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Long-term (42 years) effect of thinning on soil CO_2 emission in a mixed broadleaved-Korean pine (*Pinus koraiensis*) forest in Northeast China

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ABSTRACT

Thinning is an important forest management practice that has great potential to influence regional soil carbon storage and dynamics. The present study measured soil respiration (R_S, the efflux of CO_2 emitted) and its two components (heterotrophic (R_H) and autotrophic (R_A) respiration) from soil 42 years after thinning in comparison to un-thinning (control). Autotrophic respiration was significantly greater in the thinning plot, approximately 44% higher compared to the control, while both R_S and R_H were slightly, but not significantly, higher in the thinning plot. Higher fine root biomass might have contributed to the higher R_A in the thinning plot. Both R_S and R_H showed clear soil temperature-dependent seasonal patterns, whereas R_A was less responsive to changes in temperature, especially within one specific season. The annual and season-specific temperature sensitivities of R_S and R_H were lower in the thinning plot, specifically during the mid-growing season. Furthermore, variations in the season-specific temperature sensitivity of R_S and R_H were less intense in the thinning plot. We conclude that forest thinning can reduce the temperature sensitivity of R_S and R_H during the mid-growing season and increase soil CO_2 emission in the long term.

Key Words: autotrophic respiration, heterotrophic respiration, microbial decomposition, rhizosphere respiration, soil respiration, soil temperature, temperature sensitivity

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INTRODUCTION

More than two-thirds of terrestrial carbon (C) is retained in soil pools (Hibbard *et al*., 2005). Soil respiration (R_S), the efflux of CO_2 emitted from soil, is the second-largest C flux in forest ecosystems, next to photosynthesis (Schlesinger, 1997). A large amount of C (75–100 Pg) is released through the R_S pathway to the atmosphere as CO_2, exceeding that from fossil fuel combustion by ten-fold (Bond-Lamberty and Allison, 2010). Therefore, R_S is a key process that requires a clear understanding to improve the accuracy of predicting terrestrial C budgets.

Soil respiration is the sum of root and associated rhizosphere respiration (autotrophic respiration, R_A) and microbial decomposition (heterotrophic respiration, R_H). As a combined signal of these two processes, R_S is significantly affected by a complex series of biotic and abiotic factors, namely, soil temperature, soil moisture, soil organic C content, fine roots, and microbial biomass and activity (Hopkins *et al*., 2013; Moyes and Bowling, 2013; Han *et al*., 2016; Ali *et al*., 2018). In temperate forest ecosystems, soil temperature is considered to be the most influential factor for the seasonal variation of R_S (Han *et al*., 2018), which has been generally used to model the feedback of soil C to global warming with the temperature dependency (Q_{10}) function (Peng *et al*., 2009). In addition to the direct effects of soil temperature on the activity of roots and microbes, soil temperature can indirectly influence R_A and R_H by regulating substrate diffusion and supply (Davidson *et al*., 2006). Comparatively, the effect of soil moisture on soil CO_2 emission usually has threshold values below or over which values have contrasting effects on R_S, which could also confound the impact of soil temperature (Davidson *et al*., 1998). Other factors, such as substrates, microbial organisms, and fine roots, often exhibit more complex relationships with R_S. These factors may account for changes in R_S and its two components following forest disturbance (*e.g*., burning and harvest) (Chatterjee *et al*., 2008; Akburak and Makineci, 2016; Guo *et al*., 2016; López-Serrano *et al*., 2016).

Forest management plays an important role in improving forest sustainability and C sequestration (Templeton *et al*., 2015). As a silvicultural tool, thinning is widely used to reduce competition and wildfire risk and, consequently, to improve tree productivity and preserve the health of forests. The opening of the forest canopy and removal of stand biomass would bring about changes in soil microclimate, root

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density and activity, soil organic matter, and soil microbes (Chatterjee *et al*., 2008; Tian *et al*., 2010; Bolat, 2014; Akburak and Makineci, 2016). However, current thinning practices have ambiguous effects on R_S rates, including positive, negative, or neutral effect (Stoffel *et al*., 2010; Cheng *et al*., 2015; Akburak and Makineci, 2016; Pang *et al*., 2016). In a northern hardwood forest, soil surface CO_2 flux after thinning was not significantly altered (Stoffel *et al*., 2010). However, Lei *et al*. (2018) showed that either light or heavy thinning significantly increased R_S and its two components in a pine plantation. Conversely, a negative effect of thinning on R_S has also been reported in temperate pine forests (Tang *et al*., 2005; Bolat, 2014).

There are different factors affecting R_S rates after thinning, including forest type, thinning intensity, site-specific environmental factors, and the time period after thinning (Nilsen and Strand, 2008; Akburak and Makineci, 2016; Pang *et al*., 2016; Lei *et al*., 2018). For example, a reduction in root density following tree removal can result in decrease in R_A (Tang *et al*., 2005), but the increase in decomposition of remaining residues after logging may more than compensate for this negative effect on R_S (Shabaga *et al*., 2015). It is important to determine the influence of forest management practices over a period (*i.e*., a diachronic study), as no general conclusive results about soil C dynamics is available to elucidate the time span elapsed when a forest returns to its pre-treated condition (Nilsen and Strand, 2008; López-Serrano *et al*., 2016). Until now, however, most of the studies concerning the effects of thinning practices on R_S were based on short-term experimental design, with measurements starting less than 1 year immediately following thinning treatment (Akburak and Makineci, 2016; López-Serrano *et al*., 2016).

The Asian temperate mixed forest is one of the three largest temperate mixed forests worldwide and is predominantly distributed in northeastern China, accounting for one-third of the total national forested land area and forest stock (Ministry of Forestry of China, 1994). The primary mixed broadleaved-Korean pine (*Pinus koraiensis* Siebold & Zucc.) forest is the zonal climax vegetation in northeastern China. Since the 1970s, thinning has been the most commonly used forest management practice to obtain wood and achieve local regeneration to improve ecological benefits in mixed broadleaved-Korean pine forest. There is no study examining the long-term effect of thinning on soil CO_2 efflux in primary mixed-broadleaved forests, and only a few studies have examined the long-term effect of forest thinning on C storage and dynamics (Nilsen and Strand, 2008). In the current study, we aimed to: i) investigate the long-term effect of early thinning on soil respiration and its components in a primary mixed broadleaved-Korean pine forest, ii) evaluate the relationships between R_S and its components and biotic and abiotic factors across un-thinning (control) and thinning plots, and iii) identify the factors driving the changes in R_S, R_H, and R_A after a long-term period following thinning. We hypothesized that both R_H and R_A are lower in thinning plot compared to the control due to the reduction in C input and tree roots after thinning, and soil moisture is another important factor inhibiting R_S with higher throughfall in the thinning plot than in the control.

