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Individual- and stand-level stem CO_2 efflux in a subtropical *Schima superba* plantation

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Abstract. Stem respiration is an important, but poorly studied component of total forest ecosystem respiration. Stem CO_2 efflux was investigated with an open gas exchange system while stand microclimate and stem temperature were continuously monitored in a *Schima superba* plantation in South China for several days in August and December 2010. The temperature response of respiration in the different seasons, the vertical variation in stem CO_2 efflux along the stem, and the stand-level stem CO_2 efflux were examined. Stem volume was identified as the better correlate for stem CO_2 efflux and was used as the scalar for the stand-level estimates of stem CO_2 efflux in this *S. superba* plantation. Volume-based stem CO_2 efflux was higher at 2 m than at 1.3 m. Mean stem CO_2 efflux was 268.9 and 104.6 µmol m^{-3} s^{-1} in August and December, respectively, indicating a dramatic seasonal variation of stem CO_2 efflux. The temperature response of stem CO_2 efflux remained constant during our study period with Q_{10} values of 1.9 and 1.8. In this subtropical *S. superba* plantation, stem CO_2 efflux per unit ground area averaged 3.36 and 1.26 µmol m^{-2} s^{-1} based on the measurement data at 1.3-m height of the stem in August and December, respectively. Our results suggest that stem CO_2 efflux has a constant temperature response, and the seasonal variation in stem CO_2 efflux is mainly controlled by stem temperature, and the vertical variation in stem CO_2 efflux needs to be considered in the stand-level estimation.

1 Introduction

Forest carbon storage is an important carbon pool in the terrestrial ecosystem. Respiration is the dominant physiological process accounting for the variations in ecosystem production, and autotrophic respiration can consume 30–70 % of net primary production (Valentini et al., 1996; Ryan et al., 1997; Litton et al., 2007; Tang et al., 2008). Since woody tissue constitutes the largest part of forest biomass, its respiration makes an important contribution to the carbon balance of forest ecosystems (Kramer and Kozlowski, 1979; Harris et al., 2008). Zha et al. (2004) concluded that stem respiration made up 9 % of the ecosystem carbon loss and consumed 8 % of the gross primary production. Recent studies emphasize the utility of in situ chamber measurements for stand-level estimation, but woody tissue respiration is usually measured only at a given point of the stem (Ryan, 1990; Sprugel, 1990; Harris et al., 2008; Robertson et al., 2010). One of the main problems involved in scaling up the chamber measurements to the forest is the difficulty in measuring stem surface area or stem volume at the stand level due to the different tree structures of tree species (Lavigne et al., 1996; Ryan et al., 1996; Levy and Jarvis, 1998; Kim et al., 2007). The surface area and volume are generally estimated using the allometric equations with diameter and tree height (Chambers et al., 2004; Kim et al., 2007; Robertson et al., 2010). Damesin et al. (2002) also raised several problems about scaling up respiration to the stand level, including the seasonal and vertical changes of stem respiration. Respiration rates in the tree crown are 19–42 times greater than at the stem base (Sprugel, 1990; Damesin et al., 2002). So, it is very essential to consider the spatial changes in woody tissue respiration when estimating

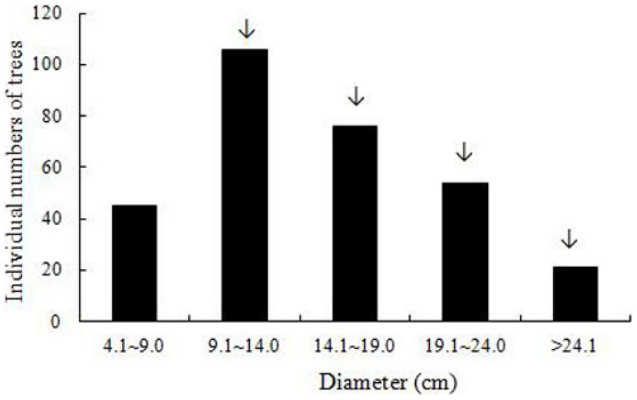

Fig. 1. Distribution of tree stem diameters at the experimental site. All diameters were measured at 1.3-m height. The arrows indicate the diameters of sample trees used for stem CO_2 efflux measurements.

Fig. 2. Photograph of stem respiratory chamber. Air entered chamber through PVC tube. The PVC tube on the other side of the chamber was connected to IRGA. When measurements were made, the chamber was attached to the stems with adjustable cords to keep it airtight. After the reading was stable, the cords were loosened to make the chamber open.

the stand-level respiration (Wieser and Bahn, 2004; Zach et al., 2008). It is also important to determine the most reasonable unit for estimating wood CO_2 efflux at the stand level. In some studies, stem surface area has been identified as the best correlate for respiration (Lavigne et al., 1996; Levy and Jarvis, 1998), while stem volume is considered as the better unit for expressing stem CO_2 efflux by other researches (Ryan, 1990; Lavigne et al., 1996; Law et al., 1999).

