

# Effects of Spatial-Temporal Variation and Biological Factors on Stem Respiration of *Larix principis-rupprechtii* Mayr

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## Abstract

This study was conducted to expose the rule of stem respiration change in temporal variations, spatial variations, biological factors and analyze the reasons of the stem respiration change for investigated stem respiration rate ( $R_s$ ) in Prince Rupprecht's Larch (*Larix principis-rupprechtii* Mayr) plantation using the soil carbon flux system (Li-8100) during the growing season (May to September) and the non-growing season (October) in Saihanba National Forest Park. The results are listed below. (1) The daily dynamics and seasonal dynamics of  $R_s$  obeyed single-peak curves. (2) Except for September,  $R_s$  significantly differed among stem heights. (3) The annual  $R_s$  changed with the increased thinning intensity (TI) as follows: TI 20% ( $1.68 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) < TI 15% (1.83) < control (1.89) < TI 30% (1.92) < TI 35% (2.82). (4) The annual  $\text{CO}_2$  emission per unit area changed with crown height (CH) as follows: CH 2:3 ( $8.32 \text{ t ha}^{-1}$ ) (control, non-pruned) > CH 1:3 (7.60) (intense pruning) > CH 1:2 (7.21) (slight pruning). (5) The  $R_s$  of trees with large and middle diameter grades (diameter at breast height DBH 170-210 vs. 120-160 mm) were not significantly different, but were both higher than trees with small diameter grade (DBH 70-110 mm). This study clarifies the response of stem respiration rate to various influencing factors and helps to accurately estimate the carbon emissions from stem respiration.

**Keywords:** biological factors, carbon emission, *Larix principis-rupprechtii*, spatial-temporal variations, stem respiration

## Introduction

The respiration of trees generally consumes 30-60% of the carbon fixed via photosynthesis (Kozłowski 1992). Stem respiration annually accounts for 14-48% of autotrophic respiration (Zeng et al. 2000, Vose and Ryan 2002, Xiao et al. 2005). Moreover, forests cover about 40% of global lands, and store 76-98% of the organic carbon in terrestrial ecosystems (Fang et al. 2007, Dixon et al. 1994). Therefore, investigation into the laws and influencing factors of stem respiration is a major part in estimation of forest carbon balance and is significant for revealing the carbon sequestration capacity of forest ecosystems.

Research on temporal variation is the basis for studying the laws of stem respiration. The existing research focuses on time scales of day and month, but rarely on time scale of 10 days. Furthermore, the existing studies at time scale of day are very inconsistent. Daily dynamic curves of stem respiration can be divided into single-peak curves (Shi et al. 2010, Wang et al. 2008, Wang et al. 2003), double-peak curves (Hu and Sha 2010, Yan et al. 2006), and S-shaped

curves (Wang et al. 2005). Many tests about the spatial variation of stem respiration focus on the north-south differences (Yan et al. 2009), but in fact, the competition due to density differences is a key factor affecting the growth of trees (Yao et al. 2013). Faster growth causes remarkable  $R_s$  increase (Daudet 2005). Therefore, whether density has any significant effect on  $R_s$  is to be researched. Pruning is a key measure in tree cultivation, as it can regulate the forest microclimate by changing the crown height. Accordingly, research on the effects of crown height on stem respiration will facilitate tree cultivation. The same-aged forests with different diameter grades have a significant difference in metabolism which results in  $R_s$  change (Teskey and McGuire 2007). Therefore, it is worth studying further whether trees with larger diameter grade have a higher  $R_s$ . Prince Rupprecht's larch (*Larix principis-rupprechtii* Mayr) is a major reforestation species in the sub-alpine areas of China's warm temperate zone (Wang 2002), and plays important roles in wood production, water-soil conservation, and ecological regulation in North China (Wang et al. 1992). It is essential to verify and clear the influence of temporal varia-

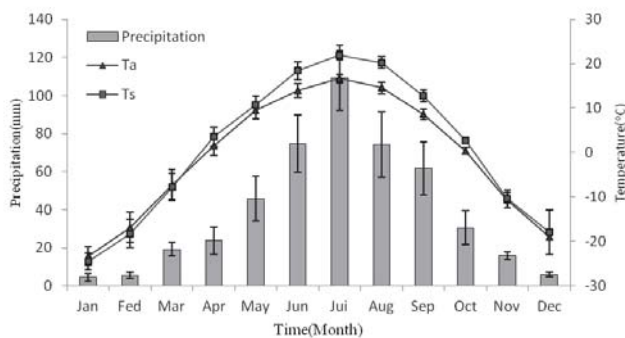
tions (daily dynamics, seasonal dynamics) spatial variations (vertical height and stand density) and biological factors (crown height, diameter grades) on stem respiration of *Larix principis-rupprechtii*, which can provide data and theory on carbon cycle mode construction, help to search for the causes on stem respiration change, and point the way to the further research on mechanism.

The aim of the study was (1) to evaluate the effects of temporal spatial variations and biological factors on the stem respiration of *Larix principis-rupprechtii*, (2) to analyze the reasons of the stem respiration change, and (3) to determine the direction of future research.

## Materials and Methods

### Site Description

The study area was located in Saihanba National Forest Park (E 116°51' -117°39'; N 42°02' -42°36') of Weichang Manchu and Mongolian Autonomous County in northeastern Hebei Province. This area belongs to the semi-arid monsoon climate zone in cool temperature zone. The basic information is listed as follows: elevation 1600-1800 m, annual average temperature -1.5 °C, extreme maximum temperature 29.7 °C, extreme minimum temperature -38.7 °C, active accumulated temperature ( $\geq 10$  °C) 1,663.5 °C, and average annual rainfall 433 mm. The precipitation in June and August is 55% of the total annual precipitation (Figure 1). The soils are composed mainly of dark gray forest soil, and *Larix principis-rupprechtii* is the dominant tree species. The tested forests included 16- (Young Larch), 25- (Immature Larch), and 41-year-old (Mature Larch) artificial pure forests of *L. principis-rupprechtii*. The density and size of trees of the study sites, as shown in Table 1, were obtained for the three forest ages through wood seized feet.



**Figure 1.** Monthly mean precipitation, air temperature ( $T_a$ ) and soil temperature ( $T_s$ ) in Saihanba National Forest Park from 1996 to 2013. Bars are means  $\pm$  standard error,  $n=9$

## Methods

### Measurement of stem respiration

Stem respiration was measured using a soil carbon flux system (Li-8100). The steps are as follows: Polyvinyl chlo-

**Table 1.** Information on sample plots investigated in stands of *Larix principis-rupprechtii*

Forest age	Number of trees ( $\text{ha}^{-1}$ )	Mean DBH <sup>a</sup> (mm)	Mean tree height (m)	Stem surface area of one tree ( $\text{m}^2$ )	Stem surface area <sup>b</sup> ( $\text{m}^2 \text{ha}^{-1}$ )
16	2915	86.4	7.8	1.49	4343.35
25	1797	114.0	10.07	4.38	7870.86
41	652	219.7	17.5	9.57	6239.64

<sup>a</sup> DBH: Diameter at Breast Height.