MATERIALS AND METHODS

Site description

A field experiment was conducted in a mixed broadleaved-Korean pine forest located in the Heilongjiang Liangshui National Nature Reserve (47°10′50″ N, 128°53′20″ E), northeastern China. The site has a continental monsoon climate regime with a mean annual precipitation of 676 mm falling primarily in summer. The mean annual temperature is −0.3 °C, and the frost-free period is 100–120 d. The dominant soil type at this site is classified as Humaquept according to soil taxonomy (Soil Survey Staff, 1999). The primary mixed broadleaved-Korean pine forest in this region is the zonal climax vegetation in Northeast China and accounts for 63.7% and 77.4% of the forested area and standing tree volume in the entire reserve, respectively.

Thinning treatment and sampling design

In 1971, thinning was conducted with *ca*. 30% of the tree basal area removed (only boles), including mixed sizes. The harvested tree species was *Pinus koraiensis*. Table I provides information on the tree stand characteristics of the un-thinning and thinning plots. The two treatments were replicated three times, and each of the six plots was 20 m ×

TABLE I

Primary characteristics of un-thinning and thinning plots in the field experiment

Primary characteristic	Un-thinning	Thinning
Tree density (trees ha^{-1})	3 406 ± 345[a)]	2 867 ± 384
Basal area (m^2 ha^{-1})	33.0 ± 0.9	28.1 ± 4.7
Mean DBH[b)] (cm)	11.2 ± 0.6	11.3 ± 1.2
Mean annual air temperature (°C)	10.82 ± 0.12	10.55 ± 0.13
Mean annual air humidity (%)	78.29 ± 0.26	76.90 ± 0.28
Primary species composition	*Pinus koraiensis*, *Betula costata*, *Tilia amurensis*, *Acer ukurunduense*, *Abies nephrolepis*	*Pinus koraiensis*, *Betula costata*, *Tilia amurensis*, *Acer mono*, *Acer ukurunduense*

[a)] Means ± standard errors ($n = 3$).
[b)] Diameter at breast height.

30 m, with tens to hundreds of meters of buffer zone outside the plots. In each plot, eight polyvinyl chloride (PVC) collars, 10.4 cm in inner diameter and 6 cm in height, were inserted into the soil for R_S measurements, with an insertion depth of 1–4 cm to ensure gas tightness and minimal disturbance of superficial roots. To distinguish the two components of R_S, four root-free subplots (2 m × 2 m) were established in each plot in 2009. On the edges of the subplots, trenches were dug to 50–80 cm, below which few roots exist. Trenches were lined with double-layer nylon mesh (37 μm in pore size) and carefully refilled with the excavated soil. All plants growing in trenched plots and inside collars were removed every 2 weeks throughout the growing season during the entire experimental period. Three PVC collars were randomly installed in each subplot for R_H measurements.

Soil respiration and soil microclimate

Soil respiration was measured biweekly on rainless days using an LI-6400 portable CO_2 infrared gas analyzer connected with a 0.991 L chamber (LI-COR Inc., USA) during the growing seasons of two consecutive years (2013 and 2014) for a total of 20 measurement periods throughout the entire experiment. As mentioned above, 20 measurement collars were randomly installed within each plot, with 8 of them used to measure R_S and 12 of them used to measure R_H.

Soil temperature was measured at a depth of 5 cm using a probe connected to LI-6400, and soil moisture (volumetric water content) was measured at a depth of 5 cm using a time-domain reflectometry probe (IMKO, Germany) next to each collar.

The growing season was defined as the duration of time when the surface soil temperature rose above 0 °C (Chen *et al*., 2010). We measured soil respiration from May to October, and three specific periods of the growing season were defined: the early growing season (May–June), the mid-growing season (July–August), and the late growing season (September–October). Because the analyzer could not operate at temperatures below 0 °C, we did not conduct measurements beyond the growing seasons.

Soil properties and fine root biomass

Four soil samples were collected randomly using a soil auger (5 cm in inner diameter) at a depth of 10 cm in each plot at the beginning of each month from May to October (except for June) 2013. Soil samples were passed through a 2-mm sieve and pooled as one sample and then preserved at 4 °C for soil microbial biomass C analysis within one week. The chloroform fumigation-extraction method (Vance *et al*., 1987) was used to determine soil microbial biomass C. For each sample, one subsample was extracted with 0.5 mol L^{-1} K_2SO_4. A second subsample was fumigated with chloroform for 24 h in a vacuum and then extracted with 0.5 mol L^{-1} K_2SO_4. After filtering, the organic C content in the extracts was analyzed using a multi N/C 2100 analyzer (Analytik Jena AG, Jena, Germany). Soil microbial biomass C was estimated as the difference between fumigated and non-fumigated extracts and corrected with a coefficient of 0.45 (Brookes *et al*., 1985; Vance *et al*., 1987):

$$\text{Soil microbial biomass C} = \text{EC}/0.45 \quad (1)$$

where EC is the difference in organic C content between the fumigated and non-fumigated extracts.

In September 2013, some additional soil samples were collected near R_S measurement points in each plot to determine other soil properties. These soil samples were pooled as one sample and then air-dried. The light fraction of soil organic C was extracted according to the method of Janzen *et al*. (1992). Soil organic C and its light fraction were determined using the multi N/C 2100 analyzer. Soil total nitrogen (N) was determined using a Hanon K9840 Auto Kjeldahl Analyser (Jinan Hanon Instruments Co., Ltd, China). Soil C:N ratio was calculated from soil organic C and total N. Soil pH was measured in 1 mol L^{-1} KCl extract (1:2.5, weight/volume) using a laboratory pH meter (S210-K, METTLER TOLEDO, Switzerland).

Ten soil cores were collected from the 0–40 cm soil layer in each plot using a soil corer (5-cm inner diameter) from May to September 2013. We separated each soil sample into four parts in 10 cm increments. All living fine roots (< 2 mm in diameter) were picked out according to color and flexibility and then oven-dried at 60 °C until they reached a constant weight.

