Temporal dynamics and vertical variations in stem CO₂ efflux of *Styphnolobium japonicum*

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Abstract CO₂ efflux (E_{CO_2}) from stems and branches is highly variable within trees. To investigate the mechanisms underlying the temporal dynamics and vertical variations in E_{CO_2} , we measured the stem E_{CO_2} by infrared gas analysis (IRGA) and meteorological conditions at 10 different heights from 0.1 to 3.7 m aboveground on two consecutive days every month for 1 year in six *Styphnolobium japonicum* trees with a similar size. The results indicated that the seasonal change in E_{CO_2} roughly followed the seasonal variations in woody tissue temperature (T_w) and stem radial diameter increment (Di). Together, T_w and Di explained the monthly change in E_{CO_2} , and the contributions of T_w and Di changed with the stem positions and growth stages. The diurnal patterns of E_{CO_2} differed greatly between the growing and dormant season, showing a bimodal distribution with an obvious midday depression in the former and a unimodal distribution in the latter. The strong vertical variation in the day-time E_{CO_2} of the growing season was mainly caused by the vertical gradients of T_w , Di and difference in sapwood volume per unit of the stem surface along the trunk. The temperature-sensitivity coefficient (Q_{10}) was not constant, as assumed in some models, but was instead vertically altered and highly dependent on the

measurement temperature. For all stem positions, the highest Q_{10} value appeared at approximately 5 °C, and both higher and lower temperatures decreased Q_{10} . Our study demonstrated that application of a constant Q_{10} would cause an estimation error when scaling up chamber-based measurements to annual carbon budgets at the whole-stem level.

Keywords Q_{10} · Temperature-sensitivity coefficient · Temporal dynamics · Vertical variations · Stem CO₂ efflux

Introduction

CO₂ efflux (E_{CO_2}) from stems and branches is important in the regulation of biomass productivity (Valentini et al. 1996; Zha et al. 2004) and maintenance of carbon balance in terrestrial ecosystems (Cernusak et al. 2006; Maier et al. 2004), as 50–70% of the net photosynthetic production (NPP) has been estimated to be consumed by plant respiration, and woody tissue alone accounts for ca. 11–23% (Ryan 1991; Ryan et al. 1994). Despite its importance, uncertainties relevant to the variations in E_{CO_2} remain poorly assessed due to the lack of continuous sampling both in time series and space sequences.

E_{CO_2} is a physiological process that is sensitive to temperature. The increase in temperature could promote the activities of enzymes involved in respiration, and also decrease the gas solubility and improve the diffusion coefficient of CO₂. The temperature response of E_{CO_2} is usually expressed in terms of the temperature-sensitivity coefficient (Q_{10}), representing the times of change in E_{CO_2} with an increase in temperature of 10 °C (Stockfors 2000; Valentini et al. 1996). In some process-based models, Q_{10} is set as a constant value of 2.0 (Melillo et al. 1993; Ryan et al.

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1995). However, this is surprising in some respects because it has been reported that Q_{10} is neither constant nor near 2.0 except for some specific species over a limited temperature range (Atkin et al. 2003). Among different species or different individuals of the same species, Q_{10} values are highly variable (Atkin et al. 2002; Covey-Crump et al. 2002; Loveys et al. 2003; Turnbull et al. 2001; Yang et al. 2014). A recent report examining the temperature-sensitivity of woody tissue E_{CO_2} revealed that Q_{10} ranged from 1.00 to 6.40, with an average of 2.0 (Yang et al. 2014). Within the same individual, Q_{10} was higher in the canopy or mid-stem than at breast height (Ceschia et al. 2002; Damesin et al. 2002).

Generally, E_{CO_2} measurements were conducted during the daytime at a given point (usually at breast height) (Maier and Clinton 2006; Teskey et al. 2008), and estimation of E_{CO_2} at the tree- or stand-level was subsequently scaled up from the infrequent chamber-based measurements with the assumption of breast height E_{CO_2} being representative of the entire stem (Chambers et al. 2004; Harris et al. 2008; Robertson et al. 2010). In fact, large temporal and vertical variations in E_{CO_2} have hitherto been revealed, resulting in over- or under-estimation of the large-scale carbon budget (Acosta et al. 2008; Brito et al. 2010; Ceschia et al. 2002; Edwards and Hanson 1996; Katayama et al. 2014; Maunoury et al. 2007; Stockfors and Linder 1998; Tarvainen et al. 2014; Wieser and Bahn 2004). The temporal variations, including seasonal dynamics and diurnal fluctuations, have been reported to be caused by the complicated interactions of temperature (Paembonan et al. 1991), growth processes and the cambial active-dormancy cycle (Maunoury et al. 2007). In contrast, the vertical variation may be attributed to significant gradients in the woody tissue temperature (Edwards and Hanson 1996) and the fraction of living cells (Stockfors 2000). Along the trunk, E_{CO_2} commonly increased with stem height, i.e., small diameter branches have a relatively higher E_{CO_2} than lower stems (Araki et al. 2010; Cavaleri et al. 2006; Damesin et al. 2002). Although there is now ample evidence to show that these variations can cause considerable errors in the point-based up-scaling estimation (Araki et al. 2010; Ryan et al. 2009; Stockfors 2000; Tarvainen et al. 2014), very few models have taken this phenomenon into account due to the lack of a comprehensive, systematic understanding of E_{CO_2} (Ceschia et al. 2002; Stockfors 2000). Quantitative analysis of E_{CO_2} in temporal dynamics and vertical variations, as well as the factors driving these changes, would help to improve our knowledge of E_{CO_2} processes and understand how climatic changes affect forest carbon budgets (Vose and Ryan 2002).

Thus, the hourly stem E_{CO_2} and meteorological conditions at continuous heights of six *Styphnolobium japonicum* (L.) Schott trees were determined on two consecutive

days per month throughout 2014, in an artificial mixed forest plantation near Beijing. The aims of this study were (1) to clarify the temporal dynamics and vertical variations in E_{CO_2} of *Styphnolobium japonicum* in Dongsheng Country Park; (2) to elucidate predominant factors regulating the seasonal and vertical variations in E_{CO_2} ; (3) to obtain a monthly position-specific E_{CO_2} at the reference temperature 0 °C (E_0) and temperature-sensitivity coefficient (Q_{10}); and (4) to establish an effective method to estimate the annual carbon emission at the whole-stem level.

