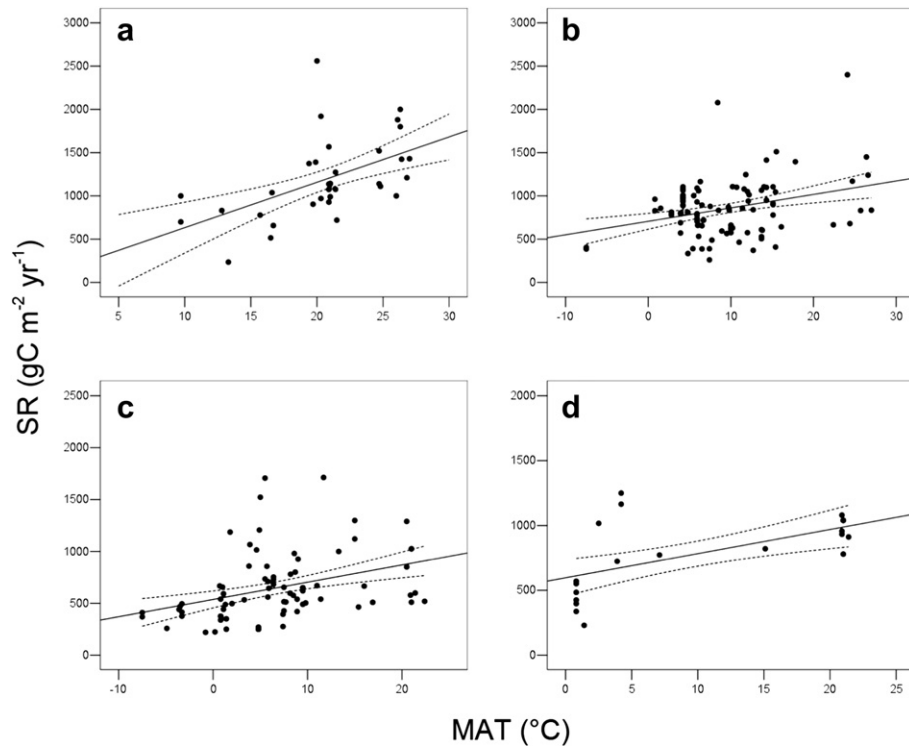
Fig. 4. SR correlates linearly with MAT within evergreen broadleaf forest (EBF) (a: $Y = 109 + 52.4\ X$; $R^2 = 0.28$, $P = 0.001$), deciduous broadleaf forest (DBF) (b: $Y = 706 + 15.5\ X$; $R^2 = 0.10$, $P = 0.002$), evergreen needleleaf forest (ENF) (c: $Y = 537 + 16.6\ X$; $R^2 = 0.13$, $P < 0.001$) and needle and broadleaf mixed forest (MF) (d: $Y = 597 + 18.6\ X$; $R^2 = 0.34$, $P = 0.008$). MAT = Mean Annual temperature. SR = Soil Respiration. Dash lines showed 95% confidence intervals.

Different forest types differed in their responses to MAP (Fig. 6). SR increased linearly with MAP, when below the thresholds of 1800 mm, 1113 mm and 813 mm for EBF, ENF and MF, respectively; every 100 mm increase in MAP, additional emissions were released by 79, 62, 140 g C m^{-2} yr^{-1} for EBF, ENF, MF, respectively. However,

when above these thresholds, SR kept relatively constant (Fig. 6). In DBF, SR increased linearly by 14.6 g C m^{-2} yr^{-1} with 100 mm increased in MAP.

