Effect of thinning intensity on the stem CO_2 efflux of *Larix principis-rupprechtii* Mayr

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Abstract

Background: Stem CO_2 efflux (E_S) plays a critical role in the carbon budget of forest ecosystems. Thinning is a core practice for sustainable management of plantations. It is therefore necessary and urgent to study the effect and mechanism of thinning intensity (TI) on E_S.

Methods: In this study, five TIs were applied in *Larix principis-rupprechtii* Mayr 21-, 25-, and 41-year-old stands in North China in 2010. Portable infrared gas analyzer (Li-8100 A) was used to measure E_S and its association with environmental factors at monthly intervals from May to October in 2013 to 2015. In addition, nutrients, wood structure and nonstructural carbon (NSC) data were measured in August 2016.

Results: The results show that E_S increased with increasing TI. The maximum E_S values occurred at a TI of 35 % (3.29, 4.57 and 2.98 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and were 1.54-, 1.94- and 2.89-fold greater than the minimum E_S value in the CK stands (2.14, 2.35 and 1.03 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in July for the 21-, 25- and 41-year-old forests, respectively. The E_S of the trees in low-density stands was more sensitive to temperature than that of the trees in high-density stands. Soluble sugars (SS) and temperature are the main factors affecting E_S. When the stand density is low enough as 41-year-old *L. principis-rupprechtii* forests with TI 35 %, bark thickness (BT) and humidity should be considered in addition to air temperature (T_a), wood temperature (T_w), sapwood width (SW), nitrogen concentration (N) and SS in the evaluation of E_S. If a change in stand density is ignored, the CO_2 released from individual 21-, 25- and 41-year-old trees could be underestimated by 168.89 %, 101.94 % and 200.49 %, respectively. CO_2 release was estimated based on the stem equation in combination with the factors influencing E_S for reference.

Conclusions: We suggest that it is not sufficient to conventional models which quantify E_S only by temperature and that incorporating the associated drivers (e.g. density, SS, SW and N) based on stand density into conventional models can improve the accuracy of E_S estimates.

Keywords: Stem CO_2 efflux, Thinning intensity, Environmental factors, Nutrient content, Wood structure, Nonstructural carbon, *Larix principis-rupprechtii*

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Introduction

Forest ecosystems play a pivotal role in the global carbon cycle, and the balance between carbon assimilation by forests and its release through respiratory processes is important in regulating the rate of CO_2 accumulation in the atmosphere (Dixon et al. 1994). Among the largest C flux pathways in forests is emission of CO_2 from stem surfaces (E_S; Ryan et al. 2009); for example, Yang et al. (2016) estimated that annual global E_S of forests was 6.7 +/− 1.1 Pg per year, comparable in magnitude to burning of fossil fuels. Despite considerable recent research, the mechanisms and controls of E_S at the individual tree and forest stand level are not fully understood, constraining our ability to predict responses of this flux to changes in climate, forest composition and structure, and other potential drivers (Trumbore et al. 2013; Tu et al. 2017).

Although respiration by living cells in the stem (R_S) is the dominant process contributing to E_S in trees, interpretation of E_S measurements is complicated by CO_2 transport processes either or both to and away from the chamber location, primarily in xylem sap (Ft; Saveyn et al. 2008; Salomón et al. 2016b). The principal environmental factor regulating cellular respiration is temperature because the rate of most enzyme-catalyzed biochemical reactions increases exponentially with temperature. This effect is often represented using the Q_{10} convention which specifies the proportional increase in reaction rate (or flux) for every 10ºC increase in temperature, i.e. the temperature sensitivity. Both cell maintenance and growth respiration can contribute to the total R_S, and maintenance respiration (Rm) is much more temperature sensitive than growth respiration (Rg; Adu-Bredu et al. 1997). Soil nutrient availability also might influence R_S because cellular respiration often depends upon tissue nutrient (especially N) concentration (Stockfors and Linder 1998; Vose and Ryan 2002).

Regarding internal biotic factors influencing E_S, the mass of living tissues directly determines R_S (Gruber et al. 2009; Fan et al. 2017). Three principal tissues are inner bark, cambium and parenchyma in the sapwood. Typically inner bark is thought to comprise the largest proportion of R_S (Gruber et al. 2009). Bark thickness can also influence E_S through its resistance to CO_2 diffusion from stem to atmosphere (Steppe et al. 2007). On a whole-tree basis both E_S and R_S increased with gross production and stem growth rate (Yang et al. 2016), and phloem girdling studies have also demonstrated that locally higher stem growth above the girdle results in higher E_S and R_S (Maier et al. 2010; Yang et al. 2019). However, this relationship is complicated by the local increase in substrate availability above the girdle which may stimulate R_S independently of growth; Maier et al. (2010) suggested that increased R_S with higher substrate supply could reflect up-regulation as a means to avoid end-product suppression of photosynthesis. In sum, the environmental and biotic factors

affecting E_S are complex, resulting in challenges to predicting the response of this important C flux pathway to global change and forest management (Trumbore et al. 2013).

Pre-commercial forest thinning is a standard and widely adopted silvicultural practice to enhance the growth in value of a forest stand by directing the wood production into the most valuable trees while maintaining favorable stem form (Kerr and Haufe 2011). Routine thinning is conducted in young, even-aged forest stands of both natural and plantation origin. After thinning the growth of the remaining trees increases and the crowns of individual trees gradually expand increasing gross photosynthesis (Binkley et al. 2004). Opening the canopy increases the penetration of solar radiation and alters the microclimate in the forest (Aussenac 2000). These changes in forest environment, structure, growth and physiological activity would be expected to cause profound responses in E_S, but to our knowledge few detailed studies have been reported (Lavigne 1987). Because a large proportion of the world's forests is managed by thinning, it is important to understand both the response of E_S to thinning and the underlying mechanisms.

The objective of this study was to quantify the effect of different levels of pre-commer cial thinning on individual tree and whole-stand E_S of *Larix principis-rupprechtii*, a widely-distributed tree species in both natural and plantation forests of northern China (Yao et al. 2013). Three plantations were thinned at four different intensities (15 %−35 % removal) in 2010, and E_S was measured monthly during the warm season in 2013−2015 using a Li-8100 A CO_2 flux system. Due to the loose bark of *Larix principis- rupprechtii*, DBH growth rate can not accurately reflect the stem growth rate. Therefore, we use the sapwood growth rate to represent the stem growth rate. There were five primary aims of this study: (1) to clarify the variation in E_S with thinning intensity (TI); (2) to explore the mechanism by which TI influences E_S; (3) to evaluate the effect of various influencing factors on E_S; (4) to determine the TI-related response and mechanism of temperature sensitivity in E_S; and (5) to evaluate the degree of error in the estimations of annual tree-scale and stand-scale CO_2 efflux if the effect of stand density on E_S in the three forest ages is not considered and establish an estimation equation for E_S that incorporates the factors influencing E_S.

Materials and methods
Site description
The study was conducted at the Saihanba National Forest Park (SNFP, 42°02′−42°36′ N; 116°51′−117°39′ E, altitude 1600−1800 m) of Weichang Manchu and Mongolian Autonomous county in Hebei Province, northern China. The climate is semiarid monsoon climate. The mean annual temperature was −1.5 °C; and average annual rainfall was
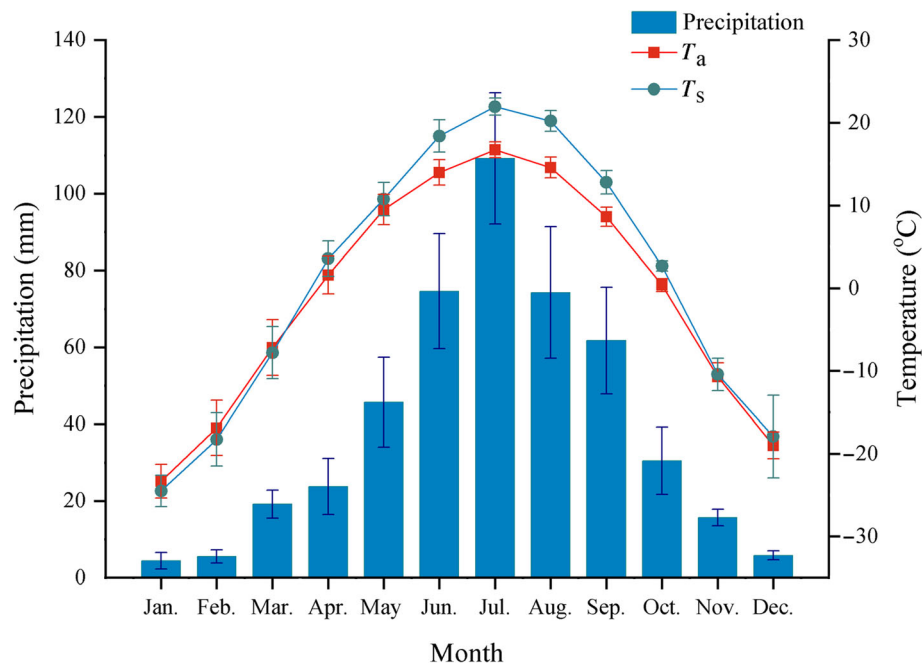
Fig. 1 Monthly mean precipitation, air temperature (T_a) and soil temperature (T_s) in the Saihanba National Forest Park (SNFP) (1996–2013). Error bars indicate the standard error, $n = 9$ (Zhao et al. 2018b)