<sup>b</sup> Stem surface area were calculated from stem diameters at 1 m-intervals along the stem, assuming that the shape of each stem segment was a truncated cone

ride (PVC) collars (diameter 7.5 cm) were fixed with silicone adhesive onto the tested stem part. After drying, the residual silicone adhesive was removed, and the areas between the stem and the PVC collars were sealed. The volume of the PVC collar was measured using volume replacement method: a pore was opened on the upside of the collar; the other end of the collar was covered with a flat lid, and then the collar was filled fine sands through the pore. After that, the in-filled sand (or water) was pulled into a marked cylinder, and the volume of the fine sand is exactly the volume of the collar. During the measurement, the Li-8100 (LI-COR, Lincoln, Nebraska, US) chamber was fixed with string onto the PVC collar. The stem surface area per hectare of forests was computed on basis of the records of each scale and via an equation. The stem respiration flux per hectare of forests was defined as the respiration rate per unit area of stem ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) multiplied by stem surface area per hectare of forests.

### Measuring Methods

The *Larix principis-rupprechtii* in Saihanba starts bud flushing, sprouting and shoot growth in the middle of May, and reaches the growth peak in July. It defoliates since middle and later August, enters the dormancy period since late September and enters full dormancy stage in October. During the dormancy, the stem respiration is dominated by maintenance respiration, the growth respiration then is negligible (Adu-Bredu et al. 1997). Therefore, the period from May to October was selected for monitoring stem respiration rate.

### Effects of temporal variation on stem respiration

(1) The 16-, 25- and 41-year-old forest were tested. From three 20 m  $\times$  20 m plots, 3 standard trees were selected and each was installed with a respiration device at 1.3 m height.

(2) Between May to October 2013, 3 days from each 10 days were selected (with basically similar weather conditions) to measure  $R_s$  at 1.3 m height. From 8:00 am on each test day to 8:00 am the next day, one cycle was set every 2 hours (totally 12 cycles) to measure the daily dynamics of the 16-year-old forest; we measured the seasonal dynamics of the 16-, 25- and 41-year-old forest at 8:00 am. Meanwhile, the air temperature and stem surface temperature were meas-

ured using an instantaneous digital thermometer; the temperature 1 cm behind the skin and the relative air humidity were measured using the devices in the Li-8100 system.

*Effects of vertical height on stem respiration*

(1) Three trees of normal growth and good development were selected from the 16-year-old forest for measurement.

(2) Respiration devices were installed in the south side at each of five heights (0.2, 0.7, 1.0, 1.3, and 1.8 m) in each tree, and there were totally 15 devices.

(3) From May to October 2013,  $R_s$  were monitored once every 10 days. In the same day, only one tree was monitored. Each cycle was set every two hours between 8:00 and 18:00 with a total of 6 cycles. Air temperature, stem surface temperature, temperature at 1 cm under skin, and air relative humidity were measured with the above methods.

*Effects of thinning density (TI) on stem respiration*

(1) The 25-year-old forests were tested. According to stand volume calculation, 15 standard plots (each 20 m×20 m) were set with 5 TIs (control, weak, medium, strong, and very strong), respectively (Table 2), in 2010, each TI took 3 standard plots.

**Table 2.** The thinning parameters of 25-year-old *Larix principis-rupprechtii*

Thinning intensity	Stand volume before thinning (m <sup>3</sup> /hm <sup>2</sup> )	Stand density before thinning (Plant/hm <sup>2</sup> )	Stand volume after thinning (m <sup>3</sup> /hm <sup>2</sup> )	Stand density after thinning (Plant/hm <sup>2</sup> )
TI 0%	117.72	2425	117.72	2425
TI 15%	140.94	3025	119.48	1750
TI 20%	111.87	2400	89.29	1425
TI 30%	121.17	3050	84.72	1550
TI 35%	127.3	2925	82.79	1425

(2) In each plot, 3 standard trees were selected according to average DBH and average tree height. Totally, 45 trees were selected and each was installed with a respiration device at the DBH.

(3) From May to October 2013,  $R_s$  at 1.3 m height were measured for trees with different cultivation measures. One day was selected from every ten days, and at 8:00 am, the air temperature, stem surface temperature, temperature 1 cm under bark, and air relative humidity were measured with the above methods.

*Effects of crown height (CH) on stem respiration*

(1) Study was performed in 16-year-old forest. In 2013, nine standard plots (each 20 × 20 m) were selected and pruned to different degrees (computed as CH): control (2:3), slight (1:2), and severe (1:3). Each CH took 3 standard plots. Three trees in normal growth and good development were selected and pruned at each plot. A PVC collar was fixed via waterproof silicone adhesive onto each stem at 1.3 m height.

(2) From May to October 2013, stem respiration was monitored once every 10 days. Each cycle was set every

two hours (8:00-18:00), with a total of 6 cycles. Air temperature, trunk surface temperature, temperature 1 cm under skin, and air relative humidity were measured with the above methods.

*Effects of diameter grades on stem respiration*

(1) The 25-year-old forest was tested. From three 20 m×20 m plots, trees in normal growth and good development were selected at three diameter grades (70-110, 120-160, and 170-210 mm, each grade with 3 trees). Totally, 27 trees were selected, and each was installed with a respiration device at DBH.

(2) From May to October 2013,  $R_s$  at 1.3 m height were measured for trees with different diameter grades. One day was selected from every ten days, and at 8:00 am, the air temperature, stem surface temperature, temperature at 1 cm under skin, and air relative humidity were measured with the above methods. Data for the late October of  $R_s$  measurement were not available because of a malfunction of the equipment.

*Calculation of stem surface area*

To compute the CO<sub>2</sub> emission per single tree due to stem respiration, five standard trees were selected from each forest age in July 2013, depending on average tree height

and average DBH (totally 15 trees). Trees were segmented every 1 m from 0.5 m height. The surface area of each segment was computed by considering it as a circular truncated cone. The surface area at treetop was computed as per the equation for cone. Through data analysis, the stem surface area of individual tree and the trunk surface area per hectare were obtained at the three forest ages (Table 1).

*Statistic analysis*

For statistical analysis of the effect of each factor (daily dynamics, seasonal dynamics, vertical height, stand density, crown height and diameter grades) on stem respiration, the Kolmogorov-Smirnov test and the Levene test were firstly used to verify the assumptions of normality and homogeneity of variances for the data for each variable, respectively. If a variable did not conform to these assumptions, it was mathematically transformed. Finally, one-way ANOVAs were carried out to determine the effect of daily dynamics, seasonal dynamics, vertical height, stand density, crown height and diameter grades on stem respiration rate. The significant differences among the levels of each

factor were checked with Duncan's multiple range test ( $P = 0.05$ ). The Kruskal-Wallis test was used to determine the data, if the transformed data still did not conform to the homogeneity assumption. All the above data analyses were performed with SPSS Statistics package (v. 18.0, SPSS Inc., Chicago IL, USA) and Origin software (v. 8.0, OriginLab, Washington, USA).