Harris et al. (2008) studied stem respiration at species and ecosystem level and concluded that species composition and stem temperature were the main factors determining ecosystem-level stem respiration. The respiratory flux from woody tissue significantly varies among the stands and with temperature (Lavigne et al., 1996; Ryan et al., 1997; Ryan, 1991). To our knowledge, although some studies have been done in temperate, boreal and tropical zones, measurements of stem CO_2 efflux in subtropical forests are rather rare (Maier, 2001; Damesin et al., 2002; Meir and Grace, 2002; Cavaleri et al., 2006; Robertson et al., 2010). In the subtropical zone of South China, there is sufficient rainfall and high air temperature, which can result in strong energy exchange between forest and atmosphere. It is necessary to understand stem respiration characteristics for estimating carbon loss of a forest ecosystem. In this study, stem CO_2 efflux, stem temperature and environmental parameters in a subtropical *Schima superba* plantation were monitored in August and December 2010. The study was intended (1) to discern the better unit for expressing stem CO_2 efflux and for extrapolating to the forest; (2) to investigate the seasonal and vertical changes in stem CO_2 efflux; and (3) to quantify the stem CO_2 efflux per unit ground area.

2 Materials and methods

2.1 Site description

The experiment was conducted in a *S. superba* plantation of the ecological observation station located within the South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China (23°10′ N, 113°21′ E, altitude 41 m). The plantation grows on a gentle slope (11.7°) with a northeast exposure. This area is dominated by a subtropical monsoon climate with mean annual precipitation of 1696.5 mm and mean annual air temperature of 21.9 °C. Detailed information about climate characteristics of the experimental site are available in Zhu et al. (2012). The area of study plot is 2885 m^2. The soil is a loam with pH of 4.0, organic content of 2.3 % and total nitrogen content of 0.07 %. The plantation is approximately 30 years old. The mean stem diameter at breast height (DBH) is 14.7 ± 5.6 cm, and understory plant is sparse. The annual leaf area index (LAI) averages 4.3 ± 0.3, based on the monthly-measured data (with LI-2000) from November 2007 to October 2008. A histogram of tree stem diameter distribution at the site is presented in Fig. 1.

2.2 Stem CO_2 efflux measurements

Stem CO_2 efflux measurements were performed every 1 h with an open gas exchange system which consisted of a respiration chamber, flow meter and an infrared gas analyzer (IRGA) (LI-6262; Li-cor, Lincoln, NE, USA). Chambers were made of a flexible acrylic film, on two sides of which metal tubes with a small hole were distributed. Chambers were attached to the stems with adjustable cords to keep

Table 1. Diameter at breast height (DBH), tree height, under-branch height and canopy size of sample trees.

No.	DBH (cm)	Tree height (m)	Under-branch height (m)	Canopy size (m^2)
1	16.0	15.3	6.0	14.7
2	20.5	12.6	8.1	28.8
3	14.9	12.1	5.9	10.4
4	25.6	15.3	4.4	37.0
5	9.6	11.0	4.4	1.1
6	19.7	12.9	6.8	27.5
7	10.1	9.7	5.3	13.3
8	9.3	9.5	4.8	6.0
9	28.1	16.9	4.0	43.4
10	14.9	11.2	6.7	12.5
11	9.6	12.0	6.4	5.6
12	17.0	13.1	7.3	13.6
mean	16.3	12.6	5.8	17.8

them airtight (Fig. 2). A constant flow rate ($1\,l\,min^{-1}$) was maintained by the electromagnetic pump within the IRGA. Before entering the chambers, the ambient air was passed through a plastic buffer bottle with a volume of 1.5 l to aquire evenly-mixed sample air with a relatively constant CO_2 concentration. Chambers of two sizes were applied in this study. The chambers covering a bark area of 10×10 cm were for the larger trees, and those of 10×6 cm were for the smaller trees, and all were orientated to the north to minimize the effect of possible direct sunshine. 12 *S. superba* trees were selected for stem CO_2 efflux measurements on 31 July–5 August, and 22–25, 29–31 December 2010. Sampling was designed to account for a range of stem sizes in the experimental site. Size characteristics of sample trees were shown in Table 1. According to Meir and Grace (2002), the measured stem CO_2 efflux of different points around the circumference of stems varied little. The canopy of this *S. superba* plantation was relatively dense, which could result in similar temperatures around the circumference of stems. So the respiration chambers were installed in only one direction.

In order to observe the vertical variation in stem CO_2 efflux along the stem, stem CO_2 efflux was measured at 1.3- and 2-m height for four *S. superba* trees. The stem diameters at the two heights are shown in Table 2.