433 mm. The precipitation from June to August accounts for 55 % of the total annual precipitation (Fig. 1). The soil is classified as gray forest soil (Xi 1994). The soil parent materials are eluvium, alluvium, and saprolite. The thickness of the organic surface horizon is approximately 3–8 cm in all stands (Zhao et al. 2018b). The stand is dominated by *L. principis-rupprechtii* (Yao et al. 2013).

Experimental design

In our study, to be more convincing, the experimental site included 21- (young larch), 25- (immature larch), and 41-year-old (mature larch) artificial forests of *L. principis-rupprechtii*. Fifteen permanent plots of 400 m² (20 m × 20 m) with essentially the same site and stand conditions were randomly established in larch plantations for each forest age, a total of forty-five plots. According to stand volume calculation, the five TIs were expressed as the percentage of felled trees to the total volume of trees in each plot: 0 % (unmanaged, control), 15 % (weak thinning, TI 15 %), 20 % (moderate thinning, TI 20 %), 30 % (strong thinning, TI 30 %) and 35 % (very strong thinning, TI 35 %; Table 1; Shen 2001). In 2010, we randomly implemented these five TIs in fifteen plots for each forest age, with three replicates for each intensity. To minimize edge effects, a 6-m-wide buffer area was established around the inner edge of each plot. The rate of E_S was monitored in three model *L. principis-rupprechtii* trees per standard plot.

Stem CO_2 efflux measurements

We used a portable infrared gas analyzer-Li-8100 A (LI-COR, Lincoln, Nebraska, USA) with 8100 – 103 chamber to monitor E_S at breast height (approximately 1.3 m) of 45 sample trees. The 8100 – 103 chamber was sealed over the collar with gasket, and the chamber volume seals with its own gasket when it closes. Use gaskets to minimize leaks and wind effects. The installation steps were as follows: polyvinyl chloride (PVC) collars (with diameters of 7.5 cm) were fixed with environmentally friendly neutral silicone adhesive onto the tested parts of the stems. After drying, the residual silicone adhesive was removed, and the areas between the stem and the PVC collars were sealed. During the measurement, the Li-8100 A chamber was fixed onto the PVC collar with a string. Before the measurement, the seal was checked by exhaling on and around the chamber and the collar to ensure no rapid change in CO_2 concentration in real time (in a properly sealed chamber, the CO_2 concentration should increase by no more than 2 ppm) and by the leak test function of the Li8100A. After the measurement, the change in the CO_2 concentration and the coefficient of variation (CV) value recorded in the Li-8100 A were analysed to ensure the sealing of the Li-8100 A and collar and the accuracy of the data. More details of instrument tightness testing methods are described in Reference (Zhao et al. 2018b). Our previous study found that the daily mean E_S could be determined from measurements taken from 9:00 to 11:00 during the daily dynamic monitoring of E_S over a one-year

Table 1 Stand characteristics for 21-, 25- and 41-year-old *Larix principis-rupprechtii* plantations

Stand age	Thinning intensity	Density (Plant·ha⁻¹)	Stand volume (m³·ha⁻¹)	Stem surface area (m²·plant⁻¹)	Canopy density	Altitude (m)
21	Control	4150 ± 125	114.61 ± 4.36	1.30	0.85	1673.9
	TI 15 %	3400 ± 132	104.73 ± 4.87	1.42	0.82	1667.0
	TI 20 %	3083 ± 52	100.22 ± 2.57	1.47	0.80	1668.4
	TI 30 %	2625 ± 100	89.18 ± 8.88	1.48	0.75	1665.4
	TI 35 %	2242 ± 76	74.65 ± 5.56	1.66	0.70	1660.1
25	Control	3083 ± 104	113.34 ± 10.07	3.29	0.76	1683.5
	TI 15 %	2308 ± 407	109.93 ± 15.68	3.42	0.72	1679.3
	TI 20 %	1883 ± 63	97.25 ± 9.30	3.47	0.70	1675.2
	TI 30 %	1600 ± 66	87.14 ± 3.29	3.55	0.68	1674.8
	TI 35 %	1125 ± 175	85.31 ± 4.71	4.02	0.65	1671.5
41	Control	925 ± 25	273.57 ± 4.29	5.38	0.75	1703.3
	TI 10 %	750 ± 25	217.31 ± 30.98	7.28	0.71	1707.8
	TI 20 %	667 ± 38	217.45 ± 17.33	7.54	0.65	1701.1
	TI 30 %	542 ± 14	183.35 ± 15.49	8.93	0.62	1701.6
	TI 35 %	475 ± 25	155.65 ± 11.41	9.26	0.60	1707.5

period (Zhao et al. 2018a). During the study period, nine days with roughly homogeneous weather conditions were selected from every month, and the E_S at each measurement point was measured from 9:00 to 11:00. The air temperature (T_a), wood temperature (T_w, 1 cm below bark) and relative humidity (RH, %) were simultaneously measured with a Li-8100 A instantaneous digital thermometer. The air moisture content (M_a, mmol·mol⁻¹) was measured using the Li-8100 A system. The temperature and moisture data were acquired simultaneously with the E_S measurements. The measured area of the stem was calculated by the ellipse area formula: fix a piece of white paper on the surface of the stem to be measured and press it with the treated PVC pipe. The indentation area on the white paper is the measured area of the stem.

Analysis of wood structure, nutrient content and nonstructural carbon

In August 2016, before the leaves turned yellow, E_S values were measured, and nine increment cores were taken at a height of 1.3 m from the stems of forty-five trees in each stand age using a wood core sampler. Three cores measured the wood structure by LINTAB 5 tree-ring measurement station (RINNTECH, Heidelberg, Germany) after polished smooth. The growth rate of sapwood is equal to the width of sapwood after thinning divided by the number of annual rings. The other three cores were dried at 70 °C for 48 h, milled and analysed of the nutrient content. The N and P were analyzed by means of an AA3 HR AutoAnalyzer (Seal Analytical Ltd., Southampton, UK); and K were analyzed by Lumina3300 (Aurora Biomed Inc., Vancouver, Canada).

The remaining three cores were immediately placed in a cooler and transported to our laboratory. SS and starch were analyzed through an enzymatic assay (McCleary et al. 1997; Yang et al. 2019).

Data analysis

During dormancy, E_S is dominated by maintenance respiration, and growth respiration is negligible (Adu-Bredu et al. 1997). In this study, during the cold season (November to April), the respiration rates were too low and the variation too high to meet the standard criterion, which states that the CV of the measurements should be below 2, so we were unable to obtain reliable measurements of E_S. Thus, the E_S values in October were used to represent the E_S values during dormancy. The period from May to October 2013−2015 was selected for monitoring E_S, and the E_S values during the period from November to April were estimated using the mature tissue method with T_a and the change in E_S resulting from a 10 °C increase in temperature (Q_{10}) (Amthor 1989).

The assumptions of normality and homogeneity of the variance in the data for each variable were verified using Shapiro-Wilk test and the Levene test. The variables that did not conform to these assumptions were mathematically transformed using logarithms or reciprocal functions. We performed statistical analysis separately for each stand age to statistically analyze the effects of TI and each factor (environmental factors, nutrient content, wood structure and NSC) on E_S.

