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Temporal variations of soil respiration at multiple timescales in a spruce-fir valley forest, northeastern China

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Abstract

Purpose There is a paucity of data regarding the multiple timescale variations of heterotrophic respiration (R_H) and autotrophic respiration (R_A) as well as the primary controlling factors. The objective of this study is to find the temporal variations of total soil respiration (R_S) and its components, revealing the driving factors at different timescales.

Materials and methods A trenching method was used to distinguish R_S, R_H, and R_A in a spruce-fir valley forest in northeastern China. We used the closed dynamic chamber method to measure the soil respiration rate. Analyses of R_S, R_H, and R_A in relation to biotic and abiotic factors were conducted to realize the temporal variations at different timescales.

Results and discussion Only R_S and R_H showed a distinct diurnal variation and soil temperature (T_S) can explain 68 and 59 % of the daily variation, respectively. R_S, R_H, and R_A showed a pronounced, single peak curve seasonally, and T_S can explain 11–95 % of the seasonal variation. Soil moisture (W_S) maintained at a relatively high level and was not related to R_S, R_H, or R_A on a seasonal scale, and there was no significant relationship between the seasonal R_S, R_A, and root biomass. However, for 5 years, only the mean R_A of the growing season was significantly related to the mean W_S, which can explain 39 % of the inter-annual variation of R_A. The annual variations of litterfall and the relative growth rate of stems were not related to R_S, R_H, or R_A. The contribution of R_H to R_S was larger, and the temperature sensitivity was 2.01–3.71 for R_S, 1.90–3.08 for R_H, and 2.20–5.65 for R_A.

Conclusions R_S, R_H, and R_A show different temporal variations at multiple timescales. When W_S is not restricted, T_S is the primary driving factor of daily and seasonal variation of R_S and R_H. In this site, R_H accounts for a large proportion of R_S and plays a crucial role in determining the magnitude and temporal variation of R_S.

Keywords Microbial respiration · Root respiration · Soil respiration · Temporal variation · Temperature sensitivity

1 Introduction

Soil respiration (R_S) is the second largest carbon efflux between terrestrial ecosystems and the atmosphere (78–98 Gt C yr^{-1}) (Raich et al. 2002; Bond-Lamberty and Thomson 2010). The annual emission of R_S is 10 times greater than the combustion of fossil fuels (Schlesinger 1997). R_S plays a crucial role in regulating soil carbon dynamics and global climate change. Generally, R_S is considered to be composed of heterotrophic (R_H, respiration by soil microbes and fauna) and autotrophic components (R_A, respiration by root and rhizosphere microorganisms) (Scott-Denton et al. 2006). Different responses of these two components determine the important role of R_S in regulating the global carbon balance (Schuur and Trumbore 2005).

Some studies have shown that R_S exhibits variations at different timescales (Savage and Davidson 2001; Ohashi et al. 2008; Hanpattanakit et al. 2015). Generally, R_S changes

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along with soil temperature (T_S) throughout the day (Shi et al. 2006; Hanpattanakit et al. 2015), whereas Yuste et al. (2004) found the short-term variation of R_S to be related to the diurnal pattern of plant phenology and productivity. In temperate and boreal forests, T_S is the primary driving factor that controls the seasonal change of R_S (Vargas et al. 2010; Pang et al. 2013), whereas soil moisture (W_S) is the restricting factor in tropical or semi-arid areas (Ohashi et al. 2008; Moyes and Bowling 2012). At large timescales, such as inter-annual, decadal, or even larger, R_S may be controlled by abiotic factors such as soil texture, T_S, W_S, and annual precipitation (Bonal et al. 2008; Moyes and Bowling 2012; You et al. 2013). The long-term change of the soil carbon pool could be the result of strong feedback between climate and the ecosystem carbon balance, which depends on the cumulative effect of litterfall products and its decomposition in R_S (Schmidt et al. 2011). Previous studies on the temporal dynamics of R_S have primarily concentrated on the single timescale, and overlooking the components of R_S. Our understanding of the multiple timescale variations and controlling factors of R_H and R_A are still limited.

Multiple variations of R_H and R_A are influenced by different biotic and abiotic factors. The short-term variation of R_H is primarily controlled by T_S and W_S (Li et al. 2011; Savage et al. 2013). Moreover, the variations of substrate availability, and microbial composition and its quantity, also have a large impact (Hopkins et al. 2014; Whitaker et al. 2014). Aside from T_S and W_S, photosynthesis, transportation of photosynthates from canopy to roots, and phenological characteristics also have significant effects on the short-term variation of R_A (Kodama et al. 2008; Savage et al. 2013). Li et al. (2011) found the decomposition of soil organic carbon was positive related to T_S, whereas the variation of R_A was the opposite. Savage et al. (2013) showed a positive relationship between photosynthetically active radiation and R_A. The R_S increased linearly with an increase in gross primary productivity (GPP); GPP and T_S could explain 53 % of the daily variation of R_S (Han et al. 2014). Comparatively, T_S is a variable that changed drastically by season in temperate forests, primarily restricting the seasonal pattern of R_H. However, R_A is affected by plant physiological changes (e.g., root growth and turnover, change of leaf area) (Luo and Zhou 2006; Prolingheuer et al. 2014). Although some studies have indicated that the changes of a series of physiological and ecological processes due to climate change would cause inter-annual variations of R_S (King et al. 2004; Luo and Zhou 2006), there is still a paucity of knowledge about the inter-annual variations of R_H and R_A, especially the relationships between multiple temporal variations, and the annual litterfall (LF), root biomass (RB), and relative growth rate of stems (RGR) are not recognized adequately. Because the multiple timescale variations of R_H and R_A are driven by different environmental factors, the sensitivity of R_S to T_S and W_S depends on the ratios of these two components (Butler et al. 2012). A wide range of the contribution of R_A to R_S (*RC*) has been reported (33–89 %) (Raich and Tufekciogul 2000; Subke et al. 2006; Wang and Yang 2007). It is vital to improve our understanding of how R_H and R_A respond to different environmental factors to accurately estimate the regional soil carbon dynamics, as well as the response to global climate change.

The Asian temperate mixed forest, one of the three largest temperate mixed forests in the world, is predominantly distributed in northeastern China, accounting for one third of the nation's total forests (Department of Forestry of PR China 1994). As an important component of dark coniferous forests, which are widely distributed in north temperate zones, spruce-fir forests typically distribute in subalpine regions; however, due to the existence of an inversion layer, they are generally distributed in narrow valleys and local gullies in the eastern mountainous region of northeastern China. Therefore, we refer to them as spruce-fir valley forests. Spruce-fir valley forests are characterized by relatively high soil moisture and low soil temperatures. As a consequence of global warming, island permafrost is melting and the natural southern boundary of the spruce-fir valley forest will move northward. All of this will result in great changes to the habitat of the spruce-fir valley forest, which greatly influences the regional carbon cycle. However, the studies regarding the multiple timescale variations of R_S, R_H, and R_A in this region have not been conducted; it is crucial to study how R_S and its components vary at different timescales for this site, to accurately estimate the soil carbon dynamics of boreal forests in the context of global warming. In this study, we conducted continuous measurements of R_S, R_H, and R_A in a spruce-fir valley forest during the growing season from 2010 to 2014. Our main objectives were to analyze the temporal variations of R_S, R_H, and R_A at different timescales with a specific emphasis on the roles of biotic (LF, RGR, and RB) and abiotic factors (T_S and W_S).