Materials and methods

Site description

This study was conducted in *Dongsheng Country Park* (39°58' N, 116°18' E, 43.7 m a.s.l.) situated in Haidian District, Beijing City of China (Appendix Fig. S1). The site is characterized by a warm temperate continental monsoon climate with a mean annual precipitation of approximately 550–600 mm, greater than 90% of which occurs in July and August, and a mean annual temperature of 17.8 °C with a long cold winter and a high-temperature humid summer. The selected experimental plots occupied a total of 101.45 hectares. *Styphnolobium japonicum* and *Salix matsudana* were the dominant deciduous trees, and the coniferous species were *Larix principis-rupprechtii* and *Platycladus orientalis*. The stem density of *Styphnolobium japonicum* in this site was 216 ± 12 stem ha^{-1} , with an average height of 10.6 ± 2.2 m and an average diameter at breast height (DBH) of 24.4 ± 3.1 cm. According to the F.A.O. classification, the soil was predominantly dark brown sandy clay loam. Measurements of soil physical and chemical properties were conducted for three soil layers (0–10, 10–20 and 20–40 cm). The average soil bulk density, C:N ratio and soil pH (soil: water, 1:2) of the three soil layers were 1.563 ± 0.102 , 24.49 ± 2.68 and 8.57 ± 0.20 g cm^{-3} , respectively.

Sampling design

Based on the frequency distribution of the diameter at breast height (DBH), six individuals of the locally dominant deciduous species (*Styphnolobium japonicum*) were chosen as subjects (Appendix Fig. S2). The six sampled trees were very similar in height (ranging from 10.7 to 11.2 m with a variation coefficient of 1.81%) and DBH (ranging from 22.5 to 26.3 cm with a variation coefficient of 5.97%). The detailed size characteristics of the sampled trees are listed in Table 1. For each sampled tree, 10 continuous heights at approximately 40-cm intervals, starting from the base of the trunk (10 cm aboveground),

Table 1 Size characteristics of six sampled *Styphnolobium japonicum* trees for CO₂ efflux measurements

Trees	H (m)	DBH (cm)	Height of lowest living branch ^a (m)	Crown height ^b (m)	Crown ratio ^c (%)	Stem area ^d (m ²)	Sapwood volume ^e (m ³)
S ₁	10.7	22.5	3.38	4.24	39.63	2.463	0.199
S ₂	10.9	23.2	3.52	3.88	35.60	2.628	0.241
S ₃	10.9	23.6	3.41	4.57	41.93	2.467	0.229
S ₄	11.1	24.7	3.47	4.71	42.43	2.766	0.217
S ₅	11.2	26.3	3.55	5.06	45.19	2.832	0.259
S ₆	11.2	25.5	3.61	5.32	47.50	2.884	0.263

Sampled trees were named from S₁ to S₆ in ascending order of height; *H* height of the sampled trees (measuring method is shown in Appendix Fig. S3); *DBH* diameter at breast height

^aThe height of the lowest living branch was defined as the above-ground height of lowest intersection point between the stem and the first-order branching of the main stem (Appendix Fig. S3)

^bCrown height referred to the vertical height from the base of the crown to the top of the tree (Appendix Fig. S3)

^cCrown ratio was calculated as the ratio of crown height to total height of the tree (*H*)

^{d,e}Stem area (sapwood volume) was the sum of the estimated stem or branch surface area (sapwood volume) of 10 segments (Katayama et al. 2014) (detailed partition method of segments and calculation formula for stem area and sapwood volume of each segment are shown in Appendix Fig. S4)

were chosen as the measurement points (approximately 0.1, 0.5, 0.9, 1.3, 1.7, 2.1, 2.5, 2.9, 3.3 and 3.7 m above the ground) (Appendix Fig. S4a), among which nine points (0.1–3.3 m) were located in the stem and the highest point was located in the first-order branching of the main stem. The diameters of these measurement positions ranged from 12.5 to 31.6 cm (mean = 22.05 cm, *n* = 60). Detailed information for the measurement points is listed in Appendix Table S1.

Field preparation and instrumentation

The CO₂ released by stems or branches was captured using a simple technique: a custom-built polyvinyl chloride (PVC) collar (Polyvinyl Chloride, 60P) (Xu et al. 2000). Before the experiment, two inner diameters of 7.0 cm and 10.6-cm PVC pipes were cut perpendicular into the length of 5-cm cylindrical collars (Appendix Fig. S5). To firmly attach the collar to the trunk, the loose bark was removed, and one end of these collars was cut into the curve to conform to the trunk surface. One-component polyurethane foam sealant was used to glue the collars to the trunk. For the points with a large diameter (*D* > 15 cm), we adopted collars of 10.6 cm in inner diameter, and for points with a small diameter (*D* ≤ 15 cm), we adopted the 7.0-cm ones. At each height at which the collar was installed, pairs of HOBO Pro V2 U23-002 temperature/relative humidity (RH) and U23-004 temperature probes (Onset Computer Corporation, Bourne, MA, USA) were placed in preparation for the observation of meteorological conditions (Appendix Fig. S4a).

Measurements

Stem E_{CO2} measurements

The hourly stem E_{CO2} was measured on two consecutive days for each month using a portable closed chamber system (LI-8100, Li-Cor, Inc., Lincoln, NE, USA). Immediately before measurement, a diffusion-tight chamber connected to the LI-8100 gas channels sequentially covered the collars that had been installed previously. In measurement mode, a non-dispersive infrared gas analyser (IRGA) was used to monitor the change in CO₂ concentration inside the closed chamber. The data logger computed the change rate of the CO₂ mixing ratio based on a linear increase in chamber CO₂ concentrations over time, and then stored the rates of E_{CO2}. The air was circulated through the chamber at a flow rate of 0.5 L min⁻¹ after warming up the LICOR. For each point, approximately 1.5 min was required: 60 s for the CO₂ measurements and 30 s for the observation delay. The total 60 repetitive operations (10 points tree⁻¹ × 6 trees), therefore, could not be achieved within an hour. For each month, two consecutive days of hourly stem E_{CO2} measurements were conducted for three trees (S₁, S₂ and S₃), and similar measurements were acquired for the remaining trees (S₄, S₅ and S₆) on another two consecutive days with similar meteorological conditions.