Pearson's rank correlations and ordinary least square regression (OLS) were used to determine the relationships between the E_S and each factor (including the

stand density caused by the five TIs). The relative weight method was used to compare the weights of each prediction variable and closely approximated the average increase in R-square obtained by adding a predictor variable across all possible submodels (Johnson 2004; Johnson and Lebreton 2004; Lebreton and Tonidandel 2008). The quantitative relationships between E_S and the factors were determined and modeled by all-subsets regression analysis, during which the variance inflation factor (VIF) was used to test the multicollinearity of predicted variables. Based on a comparison of the weights of predictive variables with multicollinearity problems, the predictive variables with smaller weights were excluded, and a new equation was established. Then, the goodness of fit between the old and new models was compared by analysis of variance (ANOVA) and the Akaike information criterion (AIC). The temperature coefficient (Q_{10}) was computed by E_S and temperature; the surface area was estimated by the circular truncated cone surface area equation. Estimation of yearly stand-scale and tree-scale Es and calculation of Q_{10} were done according to Zhao et al. (2018b).

Statistical analysis was performed with the R v.3.5.0 statistical software (R Foundation for Statistical Computing, Vienna, Austria) and at a $P < 0.05$ significance level. All figures were created using Origin 8 (OriginLab, Northampton, MA, USA) and the R v.3.5.0 statistical software.

Results
Thinning intensity variation in E_S and influencing factors
As shown in Fig. 2, the E_S increased with increasing TI for the 21-, 25- and 41-year-old forests. The E_S of each stand was the highest in July of each year; the maximum E_S values occurred at TI 35 % (3.29, 4.57 and 2.98 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and were 1.54-, 1.94- and 2.89-fold greater than the minimum E_S values at control (2.14, 2.35 and 1.03 $\mu mol \cdot m^{-2} \cdot s^{-1}$) in July for the 21-, 25- and 41-year-old stands, respectively. The seasonal E_S variation range in the 21-, 25- and 41-year-old forests increased with increasing TI. The amplitudes of variation at TI 35 % were the highest (2.26, 3.57, and 2.55 $\mu mol \cdot m^{-2} \cdot s^{-1}$), and the amplitudes of variation at control were the lowest (1.74, 1.69, and 1.12 $\mu mol \cdot m^{-2} \cdot s^{-1}$). In the 21- and 25-year-old stands, there were significant differences in E_S under different TIs ($P < 0.05$) in July, August and September. In the 41-year-old stands, except for in May and October, there were significant differences in E_S under different TIs ($P < 0.05$).

In the 21-year-old forest stands, the variables with significant differences among the five TIs were SR ($P = 0.012$) and ST ($P = 0.002$); the maximum SR values occurred at TI 35 % (13.73 $cm^2 \cdot yr^{-1}$), which was significantly higher than other plots (Fig. 3); the maximum ST values occurred

at TI 15 % (19.25 mg·g^{-1}) (Fig. 4). In the 25-year-old forest stands, the variables with significant differences under different TIs were T_a ($P = 0.020$), HS ($P = 0.015$) and SR ($P = 0.060$); the maximum T_a values occurred at TI 35 % (14.44ºC) (Fig. 5); HS showed a single peak curve with thinning intensity, and the maximum value appeared at TI 20 % (0.64) (Fig. 5). In the 41-year-old forest stands, the variables with significant differences were T_a ($P = 0.029$), BT ($P = 0.001$), SW ($P = 0.023$), HS ($P = 0.000$) and SR ($P = 0.054$); BT showed "V" shape with the increase of thinning intensity, the minimum value is 0.40 cm, which appears in TI 20 % (Fig. 3).

Effects of environmental factors, nutrient content, wood structure and nonstructural carbon on$E_S$in forests of different ages
In the 21-year-old forest, E_S was significantly correlated with T_a ($r = 0.57$, $P < 0.01$), SW ($r = 0.39$, $P = 0.03$), N ($r = 0.51$, $P < 0.01$) and starch ($r = 0.37$, $P = 0.04$) when the data from all TIs over the 21-year-old forests were included, as shown in Fig. 6a. The results of the model selections based on the all-subsets regression analysis and VIF testing (VIF of SW = 12.82, VIF of SR = 7.28, SW and SR exhibit multicollinearity) demonstrated that the best model used T_a, density, BT, SW, HS, N and starch to explain the TI variation in E_S in the 21-year-old forest stands ($R^2 = 0.905$) (Table 2).

The T_w ($r = 0.66$, $P < 0.01$), M_a ($r = 0.48$, $P = 0.01$) and SS ($r = 0.49$, $P = 0.01$) were significantly correlated with E_S in 25-year-old forests (Fig. 6b). T_w was significantly correlated with T_a ($r = 0.43$, $P < 0.01$), M_a ($r = 0.86$, $P = 0.02$) and RH ($r = 0.76$, $P < 0.01$). The results of the model selections based on the all-subsets regression analysis and VIF testing demonstrated that the best model used T_w, density, BT, HS, SR, N, K and SS to explain the TI variation in E_S in the 25-year-old forest stands ($R^2 = 0.863$) (Table 2).

In the 41-year-old forest, the M_a ($r = 0.53$, $P < 0.01$), T_a ($r = 0.37$, $P = 0.04$), density ($r = -0.65$, $P = 0.01$), N ($r = 0.46$, $P = 0.01$) and SS ($r = 0.54$, $P < 0.01$) were significantly correlated with E_S (Fig. 6c). RH was significantly correlated with M_a ($r = 0.87$, $P < 0.01$). The results of the model selections based on the all-subsets regression analysis and VIF testing demonstrated that the best model used T_a, M_a, density, BT, HS, N and SS to explain the TI variation in E_S for the 41-year-old forests ($R^2 = 0.907$) (Table 2).