2.3 Stem temperature measurements

Stem temperature was monitored using self-made thermistors. The sensors were inserted into 20 mm of sapwood depth adjacent to the respiration chambers for six or eight sample trees. For the observation of vertical variation in stem CO_2 efflux, three sample trees were selected for stem temperature measurements.

2.4 Environmental parameters measurements

Air temperature and humidity were monitored respectively using AT2 and RHT2 sensors (Delta-T Devices, Ltd., Cambridge, UK) in an instrument shelter installed under the forest. Soil moisture was measured using three sensors (SM200, Delta-T Devices Ltd., Cambridge, UK). Both environmental factors and stem temperature were read every 30 s, averaged and recorded every 10 min with a data logger (DL2e, Delta-T Devices, Ltd., Cambridge, UK).

2.5 Stem CO_2 efflux per surface area vs. volume

It is important to determine the best unit for expressing stem CO_2 efflux when scaling stem CO_2 efflux to stand level. According to Levy and Jarvis (1998), if the CO_2 efflux is proportional to volume, measured CO_2 efflux on an area basis will be positively and linearly correlated with diameter. If stem CO_2 efflux is dependent on surface area, measured stem CO_2 efflux on a volume basis will be positively and linearly related to the reciprocal of diameter. Analysis of the relationship between CO_2 efflux and surface area or volume will also help us better understand the main source of CO_2. If stem CO_2 efflux is related to volume, it indicates that CO_2 diffused to atmosphere is mainly produced by the xylem parenchyma. Alternatively, if stem CO_2 efflux is related to surface area, it indicates that CO_2 efflux is produced by the cambial and phloem cells (Meir and Grace, 2002). So we examined the relationship between diameter at the breast height and stem CO_2 efflux on an area and a volume basis for 12 sample trees in order to discern the best unit for extrapolating the measured stem CO_2 efflux of sample trees to the whole forest stand.

2.6 Calculations

Stem CO_2 efflux was calculated as

$$E_s = \Delta CO_2 \frac{F}{A} \quad \text{or} \quad \Delta CO_2 \frac{F}{v}. \tag{1}$$

Where E_s is the stem CO_2 efflux ($\mu mol\,m^{-2}\,s^{-1}$ or $\mu mol\,m^{-3}\,s^{-1}$), ΔCO_2 is the difference between ambient (reference gas) and chamber (sample gas) CO_2 concentration, F is the air flow rate passing through the chamber, and A and v are the surface area and the stem volume of the enclosed stem segment, respectively.

Meanwhile, a simulated E_s was obtained by applying an exponential model:

$$E_s = E_o \exp(bT_s). \tag{2}$$

Where E_o is the stem respiration rate at 0 °C, T_s is the stem temperature in °C, and b is a constant parameter (Ryan, 1990) presenting a temperature coefficient of E_s.

Q_{10} (the proportional increase in stem CO_2 efflux with a 10 °C temperature increase) was calculated as

$$Q_{10} = \exp(10b). \tag{3}$$

Table 2. Diameter (d, cm), mean stem CO_2 efflux ($\overline{E}_s$, μmol m^{-3} s^{-1}) and mean stem temperature ($\overline{T}_s$, °C) of the stems at two heights of sample trees. Measurement positions were at 1.3 and 2 m above the ground, respectively.

Height above the ground (m)	Tree 3			Tree 4			Tree 8			Tree 12		
	d	$\overline{E}_s$	$\overline{T}_s$	d	$\overline{E}_s$	$\overline{T}_s$	d	$\overline{E}_s$	$\overline{T}_s$	d	$\overline{E}_s$	$\overline{T}_s$
1.3	14.9	115.5[a]	19.7[a]	25.6	24.5[a]	18.5[a]	9.3	23.2[a]	19.1[a]	17.0	47.2[a]	–
2	14.2	125.0	20.4	23.9	75.4	19.6	8.9	40.4	19.3	16.2	62.9	–

[a] value significantly different from 2-m height at $P < 0.01$.

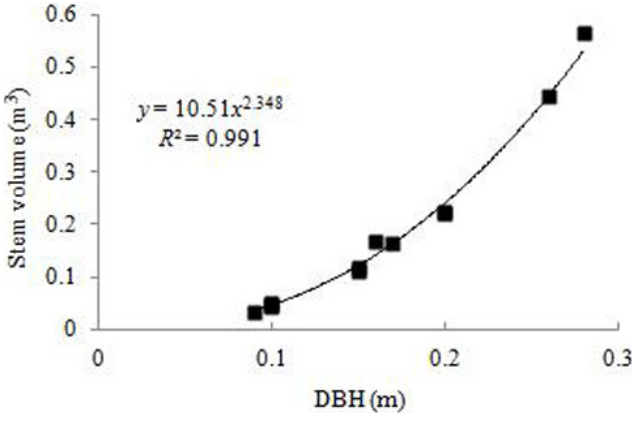

Fig. 3. An allometric relationship between stem volume and DBH.