Microclimate records

Throughout the year 2014, air temperature (*T_A*) and RH were monitored every 2 min by HOBO Pro V2 U23-002 probes, and the woody tissue temperature (*T_W*) was

measured by HOBO Pro V2 U23-004 probes with the same observation frequency. The accuracy of the temperature and RH probes is $\pm 0.21^\circ\text{C}$ (applicable range between 0 and 50°C) and $\pm 2.5\%$ (applicable range between 10 and 90%), with respective resolutions of 0.02°C and 0.1% under conditions of 25°C . The U23-004 probes were inserted at a depth of 3 cm beneath the bark of stems or branches (the total length of the probe was inserted into the trunk to prevent direct sunlight), and the U23-002 probes were positioned close to the U23-004 exposure to air (Appendix Fig. S4a). All probes were connected to the smart sensor-compatible HOBO loggers (15 data channels).

Dendrometer

In this study, we selected four representative heights (10, 130, 250 and 370 cm) to investigate the growth rates of *Styphnolobium japonicum* trees. The rates of the stem radial diameter increment (Di) were continuously monitored using automatic point dendrometers with a resolution of $1\text{ }\mu\text{m}$ and temperature coefficient $<0.1\text{ }\mu\text{m K}^{-1}$ (Agricultural Electronics, Tucson, Arizona, USA). Depending on stem expansion or contraction, the linear variable differential transformer (LVDT) moves in or out and transmits a signal to the potentiometer. To minimize heating by direct solar radiation, all the electronic point dendrometers were installed at the north-facing side of the trees. Before installation, the outer parenchyma was removed to avoid the influence of diameter fluctuations caused by water absorption or dehydration. Data were obtained every 30 min, and 15-day means were automatically recorded with a data logger (CR10X, Campbell Scientific, Logan, UT, USA).

Data processing

Calibration of the stem E_{CO_2}

In this paper, the instrument-derived E_{CO_2} was expressed as the unit of surface area of stem ($E_{\text{CO}_2-\text{S}}$, $\mu\text{mol m}^{-2}\text{ s}^{-1}$). As the stem surface was not regular, the stem surface area covered by the collar and the air volume enclosed in the chamber were different among measurement points. Hence, the stem surface area-based $E_{\text{CO}_2-\text{S}}$ should be calibrated with the following expression (Xu et al. 2011):

$$E'_{\text{CO}_2-\text{S}} = \frac{V + V' - \pi\left(\frac{D}{2}\right)^2 h}{V} \times \frac{S}{S'} \times E_{\text{CO}_2-\text{S}}, \quad (1)$$

where $E_{\text{CO}_2-\text{S}}$ and $E'_{\text{CO}_2-\text{S}}$, both in units of $\mu\text{mol m}^{-2}\text{ s}^{-1}$, respectively represented the stem area-based CO_2 release rates before and after calibration. V and S were the default

values of the systemic chamber volume (854.2 cm^3) and area (83.7 cm^2), while V' and S' were the actual volume of the chamber and surface area of the curved edge of the collar (the determination method for V' and S' is shown in Appendix Fig. S6). D was the external diameter of the chamber, and h was the depth of the chamber inserted into the collar.

Conversion of expression units

According to the theory of Levy and Jarvis, all E_{CO_2} used for following analysis was expressed as a unit of sapwood volume ($E'_{\text{CO}_2-\text{V}}$, $\mu\text{mol m}^{-3}\text{ s}^{-1}$) because of the positive relationship between area-based $E'_{\text{CO}_2-\text{S}}$ and diameter (Levy and Jarvis 1998). The conversion of $E'_{\text{CO}_2-\text{V}}$ and $E'_{\text{CO}_2-\text{S}}$ was performed as follows:

$$E'_{\text{CO}_2-\text{V}} = E'_{\text{CO}_2-\text{S}} \times \frac{1}{\text{SVS}}, \quad (2)$$

where SVS represents the sapwood volume per unit of stem surface ($\text{m}^3\text{ m}^{-2}$).

Calculation of the temperature-sensitivity coefficient (Q_{10}).

For all stem positions, the hourly measured stem $E'_{\text{CO}_2-\text{V}}$ was highly correlated with T_{W} (data not listed). To investigate the temperature sensitivity of $E'_{\text{CO}_2-\text{V}}$, we fit the hourly $E'_{\text{CO}_2-\text{V}}$ against T_{W} according to the following exponential equation for each month “i”:

$$E'_{\text{CO}_2-\text{V}} = E'_{\text{CO}_2-\text{V}-0} \times e^{K_i T_{\text{W}}} (i = 1, 2, \dots, 12), \quad (3)$$

where $E'_{\text{CO}_2-\text{V}-0}$ is the $E'_{\text{CO}_2-\text{V}}$ normalized to the reference temperature 0°C , and K_i is the regression coefficient describing the temperature sensitivity of $E'_{\text{CO}_2-\text{V}}$. The temperature-sensitivity coefficient (Q_{10}) was then calculated as follows:

$$Q_{10} = e^{10 \times K_i}, \quad (4)$$

The monthly $E'_{\text{CO}_2-\text{V}-0}$, K_i and Q_{10} at all heights are listed in Appendix Table S2.

Up-scaling of $E'_{\text{CO}_2-\text{V}}$ at the whole-stem level.

In this study, the daily $E'_{\text{CO}_2-\text{V}}$ of whole stem (E_{D} , $\text{mmol stem}^{-1}\text{ day}^{-1}$) was determined via three approaches, and the results were compared. In the first approach, the whole stem was divided into 10 segments (detailed partition method of the segments described in Appendix Fig. S4a), and E_{D} was calculated as the sum of the daily $E'_{\text{CO}_2-\text{V}}$ of 10 segments (E_{d} , $\text{mmol segment}^{-1}\text{ day}^{-1}$). For each segment, E_{d} was calculated as the product of the daily mean $E'_{\text{CO}_2-\text{V}}$ ($E'_{\text{CO}_2-\text{V}-\text{d}}$, $\mu\text{mol m}^{-3}\text{ s}^{-1}$, the average of instantaneous $E'_{\text{CO}_2-\text{V}}$ measured hourly for 24 h), sapwood volume of the segment (S_{v} , m^3 , estimation method shown in Appendix Fig. S4b) and a constant, 86.4 [the integration of unit

conversion from $\mu\text{mol m}^{-3} \text{s}^{-1}$ to $\text{mmol m}^{-3} \text{s}^{-1}$ ($1 \mu\text{mol m}^{-3} \text{s}^{-1} = 10^{-3} \text{mmol m}^{-3} \text{s}^{-1}$) and 86400 s per day]:

$$E_D = \sum_{S=1}^{10} E_d = \sum_{S=1}^{10} E'_{\text{CO}_2\text{-V-d}} \times S_v \times 86.4, \quad (5)$$

where S is the serial number of separate segments where $E'_{\text{CO}_2\text{-V}}$ was measured.