The above models were compared with the equation fitting E_S with all 14 predictive variables by ANOVA and AIC for 21- (AIC: 28.03 VS 39.60, $P = 0.60$), 25- (AIC: −6.94 VS −2.13, $P = 0.78$) and 41-year-old (AIC: −70.24 VS −54.70, $P = 0.75$) forests.
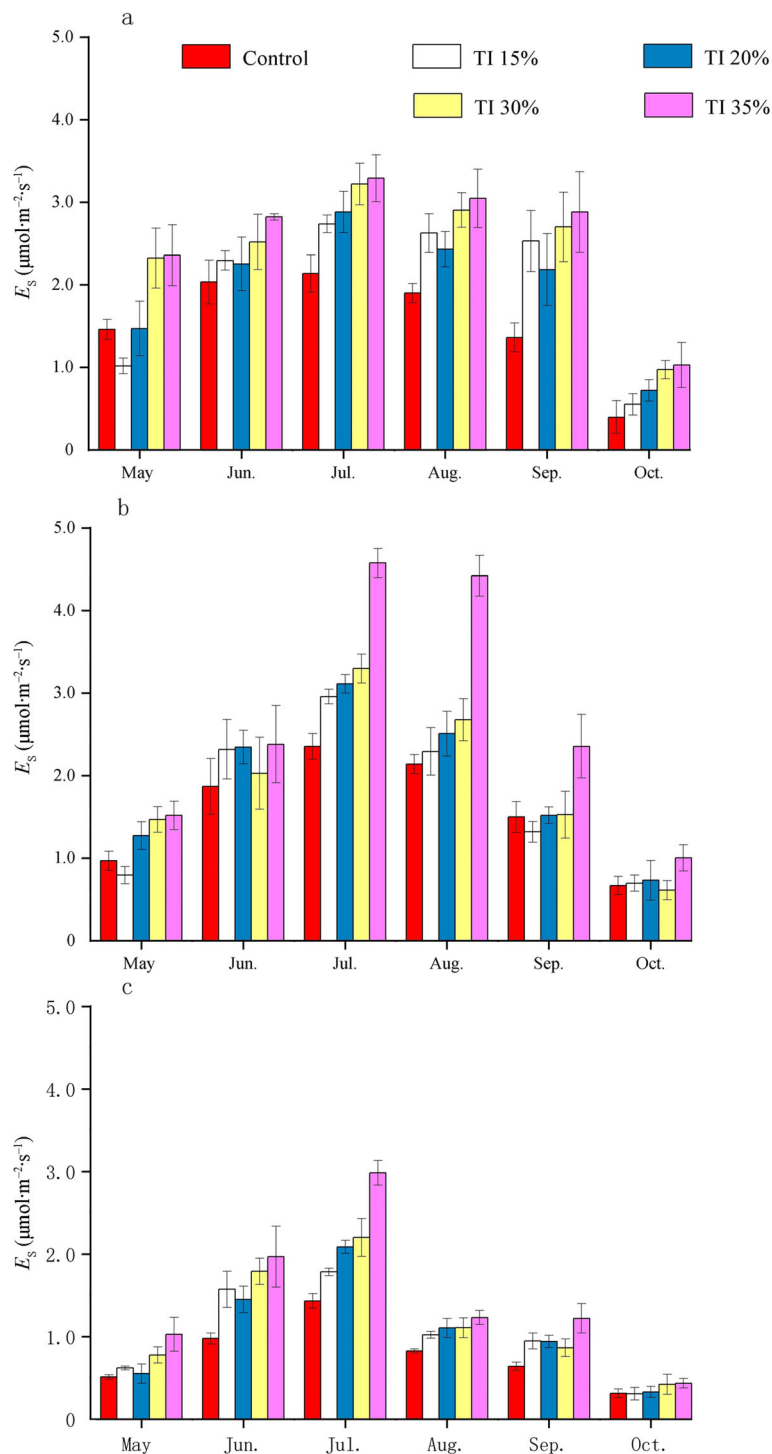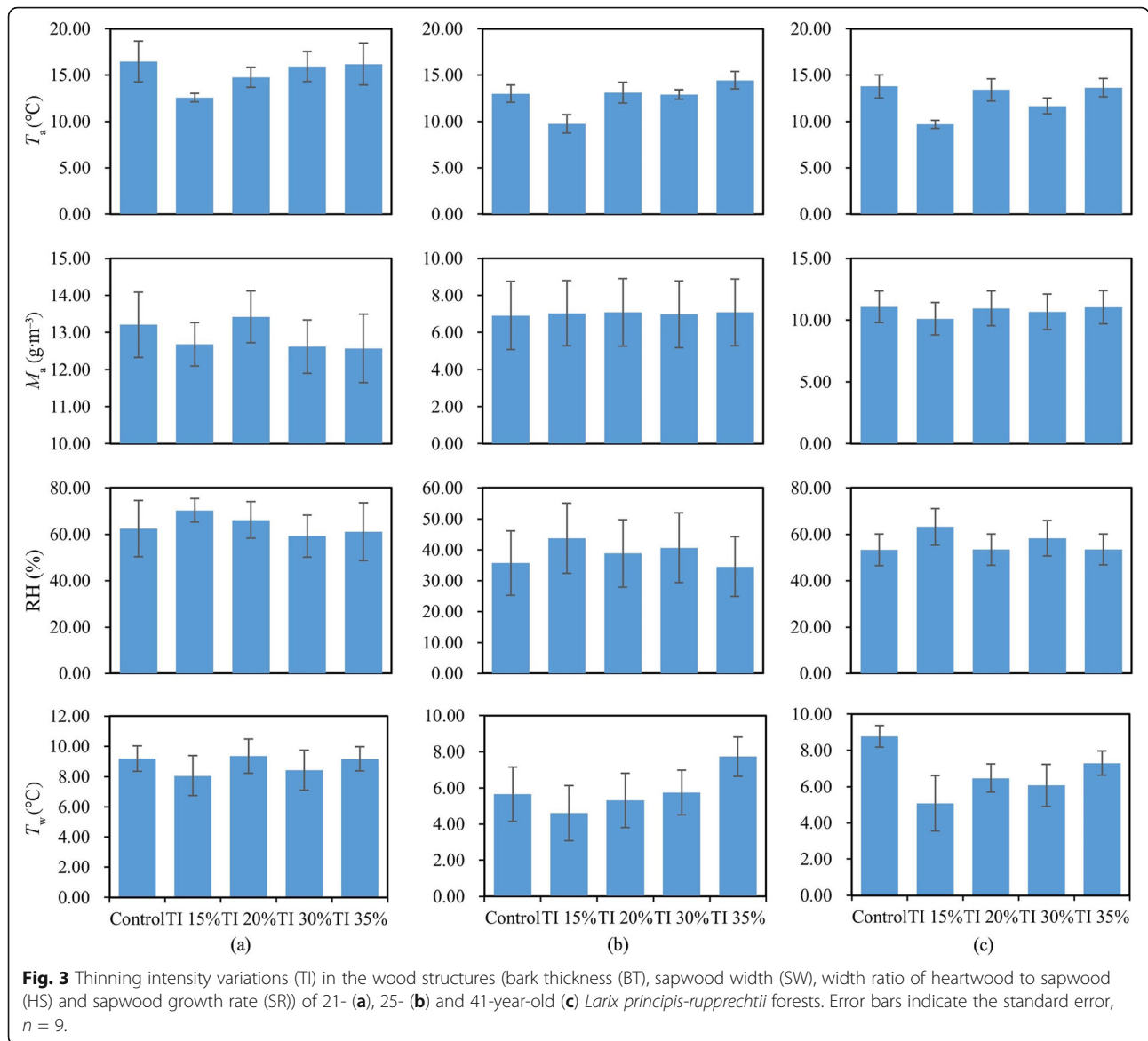
Fig. 2 Thinning intensity (TI) variations in the monthly stem CO_2 efflux (E_S) of 21- (**a**), 25- (**b**) and 41-year-old (**c**) *Larix principis-rupprechtii* forests from May to October 2013–2015. Error bars indicate the standard error, $n = 3$

Q_{10} change in thinning intensity

Exponential fitting of the annual E_S and T_a at different TIs was conducted to evaluate the mechanism by which temperature affects E_S (Table 3). For the three stand ages, the E_S of the trees with lower density was more sensitive to temperature than that of the trees with higher density. In the 25- and 41-year-old forest stands, the E_S of TI 35 % was the most sensitive to temperature (Q_{10} = 3.33 and 3.86). In the 21-year-old forest stands, the E_S of the TI 30 % stand was the most sensitive to

Fig. 3 Thinning intensity variations (TI) in the wood structures (bark thickness (BT), sapwood width (SW), width ratio of heartwood to sapwood (HS) and sapwood growth rate (SR)) of 21- (**a**), 25- (**b**) and 41-year-old (**c**) *Larix principis-rupprechtii* forests. Error bars indicate the standard error, $n = 9$.