3.2. Climatic control over HR and AR

On a global scale, both HR and AR were positively and linearly correlated with MAT (Fig. 7a, c). MAT explained 29% and 12% of the variation in HR and AR, respectively, indicating that AR was less influenced by MAT than HR. Two possible mechanisms could account for the fact that AR had a lower dependence on temperature. First, AR has been reported to be more dependent on photosynthesis than on temperature (Högberg et al., 2001; Bhupinderpal-Singh et al., 2003; Edwards et al., 2004; Heinemeyer et al., 2007). Root respiration (Luo et al., 2001; Hartley et al., 2007a) and root-associated respiration of ectomycorrhizal (Malcolm et al., 2008) and arbuscular mycorrhizal fungi (Heinemeyer et al., 2006) were reported to be relatively insensitive to temperature when compared with the temperature sensitivity of HR. This higher dependence on photosynthetic substrate supply may therefore reduce the dependence of AR on temperature (Kirschbaum, 2006). When we pooled the values for DBF and ENF with relatively sufficient observation numbers, we confirmed that MAT explained less variation in AR than HR (Table 1), especially in DBF. In addition, physiology and phenology of trees may play important roles in determining the amount of roots active at particular times of the year (Lenton and Huntingford, 2003). For example, AR was found to peak in spring, coinciding not only with high temperatures but also with leaf flush, and to peak again in autumn prior to litterfall (Dickmann et al., 1996).

AR and HR also responded differently to MAP. HR increased linearly with MAP (Fig. 7d). AR responded non-linearly to MAP with the threshold of 1000 mm. Before the threshold, AR increase by
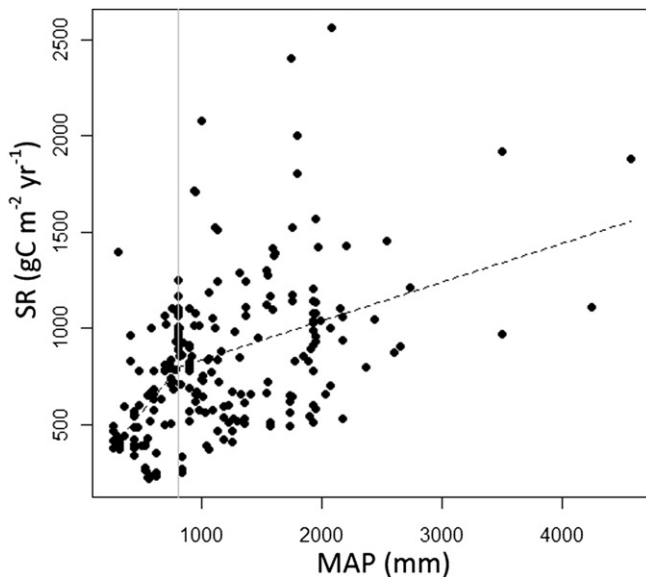