According to Levy and Jarvis (1998), stem volume per unit ground area is defined as stem volume index (SVI) in this paper. Stem volume per sample tree was calculated with DBH and under-branch height (Height from ground to crown base).

$$V = f_{1.3} g_{1.3} h \quad (4)$$

Where V is the stem volume, $f_{1.3}$ is the form factor of breast-height, $g_{1.3}$ is the basal area of breast-height, and h is the under-branch height.

Stem volumes of other trees were calculated from an allometric equation developed with stem volume of sample tree and DBH (Fig. 3). Stem volume per unit ground area (SVI) was determined from stem volume per tree and number of trees per unit ground area.

2.7 Statistical analysis

Relationship between stem CO_2 efflux and DBH was analyzed by using linear correlation. The comparion of Q_{10} between the two seasons was examined by t-test. The differences in stem CO_2 efflux between the different heights along the stem were analyzed by paired t-test. The effect of stem temperature on stem CO_2 efflux on the seasonal scale was analyzed from the means of all sample trees. All the statistical analyses were carried out using SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

3 Results

3.1 Seasonal changes of microclimate parameters in the experimental site

Means of air humidity and temperature were 76.3 % and 31.3 °C in August, and 62.7 % and 15.1 °C in December, respectively. Air temperature changed diurnally, typically reaching the maximum at about 16:00 LT and the minimum at about 07:00. Air humidity was opposite of the diurnal pattern of air temperature with the maximum in the morning and the minimum in the afternoon (Fig. 4). Soil volumetric water content monitored at 30-cm depth averaged 45.8 % and 21.1 % in August and December, respectively. Therefore, there were distinct wet and dry season dynamics in our study site.

3.2 Temperature response of stem CO_2 efflux

There was a linear increase in E_s per unit surface area with diameter at the breast height (Fig. 5a, $r^2 = 0.40$, $n = 10$, $P < 0.05$), but no relationship between reciprocal of diameter and E_s per unit volume (Fig. 5b) was observed. Thus, the data indicated that E_s was proportional to stem volume and the major respiratory source was volume-related according to Levy and Jarvis (1998). Therefore, the stem volume contributed more to E_s and was the better unit for expressing E_s in our study.

As shown in Fig. 6, both E_s and stem temperature (T_s) presented a daily dynamic. Coefficients of variation (CVs) of E_s and T_s were respectively 4 % and 1 %, indicating that E_s values showed a larger coefficient of variation among the measured sample trees than T_s. Mean E_s and T_s for all measured trees were 268.9 μmol m^{-3} s^{-1} and 29.9 °C in August, and 104.6 μmol m^{-3} s^{-1} and 15.9 °C in December, respectively. Mean daily E_s in August was higher than in December ($P < 0.05$). The exponential relationship between E_s and T_s was established (Fig. 7). The intercept (E_s at 0 °C) and temperature coefficient were a little higher in August than in December. Based on the exponential equation, the estimated Q_{10} was 1.9 and 1.8 in August and December, respectively, and the differences in Q_{10} between the seasons were not significant ($n = 3$, $P > 0.05$), indicating similar responses of E_s to T_s and a similar proportional increase in E_s derived from