**Fit model for stem respiration and temperature**

Stem respiration (R) and temperature (T) were exponentially fitted as follows:

$$R = a \cdot e^{bT} \tag{1}$$

where a and b are coefficients. The relationship between stem respiration and corresponding stem temperature can be described by an exponential function.

Temperature coefficient  $Q_{10}$  (increase of stem respiration with increase by 10 °C) was computed as follows:

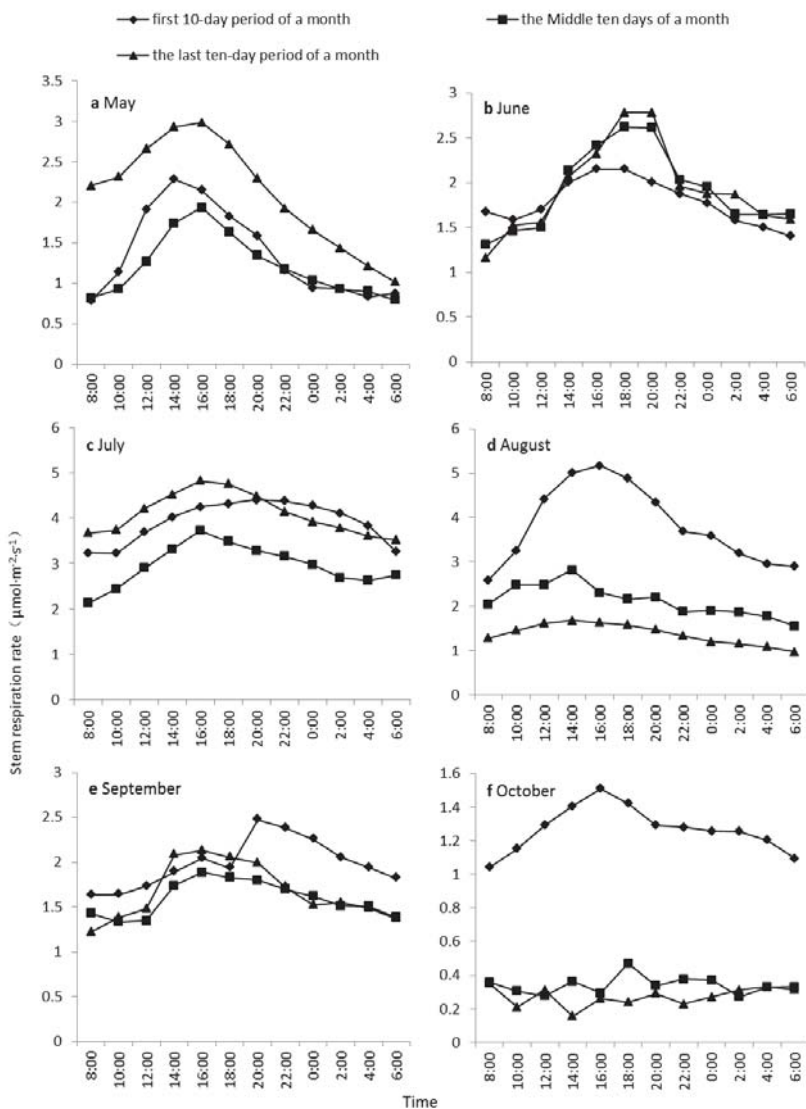
$$Q_{10} = e^{10b} \tag{2}$$

**Results**

**Temporal variation of stem respiration**

*Daily dynamics of stem respiration*

The daily dynamics of  $R_s$  of the 16-year-old trees obeyed a single-peak curve (Figure 2). (1) In growing season (May to September), the daily  $R_s$  changed as follows:  $R_s$  at night was mostly maintained at very low level, and was minimized at 6:00-8:00 ( $0.78-3.52 \mu\text{mol m}^{-2} \text{s}^{-1}$ );  $R_s$  gradually rose since 8:00 and peaked at 14:00-16:00 ( $1.67-5.17 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Table 3). (2) In non-growing season (October),  $R_s$  changed irregularly in a multi-peak curve with small amplitude of fluctuation.  $R_s$  was 0.47, 0.20 and  $0.12 \mu\text{mol m}^{-2} \text{s}^{-1}$  in early, middle and late October, respectively.  $R_s$  in middle and late October fluctuated between  $0.27-0.21$  and  $0.47-0.33 \mu\text{mol m}^{-2} \text{s}^{-1}$ . In early August (most vigorous period),  $R_s$  range was maximized to be  $2.58 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which was 21.50-fold higher than in non-growing season (late October,  $0.12 \mu\text{mol}$



**Figure 2.** Daily dynamics of 16-year-old *Larix principis-rupprechtii* stem respiration rate from May to October. Different lines indicate the diurnal variation of stem respiration rate in different periods of each month. Bars are means  $\pm$  standard error,  $n=9$



**Table 3.** Extreme values of daily *Larix principis-rupprechtii* stem respiration and the occurring periods

Dates	Maximum occurrence time	Maximum ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Minimum occurrence time	Minimum ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
Early May	14:00	2.29	8:00	0.78
Middle May	16:00	1.93	6:00	0.79
Late May	16:00	2.99	6:00	1.02
Early Jun.	18:00	2.15	6:00	1.41
Middle Jun.	18:00	2.62	8:00	1.31
Late Jun.	20:00	2.78	8:00	1.16
Early Jul.	20:00	4.40	10:00	3.22
Middle Jul.	16:00	3.73	8:00	2.13
Late Jul.	16:00	4.82	6:00	3.52
Early Aug.	16:00	5.17	8:00	2.59
Middle Aug.	14:00	2.82	6:00	1.55
Late Aug.	14:00	1.67	6:00	0.97
Early Sep.	20:00	2.48	8:00	1.64
Middle Sep.	16:00	1.89	10:00	1.33
Late Sep.	16:00	2.13	8:00	1.22
Early Oct.	16:00	1.51	8:00	1.04
Middle Oct.	18:00	0.47	12:00	0.27
Late Oct.	4:00	0.33	10:00	0.21

$\text{m}^2 \text{s}^{-1}$ ). (3) The daily  $\text{CO}_2$  emissions from stem in all tested months are listed in Table 4. The emission was maximized in July and minimized in October ( $60.39$  vs.  $10.34 \text{ kgCO}_2 \text{ ha}^{-1} \text{ d}^{-1}$ ), and the emission in the growing season was 2.49-5.84 times higher than in the non-growing season.