2 Materials and methods

2.1 Site description and experimental design

This study was conducted in a spruce-fir valley forest in the Liangshui National Reserve (128° 53′ 20″ E, 47° 10′ 50″ N) in northeastern China. The elevation is 280–707 m, and the climate is classified as continental monsoon. The mean annual temperature is −0.3 °C, with a frost-free period of 100–120 days and snow period of 130–150 days. The mean annual precipitation is 676 mm and occurs during the summer, and the annual average evaporation is 805 mm. The soil is dark-brown forest soil (by Chinese classification), which is equivalent to Humaquepts or Cryoboralfs, based on the American Soil Taxonomy (Soil Survey Staff 1999), with 60–80 cm of soil thickness. The soil properties are as follows: 90.9 g kg^{-1}

soil organic carbon (C), 7.5 g kg^{-1} total nitrogen (N), C: N 11.5, pH 4.8, soil bulk density 0.47 g cm^{-3}, and see details in Shi and Jin (2016). The spruce-fir valley forest is the non-zonal climax vegetation, which is greater than 300 years, and belongs to the evergreen coniferous forest. The forest is primarily composed of *Abies nephrolepis*, *Picea koraiensis*, *Acer ukurunduense*, *Pinus koraiensis*, *Betula costata*, and *Larix gmelinii*.

We established three 20 m × 30 m replicate plots in the spruce-fir valley forest. Eight polyvinyl chloride (PVC) collars (10.4-cm inside diameter, 6-cm height) were randomly inserted into the soil in each plot to a depth of 4 cm (including the litter layer) to measure the R_S, which was considered to be the total soil respiration rate. Four subplots (2 m × 2 m) were randomly established in each plot in October 2009. On the outside boundaries of the subplots, we dug a trench to the bedrock or below where few roots existed. To prevent root growth into the trenched plots, and avoiding the blockage of air circulation and water, we used a double-layer of nylon mesh to line the trenches and then refilled the trenches with the same excavated soil. Additionally, we removed all of the living plants and kept the surface free of seedlings and herbaceous vegetation throughout the study. We installed three PVC collars in each subplot. To minimize the effects of soil disturbance and fine root decomposition following trenching, we began measuring the soil respiration rate of the trenched subplots and untrenched plots starting in the growing season of 2010 and ending in 2014. The soil respiration rate of the trenched plots represents measured R_H.

2.2 Soil respiration measurement

We used an LI-6400 portable CO_2 infrared gas analyzer (IRGA) (LI-COR Inc., Lincoln, NE, USA) to measure the soil respiration rate approximately every 2 weeks during the growing season from 2010 to 2014. The soil respiration rate was measured on rainless days a total of 49 times. Due to the analyzer cannot run at low temperatures, we did not conduct measurements during non-growing seasons (T_S lower than 0 °C). The T_S at a depth of 5 cm was concurrently measured with the soil respiration rate next to each collar using a portable temperature probe provided with the LI-6400. Simultaneously, W_S at a depth of 5 cm was measured using a time-domain reflectometry (TDR). Additionally, we measured the R_S and R_H every 2 h during the daytime from 0600 to 1800 hours and every 3 h at night from 1800 to 0300 hours on rainless days in August 2012, as well as the T_S, a total of 10 times.

2.3 Relative growth rate of stems measurement

The diameter at breast height (DBH) was measured for trees with a DBH greater than 10 cm that were within 3–8 m of each collar in the untrenched plots. We numbered and positioned each of the trees and installed self-made tree measuring devices to monitor the DBH growth. If some tree measuring devices were damaged or the DBH of some trees grew to be 10 cm during the measurement period, then those devices were replaced or the trees were installed with new devices, recording their number and position. If some large trees fell, those were recorded as well. Then, the relative growth rate of the stem diameter (RGR/cm cm^{-1} year^{-1}) was calculated as follows (Poorter et al. 2008):

$$\mathrm{RGR} = (\log(\mathrm{DBH}_t) - \log(\mathrm{DBH}_0))/t \tag{1}$$

where DBH_0 and DBH_t represent the DBH early and late in the growing season, respectively, and t represents the time.

2.4 Litterfall measurement

To measure the litterfall (LF), six square litter traps (area 1 m^2) composed of wire (diameter 8 mm) and nylon mesh (bore diameter 1 mm, depth 0.5–0.6 m) were randomly placed in each plot. The distance from the bottom of the litter traps to the forest floor was 0.5 m. We collected LF once a month from 1 May to November (a period within which most LF occurs) between 2009 and 2014. Each sample was weighed after being oven dried at 65 °C. We summed up the LF of each litter trap from May to November and then averaged to get the mean LF of each year.

2.5 Root biomass measurement

Ten soil cores were randomly taken to estimate the root biomass (RB) using a 5-cm diameter corer at each plot, once at the end of each month from May to September 2012. The soil cores were taken from the forest floor surface down to 40 cm. Next, small roots (<5 mm in diameter) in the samples were collected, dried at 60 °C to a constant mass, and weighed.

2.6 Data analysis

The following exponential function (Luo et al. 2001) was used to describe the temperature dependence of soil respiration:

Table 1 The models that are used to correct the measured heterotrophic respiration (R_H) of trenched plots

Year	Model
2010	Model $R_H = 0.854e^{0.064T}$
2011	Model $R_H = 0.562e^{0.113T}$
2012	Model $R_H = 0.839e^{0.096T}$
2013	Model $R_H = 0.817e^{0.084T}$
2014	Model $R_H = 0.699e^{0.087T}$