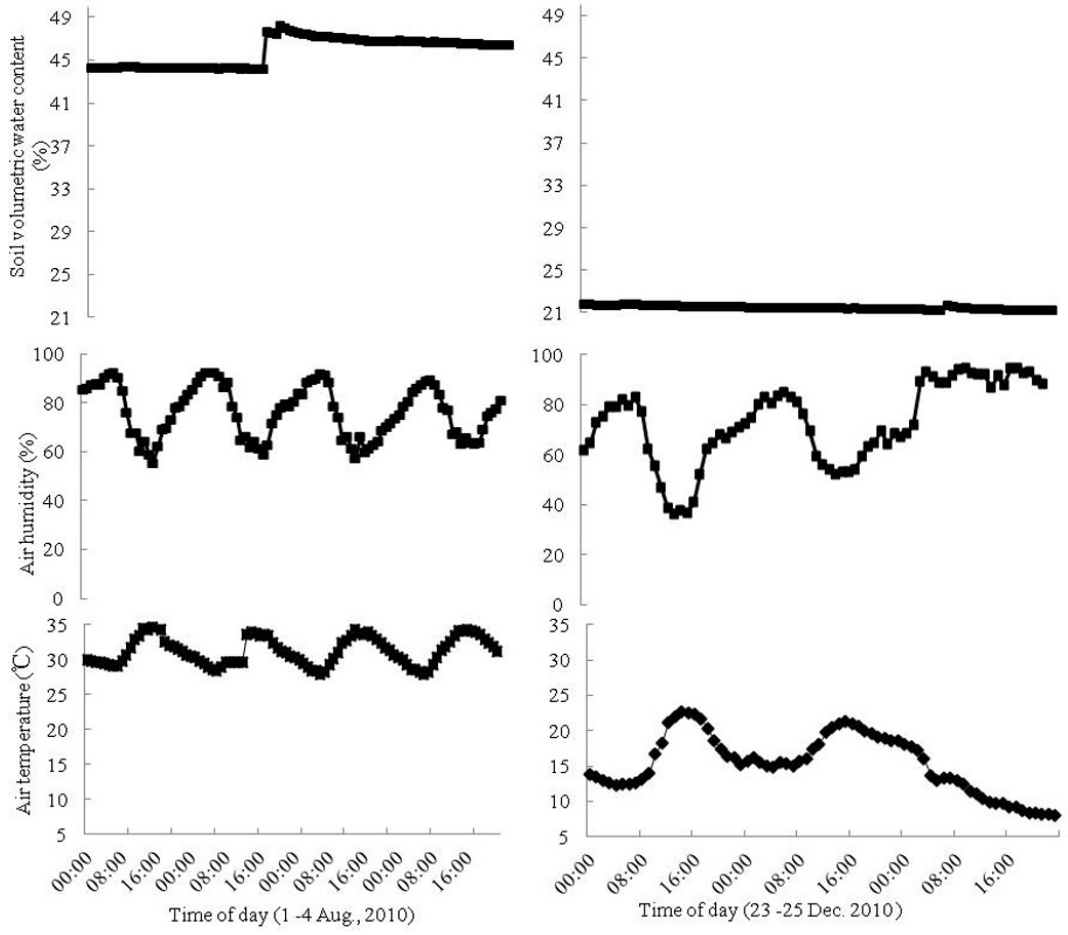

Fig. 4. Diurnal variation in soil volumetric water content, air humidity and air temperature on 1–4 August and 23–25 December 2010.

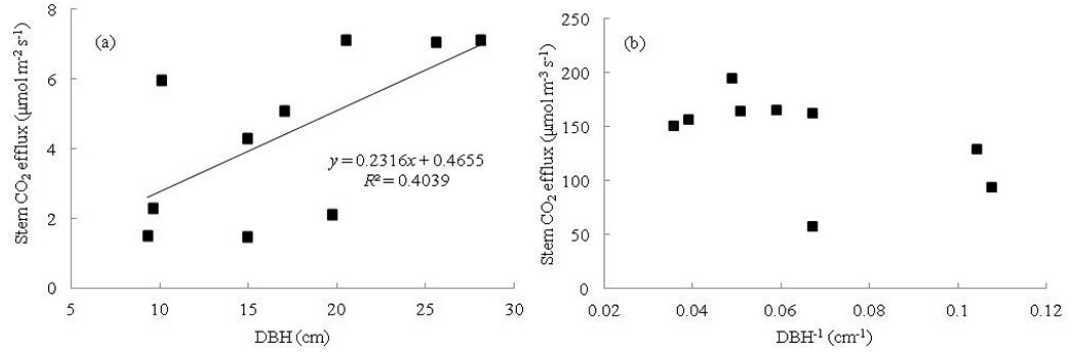

Fig. 5. Relationship between stem CO_2 efflux and diameter at the breast height (DBH). **(a)** surface-based stem CO_2 efflux and DBH; **(b)** volume-based stem CO_2 efflux and DBH^{-1}. Surface-based stem CO_2 efflux was positively linearly correlated with DBH ($P < 0.05$, $R^2 = 0.40$), but volume-based stem CO_2 efflux was not correlated with DBH^{-1} ($P > 0.05$).

the increase of T_s in the different seasons during our study period.

3.3 Stem CO_2 efflux at the stand level

Significant differences in E_s or T_s at different tree heights were observed (Table 2). Mean E_s at 2 m was 2.0 times higher than at 1.3 m, although E_s (ranging from 1.2 to 3.1) did not vary by the same amounts among the individuls. To