Fig. 5. Response of SR to MAP in naturally-regenerated forests. The breakpoint occurred at 813 mm MAP ($P = 0.003$) with 95% confidence interval between 640 mm and 1106 mm ($R^2 = 0.26$, $P < 0.001$). Before the breakpoint, slope = 0.753, $P < 0.001$; after the breakpoint, slope = 0.203, $P < 0.001$. SR = Soil Respiration, MAP = Mean Annual Precipitation.
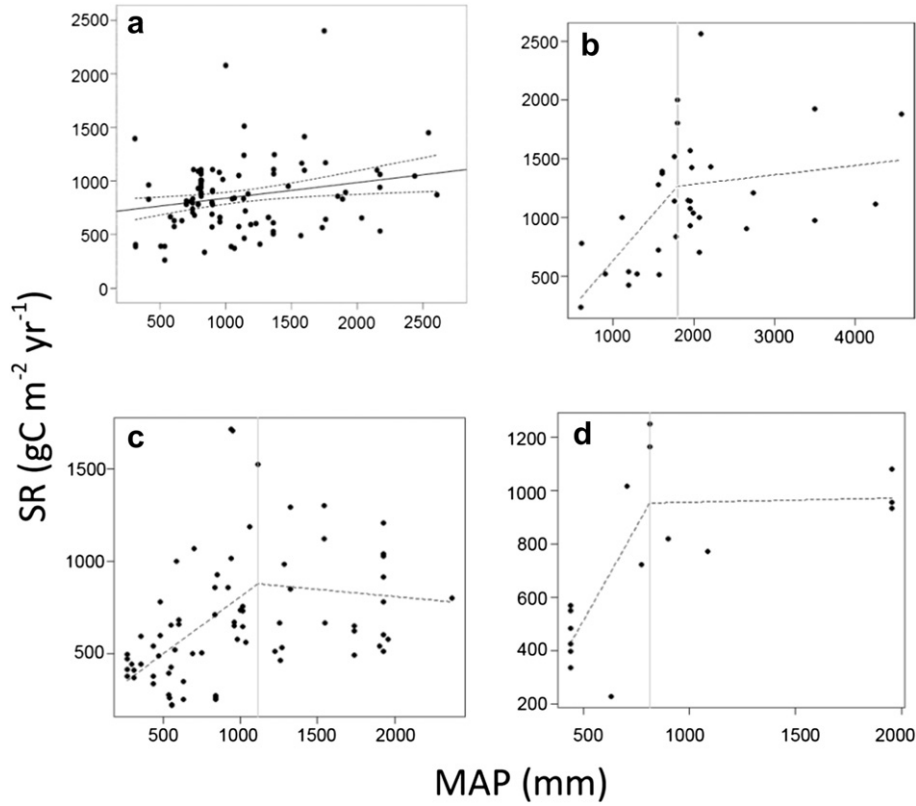
Fig. 6. Response of SR to MAP within deciduous broadleaf forest (DBF) (a: $Y = 693 + 0.146 X$; $R^2 = 0.34$, $P = 0.026$), evergreen broadleaf forest (EBF) (b: breakpoint = 1800 mm, $P = 0.02$, $R^2 = 0.34$; when MAP < 1800 mm, slope = 0.79, $P < 0.05$; when MAP > 1800 mm, slope = 0.08, $P > 0.05$), evergreen needleleaf forest (ENF) (c: breakpoint = 1113 mm, $P = 0.004$, $R^2 = 0.26$; when MAP < 1113 mm, slope = 0.62, $P < 0.05$; when MAP > 1113 mm, slope = −0.08, $P > 0.05$) and needle and broadleaf mixed forest (MF) (d: breakpoint = 813 mm, $P = 0.006$, $R^2 = 0.64$; when MAP < 813 mm, slope = 1.40, $P < 0.05$; when MAP > 813 mm, slope = 0.02, $P > 0.05$). MAT = Mean Annual Temperature. SR = Soil Respiration. Dash lines (a) showed 95% confidence intervals.
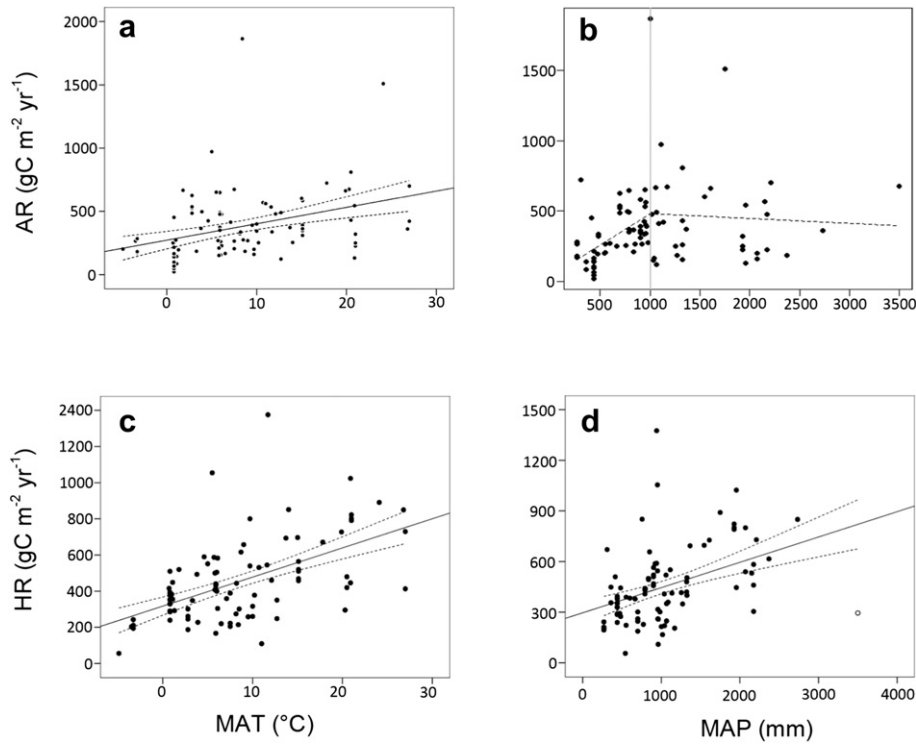