Calculations and statistical analyses

We first calculated the mean R_S and R_H from the corresponding collars in each plot, and then the mean R_A at the plot level was calculated using the mean R_S subtracted from the mean R_H. The mean values of soil respiration rate were applied in the following analyses. Repeated measures analysis of variance (ANOVA) were performed to analyze the individual and interactive effects of thinning and measurement date on R_S, R_H, R_A, fine root biomass, and soil microbial biomass C. We used one-way ANOVA to test the differences in soil microbial biomass C and fine root biomass between the un-thinning and thinning treatments ($n = 3$). Regression analyses were performed to determine the relationships between soil respiration and biotic and abiotic factors.

To describe the temperature dependency (Q_{10}) of soil respiration rates, the following exponential function was used:

$$R = R_0 \times \mathrm{e}^{\beta T} \quad (2)$$

where R is soil respiration rate, R_0 is respiration rate at 0 °C, β is temperature response coefficient, and T is soil temperature. Apparent Q_{10} values were calculated using Eq. 3:

$$Q_{10} = \mathrm{e}^{10\beta} \quad (3)$$

The apparent Q_{10} was used to describe the annual temperature sensitivity using the whole dataset during the growing season. In addition, the Q_{10} function was also fitted for each period of the growing season to describe the season-specific temperature sensitivity (Mo *et al*., 2005; Noh *et al*., 2017).

All statistical analyses were performed using SPSS statistical software (SPSS Inc., USA). The significance level was set at 0.05. Graphs were generated using OriginPro 2016 (Origin Lab Inc., USA).

RESULTS

Soil properties and fine root biomass

Over the two consecutive growing seasons, there were no significant differences in soil temperature and soil moisture between the thinning and control plots (Table II). Soil organic C of the thinning plot was 29% higher than that of the control. Total N, C:N ratio, and light fraction of organic C of the thinning plot were all slightly higher compared to the control, but the differences were not statistically significant (Table III). Both soil microbial biomass C and fine root biomass changed markedly with sampling time (from May to October) (Table II). Soil microbial biomass C in the thinning plot was slightly higher than that of the control, and the difference was significant in September; however, contrasting results were observed in August (Table IV). Fine root biomass was 4%–44% higher in the thinning plot than in the control plot throughout the measurement period, while it was only significant in August.

Soil temperature exhibited pronounced seasonal variations, peaked between July and August, and reached the lowest values in the early or late growing season (Table II, Fig. 1). Comparatively, soil moisture fluctuated significantly among different measurement periods, especially in 2013. However, there were no consistent or regular seasonal trends for soil moisture. Seasonal changes in soil temperature and soil moisture were similar between the control and thinning plot within each year (Fig. 1), with average seasonal coefficients of variation (CV) of 33% and 25%, respectively.

Soil respiration and soil microclimate

Mean values of R_S, R_H, and R_A in the thinning plot were approximately 23%, 15%, and 44% higher compared to the control, respectively, and the difference in respiration rates between the thinning plot and the control was significant for R_A (Table III). The contribution of R_A to R_S in the thinning plot was about 17% higher ($P < 0.05$) compared to the control. Both R_S and R_H showed pronounced seasonal variations, and basically changed along with soil temperature (Table II, Fig. 2). Although we did not directly determine R_A, the repeated measurement ANOVA indicated that R_A exhibited significant seasonal variations (Table II). In a comparison between the control and thinning plot, R_S showed

TABLE II

Repeated measures analysis of variance results of the effects of thinning and sampling time (ST) on soil respiration (R_S), heterotrophic respiration (R_H), autotrophic respiration (R_A), soil temperature, soil moisture, soil microbial biomass C (SMBC), and fine root biomass (FRB)

Item	R_S		R_H		R_A		Soil temperature		Soil moisture		SMBC		FRB	
	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value	F value	P value
2013														
Thinning	3.79	0.12	0.59	0.49	6.54	0.06	0.93	0.39	3.95	0.12	3.46	0.14	14.18	0.02
ST	54.10	< 0.001	18.21	< 0.001	5.76	0.001	380.60	< 0.001	28.75	< 0.001	52.86	<0.001	0.46	0.76
Thinning × ST	1.80	0.11	0.68	0.71	2.12	0.06	2.95	0.01	2.86	0.02	33.81	< 0.001	0.77	0.56
2014														
Thinning	2.02	0.23	1.58	0.28	0.65	0.47	1.39	0.30	0.12	0.75				
ST	79.21	< 0.001	23.41	< 0.001	7.86	< 0.001	446.00	< 0.001	28.38	< 0.001				
Thinning × ST	2.12	0.05	1.23	0.30	0.52	0.86	6.55	< 0.001	3.07	0.006				

TABLE III

Soil respiration (R_S), heterotrophic respiration (R_H), autotrophic respiration (R_A), soil temperature, soil moisture, and other soil chemical and physical properties in un-thinning and thinning plots

Plot	R_S	R_H	R_A	Organic C	Total N	C:N ratio	Light fraction of organic C	pH
	μmol CO_2 m^{-2} s^{-1}			g kg^{-1}			g kg^{-1}	
Un-thinning	2.44 ± 0.22[a)] a[b)]	1.72 ± 0.15a	0.72 ± 0.09a	47.8 ± 6.60a	7.0 ± 0.90a	6.7 ± 0.30a	23.2 ± 4.10a	5.9 ± 0.10a
Thinning	3.01 ± 0.26a	1.97 ± 0.19a	1.04 ± 0.10b	61.7 ± 7.0b	8.3 ± 0.80a	7.4 ± 0.50a	28.7 ± 4.70a	5.9 ± 0.10a

[a)] Means ± standard errors ($n = 3$).
[b)] Means followed by different letters within each column are significantly different ($P < 0.05$).

TABLE IV

Soil microbial biomass C and fine root biomass in un-thinning and thinning plots from May to October 2013

Month	Soil microbial biomass C		Fine root biomass	
	Un-thinning	Thinning	Un-thinning	Thinning
	g kg^{-1}		g m^{-2}	
May	0.46 ± 0.17[a)]a[b)]	0.55 ± 0.17a	168.19 ± 40.68a	300.56 ± 67.71a
July	1.51 ± 0.09a	1.61 ± 0.16a	209.59 ± 28.58a	217.60 ± 52.52a
August	2.76 ± 0.07b	1.04 ± 0.06a	160.16 ± 9.39a	213.95 ± 16.1b
September	0.96 ± 0.10a	1.81 ± 0.09b	185.44 ± 36.38a	219.74 ± 10.36a
October	0.63 ± 0.10a	0.70 ± 0.05a	187.95 ± 31.38a	255.13 ± 3.12a

[a)] Means ± standard errors ($n = 3$).
[b)] Means followed by different letters within each row are significantly different for soil microbial biomass or fine root biomass ($P < 0.05$).