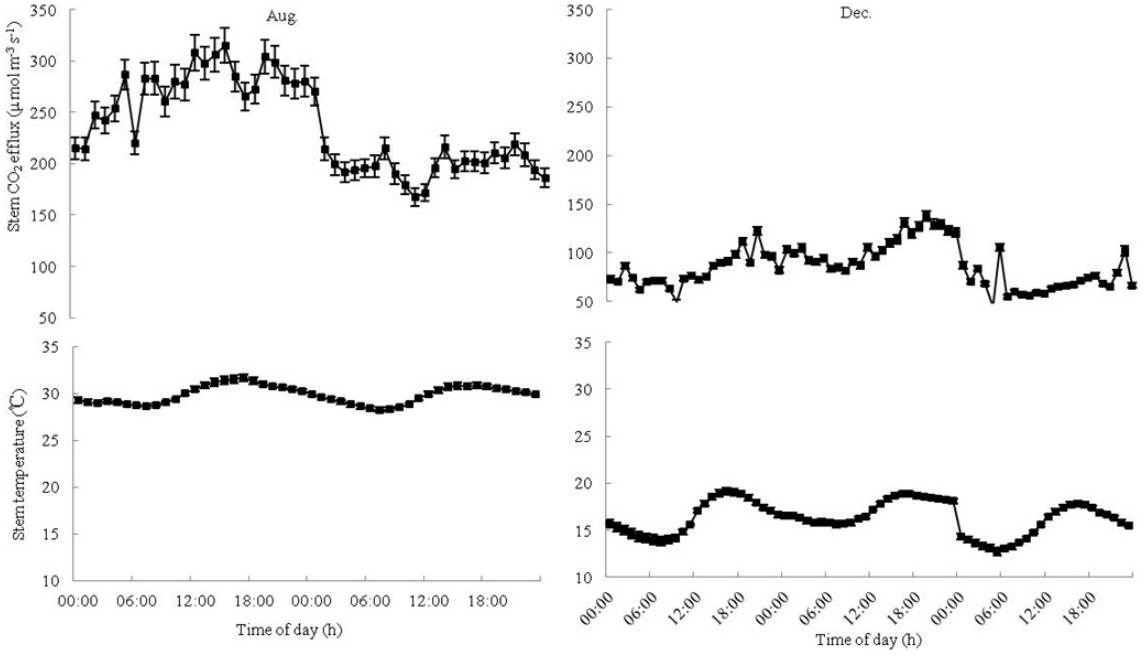

Fig. 6. Diurnal variation in mean stem CO_2 efflux and mean stem temperature of sample trees on 1, 3 August and 23–24, 30 December 2010. Error bars show standard error (SE).

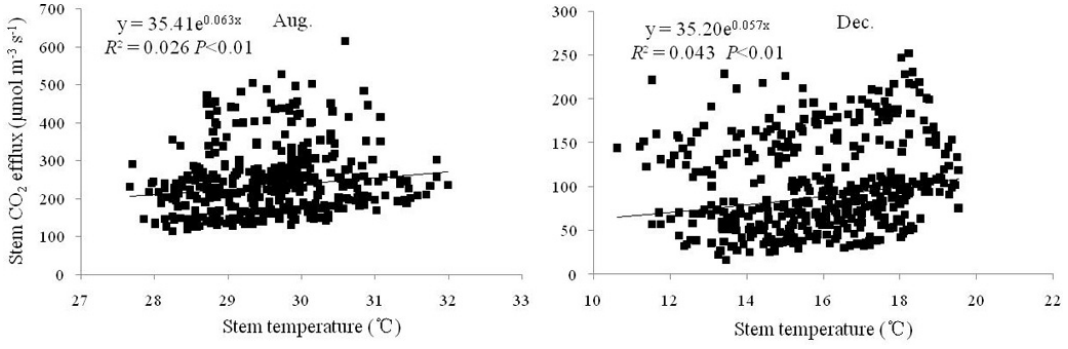

Fig. 7. Dependence of stem CO_2 efflux for all measured trees on stem temperature in August and December 2010.

calculate E_s per unit ground area, mean volume-based E_s from the measured trees, stem volume for all trees in the experimental site and ground area were needed. Stem volume per unit ground area (SVI) in this study was 0.015 m^3 m^{-2}. As a result, E_s per unit ground area averaged 3.36 and 1.26 μmol m^{-2} s^{-1} in August and December, respectively (Fig. 8). The stand-level E_s was estimated based on the assumption that E_s kept constant along the stem (Araki et al., 2010). However, in this study the vertical variation in E_s was observed, which would lead to miscalculation of the real stem respiration based on such assumption.

4 Discussion

4.1 Unit for expressing stem CO_2 efflux

Ryan (1990) found that stem growth or the amount of living cells did not vary directly with surface area and biomass and argued that these two characteristics could not be used to estimate the stand-level stem respiration. In our study, the stem volume was determined to be the best unit for expressing stem CO_2 efflux, based on the relationship between stem CO_2 efflux and stem size. This indicated that the major stem CO_2 efflux source was volume-related according to Levy and Jarvis (1998). Additionally, it suggested that the respiring tissue was associated with the xylem cells (Levy and Jarvis, 1998; Meir and Grace, 2002; Cavaleri et al., 2006). This may be because (1) the xylem tissue, in thickness, contributed to