**Table 4.** *Larix principis-rupprechtii* stem  $\text{CO}_2$  emissions during vegetation season

Month	May	June	July	August	September	October
Daily $\text{CO}_2$ emission ( $\text{kgCO}_2 \text{ ha}^{-1} \text{ d}^{-1}$ )	$25.81 \pm 4.60$	$30.98 \pm 0.75$	$60.39 \pm 5.85$	$40.28 \pm 12.03$	$28.84 \pm 1.98$	$10.34 \pm 5.30$
Month $\text{CO}_2$ emission ( $\text{kgCO}_2 \text{ ha}^{-1} \text{ month}^{-1}$ )	$800.11 \pm 142.70$	$929.4 \pm 22.55$	$1872.09 \pm 18.43$	$1248.68 \pm 373.07$	$865.20 \pm 59.52$	$310.2 \pm 164.25$

Data are means  $\pm$  standard error,  $n=9$ .

*Seasonal dynamics of stem respiration at different forest ages*

$R_s$  at three ages (16, 25, and 41 years old) was continuously monitored, and the  $R_s$  in the growing season was significantly higher than in the non-growing season (Figure 3). (1) As *Larix principis-rupprechtii* started to sprout and expand in middle May,  $R_s$  gradually increased; the trees grew vigorously from late June to early August, and  $R_s$  reached

$0.93$ - $3.84 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which was significantly higher than in other months. As air temperature declined since middle August,  $R_s$  gradually decreased. The trees started to defoliate in late August, but the nearly stopped growing in late September, and the  $R_s$  was minimized to  $0.27$ - $0.42 \mu\text{mol m}^{-2} \text{s}^{-1}$  since middle October. (2) From early May to early October, the mean of  $R_s$  at the three forest ages all ranked as follows:  $16 (2.22 \mu\text{mol m}^{-2} \text{s}^{-1}) > 25 (1.93) > 41 (0.92)$  years old. In middle and late October,  $R_s$  ranked as follows:  $41 (0.38 \mu\text{mol m}^{-2} \text{s}^{-1}) > 25 (0.32) > 16 (0.29)$ -year-old. (3) The annual  $\text{CO}_2$  emission per unit area during stem respiration ranked by forest age as follows:  $25 (14.50 \text{ t ha}^{-1}) > 16 (7.84) > 41 (4.41)$  years old. As shown in Table 5, one-way analysis of variance (ANOVA) shows that  $R_s$  significantly changed among the three forest ages ( $P < 0.01$ ). (4)  $R_s$  of the three forest ages (16, 25, 41-year-old) had an obvious exponential relationship with temperature (Figure 4,  $R^2 = 0.85, 0.77, 0.58, P < 0.01$ ), respectively. The daily and seasonal changing trends of  $R_s$  were consistent with that of temperature, with  $Q_{10}$  of 2.77 (16-year-old), 2.66 (25), and 2.39 (41).

*Spatial variation of stem respiration*

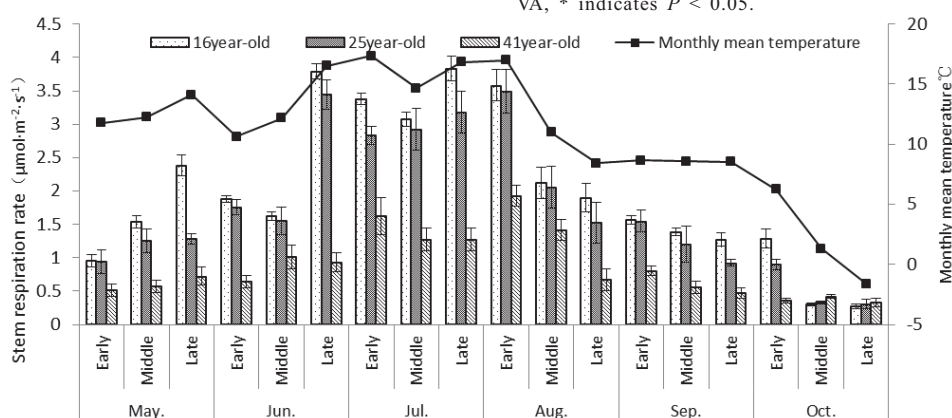
In order to estimate the effects of spatial factors on  $R_s$ , the values of  $R_s$  from different vertical height and stand density were investigated, respectively.

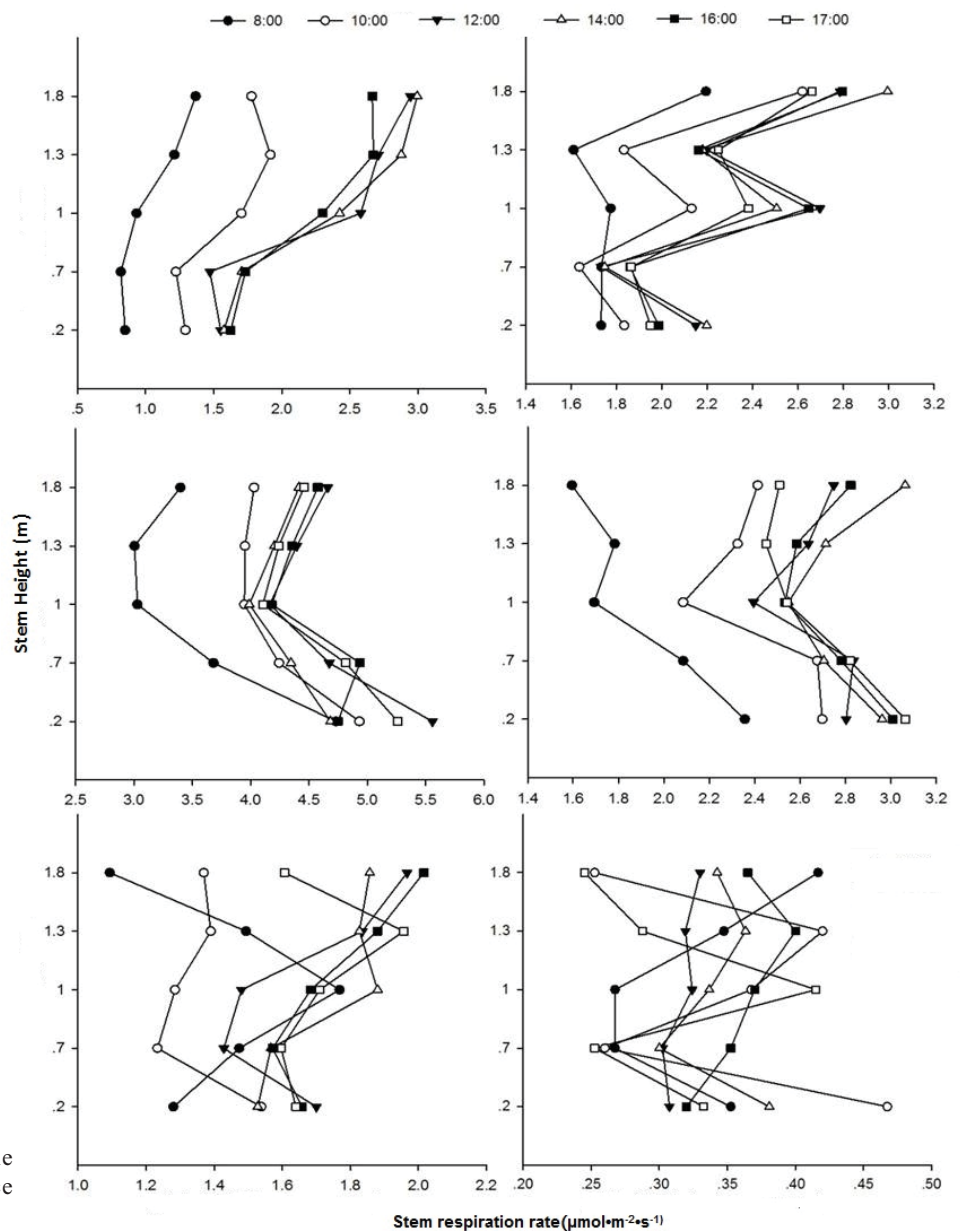
**Table 5.** Analysis of variance stem respiration rate in 16-, 25-, 41-year-old *Larix principis-rupprechtii* stand influenced by forest age