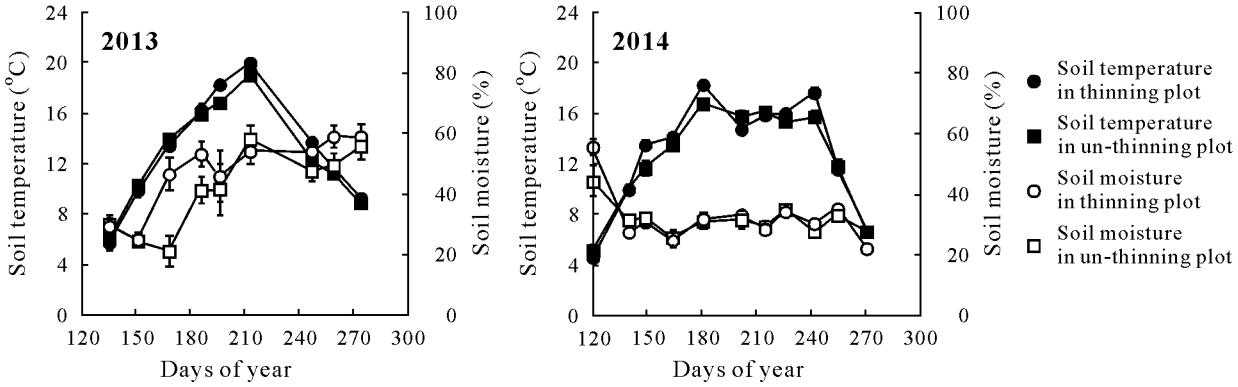

Fig. 1 Seasonal changes in soil temperature and soil moisture in un-thinning and thinning plots in 2013 and 2014. Vertical bars represent standard errors of the means ($n = 3$).

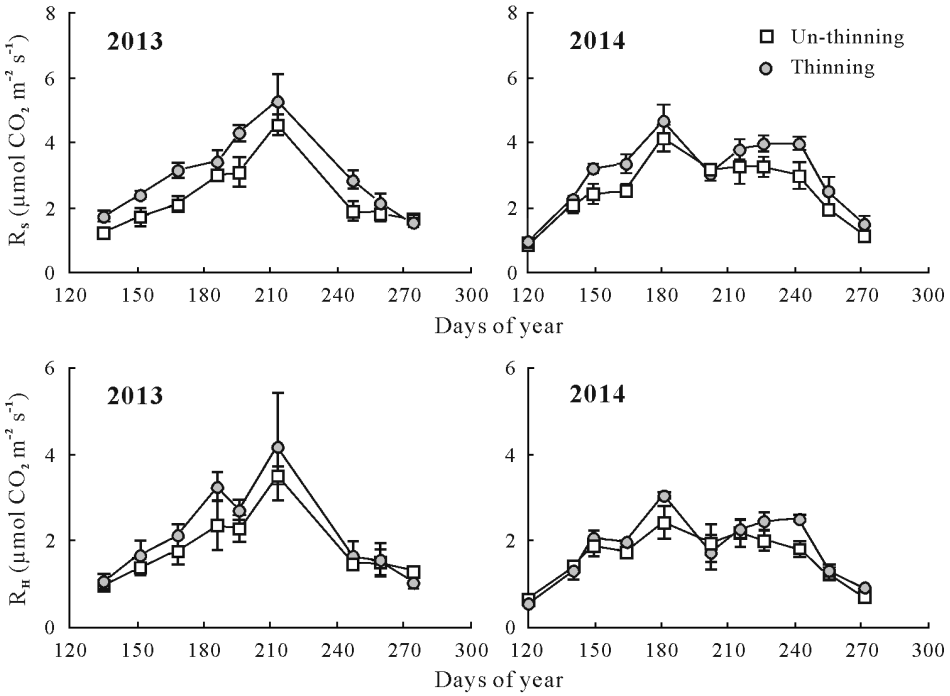

Fig. 2 Seasonal variations of soil respiration (R_S) and heterotrophic respiration (R_H) measured in un-thinning and thinning plots in 2013 and 2014. Vertical bars represent standard errors of the means ($n = 3$).

similar seasonal variations, with the CV ranging from 37% to 43%. The seasonal CV of R_H was approximately 17% higher in the latter, while the seasonal CV of R_A was approximately 28% lower in the latter.

For the control and thinning plot, R_S, R_H, and R_A were significantly and positively correlated with soil temperature,

and the exponential model could explain 84%–88%, 57%–87%, and 33%–50% of the seasonal variations, respectively (Fig. 3). Compared with R_H, R_A was less controlled by soil temperature, as indicated by its relatively lower determination coefficients. The annual Q_{10} value ranged from 2.51–3.25, 2.56–2.92, and 2.29–6.23 for R_S, R_H, and R_A, respectively. Additionally, we also measured the season-specific apparent Q_{10} of R_S, R_H and R_A. Seasonal Q_{10} of R_S and R_H changed with season, whereas R_A was not sensitive to soil temperature in most specific seasonal periods (Table V). Generally, seasonal Q_{10} of R_S and R_H was higher in the control compared to the thinning plot within the mid growing season, while no difference was found for the early and late growing seasons. Seasonal variations of Q_{10} of R_S and R_H were relatively larger in the control compared to the thinning plot. Both R_S and R_H showed a significant parabolic relationship with soil moisture in the control and thinning plot, of which the soil moisture threshold was approximately 38%–40% (Fig. 4).