T represents the T_S of untrenched plots from 2010 to 2014

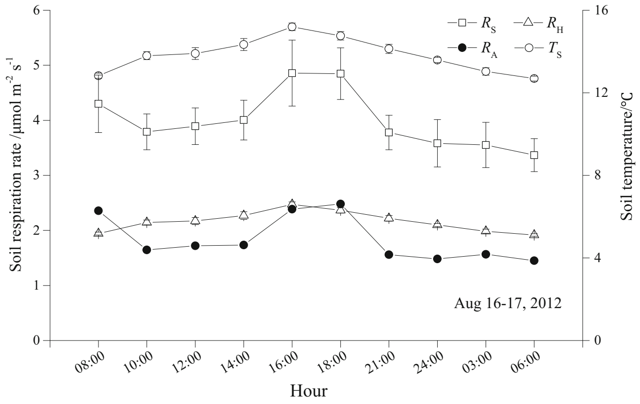

Fig. 1 The diurnal variations of soil respiration (R_S), heterotrophic respiration (R_H), autotrophic respiration (R_A), and soil temperature (T_S). The *error bars* represent standard errors of means

$$R = R_0 e^{kT} \tag{2}$$

where R is the measured soil respiration (R_S, R_H, and R_A), R_0 is the basal respiration at 0 °C, T is the soil temperature at 5 cm (°C) and k is the temperature coefficient, which is related to Q_{10} (the increasing multiples of the soil respiration rate when the temperature increases by 10 °C). Q_{10} is calculated as follows:

$$Q_{10} = e^{10k} \tag{3}$$

Due to the T_S of trenched plots was larger than the T_S of untrenched plots during the measurements (Fig. 2), which could make biases for the estimation of R_H and R_A. To ensure the comparability of soil respiration and eliminate the effects of trenching on the T_S, measured R_H was corrected where T_S diverged on trenched and untrenched plots throughout the measurements. We used a simple model to correct the measured R_H (Schindlbacher et al. 2009). The model is derived from measured R_H of trenched plots from 2010 to 2014 (Fig. 5) and the models information see detail in Table 1. Hence, we used the Model R_H to represent R_H in this paper, and R_A was calculated by the difference between R_S and R_H. The contribution of R_A (RC) was calculated by ratio of R_A to R_S. The relationship between measured R_H and Model R_H see Fig. S1 (Electronic Supplementary Material). In addition, though there were differences of W_S between trenched and untrenched plots, it was not significant. We found W_S was not the restricted variable and was not related to R_S or R_H in this site. Mean T_S and W_S of trenched and untrenched plots for 5 years see Table S1 (Electronic Supplementary Material).

We used one-way ANOVA and LSD tests to compare the differences in the mean soil respiration rate of the growing season and related factors. A regression analysis was performed to test the relationships between soil respiration and the LF, RGR, and RB. The significance level was set as 0.05. All statistical analyses were performed using SPSS 19.0 (SPSS Inc., USA). Graphs were generated using Origin Pro 9.1 (Origin Lab Inc., USA).

3 Results

3.1 The diurnal variation of soil respiration

In this study, R_S and R_H all showed a pronounced diurnal variation with a single peak curve (Fig. 1), and the diurnal coefficients of variation (CV) was 12.97 and 8.40 %, respectively. The minimum and maximum values occurred at 0600 and 1600 hours, which coincided with the T_S. The regression analysis (Eq. (2)) indicated that T_S could explain 52.3 % of the

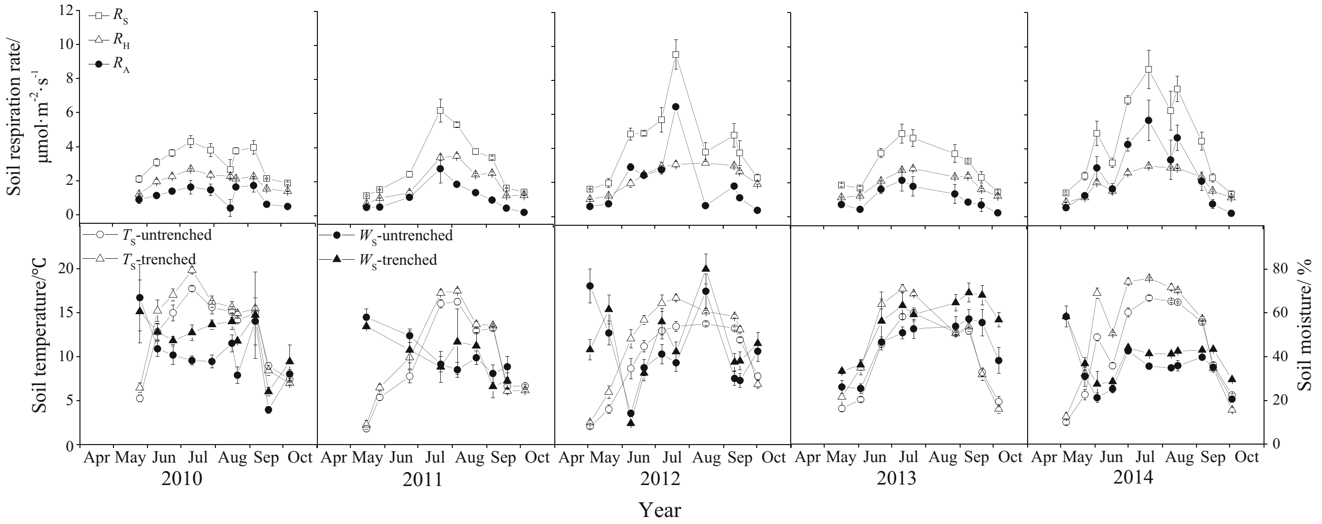

Fig. 2 The seasonal variations of soil respiration (R_S), heterotrophic respiration (R_H), autotrophic respiration (R_A), soil temperature (T_S), and soil moisture (W_S) during the growing season from 2010 to 2014. The *error bars* represent standard errors of means

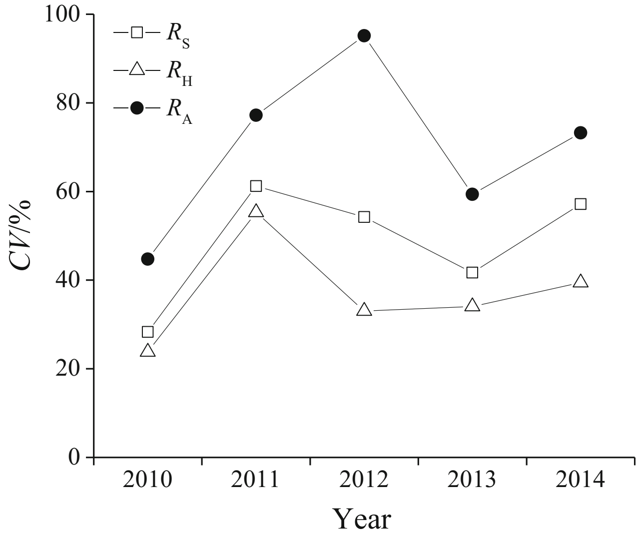

Fig. 3 The coefficients of variation (*CV*, %) of soil respiration (R_S), heterotrophic respiration (R_H), and autotrophic respiration (R_A) from 2010 to 2014

diurnal variation of R_S and 58.5 % for the measured R_H, respectively, although the diurnal difference of T_S was close to 2.5 °C, and the *CV* was below 10 %. The diurnal change of R_A was not coincided with T_S, and there was no significant relationship between them. In addition, the *CV* of R_A was 22 % and the contribution of R_A to R_S was 36–50 %.