Forest age	$R_s (\mu\text{mol m}^{-2} \text{s}^{-1})$	F	P
16	$1.93 \pm 0.25^a$	7.836	0.001*
25	$1.68 \pm 0.23$		
41	$0.84 \pm 0.10$		

For different forest age, a values are means  $\pm$  standard error,  $n=18$ . Significance for differences among three forest ages was analyzed by ANOVA, \* indicates  $P < 0.05$ .

**Figure 3.** Seasonal dynamics of *Larix principis-rupprechtii* stem respiration rate from May to October. Bars are means  $\pm$  standard error,  $n=9$





**Figure 4.** Relationship of the stem respiration per unit surface area ( $R_s$ ) with temperature

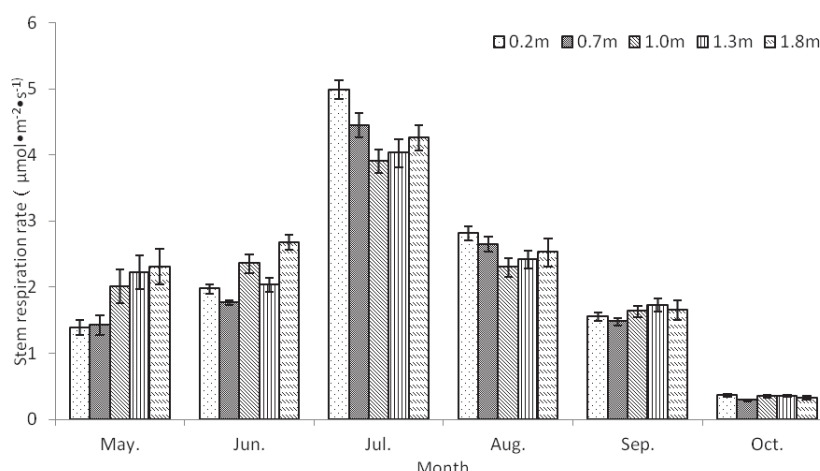
*Effects of height on stem respiration*

The  $R_s$  at varying heights in daily and monthly dynamics from May to October was studied to reveal the laws of  $R_s$ .

*Response of stem respiration to stem height within all tested months*

The stem respiration of 16-year-old trees at five heights (0.2, 0.7, 1.0, 1.3 and 1.8 m) was monitored. The results show that (1) at early growth stage (May),  $R_s$  basically increased with the rising height, and the  $R_s$  at 1.8 m height was 1.37-1.90-fold higher than at 0.2 m height (1.37-2.99 vs. 0.85-1.63  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). (2) The  $R_s$  in June was very consistent among the five heights:  $H1.8 \text{ m} > H1.0 \text{ m} > H1.3 \text{ m} > H0.2 \text{ m} > H0.7 \text{ m}$ , and the

$R_s$  at 1.8 m was 1.27-1.71-fold higher than at 0.7 m (2.20-3.00 vs. 1.64-1.87  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). (3) During the vigorous growth period (July and August), the  $R_s$  at all daytime points were very consistent among the five heights, as  $R_s$  basically first decreased and then increased with the rising height;  $R_s$  was minimized to 3.03-4.18 and 1.69-2.55  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at 1.0 m height. (4) After defoliation (September and October), the  $R_s$  did not change obviously with height, mainly because the growth and metabolism of stems were weakened or even stopped, and thus respiration rate was reduced and maintenance respiration was dominant. Moreover, the growth respiration rate changed obviously with height, and the maintenance respiration did not change largely among the five heights (Figure 5).



**Figure 5.** Vertical variations of stem respiration rate at different periods in 16-year-old *Larix principis-rupprechtii* stand from May to October. Lines indicate stem respiration rate of different height at the time point. Bars are means  $\pm$  standard error, n=9

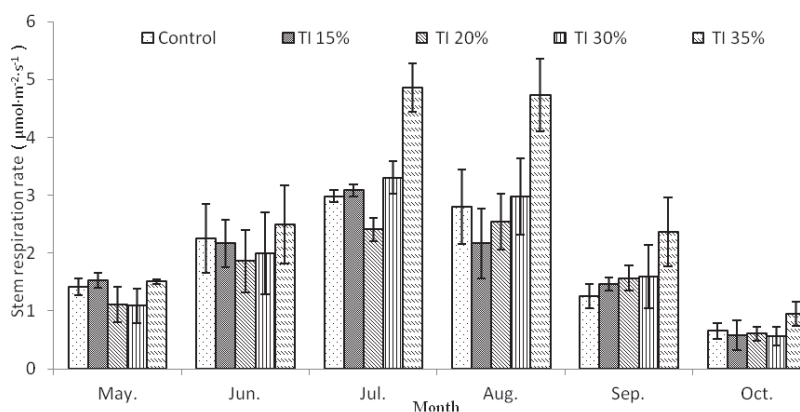
*Response of stem respiration to stem height between all tested months*

$R_s$  of 16-year-old trees at five heights in all tested months was monitored. The results show that  $R_s$  at different periods changed with height in a complex way (Figure 6). (1) The changing trends were similar between May and June, as  $R_s$  increased with the rising height: H1.8 m ( $2.31 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) > H1.3 m ( $2.23$ ) > H1.0 m ( $2.01$ ) > H0.7 m ( $1.42$ ) > H0.2 m ( $1.39$ ) in May, and H1.8 m ( $2.68 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) > H1.0 m ( $2.36$ ) > H1.3 m ( $2.04$ ) > H0.2 m ( $1.98$ ) > H0.7 m ( $1.76$ ) in June. (2) The changing trends were similar between July and August as  $R_s$  first decreased and then increased with the rising height (H0.2 m > H0.7 m > H1.8 m > H1.3 m > H1.0 m);  $R_s$  at H0.2 m was  $4.99$  and  $2.82 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively, which were 1.28- and 1.23-fold higher than at 1.0 m height ( $3.90$  and  $2.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ );

and October (all  $p < 0.05$ ) but was not significantly different in September. The variation coefficients in all months were listed below: May ( $0.234$ ) > June ( $0.165$ ) > July ( $0.098$ ) > October ( $0.087$ ) > August ( $0.079$ ) > September ( $0.060$ ).