Fig. 7. AR responded linearly to MAT (a: $Y = 273 + 12.9 X$; $R^2 = 0.12$, $P = 0.001$). AR responded non-linearly to MAP. The breakpoint occurred in 1000 mm MAP with 95% confidence intervals between 580 mm and 1655 mm ($P = 0.004$, $R^2 = 0.15$); when MAP < 1000 mm, slope = 0.445, $P < 0.05$; when MAP > 1000 mm, slope = −0.035, $P > 0.05$; HR responded linearly to both MAT (c: $Y = 317 + 16.1 X$; $R^2 = 0.29$, $P < 0.001$) and MAP (d: $Y = 296 + 0.15 X$; $R^2 = 0.17$, $P < 0.001$). MAT = Mean Annual Temperature; MAP = Mean Annual Precipitation; HR = Heterotrophic Respiration; AR = Autotrophic Respiration. Dash lines in linear regression showed 95% confidence intervals.

Table 1
Correlation between MAT (mean annual temperature) and AR (autotrophic respiration) and between MAT and HR (heterotrophic respiration) in deciduous broadleaf forest (DBF) and evergreen needleleaf forest (ENF).

	N	AR		HR	
		R^2	P	R^2	P
DBF	37	0.03	0.31	0.28	0.001
ENF	39	0.12	0.03	0.17	0.01

Note: N = sample size.

44.5 g C m^{-2} yr^{-1} for every 100 mm increased MAP. After the threshold, AR kept relatively constant (Fig. 7b). The difference may be connected with the strong dependence of AR on plant activity (Högberg et al., 2001, 2009; Liu et al., 2006; Moyano et al., 2008). Increased precipitation may be coupled with increased cloudiness (Sellers et al., 1997; Luyssaert et al., 2007), which in turn may decrease solar radiation at the forest canopy below photosynthetic light saturation. This would indirectly lead to a decline in AR.