3.2 The seasonal variation of soil respiration

The seasonal ranges of R_S, R_H, and R_A were 1.17–9.51, 0.69–3.5, and 0.19–6.45 μmol m^{-2} s^{-1}, respectively (Fig. 2). R_A had a higher *CV* of 44.74–95.15 %, whereas the *CV* of R_S and R_H were close to each other (Fig. 3). It is worth mentioning that R_H was larger than R_A during the growing season throughout the measurement and the large portion of R_S was held by R_H apart from 2014 (Fig. 4). In general, RC showed a pronounced decreasing trend from the end of July to October, while the contribution of R_H was on the contrary.

R_S, R_H, and R_A showed a similar tendency with T_S (Fig. 2), and there was a significant exponential relationship between T_S and soil respiration (Fig. 5), with R^2 ranging from 0.451 to 0.950 for R_S, from 0.608 to 0.945 for measured R_H, and from 0.114 to 0.843 for R_A. However, W_S maintained at a high level (Fig. 2), and we found that W_S could not explain the seasonal variations of R_S and its components by multivariate regression analyses (Wang et al. 2006) (Table S2, Electronic Supplementary Material). The *CV* of T_S and W_S are 32–51 and 26–43 %, respectively (data not shown). In addition, we found the RB was significantly different between different months, except the fourth soil layer (30–40 cm) (Table 2). The total RB ranged from 390.14 to 824.71 g m^{-2}, whereas we found no significant relationship between the seasonal R_S, R_A, and RB (Fig. S2, Electronic Supplementary Material).

3.3 The inter-annual variation of soil respiration

The mean R_S, R_H, R_A, and RC of the growing season exhibited pronounced inter-annual variation, and the maximum values occurred in 2012 or 2014 (Table 3); the annual *CV* for each was 20.31, 8.19, and 41.53 %, respectively, which are all less than the corresponding seasonal *CV*. Although there were significant differences in the annual mean T_S and W_S, the *CV* for both was low (10–17 %). We found only the annual mean W_S to be significantly related to the annual mean R_A, and the W_S could explain 38.7 % of its inter-annual variation (Fig. 6). The mean value of the contribution of R_A ranged from 32.23 to 47.84 %. We found the Q_{10} of R_A to have the highest maximum annual fluctuation, whereas the Q_{10} of R_S and R_H were similar (Table 3).

We measured the RGR and LF continuously, and the results are shown in Table 4. The RGR ranged from 1.11 to 3.34 % and the LF ranged from 318.92 g m^{-2} a^{-1} to 450.72 g m^{-2} year^{-1}. However, we found no significant difference of LF between years, and the regression analysis showed that both RGR and LF had no discernible relationship with the annual mean R_S, R_H, or R_A ($P > 0.05$) (Fig. S2, Electronic Supplementary Material).

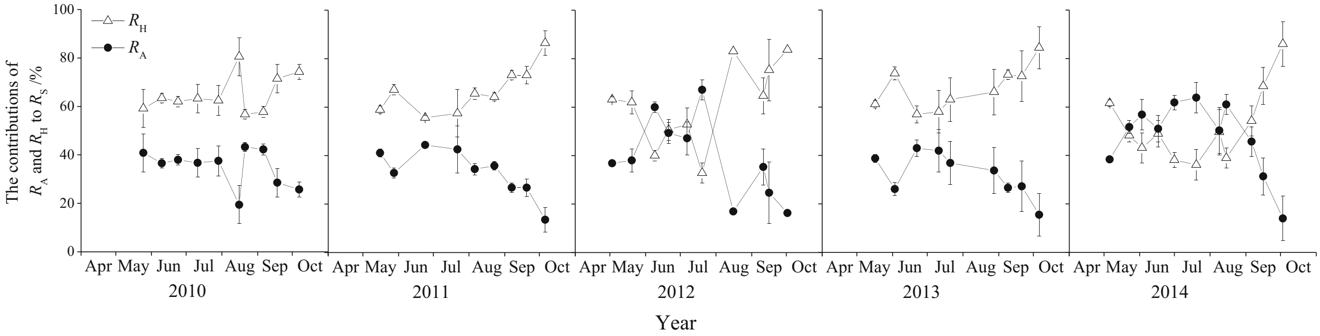

Fig. 4 The monthly average contributions of autotrophic respiration (R_A) and heterotrophic respiration (R_H) to soil respiration (R_S) from 2010 to 2014. The *error bars* represent standard errors of means

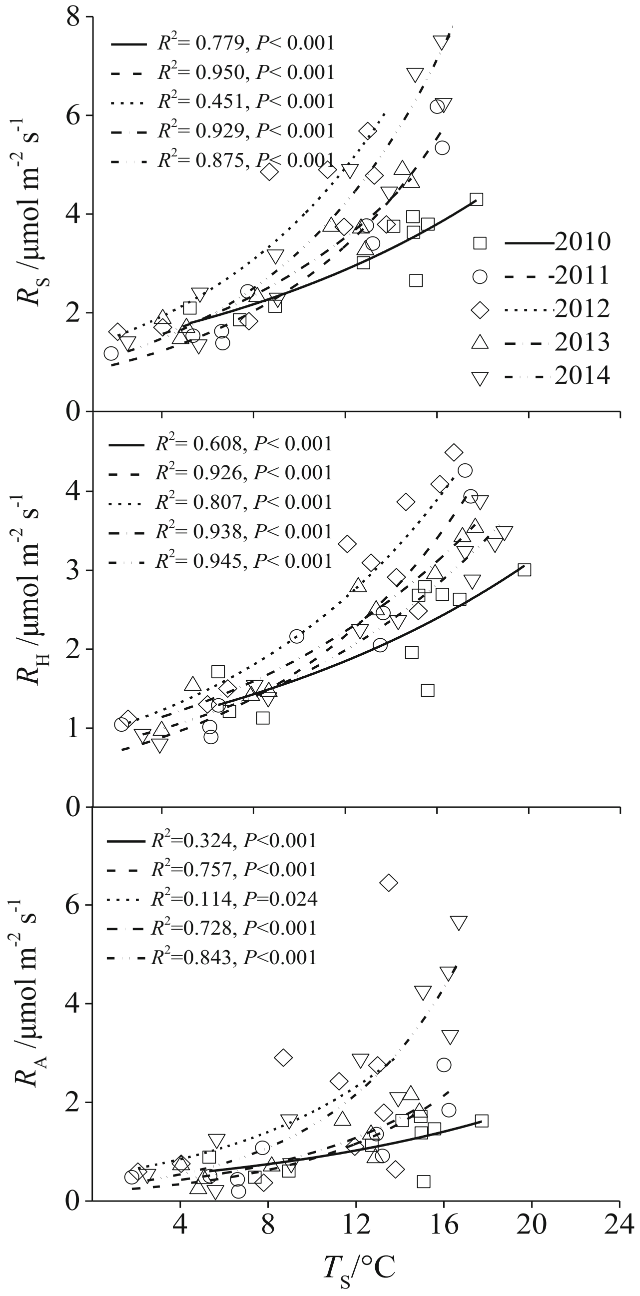

Fig. 5 Relationship of soil respiration (R_S), heterotrophic respiration (R_H), and autotrophic respiration (R_A) to soil temperature (T_S). The regression models are of the form: $R = R_0e^{kT}$, where R is R_S, R_H or R_A; T is the soil temperature at 5 cm (°C), and k is the temperature coefficient