temperature ($Q_{10} = 3.26$), and the Q_{10} of the TI 35 % stand was 3.22, which was only 1.23 % lower than that of the TI 30 % stand. The Q_{10} values of TI 35 % in the three forest ages were 1.25, 1.23 and 1.45 times higher than those in control, respectively.
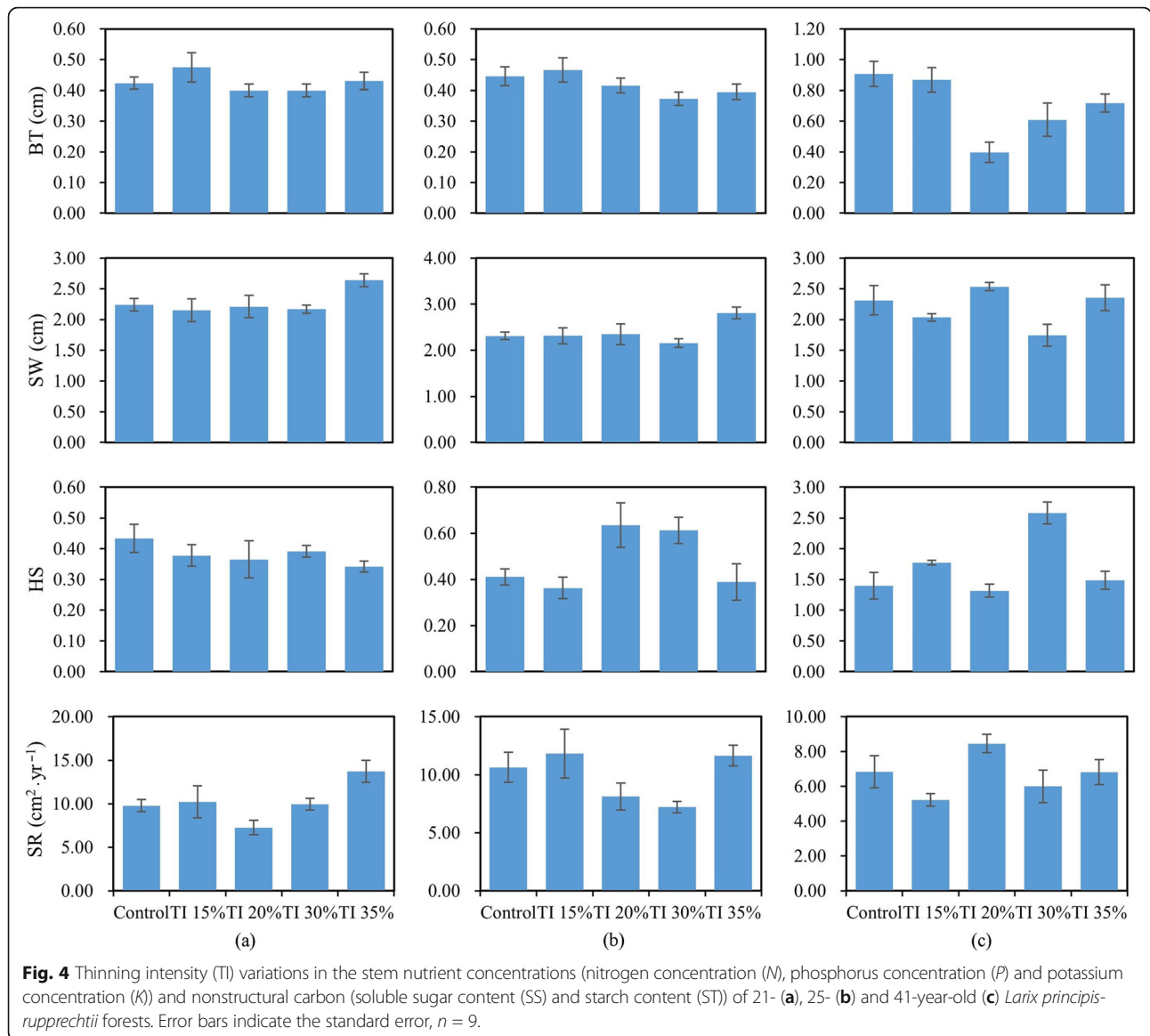
Relative weight of impact factor to E_S

As shown in Fig. 7, fourteen factors affecting E_S, including environmental factors, nutrient content, wood structure and NSC, could explain 90.9 %, 87.5 % and 89.3 % of the E_S in the three forest ages, respectively. The five variables with the highest weight for E_S in the 21-year-old stand were SS (14.51), starch (14.46), T_a (10.72), SW (9.78) and N (9.37); thus, the main environmental, nutrient content, wood structure and NSC factors that influenced the TI-related variations in E_S were T_a, SW, N

and SS, respectively. In the 25-year-old forest, the five highest weighted factors for E_S were T_w (28.37), SS (15.21), M_a (13.81), RH (9.73) and N (8.06); thus, the main environmental, nutrient content, wood structure and NSC factors that influenced the TI-related variations in E_S were T_w, SW (5.03), N and SS, respectively. In the 41-year-old forest, the five highest weighted factors for E_S were SS (17.16), BT (16.48), M_a (16.07), RH (10.53) and T_a (10.37); thus, the main environmental, nutrient content, wood structure and NSC factors that influenced the TI-related variations in E_S were M_a, BT, N (7.57) and SS, respectively.

The amount of CO_2 released from different density stands

As shown in Table 4, the maximum stand-scale CO_2 efflux value occurred at TI 35 % (10.86 ± 0.37 t $CO_2 \cdot ha^{-1} \cdot yr^{-1}$)

Fig. 4 Thinning intensity (TI) variations in the stem nutrient concentrations (nitrogen concentration (*N*), phosphorus concentration (*P*) and potassium concentration (*K*)) and nonstructural carbon (soluble sugar content (SS) and starch content (ST)) of 21- (**a**), 25- (**b**) and 41-year-old (**c**) *Larix principis-rupprechtii* forests. Error bars indicate the standard error, *n* = 9.

and was 1.45-fold greater than the minimum E_S value at control (7.47 ± 0.23 t $CO_2 \cdot ha^{-1} \cdot yr^{-1}$) in the 21-year-old forest. In the 25-year-old forest, the maximum stand-scale CO_2 efflux occurred at control, with a value of 15.89 ± 0.54 t $CO_2 \cdot ha^{-1} \cdot yr^{-1}$, and the minimum occurred at TI 30 %, with a value of 10.08 ± 0.42 t $CO_2 \cdot ha^{-1} \cdot yr^{-1}$. In the 41-year-old forest, the maximum stand-scale CO_2 efflux occurred at TI 35 % (5.87 ± 0.31 t $CO_2 \cdot ha^{-1} \cdot yr^{-1}$), similar to the 21-year-old forest, and the minimum occurred at control, with a value of 3.80 ± 0.10 t $CO_2 \cdot ha^{-1} \cdot yr^{-1}$. Under five TIs, the stand-scale CO_2 release of the 25-year-old stand was the highest among the three forest ages, and the CO_2 release of the 41-year-old stand was the lowest. There were significant differences in the stand-scale CO_2 release among the five TIs for all three forest ages ($P < 0.01$). The tree-scale CO_2 efflux increased

with increasing TI for all three forest ages. The tree-scale CO_2 release of TI 35 % (4.84 ± 0.22, 10.40 ± 0.49 and 12.35 ± 0.39 kg $CO_2 \cdot plant^{-1} \cdot yr^{-1}$) increased by 168.89 %, 101.94 % and 200.49 % compared with that of control (1.80 ± 0.21, 5.15 ± 0.27 and 4.11 ± 0.13 kg $CO_2 \cdot plant^{-1} \cdot yr^{-1}$) for the 21-, 25- and 41-year-old forests, respectively. Additionally, the tree-scale CO_2 emissions were significantly different among the five TIs for three forest ages ($P < 0.01$).