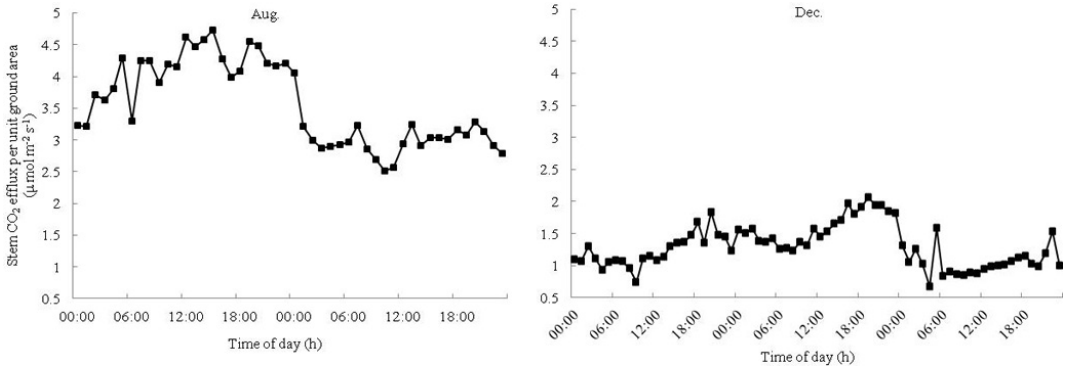

Fig. 8. Diurnal variation in mean stem CO_2 efflux per unit ground area on 1, 3 August and 23–24, 30 December 2010.

about 90 % of the stem, and (2) the living cells of the xylem tissue were very active in this *S. superba* plantation based on the high transpiration rates under the condition of sufficient water supply, which was reflected by the sap velocity of 0.83 and 0.41 g s^{-1} in the wet and dry season, respectively (Zhu et al., 2012). Teskey et al. (2008) found that the distribution of living tissue cells between the bark and xylem depended on species and tree size. In *Picea abies* trees with DBH of 7–10 cm, the xylem living cell volume was only 20–25 % of the stem living cell volume (Stockfors and Linder, 1998), while the study of Ceschia et al. (2002) indicated that the living cell of *Fagus sylvatica* xylem was almost equivalent to that of the entire stem with diameters up to 16 cm. In our study, mean DBH of sample trees was much larger (16.3 cm) compared with that (0.1–4.8 cm) in the Levy and Jarvis (1998) study, and the living tissue cells were mainly distributed in the xylem. Based on our findings, the stand-level stem CO_2 efflux in this study was estimated using stem volume.

4.2 Vertical variation of CO_2 efflux along the stem

Generally, woody tissue carbon loss estimation at ecosystem level was based on a assumption that stem respiration remained constant along the stem (Damesin et al., 2002). However, some studies showed that stem respiration varied with height (Ryan et al., 1996; Ceschia et al., 2002; Araki et al., 2010). Edwards et al. (2002) demonstrated that stem respiration rates in the upper trunk were four times higher than in the lower trunk. In our study, mean E_s was 2.0 times higher at 2 m than at 1.3 m above the ground. However, mean T_s was only 1.04 times higher at 2 m than at 1.3-m height of the stem. Therefore, differences in stem temperature with height could not totally explain why stem CO_2 efflux doubled (and more) with height. Ceschia et al. (2002) attributed the variations in stem respiration along the stem to the differences in wood composition and wood amount, the living cell and carbohydrates distribution, and temperature. Sprugel (1990) concluded that the higher respiration rates in the canopy than in stems were mainly derived from the more physiologically active cells. We thought that there were more newly produced tissue cells at the higher location of the stem and that higher sapwood volume/stem volume might increase the source of respiratory CO_2, which increased the stem CO_2 efflux.

4.3 Stem CO_2 efflux in relation to stem temperature

Ryan et al. (1994, 1996) estimated woody-tissue maintenance respiration rate was 39.6 μmol m^{-3} s^{-1} at 24.6 °C in two tropical wet forest trees. Ryan et al. (1997) estimated stem respiration rates varied from 73 to 203 μmol m^{-3} s^{-1} during June–August in boreal forest, and found that the differences in stem respiration rates among the tree species were significant. In our study, mean stem CO_2 efflux was 268.9 and 104.6 μmol m^{-3} s^{-1} in wet and dry season, respectively, which was close to the values for boreal forest but higher than the values reported for tropical forest. Meir and Grace (2002) indicated that the differences in stem CO_2 efflux between sites resulted from the discrepancy in metabolic activity. Zha et al. (2004) concluded that the variations in stem respiration rates among the tree species reflected the physiological adjustments to temperature changes and the metabolic activity. At our experimental site, *S. superba* trees grew all year round due to good water and heat condtions. The high temperature and soil moisture promoted the metabolic activity and increased the transpiration rate, which transported CO_2 from soil upwards, increasing stem CO_2 efflux at the monitored position (Zhu et al., 2012). Besides, annual mean LAI in this *S. superba* plantation reached 4.3, which could assimilate more energy from sunlight and provide sufficient substrate for stem respiration and then result in more CO_2 diffusion into the atmosphere.