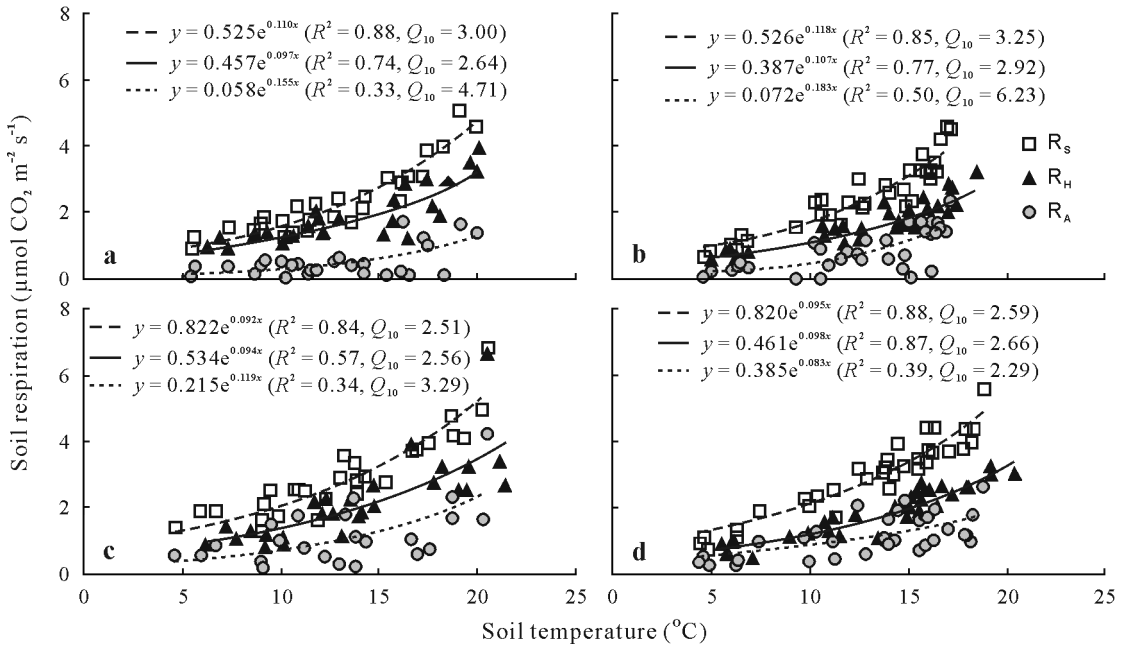

Fig. 3 Exponential relationships between soil respiration (R_S), heterotrophic respiration (R_H), and autotrophic respiration (R_A) and soil temperature in un-thinning (a and b) and thinning (c and d) plots in 2013 (a and c) and 2014 (b and d). R^2 = coefficient of determination; Q_{10} = temperature dependency.

TABLE V

Parameters[a)] derived from the exponential relationship and temperature dependency (Q_{10}) function between soil respiration (R_S), heterotrophic respiration (R_H), and autotrophic respiration (R_A) and soil temperature for each season in un-thinning and thinning plots in 2013 and 2014

Year	Component	Growing season	Un-thinning			Thinning		
			β	Q_{10}	R^2	β	Q_{10}	R^2
2013	R_S	Early	0.071	2.04	0.66	0.074	2.09	0.88
		Mid	0.139	4.00	0.76	0.135	3.86	0.81
		Late	–[b)]	–	–	0.126	3.53	0.65
	R_H	Early	0.070	2.01	0.66	0.101	2.74	0.76
		Mid	0.163	5.08	0.45	–	–	–
		Late	–	–	–	0.115	3.16	0.40
	R_A	Early	–	–	–	–	–	–
		Mid	–	–	–	0.369	40.16	0.69
		Late	–	–	–	–	–	–
2014	R_S	Early	0.118	3.26	0.91	0.121	3.34	0.94
		Mid	0.221	9.07	0.61	0.115	3.17	0.71
		Late	0.114	3.13	0.90	0.086	2.36	0.87
	R_H	Early	0.111	3.03	0.90	0.122	3.40	0.90
		Mid	0.186	6.41	0.58	0.093	2.55	0.61
		Late	0.089	2.44	0.82	0.089	2.45	0.94
	R_A	Early	–	–	–	0.120	3.31	0.62
		Mid	–	–	–	–	–	–
		Late	–	–	–	0.074	2.09	0.53

[a)] β = temperature response coefficient; R^2 = coefficient of determination.
[b)] Indicating that the regression result is not significant and thus the Q_{10} function is not applicable.

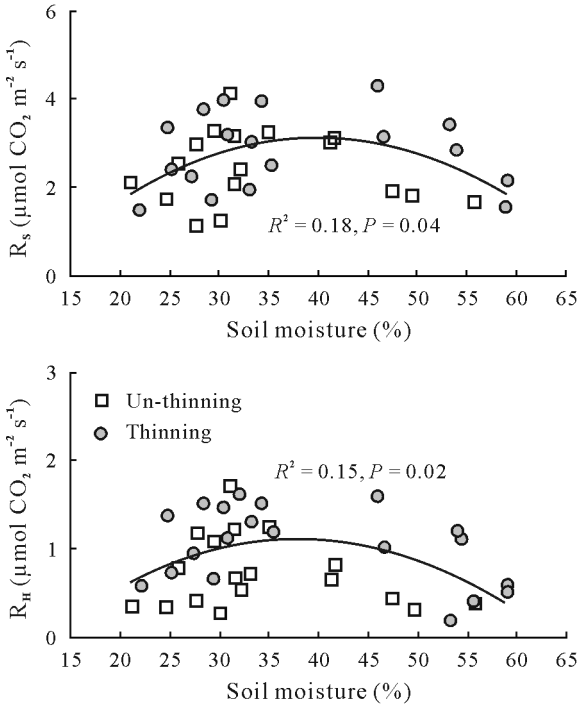

Fig. 4 Relationships between soil respiration (R_S) and heterotrophic respiration (R_H) and soil moisture in un-thinning and thinning plots. R^2 = coefficient of determination.

There were significant linear relationships between R_S and R_H and soil microbial biomass C in the two treatments when the outliers were excluded (Fig. 5).

DISCUSSION

Effect of thinning on soil respiration and soil microclimate

Following thinning, soil temperature is generally expected to increase with the opening of the canopy, *i.e.*, increased absorption of solar radiation by surface soil (Stoffel *et al.*, 2010; Bolat, 2014; Pang *et al.*, 2016). In this study, however, soil temperature was similar between the control and thinning plot, which might have been caused by the shading effects of the understory in the gap area (Schliemann and Bockheim, 2014), as many saplings, shrubs, and herbs regenerated under the opening canopy in the study site. Similarly, the difference in soil moisture between the thinning plot and control was not significant. Although gaps allow more throughfall to reach the ground, an increase in evaporation may weaken this effect (Simonin *et al.*, 2007).