Second, we used the conventional method to estimate E_D of the whole stem based on the hypothesis that the sapwood volume-based $E'_{\text{CO}_2\text{-V}}$ was constant throughout the trunk and using breast-height $E'_{\text{CO}_2\text{-V}}$ ($E'_{\text{CO}_2\text{-V-130}}$, $\mu\text{mol m}^{-3} \text{s}^{-1}$) as the representative value of whole stem. Accordingly, E_D was calculated as the product of $E'_{\text{CO}_2\text{-V-130}}$ and the sapwood volume of whole stem (S_v , m^3 , the sum of S_v):

$$E_D = E'_{\text{CO}_2\text{-V-130}} \times S_v \times 86.4 \quad (6)$$

In the third approach, E_D was estimated with breast-height $E'_{\text{CO}_2\text{-V-130}}$ normalized to the reference temperature 0°C ($E'_{\text{CO}_2\text{-V-130-0}}$), and the constant Q_{10} value of 2.0 as assumed in most models:

$$E_D = E'_{\text{CO}_2\text{-V-130-0}} \times 2.0^{\frac{T_w}{10}} \times S_v \times 86.4 \quad (7)$$

Finally, we estimated the annual $E'_{\text{CO}_2\text{-V}}$ of whole stem (E_Y , $\text{mmol stem}^{-1} \text{year}^{-1}$) considering the seasonal variation in E_D . E_Y was calculated as the sum of monthly $E'_{\text{CO}_2\text{-V}}$ (E_M , $\text{mmol stem}^{-1} \text{month}^{-1}$), and E_M was obtained by multiplying the estimated E_D by the days (N) of the current month:

$$E_Y = \sum_{i=1}^{12} E_M = \sum_{i=1}^{12} E_D \times N \quad (8)$$

Statistical analysis

To examine which factors influenced the seasonal variation in daily mean $E'_{\text{CO}_2\text{-V}}$ ($E'_{\text{CO}_2\text{-V-d}}$, $\mu\text{mol m}^{-3} \text{s}^{-1}$), we separately calculated Spearman's rank correlation coefficients (ρ) between $E'_{\text{CO}_2\text{-V-d}}$ and the seasonally changed independent variables [i.e., daily mean woody tissue temperature (T_{w-d}) and stem radial diameter increment (Di_{-d})] for 4 heights (10, 130, 250 and 370 cm) of six sampled trees in the dormant and growing season (the definitions of the growing and dormant seasons are explained in Fig. S7). Subsequently, the position-specific explanatory powers of T_{w-d} and Di_{-d} on the monthly change in $E'_{\text{CO}_2\text{-V-d}}$ were determined using generalized linear models (GLMs), in which $E'_{\text{CO}_2\text{-V-d}}$ was set as the dependent variable, and T_{w-d} and Di_{-d} were regarded as independent variables. For the 24 stem positions, we calculated the standardized regression coefficients for T_{w-d} and Di_{-d} of the position-specific GLM to determine their explanatory powers on

$E'_{\text{CO}_2\text{-V-d}}$ (Araki et al. 2015). To investigate the morphological factors affecting the magnitude of the influence of T_{w-d} or Di_{-d} , we fitted the 24 position-specific regression coefficients for T_{w-d} or Di_{-d} of GLMs (denoted as Coef. T_{w-d} and Coef. Di_{-d} , respectively, indicating the response of $E'_{\text{CO}_2\text{-V-d}}$ to the per temperature change or stem radial diameter increment) against 3 morphological characteristics of the trees (h , height of the measurement points; SVS, sapwood volume per unit of stem surface; Di_{-y} , annual stem radial diameter increment).

The factors causing the vertical variation in daytime $E'_{\text{CO}_2\text{-V}}$ during the growing season were determined by fitting the vertically changed $E'_{\text{CO}_2\text{-V}}$ against 4 vertically changed biotic (Di_{-d} and SVS) and abiotic factors (T_w and T_A). All the $E'_{\text{CO}_2\text{-V-d}}$, T_{w-d} , T_{A-d} and Di_{-d} used for analysis were calculated as the average of the daytime values (10:00–16:00) in July, when the vertical distributions of $E'_{\text{CO}_2\text{-V}}$ and other meteorological conditions were most obvious. For each height, 6 replicate samples of 6 sampled trees were incorporated into the correlation analysis.

One-way repeated measures analysis of variance (ANOVA) and the least significant difference (LSD) were used to compare the significant differences in $E'_{\text{CO}_2\text{-V}}$ among heights or months ($\alpha=0.05$). All data processing and statistical analysis were performed using SPSS19.0, and the graphs were drawn with Origin8.0.

Results

Seasonal variation in T_A , T_w and $E'_{\text{CO}_2\text{-V}}$

The seasonal patterns of air temperature (T_A) and woody tissue temperature (T_w) were characterized by unimodal inverted U curves, with daily mean T_{A-d} varying between -1.13°C (Jan 5, 2014) and 29.93°C (Jul 24, 2014) and T_{w-d} between -1.44°C (Feb 2, 2014) and 26.65°C (Jul 24, 2014) (Fig. 1a). Throughout the year, there was a good correlation between T_w and T_A . In the warm and wet period (growing season), T_A was significantly higher than T_w , but it was the opposite in the cold and dry period (dormant season) (Fig. 1a).