4 Discussion

4.1 The diurnal variation of soil respiration

T_S is a variable that changed strongly at the diurnal scale and is the primary driving factor for the diurnal variation of R_S and R_H, which can explain 52 and 59 % of the daily variation. This is consistent with the results of other terrestrial ecosystems (Tang et al. 2005; Vargas et al. 2010). Li et al. (2011) found that T_S could explain more than 60 % of the diurnal variation of R_S and R_H, which is similar to our study. Jensen et al. (1996) conducted a two-day measurement in a *Pinus radiata* forest in New Zealand and found no obvious diurnal variation of R_S, which may be caused by the little fluctuation in T_S. However, we found the diurnal pattern of R_A to not be related to T_S, which may be a result of R_A being more affected by other biotic factors, in addition to T_S. The photosynthesis intensity and the transportation of photosynthates from the canopy to roots have pronounced effects on the diurnal variation of R_A (Davidson and Holbrook 2009; Kuzyakov and Gavrichkova 2010; Vargas et al. 2010). A high-frequency measurement of the roots and microbial respiration in Harvard forest showed that the R_A was closely related to canopy photosynthesis, and that T_S could not explain the amplitude of R_A on a day scale (Savage et al. 2013). Additionally, the direct connection between solar radiation and T_S typically obscures the relativity between the R_A and these two factors (Kuzyakov and Gavrichkova 2010). The diurnal patterns of R_H and R_A were controlled by different environmental factors, and the ratios of R_H and R_A to R_S may determine the diurnal variation of R_S.

4.2 The seasonal change of soil respiration

The seasonal patterns of R_S, R_H, and R_A exhibited a single peak curve. The *CV* of the seasonal R_S is 31–60 %, which is higher than the results of Wang et al. (2006) (25 %). This difference may be caused by the composition of tree species and the soil microclimate. The spruce-fir valley forest is sensitive to hydrothermal conditions, and the local permafrost is melting as a result of global warming. All of these changes may result in a relatively high seasonal variation of soil respiration along with the seasonal changes of T_S and W_S. In addition, we found the *CV* of R_A to be higher than the R_H (Fig. 3), perhaps due to the mixed effects of the seasonal change of W_S and the plant phenology on roots. Changes in T_S, W_S, and their interaction could cause soil respiration to have a corresponding variation trend (Saiz et al. 2006; Kukumägi et al. 2014; Shi et al. 2015). In this study, T_S can explain 80–95 % of the variation of the seasonal R_S and R_H in most cases, whereas the explanation for R_A is very different throughout the 5-year study (Fig. 5). Shi et al. (2015) obtained similar results in three coniferous forests in the same area, with an R^2 ranging from 0.343 to 0.580 for R_A. In general, R_H is regulated by soil microorganisms, which are primarily controlled by T_S and the substrate availability (Han et al. 2007). Hopkins et al. (2014) found that warming increased the turnover rate of soil organic carbon, through an incubation experiment. The results of Billings et al. (1998) also indicated that the temporal variation of soil respiration was consistent with the changes of T_S when W_S was not limited. Furthermore, the contribution of R_H to R_S was 33–86 % (Fig. 4), and W_S maintained at a relatively high level (20–60 %) (Fig. 2) and was not the restricted

Table 2 The small root biomass (diameter = 0–5 mm) of four soil layers (0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm) from May to September 2012

	Soil layer	Month				
		May	Jun	Jul	Aug	Sep
RB (g m^{-2})	0–10 cm	341.72 (47.39)^{ab}	244.74 (18.98)^{b}	231.00 (21.68)^{b}	285.44 (52.99)^{ab}	379.73 (38.91)^{a}
	10–20 cm	290.15 (36.12)^{a}	94.16 (4.08)^{c}	220.53 (39.82)^{ab}	127.53 (1.83)^{bc}	242.94 (38.45)^{a}
	20–30 cm	136.20 (10.45)^{ab}	61.21 (13.27)^{b}	162.73 (61.81)^{a}	90.20 (7.08)^{ab}	165.58 (11.48)^{a}
	30–40 cm	7.49 (2.22)^{a}	0.21 (0.21)^{a}	29.13 (20.33)^{a}	11.50 (4.81)^{a}	2.26 (2.26)^{a}
	0–40 cm	795.19 (75.36)^{a}	390.14 (37.02)^{c}	666.09 (88.50)^{ab}	537.78 (39.20)^{bc}	824.71 (64.74)^{a}

Values in parentheses are standard errors of means. Different letters indicate significant differences among different years ($P < 0.05$)

RB small root biomass

variable during the measurement. Thus, R_H exerts a crucial role in determining the temporal variation of R_S in this site, and we speculate that T_S is the primary driving factor of the seasonal R_S and R_H in temperate forests when the W_S is adequate. We only measured the RB from May to September 2012, and we found there was no significant relationship between the seasonal R_A and RB (including the first soil layer and the total). Generally, R_A consists of the actual root respiration and rhizosphere microbial respiration (Scott-Denton et al. 2006); in addition to RB, the unit root respiration rate and rhizosphere microbial activity are important factors controlling the variation of R_A (Luo and Zhou 2006). The respiration by rhizosphere organisms and ectomycorrhizae contributed approximately 50 % to the R_A (Subke et al. 2011). Additionally, other than RB, the metabolic activity of root systems also has a pronounced effect on the temporal variation of R_A (Vargas and Allen 2008). R_A may be a result of complicated interactions among environmental factors. Thus, it is necessary to conduct additional controlled experiments and analyzing methods to distinguish impacts of environmental variables on R_A and to identify which processes driving the seasonal variation of R_A (Zhang et al. 2013).