Discussion

Seasonality and TI variation in E_S

The current study found that E_S increased with TI. Previous studies have presented that thinning could significantly promote the growth of tree DBH (Zhao et al. [2016]) and that DBH growth could promote E_S increase
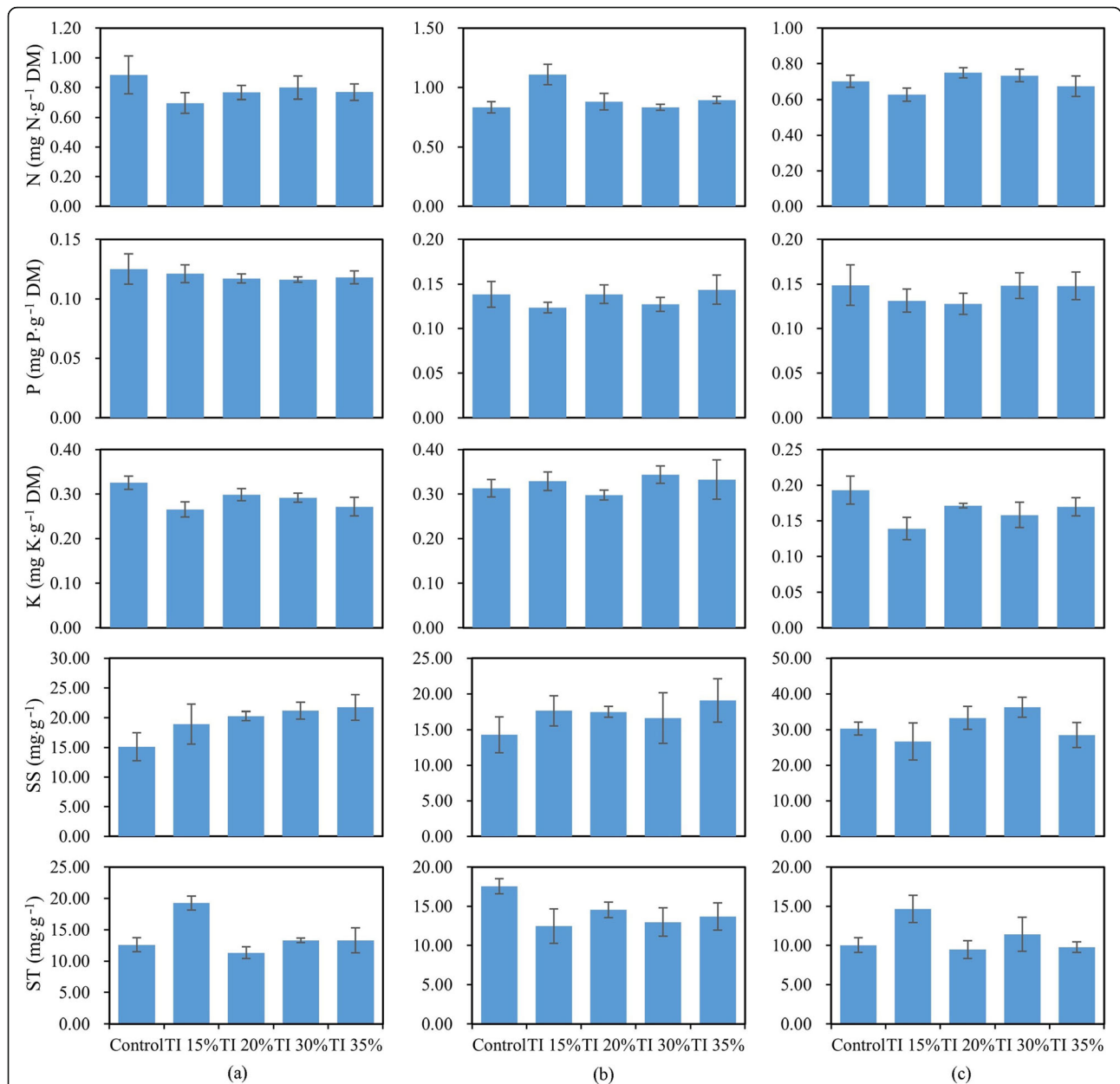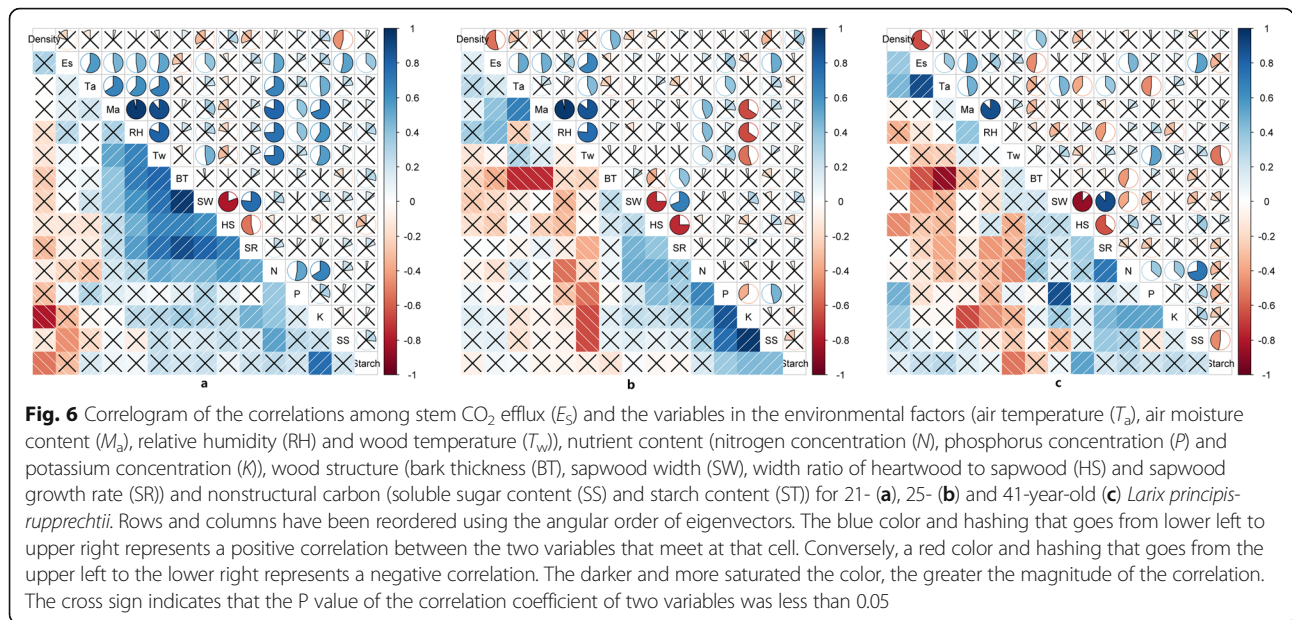
Fig. 5 Thinning intensity (TI) variations in the environmental factors (air temperature (T_a), air moisture content (M_a), relative humidity (RH) and wood temperature (T_w)) of 21- (a), 25- (b) and 41-year-old (c) *Larix principis-rupprechtii* forests. Error bars indicate the standard error, $n = 9$.

(Robertson et al. 2010; Yang et al. 2012; Araki et al. 2015; Tu et al. 2017), supporting our research results. There are several factors accounting for these complex relationships between E_S and TI. Thinning reduces tree density and opens the canopy, thus changing the microclimatic conditions by allowing greater penetration of solar radiation and wind into forest stands (Brèda et al. 1995; Aussenac 2000). In conifer forests, low-density stands with more open canopies are usually sunnier, hotter and drier than high-density stands (Meyer et al. 2001; Rambo and North 2009; Ma et al. 2010; Martín-

Benito et al. 2010; Moreno-Gutierrez et al. 2011). Consequently, there are significant differences in temperature under different TIs, thereby supporting the above point of view. E_S and temperature are strongly positively correlated (Bown and Watt 2016; Darenova et al. 2018; Salomón et al. 2019). Therefore, temperature is one of the mechanisms by which thinning affects E_S. Additionally, thinning may increase photosynthetic production because of the lower competition for light, water and mineral nutrients (López-Serrano et al. 2005; Han et al. 2006; Barbour 2007; Forrester et al. 2012; Forrester and

Fig. 6 Correlogram of the correlations among stem CO_2 efflux (E_S) and the variables in the environmental factors (air temperature (T_a), air moisture content (M_a), relative humidity (RH) and wood temperature (T_w)), nutrient content (nitrogen concentration (N), phosphorus concentration (P) and potassium concentration (K)), wood structure (bark thickness (BT), sapwood width (SW), width ratio of heartwood to sapwood (HS) and sapwood growth rate (SR)) and nonstructural carbon (soluble sugar content (SS) and starch content (ST)) for 21- (**a**), 25- (**b**) and 41-year-old (**c**) *Larix principis-rupprechtii*. Rows and columns have been reordered using the angular order of eigenvectors. The blue color and hashing that goes from lower left to upper right represents a positive correlation between the two variables that meet at that cell. Conversely, a red color and hashing that goes from the upper left to the lower right represents a negative correlation. The darker and more saturated the color, the greater the magnitude of the correlation. The cross sign indicates that the P value of the correlation coefficient of two variables was less than 0.05

Baker 2012). These changes could affect the carbohydrate levels of the remaining trees, and the accumulation of SS could increase the stem respiration rate (Yang et al. 2019). As shown in Fig. 6, thinning increased the SS and promoted the carbon emission rate of stem. Moreover, a decrease in stand density could lead to an enhancement of transpiration (Forrester 2015) and an acceleration of the transport of CO_2 in the catheter. The E_S at a given location includes the CO_2 generated by trunk and root respiration and transported in the sap flow (Teskey et al. 2008; Bloemen et al. 2014) and the CO_2 exhaled by trunk cells at the measured location (Araki et al. 2015). Thus, an increase in CO_2 transport accelerates the outward discharge of CO_2 in trunk sap flow (Saveyn et al. 2008; Bužková et al. 2015; Salomón et al. 2016b, 2019), eventually leading to an increase in E_S. Therefore, we speculate that changes in the microenvironment (temperature and humidity), transpiration tension and NSC content are key to the increase in E_S caused by thinning. Future research exploring the relationship between growth respiration and maintenance respiration under different TIs and the above influencing factors could be of great significance for explaining the relationship between thinning and E_S.