The daily mean stem radial diameter increment rates (Di_{-d}) at 4 representative heights (10, 130, 250 and 370 cm) were calculated semi-monthly and are shown in Fig. 1b. The timing of the diameter increment was almost synchronous along the trunk, which started in mid-April and ceased approximately at the end of August with a peak in July (Fig. 1b). However, the absolute diameter increment rates were significantly different at 4 representative heights, especially during the growth period of trees (from April to August). The highest annual cumulative radial increment appeared in the first-order branching of the main stem, with

Fig. 1 Seasonal variations in air temperature (T_A , °C) and woody tissue temperature (T_W , °C) at breast height (approximately 1.3 m above the ground) (a), daily mean radial diameter increment rates (Di_d , mm day⁻¹) calculated semi-monthly at 4 representative heights (10, 130, 250 and 370 cm) (b), daily mean stem CO₂ efflux per unit sap-

wood volume ($E'_{CO2-V-d}$, $\mu\text{mol m}^{-3} \text{s}^{-1}$) (c) and $E'_{CO2-V-d}$ normalized to the reference temperature 0 °C ($E'_{CO2-V-0}$, $\mu\text{mol m}^{-3} \text{s}^{-1}$) (d). Values were derived from measurements obtained for six trees throughout 2014. Means $\pm$ SD (standard deviation) are shown

an average of $56.87 \pm 3.52 \text{ mm year}^{-1}$ ($n=6$), and the lowest annual increment of $30.63 \pm 2.08 \text{ mm year}^{-1}$ ($n=6$) appeared at the base of the trunk (Fig. S7a).

Typically, seasonal changes in the daily mean E'_{CO2-V} ($E'_{CO2-V-d}$, $\mu\text{mol m}^{-3} \text{s}^{-1}$) was found in our study (Fig. 1c). The fall decline and spring increase in $E'_{CO2-V-d}$ generally followed the trends of T_W and Di_d (Fig. 1a, b), with an obvious increase in spring (April) and peak in late summer (around August), followed by a gradual decrease in the level of $E'_{CO2-V-d}$ related to the maintenance of respiration during the winter (Fig. 1c). The $E'_{CO2-V-d}$ normalized to the reference temperature 0 °C ($E'_{CO2-V-0}$, $\mu\text{mol m}^{-3} \text{s}^{-1}$) significantly varied with the month, and two apexes appeared in the seasonal pattern of $E'_{CO2-V-0}$ (Fig. 1d). For the first time, $E'_{CO2-V-0}$ peaked around April, which was anterior to the diameter increment occurrence, followed by a second peak in July corresponding to a maximum of Di_d

(Fig. 1d). The seasonal dynamic of $E'_{CO2-V-0}$ was well synchronised with Di_d in our study, except for the transition period from dormancy to growing season (reviving stage, Appendix Fig. S7).

Effects of T_{W-d} and Di_d on the monthly change in $E'_{CO2-V-d}$

For 4 heights (10, 130, 250 and 370 cm) of each sampled tree, the relationships between $E'_{CO2-V-d}$ and daily mean woody tissue temperature (T_{W-d}) were analysed for the growing and dormant season, separately. The results indicated that irrespective of the growing or dormant season, $E'_{CO2-V-d}$ was highly correlated with the monthly change in T_{W-d} , as shown in the case of 4 heights of sampled tree 1 (S1) ($0.75 \leq \rho \leq 0.94$, $P \leq 0.01$, Table 2). Additionally, the positive correlation between $E'_{CO2-V-d}$ and Di_d was also

Table 2 Summary results of Spearman's rank correlation coefficients (ρ) between the daily mean E'_{CO2-V} ($E'_{CO2-V-d}$, $\mu\text{mol m}^{-3} \text{s}^{-1}$) and independent variables (daily mean woody tissue temperature (T_{W-d} , °C) and stem radial diameter increment (Di_{-d} , mm day $^{-1}$)) at 10,130, 250 and 370 cm of the sampled tree 1 (S1), and standardized regression coefficients for T_{W-d} and of Di_{-d} of position-specific GLMs

Seasons	Heights (cm)	Spearman's correlation coefficients (ρ)		Standardized regression coefficients	
		T_{W-d}	Di_{-d}	T_{W-d}	Di_{-d}
Growing season	Tree 1				
	10	0.86**	0.74*	0.46	0.21
	130	0.83**	0.86*	0.51	0.24
	250	0.84**	0.91**	0.38	0.27
	370	0.75**	0.84**	0.35	0.41
Dormant season	Tree 1				
	10	0.90**	0.24	0.62	
	130	0.87**	0.35	0.45	
	250	0.92**	0.41	0.54	
	370	0.94**	0.57	0.66	

The growing and dormant season, respectively, referred to the months from April to August, and the remaining months when stem growth almost ceased (Fig. S7). For each height, the number of observations was 10 ($n=10$) for the growing season and 14 ($n=14$) for the dormant season

–Indicated not included in the GLMs

** And * indicated that the correlation was significant at the 0.01 and 0.05 level, respectively (2 tailed)

statistically significant for each height in the growing season ($0.74 \leq \rho \leq 0.91$, $P \leq 0.05$, $n=10$) (Table 2), but it was not significant in the dormant season ($P > 0.05$, $n=14$). These results indicated that T_{W-d} was the main factor leading to the monthly change in $E'_{CO2-V-d}$ throughout the year, and Di_{-d} was the cofactor explaining the monthly change in $E'_{CO2-V-d}$ in the growing season.

For lower stem positions (10, 130 and 250 cm) in the growing season, T_{W-d} was the better explanatory variable for the monthly change in $E'_{CO2-V-d}$ because the standardized regression coefficient for T_{W-d} was greater than that for Di_{-d} , but for the first-order branching of stem (370 cm height), Di_{-d} instead of T_{W-d} was the predominant factor leading to the monthly change in $E'_{CO2-V-d}$ (Table 2). In dormant months, Di_{-d} was not included in GLMs for most positions, indicating that Di_{-d} played a negligible role in the monthly change in $E'_{CO2-V-d}$ during this period (Table 2).