4.3 The inter-annual variability of soil respiration

Many forest ecosystems have been observed for the inter-annual variation of R_S, but there has been little observation of the R_H and R_A (Moyes and Bowling 2012; You et al. 2013). In this study, R_H exhibited a relatively low inter-annual variation, which may be due to the small fluctuation of T_S (approximately 10 %). In addition, the spruce-fir valley forest is an evergreen coniferous forest, where the annual litterfall input is relatively stable (Table 4). We found no pronounced difference in the annual litterfall during the 5-year study, and any difference was not related to the annual R_S, R_H, and R_A. However, Zimmermann et al. (2009) found that litterfall could account for 37 % of the inter-annual variation of R_S in a tropical montane cloud forest in Peru. This difference could be caused by the quantity and quality of the annual litterfall of different forest types. In tropical forests, the different decomposition rates of litterfall between dry and wet seasons in different years may result in a high annual variation of soil respiration, whereas the effect may be different in a coniferous forest. The similar values of T_S and RGR for the last 4 years of the study may cause these two factors are both not related to soil respiration. However, the mean R_A of the growing season was negatively related to the mean W_S (Fig. 6), which could explain 38.7 % of the inter-annual variation of R_A. Spruce-fir valley forests typically distribute in areas where there are rivers or streams and the W_S is relatively high (34.13–44.95 %) (Table 3). However, the normal development of roots will be restricted due to oxygen deficit with high soil-water content (Greenway and Gibbs 2003), and the R_A may decrease. In contrast, soil microorganisms can adapt to a wide variety of soil-water conditions (Luo and Zhou 2006). The negative relationship between R_A and W_S may explain why

Table 3 Mean soil respiration (R_S), heterotrophic respiration (R_H), root respiration (R_A), relative contribution of R_A to R_S (RC), soil temperature (T_S), soil moisture (W_S), and the temperature sensitivity (Q_{10}) of R_S, R_H, and R_A from 2010 to 2014

Year	R_S/μmol m^{-2} s^{-1}	R_H/μmol m^{-2} s^{-1}	R_A/μmol m^{-2} s^{-1}	RC/%	T_S/°C	W_S/%	Q_{10} R_S	Q_{10} R_H	Q_{10} R_A
2010	3.17 (0.176)^{b}	1.99 (0.086)^{ab}	1.18 (0.116)^{b}	35.42 (1.92)^{bc}	12.68 (0.73)^{a}	39.93 (2.75)^{ab}	2.01	1.90	2.20
2011	2.98 (0.344)^{b}	1.92 (0.198)^{b}	1.06 (0.172)^{b}	33.13 (2.13)^{c}	9.62 (0.95)^{b}	40.70 (2.28)^{ab}	3.50	3.08	4.60
2012	4.61 (0.470)^{a}	2.35 (0.154)^{a}	2.26 (0.392)^{a}	42.82 (3.52)^{ab}	9.66 (0.78)^{b}	40.40 (3.30)^{ab}	3.24	2.62	3.52
2013	3.07 (0.255)^{b}	1.97 (0.125)^{ab}	1.10 (0.159)^{b}	32.23 (2.59)^{c}	9.83 (0.81)^{b}	44.95 (2.81)^{a}	2.76	2.31	3.91
2014	4.48 (0.458)^{a}	1.99 (0.133)^{ab}	2.49 (0.345)^{a}	47.84 (2.95)^{a}	11.11 (0.85)^{ab}	34.13 (1.73)^{b}	3.71	2.39	5.65

Values in parentheses are standard errors of means. Different letters indicate significant differences among different years ($P < 0.05$)

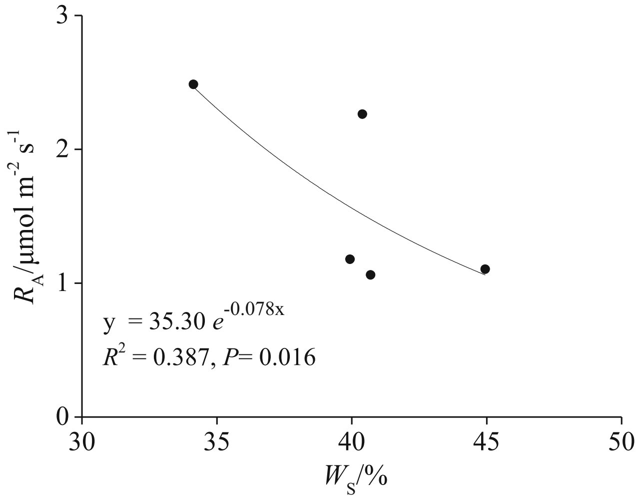

Fig. 6 Relationship of the annual mean autotrophic respiration (R_A) to the annual mean soil moisture (W_S). The regression models are of the form: $y = ae^{bx}$, where y is R_A, a and b are regression coefficients

the R_A was larger than R_H in 2014 which is the year that had the lowest W_S (Table 3). Moreover, Fig. 2 also showed the W_S throughout 2014 was lower relative to the other years which could enhance R_A, whereas the R_H was not related to W_S. R_A was more sensitive to W_S which could be due to the root and rhizosphere activity associated with phenology was restricted by W_S (Curiel yuste et al. 2004). Hence, in the case of less fluctuation of R_H (Fig. 3), the increasing of R_A in 2014 due to low W_S may lead to R_A being larger, correspondingly. Although some studies have demonstrated that W_S could account for the inter-annual variation of R_S (Martin and Bolstad 2005; Kishimoto-Mo et al. 2015), it was not the case at this site. This may be related to the large portion of R_S held by R_H. Additionally, the annual *CV* of T_S and W_S ranged from 10 to 17 %, which was far less than the annual *CV* of R_A. Therefore, only T_S and W_S could not fully explain the inter-annual variations of R_A and R_H. Changes in plant phenology and precipitation throughout the 5-year study may also be responsible for the inter-annual variation in soil respiration.

Table 4 The mean relative growth rate and litterfall (LF) in the site from 2010 to 2014

Year	RGR/%	LF/g m^{-2} year^{-1}
2010	3.34 (0.80)^a	427.48 (63.86)^a
2011	1.38 (1.16)^b	318.92 (55.85)^a
2012	1.50 (0.29)^b	366.17 (72.29)^a
2013	1.11 (0.28)^b	444.25 (61.63)^a
2014	1.33 (0.23)^b	450.72 (103.05)^a

Values in parentheses are standard errors of means. Different letters indicate significant differences among different years ($P < 0.05$)

RGR relative growth rate of trees

4.4 The contributions of R_H and R_A to R_S

The RC decreased starting approximately in the mid-growing season which coincided with T_S (Fig. 4), and it may be due to R_A was more sensitive to temperature (Table 3). Hence, the change of R_A was larger than R_H with the decreasing of T_S. RC ranged from 20 to 50 % in most cases (Fig. 4), which is similar to the result of Shi et al. (2015) (27–34 %) for three coniferous forests in the same reserve. However, the contribution of R_H to R_S was at a higher level (33–86 %). This phenomenon may be caused by the large amount of coarse woody debris in the site and the high soil-water content (Jin et al. 2009). The coarse woody debris contributes to the nutrient cycling of the forest site and has a pronounced influence on the transportation and storage of soil sediments (Jomura et al. 2008), and the accumulation of soil organic matter in the spruce-fir valley forest is high (Liu et al. 2014). In addition, the input of litterfall occurs throughout the year, which maintains a stable amount of soil microbial biomass (Liu et al. 2014) and the high W_S (Fig. 2) may restrict R_A.