*Effects of thinning intensity on stem respiration*

$R_s$  of 25-year-old trees under varying thinning intensity are presented in Figure 7. (1) In May, the forests grew very slowly, and  $R_s$  did not differ significantly among the thinning intensities (TIs) (Table 6): TI 30% ( $1.09 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) < TI 20% ( $1.11$ ) < control ( $1.42$ ) < TI 35% ( $1.51$ ) < TI 15% ( $1.53$ ). (2) In July and August,  $R_s$  under TI 35% was significantly higher than those under other TIs, and the  $R_s$  in all tested months changed with increasing TI as follows: in June,  $R_s$  first decreased and then increased: TI 20% ( $1.86 \mu\text{mol}$



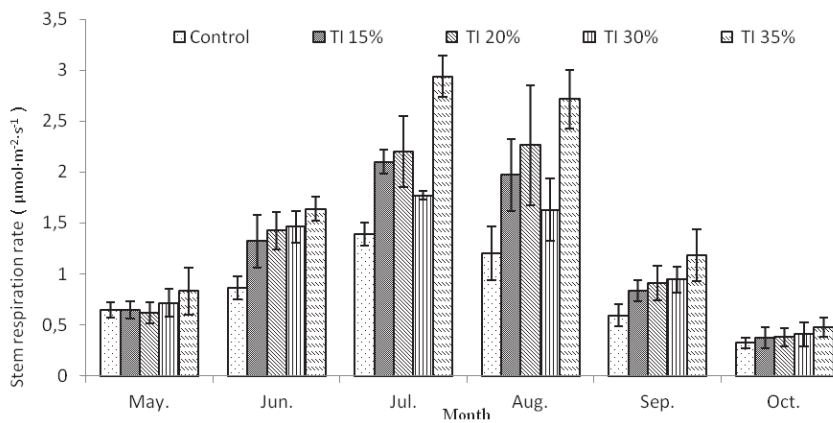
**Figure 6.** Vertical variations in monthly 16-year-old *Larix principis-rupprechtii* stem respiration rate from May to October. The significant differences among the levels of each factor were checked with Duncan's test. In the same period, significant differences became apparent at the 0.05 between the different letters, but not between the same letter. Bars are means  $\pm$  standard error, n=9

these changes were similar to those of daily changes monitored at different heights. Obviously, at the vigorous growth period, the stem parts close to the crown or roots are more active at metabolism and respiration. (3) In September,  $R_s$  was least variable among heights, with a variation coefficient of  $0.060$ , which was only  $25.6\%$  of that in May ( $0.234$ ). The stem respiration in October was dominated by maintenance respiration: H0.2 m > H1.3 m > H1.0 m > H1.8 m > H0.7 m. One-way ANOVA shows that the  $R_s$  was significantly different among the five heights in May, June, July, August,

**Table 6.** Analysis of variance monthly stem respiration rate in 25-year-old *Larix principis-rupprechtii* stand influenced by thinning density

Month	$R_s$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	F	P
May	$1.33 \pm 0.09^a$	1.065	0.461
Jun.	$2.15 \pm 0.23$	0.167	0.950
Jul.	$3.33 \pm 0.24$	13.174	0.001*
Aug.	$3.05 \pm 0.33$	2.675	0.094
Sep.	$1.65 \pm 0.18$	1.193	0.372
Oct.	$0.67 \pm 0.08$	0.738	0.587

For  $R_s$  of different thinning densities in each month, <sup>a</sup> values are means  $\pm$  standard error, n=9. Significance for differences among five thinning densities was analyzed by ANOVA, \* indicates  $P < 0.05$



**Figure 7.** Response of monthly 25-year-old *Larix principis-rupprechtii* stem respiration to different stand densities. The significant differences among the levels of each factor were checked with Duncan’s test. In the same period, significant differences became apparent at the 0.05 between the different letters, but not between the same letter. Bars are means ± standard error, n=9

$\text{m}^2 \text{s}^{-1}$ ) < TI 30% (2.00) < TI 15% (2.16) < control (2.25) < TI 35% (2.50). In July,  $R_s$  increased except under medium thinning: TI 20% (2.41  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) < control (2.98) < TI 15% (3.08) < TI 30% (3.30) < TI 35% (4.86). In August,  $R_s$  increased except for the control: TI 15% (2.17  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) < TI 20% (2.55) < control (2.80) < TI 30% (2.98) < TI 35% (4.73). In September,  $R_s$  increased: control (1.26  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) < TI 15% (1.46) < TI 20% (1.56) < TI 30% (1.59) < TI 35% (2.37). From June to September, the  $R_s$  values under TI 35% were 1.11-1.34, 1.47-2.02, 1.59-2.18, and 1.49-1.88 times higher than under other TIs. (3) In October, the forests grew very slowly or even stopped growing, and the  $R_s$  did not differ significantly among TIs: TI 30% (0.57  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) < TI 15% (0.58) < TI 20% (0.61) < control (0.65) < TI 35% (0.95). (4) Annual  $R_s$  under TIs changed as follows: TI 20% (1.68  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) < TI 15% (1.83) < control (1.89) < TI 30% (1.92) < TI 35% (2.82).

**Response of stem respiration to changes in biological factors**

In order to expose the rule that stem respiration change with biological factors, stem respiration rate from different crown height and diameter grades were analyzed respectively.

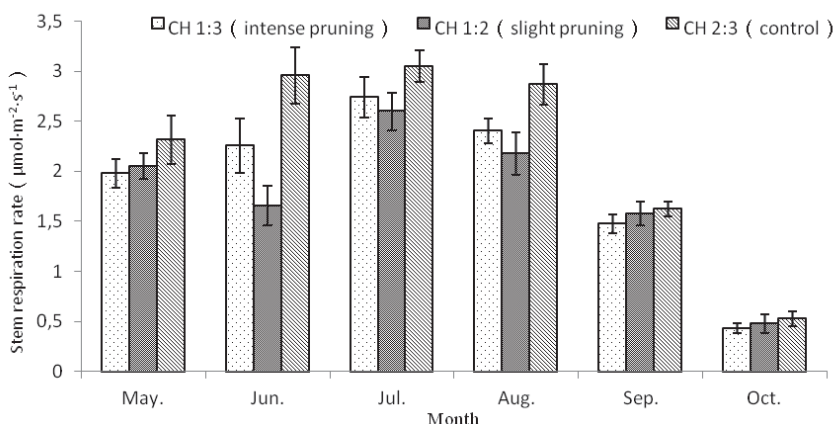
**Effects of crown height on stem respiration**

$R_s$  of 16-year-old trees at 3 crown heights (CHs) was monitored. The results are showed in Figure 8. (1)  $R_s$  of trees with different CHs changed in May as follows: CH 2:3 (2.31  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) > CH 1:2 (2.05  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) > CH 1:3 (1.98  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). (2)  $R_s$  from June to August changed with CH as follows: CH 2:3 > CH 1:3 > CH 1:2. The  $R_s$  at CH 2:3 was 1.11-1.31 and 1.17-1.79 times higher than at CH 1:3 and 1:2, respectively. (3)  $R_s$  of trees in September and October changed with CHs as follows: CH 2:3 (1.62 vs. 0.53  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) > CH 1:2 (1.58 vs. 0.48) > CH 1:3 (1.47 vs. 0.43). (4) As shown in Table 7, one-way ANOVA shows that  $R_s$  changed significantly with CH only in May, June and August. (5) Maintenance respiration was dominant only in October. The  $\text{CO}_2$  emissions by unit area changed as follows: CH 2:3 (8.32  $\text{t ha}^{-1}$ ) > CH 1:3 (7.64) > CH 1:2 (7.21).