For each sampled tree, the regression coefficient for T_{W-d} of GLMs (denoted as $\text{Coef.}T_{W-d}$, indicating the temperature sensitivity of $E'_{CO2-V-d}$) was positively correlated with the height ($P < 0.05$, $n=24$) and annual diameter increment (Di_{-y}) ($P < 0.01$, $n=24$), but negatively correlated with the sapwood volume per unit of stem surface (SVS) ($P < 0.01$, $n=24$) in the growing season (Table 3). In contrast, it was not affected by any stem characteristics in the dormant season (Table 3). The regression coefficient for Di_{-d} (denoted as $\text{Coef.}Di_{-d}$, indicating the response of $E'_{CO2-V-d}$ per stem radial

Table 3 Results of Spearman's rank correlation coefficients (ρ) between the regression coefficients for T_{W-d} and Di of GLMs (denoted as $\text{coef.}T_{W-d}$ and $\text{coef.}Di$, respectively) and the morphological characteristics of the trees (h, SVS and Di_{-y})

Seasons	Independent variables	Spearman's correlation coefficients (ρ)			N
		$\text{coef.}T_{W-d}$	$\text{coef.}Di$	Intercept	
Growing season	h	0.68* (+)	0.35	0.55* (+)	4
	SVS	0.71** (–)	0.28	0.82** (–)	24
	Di_{-y}	0.57** (+)	0.16	0.63* (+)	24
Dormant season	h	0.31	0.44	0.58* (+)	4
	SVS	0.12	0.23	0.70* (–)	24
	Di_{-y}	0.27	0.15	0.85** (+)	24

h height of measurement point, SVS sapwood volume per unit of stem surface, Di_{-y} annual diameter increment, “+” and “–” in brackets indicate the regression coefficients for T_{W-d} and Di or the intercept of GLMs are positively and negatively correlated with the morphology characteristics of trees, respectively

* Indicates the correlation is significant at the 0.05 level (2 tailed)

** Indicates the correlation is significant at the 0.01 level (2 tailed);

diameter increment) was not affected by all the morphological characteristics irrespective of the growing or dormant season ($P > 0.05$, $n=24$). In addition, the intercept of GLM, which indicates the basal E'_{CO2-V} independent of T_{W-d} and Di_{-d} , was highly correlated with Di_{-y} ($P < 0.05$, $n=24$) compared with the other two characteristics (h and SVS).

Diurnal dynamics and vertical variations in T_A , T_W and E'_{CO_2-v}

A comparative study examining the diurnal dynamics and vertical variations in T_A , T_W and E'_{CO_2-v} was carried out between the growing and dormant season, respectively, represented by two consecutive days in July (194th and 195th days of 2014) and January (22th and 23th days of 2014) (Fig. 2). In two seasons, T_A and T_W showed similar dynamics, i.e., steeply increasing from early morning, peaking in the afternoon (at approximately 14:00) and then slowly decreasing (Fig. 2a, b). In general, T_W had a relative small diurnal temperature range compared with T_A (7.76 ± 0.53 vs. 9.77 ± 0.74 °C for July and 2.93 ± 0.47 vs. 6.31 ± 0.65 °C for January). In contrast, the diurnal patterns of E'_{CO_2-v} differed greatly in two seasons: in the dormant season, E'_{CO_2-v} roughly followed the daily change in

T_A or T_W , showing an asymmetrically unimodal sequence (Fig. 2f), but in the growing season, E'_{CO_2-v} showed a varied bimodal pattern with the highest rates measured at approximately 11:30 a.m. and again approximately 16:00 p.m., with a short period of depression at noon (Fig. 2e). The mid-day depression appeared to be strongest at the highest position (370 cm) but almost absent at the lowest position (10 cm) (Fig. 2e).

Over the course of 12 months, there were no obvious differences in T_A among the different heights (Fig. 2a, b), but large gradients in T_W and E'_{CO_2-v} were observed between the upper and lower stem position during the growing season, especially in the daytime (Fig. 2c, e). Both T_W and E'_{CO_2-v} displayed a gradient increment with height along the trunk (Fig. 2c, e). The observed vertical variation in daytime E'_{CO_2-v} in the growing season could be explained by the gradient distribution of T_{W-d} , Di_{-d} and

Fig. 2 Diurnal changes in air temperature (T_A , °C) (a, b), woody tissue temperature (T_W , °C) (c, d) and sapwood volume-based CO_2 efflux (E'_{CO_2-v} , $\mu\text{mol m}^{-3} \text{s}^{-1}$) (e, f) in the growing (represented by July) and dormant season (represented by January). The temperature at different heights was distinguished by different line-types in a, b, c and d (370, 250, 130 and 10 cm heights are represented by dotted, dashed, straight and thick straight lines, respectively). E'_{CO_2-v} at different heights was distinguished by different symbols in e and f (370, 250, 130 and 10 cm heights are represented by open circles, closed circles, open squares and closed squares, respectively). Means $\pm$ SD (standard deviation) are shown

the difference in SVS (Fig. 3a, c, d). Stem $E'_{\text{CO}_2-\text{V}}$ was positively correlated with $T_{\text{W-d}}$ ($R^2=0.813$, $P<0.01$, $n=24$) and $\text{Di}_{-\text{d}}$ ($R^2=0.944$, $P<0.01$, $n=24$) but negatively correlated with SVS ($R^2=0.746$, $p<0.01$, $n=24$). Although $E'_{\text{CO}_2-\text{V}}$ was also negatively correlated with $T_{\text{A-d}}$, it was not statistically significant ($R^2=0.041$, $P=0.36$, $n=24$) (Fig. 3b).

Temperature sensitivity of $E'_{\text{CO}_2-\text{V}}$ (Q_{10})

In the current study, the regression coefficient for $T_{\text{W-d}}$ of GLM highly varied with the morphological characteristics of the trees (Table 3). To further investigate the position-specific temperature-sensitivity of $E'_{\text{CO}_2-\text{V}}$, the regression relationship between $E'_{\text{CO}_2-\text{V}}$ and T_{W} was assessed monthly for each height. In most cases, the exponential relationships between $E'_{\text{CO}_2-\text{V}}$ and T_{W} performed well ($P<0.01$, $n=288$). However, the derived monthly

$E'_{\text{CO}_2-\text{V}}$ at the reference temperature 0°C ($E'_{\text{CO}_2-\text{V}-0}$) and correlation coefficients (K_i) were strongly asymmetric (Appendix Table S2). The calculated Q_{10} was significantly higher in dormant months than in growing months for all heights (Fig. 4a). In addition, Q_{10} varied greatly among heights in the growing season, and vertical variation disappeared in the dormant season (Fig. 4a).

Throughout the year, the Q_{10} of stem $E'_{\text{CO}_2-\text{V}}$ was not constant but rather was largely dependent on the temperature used for its determination. As shown in Fig. 4b, the highest Q_{10} appeared at approximately 5°C , regardless of an increase or decrease in temperature causing a decline in Q_{10} . The single peak Gauss function was selected as a good expression of the temperature dependence of Q_{10} (Fig. 4b). Covariance analysis indicated that the functions were different among the 130, 250 and 370 cm heights ($P<0.05$), but no difference was observed between 10 and 130 cm ($P=0.074$).