Most previous studies have shown that thinning could result in an immediate (several months to years after thinning) stimulation of microbial decomposition (Cheng *et al.*, 2015; Lei *et al.*, 2018) due to extra input of both above- and below-ground residues (*e.g.*, coarse branches and dead roots) (Akburak and Makineci, 2016). However, it is usually thought that this priming effect would decline to the pre-harvest level after several years (Peng *et al.*, 2008; Akburak and Makineci, 2016). Unlike the results in the existing literature, however, our findings indicated that thinning still has a weak positive effect on R_H even after a long-term period (42 years), which was inconsistent with the first hypothesis. This may be correlated with the relatively higher content of soil organic C and its light fraction in the thinning plot. The growth of the understory, *e.g.*, shrubs and herbs, in forest gap areas provides another possible source of C into soil through root exudates (Wetzel and Burgess, 2001), although we did not measure understory biomass. Another important factor was that the soil microbial biomass C in the thinning plot was generally relatively higher compared to the control throughout the growing season, and there was a positive correlation between R_H and soil microbial biomass C in the two treatments.

Compared to the slight increase in R_H, the R_A in the thinning plot was 44% higher than that of the control, also contrary to the first hypothesis. There may be two likely reasons for this result. First, fine root biomass was relatively higher in the thinning plot, which might result in higher growth and maintenance respiration of root systems (Luo and Zhou, 2006). Root activity could be stimulated as competition for belowground nutrients and water decreased with respect to a reduction in tree density (Cheng *et al.*, 2015; Lei *et al.*,

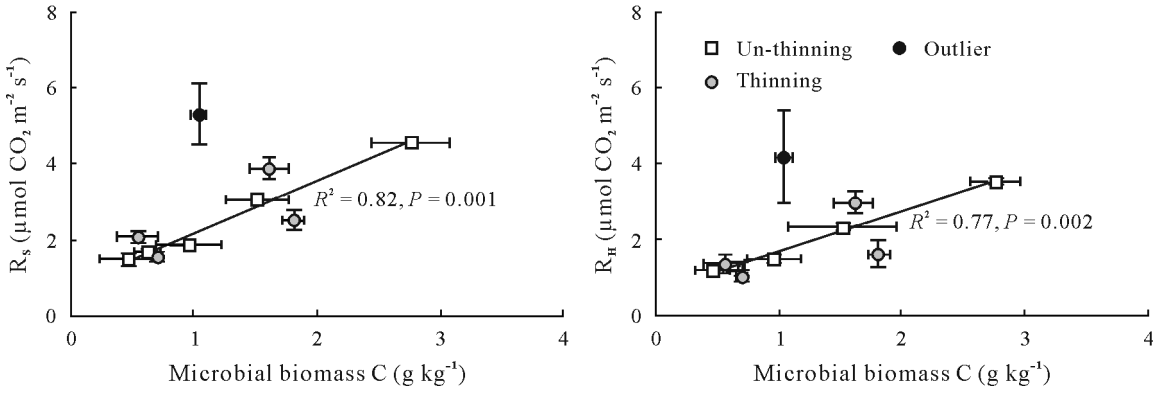

Fig. 5 Relationships between soil respiration (R_S) and heterotrophic respiration (R_H) and soil microbial biomass C in un-thinning and thinning plots. Outliers were not included in the regression analysis. Error bars represent standard errors of the means ($n = 3$). R^2 = coefficient of determination.

2018). This would increase the growth of understory shrubs and grasses, which might also contribute to increased R_A (Lei *et al*., 2018). Second, removal of trees after thinning increases the light availability within the lower canopy, which then promotes photosynthesis of aboveground parts (Forrester *et al*., 2012), and this would in turn stimulate the growth of roots (Hopkins *et al*., 2013), given that above- and belowground activities are highly correlated (Högberg *et al*., 2001).

Temperature sensitivity of soil respiration

Soil respiration was exponentially correlated with soil temperature, consistent with other studies conducted in temperate forests in northeastern China (Wang and Yang, 2007; Han and Jin, 2018). At the annual scale, the Q_{10} of R_H in the thinning plot was slightly lower compared to the control. As we mentioned above, this may be linked to the input of labile organic C resulting from enhanced root activity and higher fine root biomass in the thinning plot. According to the C quality-temperature hypothesis, the Q_{10} of microbial decomposition would decrease with improvement of C availability (Wang *et al*., 2016). Comparatively, Cheng *et al*. (2015) also found that thinning decreased the temperature sensitivity of R_H in a *Pinus tabulaeformis* plantation. Compared with microbial decomposition, root activity might be more driven by other factors in addition to soil temperature. The phenological change in root growth is closely connected to the phenology of aboveground rather than soil temperature, as canopy photosynthesis has been shown to be more important in driving root activity (Tang *et al*., 2005; Savage *et al*., 2013). Thinning resulted in a relatively large decline in the annual Q_{10} of R_A, especially in 2014. We determined the season-specific Q_{10} of soil respiration and found that it was not consistent across the growing season, which implies that this may generate substantial bias in the estimation of annual soil CO_2 emission when using a single apparent Q_{10} (Noh *et al*., 2017). The season-specific Q_{10} values of R_S and R_H were much lower in the thinning plot in the mid-growing season. This may be related to the changes in the input of available substrate during the growing season, as we mentioned above. Our results showed that fine root biomass was higher in the thinning plot. Both photosynthesis and root activity usually peak during summer (Liu *et al*., 2016), which could stimulate root exudation. In a specific season, R_A was usually not sensitive to changes in soil temperature. The apparent temperature sensitivity of soil respiration was the combined response of respiration to various environmental factors, including not only soil temperature but also soil moisture, substrate availability, photosynthesis, and root biomass (Chen *et al*., 2010; Hill *et al*., 2015; Wang *et al*., 2016; Han *et al*., 2018). Within short-term periods, the response of R_A to soil temperature in the thinning plot might be overridden by the effects of photosynthesis and fine root biomass (Högberg *et al*., 2001; Han *et al*., 2018).

Contributions of R_H and R_A to R_S

We found that changes in R_S, *e.g*., seasonal variation and temperature sensitivity, were mainly determined by R_H because of the large contribution of R_H to R_S (58%–94%) (Lei *et al*., 2018) while the contribution of R_A to R_S was relatively low (6%–42%). Forest management practices influence the balance between R_H and R_A through changes in the soil microclimate, inputs of above- and below-ground residues, and the quantities and activities of microbes and roots (Bolat, 2014; Akburak and Makineci, 2015, 2016; Lei *et al*., 2018). The contribution of R_A was 17% higher in the thinning plot than in the control. This might have been caused by the increased fine root biomass and its activity. Because we conducted the measurements a long time after thinning, in addition to the increases in root growth caused by decreased competition among trees in the thinning plot, the abundant understory shrubs and grasses may further contribute to R_A (Lei *et al*., 2018). However, it is notable that we only measured soil respiration during the growing season rather than throughout the entire year, which may lead to bias in estimating the relative contributions of R_H and R_A. The processes of root and rhizosphere metabolism tend to persist during the winter period (Subke *et al*., 2011). Furthermore, due to the thermal insulation effect of litter cover and snow pack, soil microbes might continue to decompose organic matter during the cold season (Wang *et al*., 2013; Gao *et al*., 2018). Hence, to accurately estimate the influences of forest management on the contributions of roots and microbes to total soil CO_2 emission, more annual observations are needed, especially in winter.