3.3. Q_{10} of SR and its control

3.3.1. Effect of measurement depth and forest types

Observed Q_{10} values of SR varied from 0.98 to 6.27 (Supplement Table 1). The modal Q_{10} values ranged from 2.5 to 3.0 with an overall arithmetic mean of 2.67 (Fig. 8). Our averaged estimate was slightly higher than that of global grasslands (2.13) (Wang and Fang, 2009) and that of global vegetation (2.4) (Raich and Schlesinger, 1992). Averaged Q_{10} values derived from air temperature and soil temperature at 0, 5, 10, 15, and 20 cm depths were (Mean ± SE) 1.43 ± 0.09, 2.00 ± 0.11, 2.55 ± 0.10, 3.01 ± 0.08, 3.16 ± 0.54, and 3.78 ± 0.76, respectively. As expected, Q_{10} increased with measurement depth because soil temperature fluctuates less in deeper soil. This was however only apparent in the top 10 cm soil ($P < 0.05$), whereas no difference occurred below 10 cm depth ($P < 0.05$; Fig. 9). The latter may be attributable to the attenuation and phase shift of temperature fluctuations with increasing depth (Davidson et al., 1998). At deeper depths below 10 cm, amplitudes in soil temperatures do not significantly change in response to changes in soil depth (Xu and Qi, 2001; Graf et al., 2008). Similar patterns were previously observed in several field studies with multiple temperature measurement depths within the same site (Borken et al., 2002; Wang et al., 2006; Pavelka et al., 2007). The same effect was also identified in model simulations by Hashimoto and Komatsu (2006) and was demonstrated with synthetically-
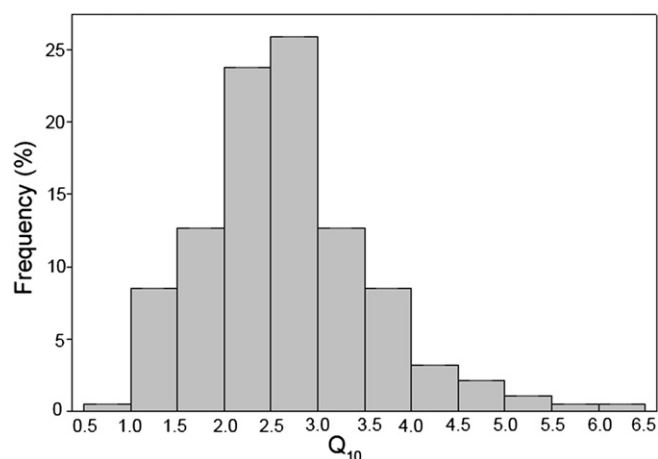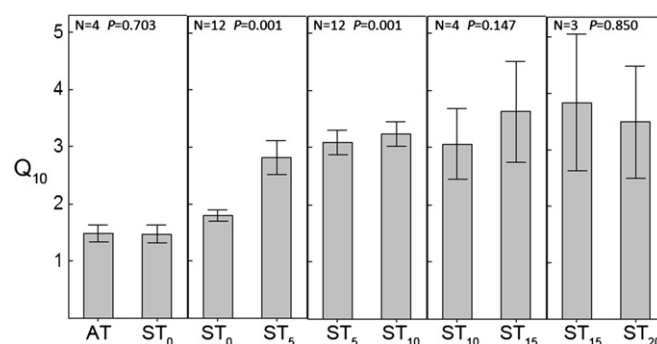

Fig. 9. Comparisons of apparent temperature sensitivity of soil respiration (Q_{10}) estimated by air temperature (AT) and soil temperature at different depths (soil surface temperature (ST_0), soil temperature at 5 cm (ST_5), soil temperature at 10 cm (ST_{10}), soil temperature at 15 cm (ST_{15}), and soil temperature at 20 cm (ST_{20})). Paired t-test was used to compare the differences in the Q_{10} values. N is the number of samples used in the paired t-test. The error bar denotes the stand error (SE) of Q_{10} at any given depth of measured soil temperature.

derived data by Reichstein and Beer (2008). Therefore, the strong dependence in Q_{10} of SR on measurement depth highlights the importance of information on soil temperature measurement depth when applying field estimation of Q_{10} values into current terrestrial ecosystem models.

Q_{10} values at a soil depth of 5 cm were as follows (Mean ± SE): EBF: 1.98 ± 0.12, DBF: 2.79 ± 0.14, ENF: 3.00 ± 0.21, MF: 2.66 ± 0.41, respectively. No significant difference existed among DBF, ENF and MF ($P > 0.05$) and between EBF and MF ($P > 0.05$). Q_{10} of EBF was significantly lower than that of DBF and ENF ($P = 0.002$ and 0.006, respectively) (Fig. 10).