Fig. 3 Correlations between the vertically changed daily mean sapwood volume-based CO_2 efflux ($E'_{\text{CO}_2-\text{V-d}}$, $\mu\text{mol m}^{-3} \text{s}^{-1}$) and woody tissue temperature ($T_{\text{W-d}}$, $^\circ\text{C}$) (a), air temperature ($T_{\text{A-d}}$, $^\circ\text{C}$) (b), stem radial diameter increment rates ($\text{Di}_{-\text{d}}$, mm day^{-1}) (c) and sapwood volume per unit of stem surface (SVS, $\text{m}^3 \text{m}^{-2}$) (d). The

values of $E'_{\text{CO}_2-\text{V-d}}$ at different heights were distinguished by different symbols (370, 250, 130 and 10 cm heights were represented by open circles, closed circles, open squares and closed squares, respectively). The dotted line in (b) indicated the correlation between $E'_{\text{CO}_2-\text{V-d}}$ and $T_{\text{A-d}}$ was not statistically significant ($P>0.05$, $n=24$)

Fig. 4 The monthly changed position-specific temperature-sensitivity coefficient of E'_{CO2-V} (Q_{10}) (a), and the correlations between the Q_{10} and T_w at 4 representative heights (10, 130, 250 and 370 cm) of trees (b). Symbols represent the Q_{10} of the base of the trunk (10 cm) indicated by closed squares, breast height (130 cm) indicated by open

squares, the top (250 cm) indicated by closed circles, and the first-order branching of the main stem (370 cm) indicated by open circles. The vertical error indicates $\pm$ SD (standard deviation) of the observations

Estimation of daily and annual E'_{CO2-V} on a whole-stem scale

The daily and annual E'_{CO2-V} of the whole-stem was estimated by three methods as described in the “Data processing” section. The results showed that in the growing month (June), the daily E'_{CO2-V} of whole-stem (E_D) estimated by considering the vertical variation in E'_{CO2-V} (Method 1) was significantly higher than that assuming the E'_{CO2-V} at breast height was constant throughout the stem (Method 2) ($P < 0.05$, $n = 6$) but significantly lower than that by setting the temperature-sensitivity coefficient Q_{10} to 2.0 as assumed in most models (Method 3) (Fig. 5). For the dormant month (represented by December in Fig. 5) and transition phases between growth and dormancy (represented by March and September), E_D was instead underestimated by Method 3 ($P < 0.05$, $n = 6$), but almost no difference was found using Method 1 and Method 2 (Fig. 5). The annual E'_{CO2-V} of whole stem (E_Y) estimated with Method 1 and

Method 2 was 140.33 ± 6.14 and 132.73 ± 4.26 mol stem $^{-1}$ year $^{-1}$, respectively, which was significantly lower than 165.86 ± 5.11 mol stem $^{-1}$ year $^{-1}$ estimated with Method 3 (Fig. 5).

Discussion

Temporal dynamics

In the current study, obvious seasonal and diurnal changes in temperature and E'_{CO2-V} were found (Figs. 1, 2). T_w was closely related to T_A , and both were good predictors of E'_{CO2-V} (Fig. 1; Table 2). The fall decline and spring increase in E'_{CO2-V} of stems generally followed the seasonal trends of T_w and Di_d (Fig. 1). This pattern was consistent with the results of previous studies (Yang et al. 2012, 2014; Zha et al. 2014). However, temperature alone could not explain the seasonal variation in E'_{CO2-V} in this

Fig. 5 The daily (E_D) and annual (E_Y) E'_{CO_2-V} of whole stem estimated by considering the vertical variation in E'_{CO_2-V} (Method 1) by assuming that E'_{CO_2-V} at breast height is constant throughout the stem (Method 2) and by setting the temperature-sensitivity coefficient Q_{10} to 2.0 as assumed in most models (Method 3). Identical letters indicate homogeneous groups with statistically insignificant differences ($P > 0.05$, $n = 6$)

study because although normalized to a reference temperature 0 °C, E'_{CO_2-V} was still significantly higher in growing months than that in dormant months (Fig. 1d, Appendix Table S2). The marked increase in E'_{CO_2-V-0} in the growth period coincided with the seasonal variation in stem radial diameter increment (Fig. 1b, d). Thus, the higher E'_{CO_2-V-0} in growing months might be explained by the greater metabolic activity and higher recently fixed photosynthate (Zha et al. 2004). The combination of T_{W-d} and Di_{-d} could explain the seasonal change in E'_{CO_2-V} , although T_{W-d} and Di_{-d} had different explanatory powers among the different stem heights (Table 2).

In the diurnal fluctuation of E'_{CO_2-V} , the factor that regulates the pattern remains unclear. Although most academics suggest that the diurnal fluctuation in E'_{CO_2-V} is mainly caused by daily temperature changes (Ryan et al. 1995; Stockfors 2000), stem temperature cannot fully explain the diurnal fluctuation in E'_{CO_2-V} as for seasonal variation. Others have argued that the differences in rates of transport processes, cambial activity and lower turgor pressure might also affect the diurnal patterns of E'_{CO_2-V} (Saveyn et al. 2007; Thorley and Cannell 2000). In a different perspective, we are more inclined to attribute the mid-daytime depression pattern of E'_{CO_2-V} in July to the daily asymmetry of Q_{10} , a phenomenon that has been reported by Yang et al. (2014). To verify this viewpoint, we calculated the four-hourly Q_{10} by fitting E'_{CO_2-V} against T_W for each 4 hours over 1 day. Coincidentally, a statistically significant difference between daytime Q_{10} (1.51 ± 0.07 at 12:00) and night-time Q_{10} (1.72 ± 0.08 at 00:00) was observed in growing months when mid-daytime depression in E'_{CO_2-V}

appeared, but no significant difference was found in dormant months (Appendix Fig. S8). The daytime depression in Q_{10} may be attributed to the deficiency of the respiratory substrate. A high midday temperature was considered to induce stomata closure and photosynthesis depression, thereby affecting stem respiration and thus influencing the temperature sensitivity of E'_{CO_2-V} . Therefore, on the day scale, a lower daytime sensitivity of E'_{CO_2-V} to temperature might reduce the daytime release of CO_2 .