Effect of soil moisture on soil respiration

As we discussed above, there was no significant difference in soil moisture between the control and thinning plot, and soil moisture contributed little to the differences in R_S between the two treatments. This contradicted our second hypothesis. Throughout the entire measurement period, we found a significant parabolic relationship between R_S and R_H and soil moisture both in the control and thinning plot. Generally, soil respiration rates are influenced by soil moisture in two ways. On the one hand, low soil water content limits the accessibility of substrates and the activity of soil microbial organisms (Davidson *et al*., 2006; Manzoni *et al*., 2012); on the other hand, high soil moisture exceeding a threshold value would restrict the oxygen diffusion in the soil pore space and reduce the transportation of CO_2 between soil layers (Davidson *et al*., 1998).

CONCLUSIONS

Our results suggest that forest thinning has positive effects on R_S and its source components even for a long-term

period (42 years) after thinning. In the thinning plot, R_A was 44% higher than in the control plot, which might have been caused by a higher fine root biomass. Thinning is expected to increase root growth and activity with the decreased competition among trees and understory plants for solar radiation, nutrients, and soil water. Simultaneously, the slight increase in R_H could be the result of changes in exudates, which are also linked to alterations in root density. Our results indicated that R_H and R_A showed different responses to temperature changes. Soil temperature was the main driving factor for seasonal variation in R_H, while R_A was less responsive to soil temperature during specific seasons. The season-specific Q_{10} values of R_S and R_H were lower in the thinning plot during the mid-growing season. Our findings are useful for predicting the long-term effects of forest management practices on soil C dynamics, and further studies concerning the mechanisms underlying forest management-induced changes in R_H and R_A are necessary in northeastern China.

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REFERENCES

Akburak S, Makineci E. 2015. Effects of thinning on soil respiration and microbial respiration of forest floor and soil in an oak (*Quercus frainetto*) forest. *Soil Res*. **53**: 522–530.

Akburak S, Makineci E. 2016. Thinning effects on soil and microbial respiration in a coppice-originated *Carpinus betulus* L. stand in Turkey. *iForest*. **9**: 783–790.

Ali R S, Kandeler E, Marhan S, Demyan M S, Ingwersen J, Mirzaeitalarposhti R, Rasche F, Cadisch G, Poll C. 2018. Controls on microbially regulated soil organic carbon decomposition at the regional scale. *Soil Biol Biochem*. **118**: 59–68.

Bolat İ. 2014. The effect of thinning on microbial biomass C, N and basal respiration in black pine forest soils in Mudurnu, Turkey. *Eur J For Res*. **133**: 131–139.

Bond-Lamberty B, Allison T. 2010. Temperature-associated increases in the global soil respiration record. *Nature*. **464**: 579–582.

Brookes P C, Landman A, Pruden G, Jenkinson D S. 1985. Chloroform fumigation and the release of soil nitrogen: A rapid direct extraction method to measure microbial biomass nitrogen in soil. *Soil Biol Biochem*. **17**: 837–842.

Chatterjee A, Vance G F, Pendall E, Stahl P D. 2008. Timber harvesting alters soil carbon mineralization and microbial community structure in coniferous forests. *Soil Biol Biochem*. **40**: 1901–1907.

Chen B Y, Liu S R, Ge J P, Chu J X. 2010. Annual and seasonal variations of Q_{10} soil respiration in the sub-alpine forests of the eastern Qinghai-Tibet Plateau, China. *Soil Biol Biochem*. **42**: 1735–1742.

Cheng X Q, Kang F F, Han H R, Liu H W, Zhang Y L. 2015. Effect of thinning on partitioned soil respiration in a young *Pinus tabulaeformis* plantation during growing season. *Agric For Meteorol*. **214-215**: 473–482.

Davidson E A, Belk E, Boone R D. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol*. **4**: 217–227.

Davidson E A, Janssens I A, Luo Y Q. 2006. On the variability of respiration in terrestrial ecosystems: Moving beyond Q_{10}. *Global Change Biol*. **12**: 154–164.

Forrester D I, Collopy J J, Beadle C L, Warren C R, Baker T G. 2012. Effect of thinning, pruning and nitrogen fertiliser application on transpiration, photosynthesis and water-use efficiency in a young *Eucalyptus nitens* plantation. *For Ecol Manag*. **266**: 286–300.

Gao D C, Peng B, Fan Z Z, Pei G T, Bai E. 2018. Different winter soil respiration between two mid-temperate plantation forests. *For Ecol Manag*. **409**: 390–398.

Guo J F, Chen G S, Xie J S, Yang Z J. 2016. Clear-cutting and slash burning effects on soil CO_2 efflux partitioning in Chinese fir and evergreen broadleaved forests in subtropical China. *Soil Use Manag*. **32**: 220–229.

Han M G, Jin G Z. 2018. Seasonal variations of Q_{10} soil respiration and its components in the temperate forest ecosystems, northeastern China. *Eur J Soil Biol*. **85**: 36–42.

Han M G, Shi B K, Jin G Z. 2016. Temporal variations of soil respiration at multiple timescales in a spruce-fir valley forest, northeastern China. *J Soil Sediment*. **16**: 2385–2394.

Han M G, Shi B K, Jin G Z. 2018. Conversion of primary mixed forest into secondary broadleaved forest and coniferous plantations: Effects on temporal dynamics of soil CO_2 efflux. *Catena*. **162**: 157–165.

Hibbard K A, Law B E, Reichstein M, Sulzman J. 2005. An analysis of soil respiration across northern hemisphere temperate ecosystems. *Biogeochemistry*. **73**: 29–70.

Hill P W, Garnett M H, Farrar J, Iqbal Z, Khalid M, Soleman N, Jones D L. 2015. Living roots magnify the response of soil organic carbon decomposition to temperature in temperate grassland. *Global Change Biol*. **21**: 1368–1375.