3.3.2. Effect of HR/SR

Raich and Schlesinger (1992) presumed HR to be 70% of SR. However, our results showed the reported HR/SR varied within a wide range from 10.3% to 94% (Supplement Table 1), with significant lower values in DBF than other types (Fig. 11). The outlier in DBF derived from an oak forest with humid climate in northwestern of France and HR was calculated through carbon balance method. The outlier when included or excluded did not significantly change the results of comparison. The differences among different forest types partly reflected diversity of the studied types
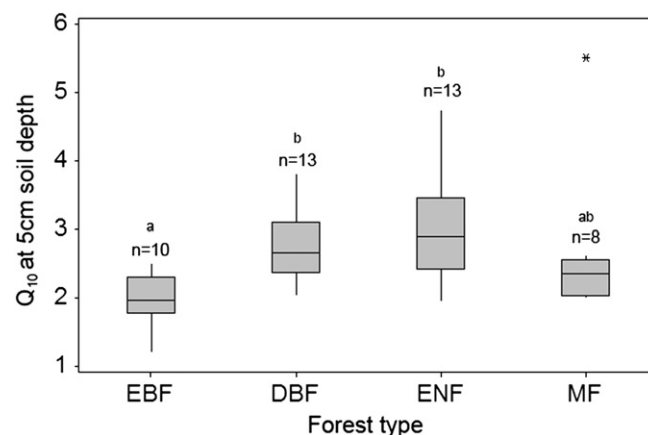

Fig. 8. Frequency distribution of Q_{10} values for in situ soil respiration as reported in the literatures.

Fig. 10. Box-plot of Q_{10} values at 5 cm soil depth for different forest types including deciduous broadleaf forest (DBF), evergreen broadleaf forest (EBF), evergreen needleleaf forest (ENF) and needle and broadleaf mixed forest (MF). 'n' indicates sample size, different lowercase letters indicate significant differences (One-way ANOVA, $P < 0.05$), and * indicates outliers.
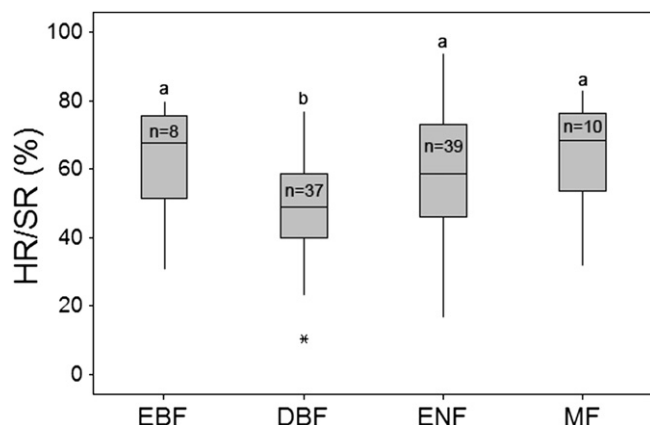
Fig. 11. Comparisons of HR/SR among deciduous broadleaf forest (DBF), evergreen broadleaf forest (EBF), evergreen needleleaf forest (ENF) and needle and broadleaf mixed forest (MF). 'n' indicates sample size, different lowercase letters indicate significant differences (One-way ANOVA, $P < 0.05$), and * indicates outliers. HR = Heterotrophic Respiration; SR = Soil Respiration.

of soils and ecosystems, however, a considerable proportion of it probably originates from the variety of measurement techniques used (Hanson et al., 2000; Kuzyakov, 2006; Subke et al., 2006; Marsden et al., 2008).

No significant relationship occurred between HR and Q_{10} of SR at 5 cm soil depth (Fig. 12b). There was a significant positive relationship between AR and Q_{10} of SR (Fig. 12a), however this relationship was largely dependent on the far right two data points. Therefore, the relationship between AR and Q_{10} still requires further investigation. A significant negative correlation was found between HR/SR and Q_{10} of SR (Fig. 12c). Among all the 18 data points for the analysis, 4 data points derived from the estimates of modeling (Luyssaert et al., 2007). When these modeled values were excluded or included, no significant effect occurred on this negative relationship ($P > 0.05$). Our results indicated that a higher contribution of AR to SR would produce higher Q_{10} of SR. Based on the negative relationship when all the data pooled, Q_{10} values of AR and HR were 3.92 ± 0.38 (HR/SR = 0) and 1.66 ± 0.29 (HR/SR = 1), respectively, suggesting apparent Q_{10} of AR were higher than that of HR. Similarly, apparent Q_{10} of AR measured in the field were significantly higher than that of HR (3.40 ± 0.32 (Mean $\pm$ SE; $n = 13$) vs. 2.42 ± 0.15 (Mean $\pm$ SE; $n = 13$)) (Supplement Table 1). Greater phenological seasonality of AR than that of HR (Boone et al., 1998; Widen and Majdi, 2001; Tierney et al., 2003) could partly account for its higher Q_{10}. For instance, apparent temperature sensitivities would be inflated if data from springtime root growing periods were included (Hanson et al., 2003). Furthermore, changes in substrate supply from photosynthesis could also largely be overlooked, resulting in additional overestimation of the temperature sensitivity of AR (Bhupinderpal-Singh et al., 2003; Davidson and Janssens, 2006). Thus, Q_{10} values derived from field measurements, including AR, could overestimate the response of heterotrophic SR to temperature changes on a future warmer earth (Borken et al., 2002).