Vertical variation

In our study, the upper stem position of trees had statistically higher T_W and E'_{CO_2-V} than the lower stems in the daytime during the growing season (Fig. 2c, e). The higher temperature in branches may be related to their location within the canopy as they are exposed to sunlight radiation for longer periods than stems, and smaller-diameter organs have more rapid equilibration between the tissue and the atmosphere. The vertical variation in E'_{CO_2-V} is consistent with the results of Araki et al. (2010) and Tarvainen et al. (2014), who observed higher CO_2 release rates in the upper stem compared with the lower stems in *Chamaecyparis Obtusa* and *Picea Abies* (L.), respectively (Araki et al. 2010; Tarvainen et al. 2014). The higher T_W and stem radial diameter increment (Di_{-d}) in upper stems were considered to be main factors leading to the vertical variation in E'_{CO_2-V} (Fig. 3a, c). In addition to T_W and Di_{-d} , another potential morphological characteristic leading to the vertical variation in E'_{CO_2-V} was the difference in SVS among stem positions (Fig. 3d).

Apart from the above factors, intra-individual differences in cortical resistance to radial CO₂ diffusion and CO₂ concentration in xylem owing to transport of CO₂ in flowing sap are attributable to the vertical variation in $E'_{\text{CO}_2-\text{v}}$ (McGuire et al. 2007; Steppe et al. 2007; Teskey et al. 2008). The higher $E'_{\text{CO}_2-\text{v}}$ in the upper stem might be induced by the smaller diffusion resistance of the thinner xylem, cambium and bark layer. Undeniably, some other processes, such as the CO₂ transported into (out) the chamber by the sap flow, or the CO₂ fixed by photosynthesis in local tissue, would also lead to the vertical pattern in $E'_{\text{CO}_2-\text{v}}$ (Araki et al. 2015).

Temperature dependence of Q_{10}

As an important parameter, Q_{10} has been highlighted in previous studies (Brito et al. 2010; Damesin et al. 2002; McGuire et al. 2007; Ryan et al. 1997; Zha et al. 2004; Yang et al. 2014). In some process-based models, stem $E'_{\text{CO}_2-\text{v}}$ is usually modelled as an exponential function of temperature with a constant Q_{10} 2.0 (Melillo et al. 1993; Ryan et al. 1995; Tjoelker et al. 2001). The values of Q_{10} in the current study fall into the range of previous studies (Yang et al. 2014) but were found highly variable, regardless of the temporal or vertical series. At the seasonal scale, the monthly calculated Q_{10} was significantly lower in growing months than in dormant months, which is in accordance with the results for 1-year-old branches of Scots Pine trees with an age of approximately 20 years, in contrast to the results obtained for 50-year-old stands of Scots Pine (Zha et al. 2004). Throughout the year, Q_{10} was highly dependent on the measurement temperature, similar to the results of previous studies on foliar and root respiration showing that Q_{10} declined by 0.043 and 0.045, respectively, in response to a 1 °C increase in temperature (Atkin and Tjoelker 2003). However, the non-linear decrease in Q_{10} with the increase in temperature was slightly different from the linear descent of foliage or root (Atkin and Tjoelker 2003; Stitt and Hurry 2002; Tjoelker et al. 2001). The decline in Q_{10} with the increase in temperature was suggested to be a result of long-term thermal acclimation (Atkin et al. 2002; Covey-Crump et al. 2002; Loveys et al. 2003; Turnbull et al. 2001; Yang et al. 2014), and the higher seasonal fluctuation in Q_{10} at the upper stem position was in accordance with the report that newly developed tissue has a higher thermal acclimation than pre-existing plant tissue (Slot and Kitajima 2015; Stitt and Hurry 2002). Thus, the monthly Q_{10} , which is exempt from seasonally confounding effects, could better reflect the biological sensitivity of respiration to temperature (CurieYuste et al. 2004; Mahecha et al. 2010). Vertically, significant differences in Q_{10} were detected among first-class branches, breast height and base of the trunk in the high temperature area ($T_w > 20^\circ\text{C}$).

This vertical variation may be caused by differences in the contents of soluble carbohydrates in plants (Atkin et al. 2002; Covey-Crump et al. 2002; Loveys et al. 2003).

Up-scaling of $E'_{\text{CO}_2-\text{v}}$ in whole stem

In this study, we up-scaled the whole-stem $E'_{\text{CO}_2-\text{v}}$ using all measured data (considering the temporal dynamics and vertical variations in $E'_{\text{CO}_2-\text{v}}$), as well as only the $E'_{\text{CO}_2-\text{v}}$ value at breast height and a constant Q_{10} value of 2.0. A neglect of vertical variation in $E'_{\text{CO}_2-\text{v}}$ caused a significant over- or underestimation of daily $E'_{\text{CO}_2-\text{v}}$ in whole stem in the growing months, but no difference was found in the dormant season or the transition phases between the growing and dormant seasons. This result indicated that the use of breast-height $E'_{\text{CO}_2-\text{v}}$ as the representative value of whole stem would cause errors in up-scaling the chamber-measured $E'_{\text{CO}_2-\text{v}}$ to the tree or stand level, especially in the growing season. The use of a constant Q_{10} value of 2.0 over- or under-estimated the daily $E'_{\text{CO}_2-\text{v}}$ in whole stem in different months and significantly overestimated the annual $E'_{\text{CO}_2-\text{v}}$. These results indicated that, regardless of the daily or annual scales, the estimation error of $E'_{\text{CO}_2-\text{v}}$ with traditional models should not be ignored. The over-estimate of the annual $E'_{\text{CO}_2-\text{v}}$ of whole stem was because the Q_{10} value was more than 2.0 during most months of the year, and thus we could reduce the error by adjusting the model parameters for this species.

The trees selected for this study were planted for city greening, and the biomass above the first-order branches accounted for no more than 20% of the total biomass due to artificial pruning. Considering the incompleteness of sealing technology for twigs and small amount of biomass, we measured only the stem and a portion of the first-order branches. The neglect of branches above the first-order branching of the main stem undeniably caused an estimation error in the up-scaling of CO₂ efflux to the tree level, and the higher CO₂ efflux rate in the crown increased the carbon emissions proportion of the branches. It is a pity that this error cannot be quantified in this report, but the focus of our future research will be on twigs in the canopy.

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