The present research shows that T_a, T_w, N and SW are the predominant environmental, nutrient content and wood structure factors that influenced on the TI variations in E_S in the 21- and 25-year-old forests. These findings also agree with our earlier observations, which were calculated by a different method (Zhao et al. 2018b). Contrary to expectations, the study of E_S under different TIs in the 41-year-old forest showed that the main influencing environmental factor was M_a, while the main influencing wood structural factor was BT. These inconsistencies might be explained as follows: the density of the 41-year-old forest stands was only approximately 25 %−33 % that of the 21-year-old and 25-year-old stands (Table 1). This lower stand density can result in drought conditions in the forest environment (Moreno-Gutierrez et al. 2011), especially in the thinned 41-year-old forest, which is more water deficient than other stands. When the forest environment is arid, the xylem CO_2 concentration becomes more sensitive to changes in air humidity, as has been reported for *Eucalyptus tereticornis* (Salomón et al. 2019), *Quercus pyrenaica* (Salomón et al. 2016a), and *Populus deltoides* (Saveyn et al. 2008). These studies demonstrate the dependency of the xylem CO_2 concentration on water availability;

Table 2 Equations for fitting E_S with influence factors in 21-, 25- and 41-year-old *Larix principis-rupprechtii* plantations in August 2016

Stand age	Data model						R^2	P-Value
21	$E_S = 0.0741 \times T_a$	$0.0004 \times$ Density	$4.4639 \times BT + 2.3568 \times SW + 9.6264 \times HS + 2.2635 \times N + 0.1363 \times$ Starch			8.8876	0.905	0.00
25	$E_S = 0.1144 \times T_w$ SS + 0.9513	$0.0002 \times$ Density + $1.1410 \times BT$	$1.3020 \times HS$	$0.0862 \times SR$	$0.2800 \times N + 1.4840 \times K + 0.0462 \times$		0.863	0.00
41	$E_S = 0.0106 \times T_a + 0.0238 \times M_a$	$0.0009 \times$ Density + $0.0286 \times BT$	$0.0878 \times HS$	$0.0916 \times N + 0.0144 \times SS + 0.9102$			0.907	0.00

Table 3 Equations for fitting E_S with air temperature and monthly mean temperature sensitivity (Q_{10}) at different thinning intensities for 21-, 25- and 41-year-old *Larix principis-rupprechtii* forests from May to October 2013–2015

Thinning intensity	Stand age: 21 years			Stand age: 25 years			Thinning intensity	Stand age: 41 years		
	Data model	R^2	Q_{10}	Data model	R^2	Q_{10}		Data model	R^2	Q_{10}
Control	$y = 0.33497e^{0.0949x}$	0.7192	2.58	$y = 0.4564e^{0.0996x}$	0.8583	2.71	Control	$y = 0.2023e^{0.0983x}$	0.6711	2.67
TI 15 %	$y = 0.3790e^{0.0973x}$	0.6573	2.65	$y = 0.5268e^{0.1051x}$	0.8436	2.86	TI 10 %	$y = 0.2314e^{0.1272x}$	0.7398	3.57
TI 20 %	$y = 0.3816e^{0.1022x}$	0.7730	2.78	$y = 0.4689e^{0.0933x}$	0.8992	2.54	TI 20 %	$y = 0.1830e^{0.1318x}$	0.7051	3.74
TI 30 %	$y = 0.2722e^{0.1181x}$	0.7587	3.26	$y = 0.4049e^{0.1179x}$	0.8958	3.25	TI 30 %	$y = 0.2373e^{0.1205x}$	0.6365	3.34
TI 35 %	$y = 0.2731e^{0.1168x}$	0.6590	3.22	$y = 0.3946e^{0.1202x}$	0.8586	3.33	TI 35 %	$y = 0.2137e^{0.1351x}$	0.7255	3.86

the change in environmental humidity in the forest can greatly increase the content of CO_2 in the xylem and promote the metabolism of the trunk. Furthermore, thinning can promote an increase in tree diameter (Zhao et al. 2016). Trunk BT increased by 1−2 mm per 10 cm increase in trunk diameter (Paine et al. 2010). The thickening of the bark helps improve trunk water retention (Teskey et al. 2008). However, the change in BT also hinders the diffusion of xylem CO_2 to the atmosphere (Aubrey and Teskey 2009; Tu et al. 2017), which makes the BT a limiting factor for E_S and makes E_S more sensitive to changes in BT. Therefore, we can conclude that the main environmental factors affecting forest E_S are T_a and T_w and that the main tree structure factor is SW. However, when the environmental humidity in a forest decreases to a certain threshold, the xylem CO_2 concentration of trees sharply decreases (Salomón et al. 2019), resulting in a decrease in forest E_S. At this time, the main environmental factor affecting E_S changes from temperature to M_a, and the tree structure factor changes from SW to BT. Therefore, the effects of humidity and BT should be considered when a low-density forest is used to study the changes of E_S.

According to the weight ranking of the influencing factors of E_S, SS is not only the main influencing factor in NSC but also plays an important role in all the influencing factors of E_S in our study. The study of loblolly pine by Maier et al. (2010) showed that SS is an important factor controlling the rates of E_S and explains much of the temporal and spatial variation in E_S in forest ecosystems, which is consistent with our results. Thinning enhances photosynthesis, and photosynthates are retained in the form of NSC (primarily SS and starch) (Hoch and Körner 2003). Although the photosynthesis and NSC concentration of the needles increased after thinning (Li et al. 2018), the responses of the NSC concentrations of the inner bark and xylem to thinning were not statistically significant. According to theory, the plant NSC pool increases when the assimilated C exceeds the demand for C but decreases when the assimilated C fails to meet demand (Sala et al. 2012). Hence,

when the tree growth is slow and the SS is in surplus, the NSC could be stored in the form of starch, whereas when the growth is rapid or conditions are dry, part of the starch could be converted to SS to promote respiration (Rodríguez-Calcerrada et al. 2014; Sevanto et al. 2014; Cui et al. 2017), and the allocation of a plant's internal carbohydrates could present a sink-driven pattern (Lambers et al. 2008). Therefore, we speculate that in a stand with a high TI, trees give priority to assigning more NSC to growth and therefore increase the availability of trunk NSC to occupy more growth space. Although the trunks of trees in stands with a high TI exhibit more NSC, the respiratory consumption of NSC also increases, resulting in lower proportions but constant concentrations of NSC in the trunk. An increase in TI can promote an increase in the DBH of trees, which also confirms this explanation. Therefore, although thinning does not cause a difference in SS, SS, like temperature, is an important factor affecting E_S.