However, there has been considerable debate on whether AR or HR is more sensitive to long-term temperature changes. For instance, Baath and Wallander (2003) showed that there were no differences in the temperature relationship between root-associated and non-root-associated organisms in a model system. A similar conclusion was also drawn by Schindlbacher et al. (2008) by warming the top soil of a mature coniferous forest stand on control and trenched plots within 24 h by 10 °C at 1 cm soil depth. However, Hartley et al. (2007b) investigated the response of belowground
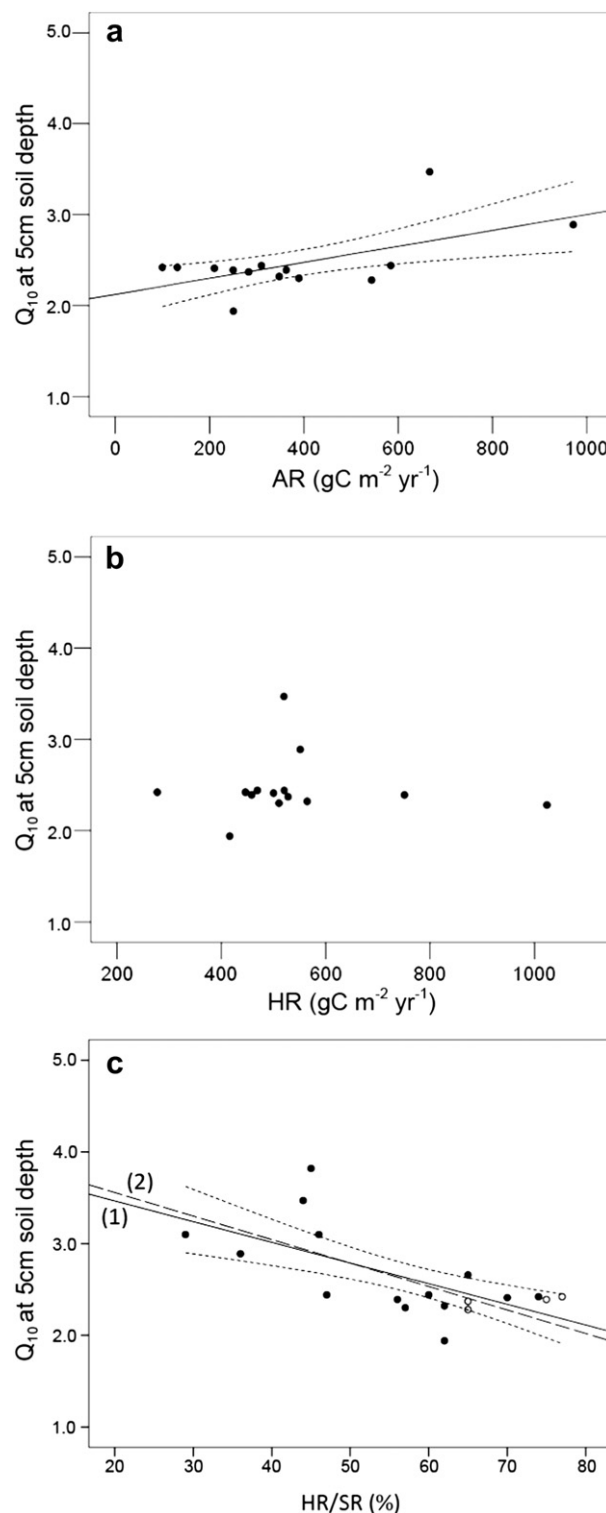