Month	$R_s$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	F	P
May	2.11±0.17 <sup>a</sup>	4.327	0.019*
Jun.	2.29±0.16	6.191	0.004*
Jul.	2.80±0.11	1.578	0.219
Aug.	2.48±0.12	3.631	0.038*
Sep.	1.56±0.06	0.565	0.573
Oct.	0.48±0.06	2.976	0.069

For  $R_s$  of different crown heights in each month, <sup>a</sup> values are means ± standard error, n=9. Significance for differences among three crown heights was analyzed by ANOVA, \* indicates  $P < 0.05$

**Table 7.** Analysis of variance monthly stem respiration rate in 16-year-old *Larix principis-rupprechtii* stand influenced by crown height



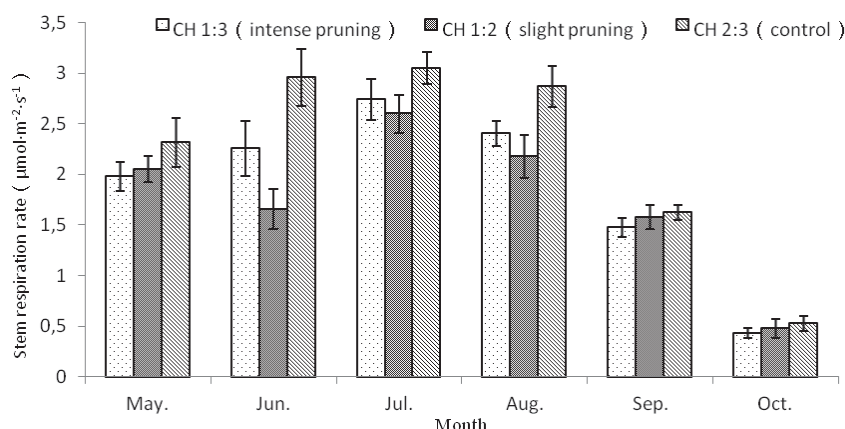
**Figure 8.** Response of monthly 16-year-old *Larix principis-rupprechtii* stem respiration to different crown height. The significant differences among the levels of each factor were checked with Duncan’s test. In the same period, significant differences became apparent at the 0.05 between the different letters, but not between the same letter. Bars are means ± standard error, n=9



**Effects of diameter grades on stem respiration**

$R_s$  of the 25-year-old trees at three diameter grades (large, medium, and small) were studied. The results show that (1)  $R_s$  of trees with large and medium diameter grades were 1.21-2.70 and 1.58-2.84 times, respectively, larger than of the tree with small diameter grade (Figure 9). (2) The seasonal changes of trees at three diameter grades all followed single-peak curves, and the  $R_s$  with large, medium, and small diameter grades all peaked in middle July: 5.02, 4.93 and 2.39  $\mu\text{mol m}^{-2} \text{s}^{-1}$  respectively. (3) One-way ANOVA shows that the  $R_s$  was not significantly variant among the three diameter grades, except for May, middle June, late August, middle September, early and middle October. (Table 8).

**Figure 9.** Response of monthly 25-year-old *Larix principis-rupprechtii* stem respiration to different diameter grades. The significant differences among the levels of each factor were checked with Duncan's test. In the same period, significant differences became apparent at the 0.05 between the different letters, but not between the same letter. Bars are means  $\pm$  standard error, n=9. Due to equipment failure, a large amount of  $R_s$  was not recorded in late October 2013



**Table 8.** Analysis of variance monthly stem respiration rate in 25-year-old *Larix principis-rupprechtii* stand influenced by diameter grades

Month	$R_s$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	F	P
Early May	1.15 $\pm$ 0.07	29.797	0.000*
Middle May	1.21 $\pm$ 0.08	33.635	0.000*
Late May	1.24 $\pm$ 0.10	15.932	0.000*
Early Jun.	1.56 $\pm$ 0.16	15.569	0.081
Middle Jun.	3.36 $\pm$ 0.28	10.413	0.001*
Late Jun.	2.95 $\pm$ 0.38	7.303	0.078
Early Jul.	3.63 $\pm$ 0.58	2.809	0.092
Middle Jul.	4.11 $\pm$ 0.60	3.072	0.087
Late Jul.	3.89 $\pm$ 0.53	1.939	0.194
Early Aug.	3.60 $\pm$ 0.37	2.914	0.085
Middle Aug.	2.91 $\pm$ 0.45	2.647	0.112
Late Aug.	2.43 $\pm$ 0.36	2.611	0.008*
Early Sep.	2.00 $\pm$ 0.22	1.920	0.189
Middle Sep.	1.24 $\pm$ 0.12	3.322	0.007*
Late Sep.	1.02 $\pm$ 0.11	1.296	0.299
Early Oct.	0.47 $\pm$ 0.04	1.655	0.016*
Middle Oct.	0.67 $\pm$ 0.06	9.135	0.001*

For  $R_s$  of different diameter grades in each month, <sup>a</sup> values are means  $\pm$  standard error, n=9. Significance for differences among three diameter grades was analyzed by ANOVA, \* indicates  $P < 0$ .

**Discussion**

From May to October, the value of  $R_s$  is inversely proportional to that of the stand age, except for middle and late October. Similar results were obtained in the study of *Larix*

*gmelinii* growth (Wang et al. 2005). The reasons are as follows: growth respiration was dominant in the growing season, and the younger trees grew and metabolized actively, and thus the growth respiration rate was high and  $R_s$  was negatively correlated with forest age. In the non-growing season, maintenance respiration was dominant, and the older trees required more energy from the maintenance respiration, and thus  $R_s$  was positively correlated with forest age (Amthor 1984).