Response of Q_{10} to TI

Q_{10} for the three forest ages ranged from 2.58 to 3.86, comparable with that observed in other species (Yang et al. 2012, 2019; Rodríguez-Calcerrada et al. 2014; Tarvainen et al. 2014; Darenova et al. 2018). Close inspection of Table 3 shows that Q_{10} basically increases with increasing TI. In contrast to our study, a previous study suggested that thinning reduces Q_{10} (Lavigne 1987). The differences in the trends probably result from the limited measuring periods (July and September) and TI levels in Lavigne (1987) and from differences among tree species. Thinning can improve the light conditions of a stand, and enhancement of photosynthesis can increase the temperature sensitivity of E_S (De Roo et al. 2019). Thinning can increase the transpiration of trees by reducing stand density and then accelerate the flow velocity of trunk sap flow; faster sap flow velocity can increase Q_{10} (Maier et al. 2010; Zhu et al. 2012; Yang et al. 2019). In addition, thinning can enhance the metabolic activity of trunk cells and carbohydrate availability (Lambers
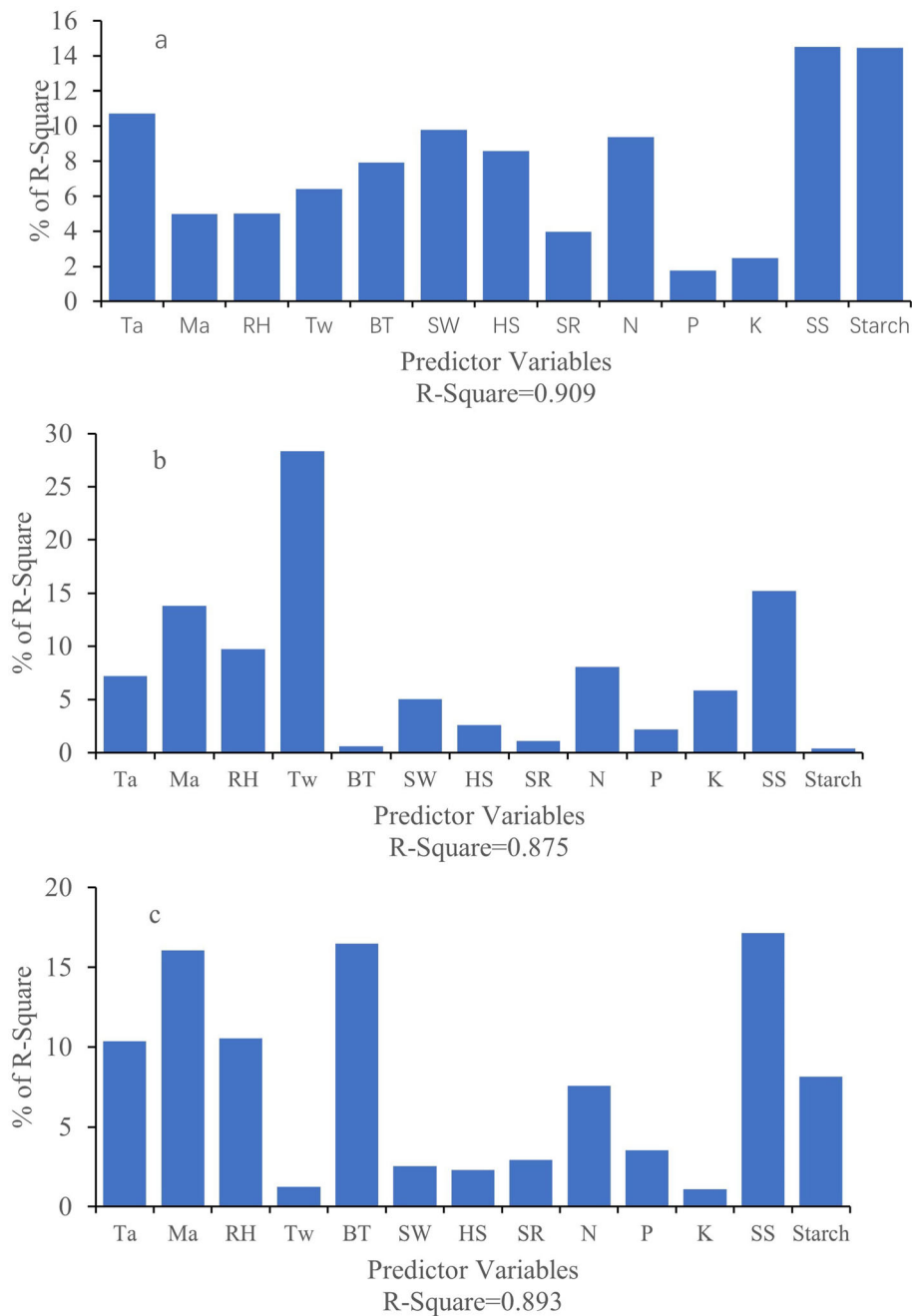
Fig. 7 Relative weight of predictive variables of 21- (**a**), 25- (**b**) and 41-year-old (**c**) *Larix principis-rupprechtii* plantations for stem CO_2 efflux (E_S)

et al. 2008; Sala et al. 2012) and increase the SS content in the trunk (Fig. 3), thereby promote the rapid growth of tree diameter, so the improvements in cell metabolic activity (Saveyn et al. 2007), carbohydrate availability (Yang et al. 2019) and soluble sugar content in stem partly explain the increase in Q_{10}. Significantly, thinning not only improved the growth respiration of trees, but also greatly improved the maintenance respiration, and the temperature

sensitivity of maintenance respiration was far greater than that of growth respiration (Adu-Bredu et al. 1997). We speculate that the increase of maintenance respiration after thinning led to the increase of temperature sensitivity of E_S. Therefore, the thinning-induced increase in Q_{10} might be partly due to the potential effects of photosynthesis, sap flow, soluble sugar content, metabolic activity of living cells and carbohydrate availability and the increase of Rm.

Table 4 Annual stem CO_2 efflux for 21-, 25- and 41-year-old *Larix principis-rupprechtii* forests. The means ± the standard deviations of the between tree variations are shown ($n = 3$)

	Stand age	Control	TI 15 %	TI 20 %	TI 30 %	TI 35 %
Stand-Scale ($t\ CO_2 \cdot ha^{-1} \cdot yr^{-1}$)	21	7.47 ± 0.23	8.53 ± 0.33	9.06 ± 0.15	9.22 ± 0.35	10.86 ± 0.37
	25	15.89 ± 0.54	13.32 ± 2.35	12.04 ± 0.40	10.08 ± 0.42	11.70 ± 1.82
	41	3.80 ± 0.10	5.14 ± 0.17	4.93 ± 0.28	5.44 ± 0.15	5.87 ± 0.31
Tree-Scale ($kg\ CO_2 \cdot plant^{-1} \cdot yr^{-1}$)	21	1.80 ± 0.21	2.51 ± 0.17	2.94 ± 0.16	3.51 ± 0.20	4.84 ± 0.22
	25	5.15 ± 0.27	5.77 ± 0.39	6.39 ± 0.29	6.30 ± 0.36	10.40 ± 0.49
	41	4.11 ± 0.13	6.85 ± 0.30	7.39 ± 0.34	10.05 ± 0.51	12.35 ± 0.39

CO_2 effluxes for each TI

The range of our annual tree-scale estimates of E_S for 21- to 41-year-old *L. principis-rupprechtii* trees (1.80 to 12.35 kg $CO_2 \cdot plant^{-1} \cdot yr^{-1}$; Table 4) are similar to those for yellow poplar (Fan et al. 2017), red oak and red maple (Reinmann et al. 2016). Our study shows that if the change in stand density is ignored, the CO_2 releases of individual trees in the three forest age groups could be underestimated by 168.89 %, 101.94 % and 200.49 %, respectively. Thinning not only promotes the release of CO_2 via stem respiration but also increases the diameter of the trees and therefore the area of the trunk. Thus, the release of CO_2 from the trunk increases considerably. On the stand scale, the promoting effect of TI on the CO_2 release from the 21- and 41-year-old stands was weakened, and the CO_2 release at the stand scale in 25-year-old stands decreased with the increase in TI. This trend is mainly because although thinning promotes E_S and increases the trunk area of individual trees, it reduces the number of trees per unit area. Nevertheless, we know from the results of this study that, regardless of tree scale or stand scale, the release of CO_2 under different TIs varies significantly. Therefore, in the estimation of stem CO_2 release, stand density is a factor that cannot be ignored, especially in the calculation of individual tree trunk respiration carbon release. Temperature has a greater effect on E_S than other factors, but T_a and T_w can only explain 11.60 %−35.56 % of R^2. Therefore, temperature is not sufficient to quantify E_S accurately, and the effect of other factors, such as stand density, on E_S must be integrated into models simulating E_S in forest ecosystems. To estimate the carbon release from the trunk more accurately, we used the E_S estimation equation combined with stand density and other factors for reference in Table 2.

Conclusions

In this study, to clarify the effects of TI on E_S and Q_{10} of *Larix principis-rupprechtii* and the related mechanisms and to evaluate the error in CO_2 emission estimates at the annual tree scale and stand scale without considering the effects of stand density on E_S, five TIs were applied to *Larix principis-rupprechtii* stands with three forest ages of 21, 25 and 41 years, and the E_S, environmental, nutritional, wood structure and NSC factors were monitored. The main findings are as follows: (1) Thinning can increase E_S by improving the microenvironment (temperature and humidity), transpiration tension and NSC content. (2) SS, like temperature, is a main factor affecting E_S. When the stand density is low enough, BT and humidity should be considered in addition to T_a, T_w, SW, N and SS in the evaluation of E_S. (3) The temperature sensitivity of E_S increases with increasing TI, and photosynthesis, sap flow, metabolic activity of living cells and carbohydrate availability may be potential influencing factors. (4) If the change in stand density is ignored, the CO_2 release of individual 21-, 25- and 41-year-old trees could be underestimated by 168.89 %, 101.94 % and 200.49 %, respectively. (5) The CO_2 estimation based on the stem equation was simulated for reference.

Authors' contributions
Kuangji Zhao: Design of the study, data collection, data analysis, and manuscript writing. Timothy J. Fahey: Guide the revision of manuscript. Xiangzhen Wang and Jie Wang: Data collection; Fang He and Chuan Fan: Data analysis and polish the manuscript. Zhongkui Jia and Xianwei Li: Supervision of the scientific experiments. The author(s) read and approved the final manuscript.

Declarations

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