Fig. 12. Q_{10} at 5 cm soil depth was positively correlated with AR (a, $Y = 2.12 + 0.001\,X$, $R^2 = 0.35$, $P = 0.026$) and uncorrelated with HR (b, $P = 0.908$). Q_{10} at 5 cm soil depth was negatively correlated with HR/SR (c). The regression equations were $Y = 3.92 - 2.26\,X$ (1) for modeled data included ($R^2 = 0.43$, $P = 0.003$) and $Y = 4.01 - 2.56\,X$ (2) when modeled data excluded ($R^2 = 0.42$, $P = 0.013$). Based on equation (1), we inferred Q_{10} of AR to be 3.92 ± 0.38 (Mean $\pm$ SE, HR/SR = 0) and Q_{10} of HR to be 1.66 ± 0.29 (Mean $\pm$ SE, HR/SR = 1). '●' shows measured data and '○' shows modeled data. Dash lines shows 95% confidence intervals. SR = Soil Respiration; HR = Heterotrophic Respiration; AR = Autotrophic Respiration.

respiration to soil warming by 3 °C above ambient in bare soil plots and plots planted with wheat and maize. They found that as the growing season progressed, HR is more temperature sensitive than AR. According to Hartley et al. (2007b), the higher Q_{10} for HR than for AR in their study was probably explained by the difference in the dependence on photosynthate supply between AR and HR.

The collected Q_{10} values in our analysis were calculated from a sequence of measurements taken over a period of time during which seasonal changes of the temperature occurred. This apparent Q_{10} may reflect the effects of plant phenological patterns (Curiel Yuste et al., 2004), desiccation stress, substrate production and allocation, and etc (Davidson and Janssens, 2006), as well as temperature sensitivity. When predicting the effects of long-term temperature changes, it is important to differentiate between the direct effect of temperature and other conditions (e.g. light), co-varying with temperature over the year (Baath and Wallander, 2003; Schindlbacher et al., 2008). The existing controversies highlight the importance of determining the intrinsic temperature response of SR in future studies. Some recent studies have made good attempts by making short-term temperate responses (Vicca et al., 2009; Curiel Yuste et al., 2010). For instance, using intact soil cores from an oak savanna ecosystem, Curiel Yuste et al. (2010) applied short-term temperature cycles to study temperature sensitivity of SR. This short-term Q_{10} is less likely to comprise confounding effects and is in general a better approximation of the intrinsic temperature response of a process (Vicca et al., 2009). Further evaluations of the feedback intensity between soil carbon efflux and global warming can thus not be satisfactorily predicted if we do not understand patterns of intrinsic temperature sensitivity.

4. Conclusions

Our results pointed to global patterns of SR, AR, HR and HR/SR in forests across a broad scale gradient of MAT and MAP. In addition, we analyzed the changes in Q_{10} of SR with measurement depth, forest types, HR, AR and HR/SR. Our results have great implications to modeling efforts and ecosystem-level C cycling studies. (i) Different responses of AR to temperature and precipitation from HR demonstrate the importance of using separate functions for modeling the responses of AR and HR to climatic variables as well as substrate supply. (ii) Strong dependence in Q_{10} of SR on measurement depth highlights the importance of information on soil temperature measurement depth when applying field estimation in Q_{10} values into current terrestrial ecosystem models. (iii) Q_{10} of SR positively correlated with AR/SR, suggesting apparent Q_{10} values derived from field measurements including AR may overestimate the temperature sensitivity of heterotrophic SR on a future warmer earth.

Acknowledgments

Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.soilbio.2010.04.013.

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