4.5 The temperature sensitivity of soil respiration

The Q_{10} of R_S ranged from 2.01 to 3.71, which is similar to the results of Wang et al. (2006) and You et al. (2013) for temperate forests in northeastern China. Ma et al. (2014) found that the range of Q_{10} for R_H and R_A was 2.69–3.03 and 3.06–4.39, respectively, in four larch plantations in northern China. However, the fluctuation of Q_{10} for R_A in this site is higher (Table 3). This indicates that the Q_{10} of R_S and R_H may be similar in temperate forests in northern China. However, the Q_{10} of R_A is different due to the tree species composition and local soil microclimate, especially the soil-water conditions, which may stimulate the sensitivity of roots to temperature. The results of Laganière et al. (2012) also indicated that the influence of boreal forest composition on soil respiration is mediated through the soil microclimate. Furthermore, the superposition effect of photosynthesis, T_S, and W_S will result in a higher Q_{10} of R_A (Subke and Bahn 2010; Jiang et al., 2013), as observed in our site. However, for R_H, the Q_{10} depends on the soil microclimate, the utilization of substrate, and the activity of soil microorganisms (Erhagen et al. 2015; Song et al. 2015). Thus, these biotic and abiotic factors should be considered simultaneously when studying the temperature sensitivity of R_S and its components.

5 Conclusions

Our results indicate that R_S, R_H, and R_A exhibit different temporal variations at multiple timescales. T_S is the fundamental driving factor of the diurnal and seasonal variation of R_S and R_H when W_S is not limited, whereas R_A may be affected by the interaction of biotic and abiotic factors, such as ectomycorrhizae, rhizosphere microorganisms, photosynthesis, and soil microclimate; this needs to be further researched. Additionally, the annual variation of W_S is an important factor that regulates the inter-annual variation of R_A in this site. The larger ratio of R_H to R_S demonstrates that R_H plays a crucial role in determining the magnitude and temporal variation of R_S. In this site, R_A is more sensitive to T_S and has a larger inter-annual fluctuation. The variability of R_H and R_A in multiple timescales is different and controlled by different environmental factors. It is necessary to consider these two components separately in carbon cycle simulations of regional ecosystems and in predicting global climate change.

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References

Billings SA, Richter DD, Yarie J (1998) Soil carbon dioxide fluxes and profile concentrations in two boreal forests. Can J Forest Res 28: 1773–1783

Bonal D, Bosc A, Ponton S et al (2008) Impact of severe dry season on net ecosystem exchange in the neotropical rainforest of French Guiana. Global Change Biol 14:1917–1933

Bond-Lamberty B, Thomson A (2010) Temperature-associated increases in the global soil respiration record. Nature 464:579–582

Butler A, Meir P, Saiz G, Maracahipes L, Marimon BS, Grace J (2012) Annual variation in soil respiration and its component parts in two structurally contrasting woody savannas in Central Brazil. Plant Soil 352:129–142

Curiel Yuste J, Janssens IA, Carrara A, Ceulemans R (2004) Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. Global Change Biol 10:161–169

Davidson EA, Holbrook NM (2009) Is temporal variation of soil respiration linked to the phenology of photosynthesis? In: Phenology of ecosystem processes: applications in global change research. Springer, New York

Department of Forestry of PR China (1994) Statistics of China's forest resources (1989 – 1993). Beijing

Erhagen B, Ilstedt U, Nilsson MB (2015) Temperature sensitivity of heterotrophic soil CO_2 production increases with increasing carbon substrate uptake rate. Soil Biol Biochem 80:45–52

Greenway H, Gibbs J (2003) Review: mechanisms of anoxia tolerance in plants. II. Energy requirements for maintenance and energy distribution to essential processes. Funct Plant Biol 30:999–1036

Han G, Zhou G, Xu Z, Yang Y, Liu J, Shi K (2007) Biotic and abiotic factors controlling the spatial and temporal variation of soil respiration in an agricultural ecosystem. Soil Biol Biochem 39:418–425

Han G, Luo Y, Li D, Xia J, Xing Q, Yu J (2014) Ecosystem photosynthesis regulates soil respiration on a diurnal scale with a short-term time lag in a coastal wetland. Soil Biol Biochem 68:85–94

Hanpattanakit P, Leclerc MY, Mcmillan AMS et al (2015) Multiple timescale variations and controls of soil respiration in a tropical dry dipterocarp forest, western Thailand. Plant Soil 390:167–181

Hopkins FM, Filley TR, Gleixner G, Lange M, Top SM, Trumbore SE (2014) Increased belowground carbon inputs and warming promote loss of soil organic carbon through complementary microbial responses. Soil Biol Biochem 76:57–69

Jensen LS, Mueller T, Tate KR, Ross DJ, Magid J, Nielsen NE (1996) Soil surface CO_2 flux as an index of soil respiration in situ: a comparison of two chamber methods. Soil Biol Biochem 28:1297–1306

Jiang H, Deng Q, Zhou G et al (2013) Responses of soil respiration and its temperature/moisture sensitivity to precipitation in three subtropical forests in southern China. Biogeosciences 10:3963–3982

Jin G, Liu Z, Cai H, Tai B, Jiang X, Liu Y (2009) Coarse woody debris (CWD) in a spruce-fir valley forest in Xiao xingan mountains, China (in Chinese with English abstract). J Nat Res 24:1256–1266

Jomura M, Kominami Y, Dannoura M, Kanazawa Y (2008) Spatial variation in respiration from coarse woody debris in a temperate secondary broad-leaved forest in Japan. Forest Ecol Manag 255:149–155

King JS, Hanson PJ, Bernhardt E, Deangelis P, Norby RJ, Pregitzer KS (2004) A multiyear synthesis of soil respiration responses to elevated atmospheric CO_2 from four forest FACE experiments. Global Change Biol 10:1027–1042

Kishimoto-Mo AW, Yonemura S, Uchida M, Kondo M, Murayama S, Koizumi H (2015) Contribution of soil moisture to seasonal and annual variations of soil CO_2 efflux in a humid cool-temperate oak-birch forest in central Japan. Ecol Res 30:311–325

Kodama N, Barnard RL, Salmon Y et al (2008) Temporal dynamics of the carbon isotope composition in a Pinus sylvestris stand: from newly assimilated organic carbon to respired carbon dioxide. Oecologia 156:737–750

Kukumägi M, Ostonen I, Kupper P et al (2014) The effects of elevated atmospheric humidity on soil respiration components in a young silver birch forest. Agr Forest Meteorol 194:167–174

Kuzyakov Y, Gavrichkova O (2010) REVIEW: time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. Global Change Biol 16:3386–3406

Laganière J, Paré D, Bergeron Y, Chen HYH (2012) The effect of boreal forest composition on soil respiration is mediated through variations in soil temperature and C quality. Soil Biol Biochem 53:18–27

Li Z, Wang X, Zhang R, Zhang J, Tian C (2011) Contrasting diurnal variations in soil organic carbon decomposition and root respiration due to a hysteresis effect with soil temperature in a Gossypium s. (cotton) plantation. Plant Soil 343:347–355