Högberg P, Nordgren A, Buchmann N, Taylor A F S, Ekblad A, Högberg M N, Nyberg G, Ottosson-Löfvenius M, Read D J. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*. **411**: 789–792.

Hopkins F, Gonzalez-Meler M A, Flower C E, Lynch D J, Czimczik C, Tang J W, Subke J A. 2013. Ecosystem-level controls on root-rhizosphere respiration. *New Phytol*. **199**: 339–351.

Janzen H H, Campbell C A, Brandt S A, Lafond G P, Townley-Smith L. 1992. Light-fraction organic matter in soils from long-term crop rotations. *Soil Sci Soc Am J*. **56**: 1799–1806.

Lei L, Xiao W F, Zeng L X, Zhu J H, Huang Z L, Cheng R M, Gao S K, Li M H. 2018. Thinning but not understory removal increased heterotrophic respiration and total soil respiration in *Pinus massoniana* stands. *Sci Total Environ*. **620**: 1360–1369.

Liu Z L, Jin G Z, Zhou M. 2016. Evaluation and correction of optically derived leaf area index in different temperate forests. *iForest*. **9**: 55–62.

López-Serrano F R, Rubio E, Dadi T, Moya D, Andrés-Abellán M, García-Morote F A, Miettinen H, Martínez-García E. 2016. Influences of recovery from wildfire and thinning on soil respiration of a Mediterranean mixed forest. *Sci Total Environ*. **573**: 1217–1231.

Luo Y Q, Zhou X H. 2006. Soil Respiration and the Environment. Academic Press, London.

Manzoni S, Schimel J P, Porporato A. 2012. Responses of soil microbial communities to water stress: Results from a meta-analysis. *Ecology*. **93**: 930–938.

Ministry of Forestry of China. 1994. Forest Resources Statistics of China (1989–1993) (in Chinese). China Forestry Publishing House, Beijing.

Mo W H, Lee M S, Uchida M, Inatomi M, Saigusa N, Mariko S, Koizumi H. 2005. Seasonal and annual variations in soil respiration in a cool-temperate deciduous broad-leaved forest in Japan. *Agric For Meteorol*. **134**: 81–94.

Moyes A B, Bowling D R. 2013. Interannual variation in seasonal drivers of soil respiration in a semi-arid Rocky mountain meadow. *Biogeochemistry*. **113**: 683–697.

Nilsen P, Strand L T. 2008. Thinning intensity effects on carbon and nitrogen stores and fluxes in a Norway spruce (*Picea abies* (L.) Karst.) stand after 33 years. *For Ecol Manag*. **256**: 201–208.

Noh N J, Kuribayashi M, Saitoh T M, Muraoka H. 2017. Different responses of soil, heterotrophic and autotrophic respirations to a 4-year soil

warming experiment in a cool-temperate deciduous broadleaved forest in central Japan. *Agric For Meteorol*. **247**: 560–570.

Pang X Y, Hu B, Bao W K, De Oliveira Vargas T, Tian G L. 2016. Effect of thinning-induced gap size on soil CO_2 efflux in a reforested spruce forest in the eastern Tibetan Plateau. *Agric For Meteorol*. **220**: 1–9.

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 Biol Biochem*. **41**: 1008–1014.

Peng Y Y, Thomas S C, Tian D. 2008. Forest management and soil respiration: Implications for carbon sequestration. *Environ Rev*. **16**: 93–111.

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

Schlesinger W H. 1997. Biogeochemistry: An Analysis of Global Change. 2nd Edn. Academic Press, San Diego.

Schliemann S A, Bockheim J G. 2014. Influence of gap size on carbon and nitrogen biogeochemical cycling in Northern hardwood forests of the Upper Peninsula, Michigan. *Plant Soil*. **377**: 323–335.

Shabaga J A, Basiliko N, Caspersen J P, Jones T A. 2015. Seasonal controls on patterns of soil respiration and temperature sensitivity in a northern mixed deciduous forest following partial-harvesting. *For Ecol Manag*. **348**: 208–219.

Simonin K, Kolb T E, Montes-Helu M, Koch G W. 2007. The influence of thinning on components of stand water balance in a ponderosa pine forest stand during and after extreme drought. *Agric For Meteorol*. **143**: 266–276.

Soil Survey Staff. 1999. Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys. 2nd Edn. USDA Natural Resources Conservation Service, Washington, D.C.

Stoffel J L, Gower S T, Forrester J A, Mladenoff D J. 2010. Effects of winter selective tree harvest on soil microclimate and surface CO_2 flux of a northern hardwood forest. *For Ecol Manag*. **259**: 257–265.

Subke J A, Voke N R, Leronni V, Garnett M H, 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 W, Qi Y, Xu M, Misson L, Goldstein A H. 2005. Forest thinning and soil respiration in a ponderosa pine plantation in the Sierra Nevada. *Tree Physiol*. **25**: 57–66.

Templeton B S, Seiler J R, Peterson J A, Tyree M C. 2015. Environmental and stand management influences on soil CO_2 efflux across the range of loblolly pine. *For Ecol Manag*. **355**: 15–23.

Tian D L, Peng Y Y, Yan W D, Fang X, Kang W X, Wang G J, Chen X Y. 2010. Effects of thinning and litter fall removal on fine root production and soil organic carbon content in Masson pine plantations. *Pedosphere*. **20**: 486–493.

Vance E D, Brookes P C, Jenkinson D S. 1987. Microbial biomass measurements in forest soils: The use of the chloroform fumigation-incubation method in strongly acid soils. *Soil Biol Biochem*. **19**: 697–702.

Wang C K, Han Y, Chen J Q, Wang X C, Zhang Q Z, Bond-Lamberty B. 2013. Seasonality of soil CO_2 efflux in a temperate forest: Biophysical effects of snowpack and spring freeze-thaw cycles. *Agric For Meteorol*. **177**: 83–92.

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

Wang Q, He N P, Yu G R, Gao Y, Wen X F, Wang R F, Koerner S E, Yu Q. 2016. Soil microbial respiration rate and temperature sensitivity along a north-south forest transect in eastern China: Patterns and influencing factors. *J Geophys Res*: *Biogeosci*. **121**: 399–410.

Wetzel S, Burgess D. 2001. Understorey environment and vegetation response after partial cutting and site preparation in *Pinus strobus* L. Stands. *For Ecol Manag*. **151**: 43–59.