During the vigorous growth period, energy is supplied via respiration to the synthesis of new cells and tissues, and also the necessary energy is provided via maintenance res-

piration for maintaining the growth of trees; in winter, the growth is slowed down or stopped, and stem respiration is dominated by maintenance respiration (Ceschia É et al. 2002a, De Vries 1975). As reported, only maintenance respiration is closely related with stem size, while the growth respiration is positively correlated with the concentrations of soluble carbohydrates in the stem and with the growth rate of stem (Ryan 1990b), which can explain the phenomena in this test. Besides, the daily and seasonal changing trends of  $R_s$  were consistent with that of temperature, with  $Q_{10}$  of 2.77 (16-year-old), 2.66 (25), and 2.39 (41). Like in other studies (Shi et al. 2010, Wang et al. 2008, Wang et al. 2003), the daily and seasonal changing trends of  $R_s$  both obeyed single-peak curves. As reported, the daily and seasonal changing trends of  $R_s$  were maximized at the highest forest temperature;  $R_s$  in the growing season was significantly larger than in the non-growing season (Ceschia É et al. 2002a, Acosta and Brossaud 2001, Adu-Bredu et al. 1997, Ceschia 2001).

Study about  $R_s$  in different vertical height shows that with the rising height,  $R_s$  at early growth stage increased;  $R_s$  at vigorous growth period first decreased and then increased, and  $R_s$  was minimized at 1.0 m height, similar to the results of *Chamaecyparis obtusa* var. *formosana* and *Ch. obt.* var. *breviramea* (Araki et al. 2010). At late stage,  $R_s$  was not significantly different among heights. The possible reasons why  $R_s$  changes with height are listed below. (1) From the

perspective of organic matter transport, the trees sprout in May and June, but produce very little organic matter. According to the principle of proximity, the sites close to the crown obtain enough nutrients, and thus stem respiration is strong and *vice versa*. In July and August, the luxuriant foliage produces abundant organic matter; the sites near the crown acquire sufficient nutrients, and the sites near the roots are supplied enough nutrients. Therefore, the respiration rate is high at the upper and lower ends of the stem, but is low at the middle part. The crown produces organic matter and transports via ATP depletion to other parts, and thus, the sites close to the crown undergo severe respiration to provide ATP needed by transport (Loka and Oosterhuis 2010). In September and October, the leaves turn yellow and fall down, the maintenance respiration is dominant, and thus the stem respiration is significantly independent of height. The differences in environmental factors (e.g. temperature and humidity) may result in different laws explaining how  $R_s$  in all tested months changes with height. (2) From the perspective of cell biology,  $R_s$  is positively correlated with the content of living cells (Ceschia *É* et al. 2002a). A higher content of living cells is generated at sites close to the roots or crown, which results in rapid growth and metabolism and thus high  $R_s$ . Furthermore, respiration of the thin cambium and phloem meristems play a dominant role in stem respiration (Maier 2001, Maier and Clinton 2006), when rapid stem growth and metabolism is observed, the  $CO_2$  concentration would be significantly increased in the cambium and phloem regions (Pruyn et al. 2002, 2003). (3) From the perspective of molecular biology, auxin and gibberellin are important regulating hormones in the production and development of plants and can promote the cell growth and division (Li et al. 2014, Nelissen et al. 2012). In July and August, the trees grow vigorously, and thus the crown produces more auxin and gibberellin, and the roots generate more gibberellin, thus increasing the contents of auxin and gibberellin at the sites close to the crown or roots (Serrani et al. 2007). Such changes promote the growth and metabolism of cells at two ends of the stem, and accelerate the stem respiration.

Stand density was altered via cultivation and thinning. From May to October, the  $R_s$  of 25-year-old trees generally increased with the decreased stand density, but sometimes it first decreased and then increased. There are three possible reasons. (1) Some trees are less adaptable to the changing environment and thus their growth is inhibited by environmental mutations (Zhao et al. 2016). (2) The stand density decreases with the increased thinning intensity, and the active effects such as growing space and radiation in the environment are enhanced. Thus, the growing environment is gradually optimized and the trees grow vigorously, and  $R_s$  is increased, especially in the growing season. Nevertheless, how stand density changes will affect stem respiration is decided by forest age and site conditions. Generally, when the inhibiting effect due to the stand density changes out-

performs the active effect,  $R_s$  decreases, and vice versa (Zhao et al. 2015). (3) The low forest density has weaker competition between the plants in water consumption to increase sap velocity (Nie et al. 2003, 2005). In the Levy et al. (1999) study, increases in apparent stem respiration with sap velocity. Therefore, appropriate forest density leads to increase  $R_s$ . It is important to note that if the density falls below a certain threshold, strengthened light intensity and decreased soil water potential could reduce sap velocity, which would result in a lower  $R_s$  ultimately.

This test changed the CH through pruning. In May, September and October with low temperature, the small CH trees have few leaves and thus produce little organic matter. As a result, the sites at 1.3 m height were not provided with enough nutrients, leading to low  $R_s$ , and thus  $R_s$  is positively correlated with CH. In June, July and August, the trees with CH 1:2 and 2:3 were all closed but the lower part with enough illumination did not turn (or only partially) to consumed branches. Therefore, the leaves on the trees with CH 2:3 produced enough nutrients, and thus underwent more active stem respiration. The trees with CH 1:3 were in strong light transmission, as the sun directly radiated to the lower part, the temperature in the forest was high, which promoted the tree growth and  $R_s$ , and thus the respiration rate was higher than in the trees with CH 1:2 (Zhao et al. 2016). In addition, some studies have shown that reductions in leaf area can reduce sap velocity (Oren et al. 1999, Cienciala and Lindroth 1995, Sala et al. 1996); Dissolved  $CO_2$  concentration of xylem water is decreasing as the sap velocity declines, which further increase  $R_s$  (Teskey and McGuire 2002, Bowman et al. 2005). But this association will be weakened at higher temperature.

The seasonal changes of  $R_s$  indicate that the  $R_s$  of young trees was larger than that of the mature trees. The  $R_s$  of the 25-year-old trees at three diameter grades shows that the  $R_s$  of large and medium diameter grades was larger compared with the trees with small diameter grade. The young trees were more vigorous than the mature trees. At the same forest age, a larger diameter grade resulted in higher metabolism. Therefore,  $R_s$  is correlated with the growth and metabolism intensities, which is proved by previous studies (Wang et al. 2005, Xu et al. 2011, Yi et al. 2012).

## Conclusions

Temporal and spatial variations and biotic factors are verified and revealed to have significant effects on stem respiration rate. (1) Temperature is one of the main factors to influence stem respiration rate which is exponential with it. And their exponential relationship is more obvious with younger stand age. (2)  $R_s$  at more metabolic sites (e.g. sites close to the roots or crown) was significantly higher than that at the middle part. (3) One forest, which is close to a stand with TI (20%) density, 1:2 crown height, and 70-110 mm

diameter grade, has the lowest  $R_s$  and the minimum carbon release in theory. The results can serve as theoretical underpinnings and data foundation for the model of forest ecosystem carbon cycling construction in the near future.

Additionally, leaf habit, active rules of cambium and phloem, water, the number of living cells and other interior factors, which might be closely related to  $R_s$ , can be further focused on in stem respiration mechanism research as physiological indexes.

#### Author contribution statement

Kuangji Zhao: design of the study, data collection, data analysis, manuscript writing. Zhongkui Jia: design of the study, manuscript reviewing. Lvyi Ma: supervise the scientific experiments.

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