Liu C, Liu Y, Jin G (2014) Seasonal dynamics of soil microbial biomass in six forest types in Xiaoxing'an Mountains, China (in Chinese with English abstract). Acta Ecol Sin 34:1–9

Luo Y, Zhou X (2006) Soil respiration and the environment. Academic Press, An imprint of Elsevier Science, London

Luo Y, Wan S, Hui D, Wallace LL (2001) Acclimatization of soil respiration to warming in a tall grass prairie. Nature 413:622–625

Ma Y, Piao S, Sun Z, Lin X, Wang T, Yue C, Yang Y (2014) Stand ages regulate the response of soil respiration to temperature in a Larix principis-rupprechtii plantation. Agr Forest Meteorol 184:179–187

Martin JG, Bolstad PV (2005) Annual soil respiration in broadleaf forests of northern Wisconsin: influence of moisture and site biological, chemical, and physical characteristics. Biogeochemistry 73:149–182

Moyes AB, Bowling DR (2012) Interannual variation in seasonal drivers of soil respiration in a semi-arid Rocky Mountain meadow. Biogeochemistry 113:683–697

Ohashi M, Kumagai TO, Kume T, Gyokusen K, Saitoh TM, Suzuki M (2008) Characteristics of soil CO_2 efflux variability in an aseasonal tropical rainforest in Borneo Island. Biogeochemistry 90:275–289

Pang X, Bao W, Zhu B, Cheng W (2013) Responses of soil respiration and its temperature sensitivity to thinning in a pine plantation. Agr Forest Meteorol 171:57–64

Poorter L, Wright SJ, Paz H et al (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology 89:1908–1920

Prolingheuer N, Scharnagl B, Graf A, Vereecken H, Herbst M (2014) On the spatial variation of soil rhizospheric and heterotrophic respiration in a winter wheat stand. Agr Forest Meteorol 195:24–31

Raich JW, Tufekciogul A (2000) Vegetation and soil respiration: correlations and controls. Biogeochemistry 48:71–90

Raich JW, Potter CS, Bhagawati D (2002) Interannual variability in global soil respiration, 1980-94. Global Change Biol 8:800–812

Saiz G, Green C, Butterbach-Bahl K, Kiese R, Avitabile V, Farrell EP (2006) Seasonal and spatial variability of soil respiration in four Sitka spruce stands. Plant Soil 287:161–176

Savage KE, Davidson EA (2001) Interannual variation of soil respiration in two New England forests. Global Biogeochem Cy 15:337–350

Savage K, Davidson EA, Tang J (2013) Diel patterns of autotrophic and heterotrophic respiration among phenological stages. Global Change Biol 19:1151–1159

Schindlbacher A, Zechmeister-Boltenstern S, Jandl R (2009) Carbon losses due to soil warming: do autotrophic and heterotrophic soil respiration respond equally? Global Change Biol 15:901–913

Schlesinger WH (1997) Biogeochemistry: an analysis of global change, Academic Press

Schmidt MWI, Torn MS, Samuel A et al (2011) Persistence of soil organic matter as an ecosystem property. Nature Nature 478:49–56

Schuur EG, Trumbore SE (2005) Partitioning sources of soil respiration in boreal spruce forest using radiocarbon. Global Change Biol 12: 165–176

Scott-Denton LE, Rosenstiel TN, Monson RK (2006) Differential controls by climate and substrate over the heterotrophic and rhizospheric components of soil respiration. Global Change Biol 12:205–216

Shi B, Jin G (2016) Variability of soil respiration at different spatial scales in temperate forests. Biol Fertil Soils. doi:10.1007/s00374-016-1100-1

Shi P-L, Zhang X-Z, Zhong Z-M, Ouyang H (2006) Diurnal and seasonal variability of soil CO_2 efflux in a cropland ecosystem on the Tibetan Plateau. Agr Forest Meteorol 137:220–233

Shi B, Gao W, Jin G (2015) Effects on rhizospheric and heterotrophic respiration of conversion from primary forest to secondary forest and plantations in northeast China. Eur J of Soil Biol 66:11–18

Soil survey staff (1999) soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. USDA Natural Resources Conservation Service, Washington, D.C

Song W, Chen S, Wu B, Zhu Y, Zhou Y, Lu Q, Lin G (2015) Simulated rain addition modifies diurnal patterns and temperature sensitivities of autotrophic and heterotrophic soil respiration in an arid desert ecosystem. Soil Biol Biochem 82:143–152

Subke JA, Bahn M (2010) On the 'temperature sensitivity' of soil respiration: can we use the immeasurable to predict the unknown? Soil Biol Biochem 42:1653–1656

Subke JA, Inglima I, Francesca Cotrufo M (2006) Trends and methodological impacts in soil CO_2 efflux partitioning: a metaanalytical review. Global Change Biol 12:921–943

Subke JA, Voke NR, Leronni V, Garnett MH, Ineson P (2011) Dynamics and pathways of autotrophic and heterotrophic soil CO_2 efflux revealed by forest girdling. J Ecol 99:186–193

Tang J, Baldocchi DD, Xu L (2005) Tree photosynthesis modulates soil respiration on a diurnal time scale. Global Change Biol 11:1298–1304

Vargas R, Allen MF (2008) Dynamics of fine root, fungal rhizomorphs, and soil respiration in a mixed temperate forest: integrating sensors and observations. Vadose Zone J 7:1055–1064

Vargas R, Detto M, Baldocchi DD, Allen MF (2010) Multiscale analysis of temporal variability of soil CO_2 production as influenced by weather and vegetation. Global Change Biol 16:1589–1605

Wang C, Yang J (2007) Rhizospheric and heterotrophic components of soil respiration in six Chinese temperate forests. Global Change Biol 13:123–131

Wang C, Yang J, Zhang Q (2006) Soil respiration in six temperate forests in China. Global Change Biol 12:2103–2114

Whitaker J, Ostle N, Nottingham AT et al (2014) Microbial community composition explains soil respiration responses to changing carbon inputs along an Andes-to-Amazon elevation gradient. J Ecol 102: 1058–1071

You W, Wei W, Zhang H, Yan T, Xing Z (2013) Temporal patterns of soil CO_2 efflux in a temperate Korean Larch (Larix olgensis Herry.) plantation, Northeast China. Trees Struct Funct 27:1417–1428

Yuste JC, Janssens IA, Carrara AR (2004) Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. Global Change Biol 10:161–169

Zhang Q, Lei HM, Yang DW (2013) Seasonal variations in soil respiration, heterotrophic respiration and autotrophic respiration of a wheat and maize rotation cropland in the North China Plain. Agr Forest Meteorol 180:34–43

Zimmermann M, Meir P, Bird M, Malhi Y, Ccahuana A (2009) Litter contribution to diurnal and annual soil respiration in a tropical montane cloud forest. Soil Biol Biochem 41:1338–1340