Zha et al. (2004) found that Q_{10} of stem respiration for Scots pine (*Pinus sylvestris*) in the growing season was higher than in the non-growing season, but the differences in Q_{10} between the seasons were small, ranging from 1.88 to 1.91. Damesin et al. (2002) estimated Q_{10} for the stem of beech was 1.7, which was relatively constant throughout the year. Zach et al. (2008) indicated that woody tissue CO_2 efflux in a tropical mountain had consistent temperature sensitivity across the differing growth environments. In contrast,

Ryan (1991) obtained a varying Q_{10} between 1.5 and 2.5, and Levy and Javis (1998) found Q_{10} for tropical tree species between 1.6 and 2.2. Our result fell within this range, and was close to the mean Q_{10} for tropical tree species. There was no significant difference in Q_{10} between the two seasons. In accordance with Meir and Grace (2002), the non-significant variation in Q_{10} may have resulted from the similar underlying biochemical process across the seasons.

Levy and Jarvis (1998) concluded that the seasonal changes in stem respiration were attributed to the growth. Woody CO_2 efflux showed a distinct seasonal change in a temperate forest where the division between the growing and non-growing seasons was definite (Demesin et al., 2002; Vose and Ryan, 2002). At our experimental site, seasonal dynamic was characterized with higher air temperature and humidity in the wet season and relatively lower air temperature and humidity in the dry season, resulting in the seasonality of stem CO_2 efflux. Due to the consistent temperature sensitivity of stem CO_2 efflux, the seasonal changes in stem CO_2 efflux might mainly result from the variations in stem temperature between the seasons. On the seasonal scale, the differences in mean stem temperature of all sample trees could explain 85.9 % of the variations in mean stem CO_2 efflux ($n = 203$, $P < 0.01$). Furthermore, Meir and Grace (2002) observed a strong positive relationship between annual aboveground woody tissue respiration rate and LAI in two tropical rain forests. Based on the data from LAI and stem CO_2 efflux, our result was consistent with their conclusion. The LAI of the *S. superba* stand was significantly higher in August ($4.9\,m^2\,m^{-2}$) than in December ($4.2\,m^2\,m^{-2}$) ($n = 3$, $P < 0.05$). It was assumed that the higher LAI increased the photosynthetic carbon assimilation, offering more respiratory substrate for stem respiration. Therefore, the higher LAI promoted stem CO_2 efflux in August, and the differences in LAI between the seasons could be presented as a contributor explaining the remaining variations in stem CO_2 efflux.

4.4 Stem CO_2 efflux at the stand level

Cavaleri et al. (2006) studied the woody tissue CO_2 efflux of many species (trees, *Pentaclethra macroloba*, palms and lianas) in a primary tropical rain forest and estimated the CO_2 efflux per unit ground area was $1.34 \pm 0.36\,\mu mol\,m^{-2}\,s^{-1}$. Ryan et al. (1996) estimated the aboveground respiration per unit ground area was higher than $2\,\mu mol\,m^{-2}\,s^{-1}$ in a boreal forest ecosystem. In this *S. superba* plantation, mean stem CO_2 efflux per unit ground area based on data for two months was $2.31\,\mu mol\,m^{-2}\,s^{-1}$, which is close to the values for boreal forest. The stem CO_2 efflux from trees of large diameter (DBH > 14 cm) contributed 90 % and 71 % of the estimated total stem CO_2 efflux in August and December, respectively. That may be because the volume of trees of large diameter accounted for 82 % of total stem volume. Our result was based on the assumption that the volume-based respiration rate was constant throughout the stem (Araki et al., 2010). However, generally stem CO_2 efflux was higher in the higher locations than in the lower locations, as mentioned in the previous section. Therefore, it could be possible that mean stem CO_2 efflux per unit ground area would be underestimated. Some studies took stem photosynthesis into consideration when estimating stem respiration. However, Pfanz et al. (2002) pointed out that the light transmittance of stems through the bark was low due to the low ratio of surface to volume. At our experimental site, stem photosynthesis was thought to be negligible considering the high LAI and the closed canopy.

5 Conclusions

In conclusion, stem CO_2 efflux was measured in a subtropical *S. superba* plantation during August and December. A similar temperature response of stem CO_2 efflux was found between the two seasons. Based on the relationship between stem CO_2 efflux and tree diameter, stem volume was determined to be the best scalar to calculate stand-level stem CO_2 efflux. Although vertical variation in stem CO_2 efflux was observed, the stand-level respiration was calculated based on the assumption that the stem CO_2 efflux was constant along the stem in this study. In the future, vertical variations in stem CO_2 efflux should be considered in estimating the whole-tree stem respiration, and should be included in the variation of stem CO_2 efflux and its response to environmental variables at the tree scale. Our findings will improve the understanding of the carbon balance of trees in the subtropical zone.

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