Biogeosciences Discussions

Individual- and stand-level Stem CO$_2$ efflux in a subtropical *Schima superba* plantation

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Abstract

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 over 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 scaling 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 was constant during our study period with Q_{10} values of 1.9 and 1.8. In this subtropical *S. superba* plantation, the averaged stem CO$_2$ efflux per unit ground area was 3.36 and 1.26 μmol m^{-2} s^{-1} in August and December, respectively, which was underestimated due to the vertical variation of stem CO$_2$ efflux along the stem. Our results suggest that stem CO$_2$ efflux has a constant temperature response on the stand scale, 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 at the stand-level estimation.

1 Introduction

Recently, the global change research has mainly focused on the carbon balance of forests (Zach et al., 2008). Respiration is the dominant physiological process accounting for the variations in ecosystem production (Valentini et al., 1996). Autotrophic respiration can consume 30–70 % of net primary production (Litton et al., 2007). Since woody tissue constitutes the largest part of forest biomass (Harris et al., 2008), its respiration makes an important contribution to the carbon balance of forest ecosystem

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(Kramer and Kozlowski, 1979). Zha et al. (2004) concluded that stem respiration made up 9 % of the ecosystem carbon loss and consumed 8 % of the gross primary production. However, it is very difficult to estimate the stand-level wood CO$_2$ efflux due to the variation in wood CO$_2$ efflux of the individual trees of different ages and sizes (Ryan et al., 2009). Cavaleri et al. (2006) pointed out that wood CO$_2$ efflux remained uncertain due to the poor sampling. Recent studies have emphasized the utility of in situ chamber measurements for the stand-level estimation (Ryan, 1990; Sprugel, 1990). Nevertheless woody tissue respiration is usually measured only at a given point of the stem (Harris et al., 2008). 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 (Levy and Jarvis, 1998). 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. Foliage respiration changes little between the seasons, while woody tissue respiration strongly differs with the seasons (Ryan et al., 1997), but the annual variation of stem respiration is very small. For example, Zha et al. (2004) found that the annual stem respiration per unit ground area is 75.97 g C m^{-2} in 2001 compared with 74.28 g C m^{-2} in 2002. 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 the stand-level respiration (Zach et al., 2008). On the other hand, it is also important to determine the reasonable unit for estimating wood CO$_2$ efflux at the stand level. In some studies, 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 in the other researches (Ryan, 1990; Lavigne et al., 1996; Law et al., 1999).

Harris et al. (2008) studied the stem respiration at species- and ecosystem-level and concluded that species composition and stem temperature were 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 sparse (Maier, 2001; Damesin et al., 2002; Meir and Grace, 2002; Cavaleri et al., 2006). 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. It was intended (1) to discern the best 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; (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 41m) that grows on a gentle slope (11.7°) with a northeast exposure. This area is dominated by subtropical monsoon climate with mean annual precipitation of 1696.5 mm and mean annual temperature of 21.9 °C. The detailed information about climate characteristics of experimental site can be available in Zhu et al. (2011). The soil is a loam with pH of 4.0, the organic content of 2.3 % and the total nitrogen content of 0.07 %. The plantation was planted in the mid-1980s. The mean stem diameter at breast height (DBH) was 14.7 ± 5.6 cm in 2010, and understory plant is rare. The annual average leaf area index was 4.3 ± 0.3 based on the monthly-measured data (with LI-2000) from Nov 2007 to Oct 2008. The histogram of tree stem diameter distribution at the site is presented in Fig. 1.

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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 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 (Fig. 2). A constant flow rate (1 L min^{-1}) was maintained by the electromagnetic pump within IRGA. Before entering the chambers, the ambient air was passed through a plastic buffer bottle with a volume of 1.5 L to aquire an evenly-mixed sample air with a relative constant CO$_2$ concentration. Chambers of two sizes were applied. The chambers covering a bark area of 10 × 10 cm were for the larger trees, and 10 × 6 cm were for the smaller trees at 1.3 m above the ground and were orientated to the north to minimize the effect of possible direct sunshine. Measurements were made under a closed canopy with unshade chambers. 12 *S. superba* trees were selected for stem CO$_2$ efflux measurements on 31 July–5 August and 22–25, 29–31 December 2010, respectively. Sampling was designed to account for a range of stem sizes in the experimental site. Size characteristics of sample trees were showed in Table 1. According to Meir and Grace (2002), the measured stem CO$_2$ efflux of different points around the circumference of stems presented pretty little radial variations. The canopy of this *S. superba* plantation is relatively density which resulted in the similar temperature at the different directions of stems. So the respiration chambers were installed in only one direction.

In order to observe the vertical variation of 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 were shown in Table 2.

2.3 Stem temperature measurements

Stem temperature was monitered using the self-made thermistors inserted into 20 mm of sapwood depth adjacent to the respiration chambers for six or eight sample trees.

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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 ennvironmental 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. Ananlysis on 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 or 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:

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

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, 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 stem temperature in $°C$, 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:

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

The measured E_s was converted into one at a common reference tempeature for separating phenology from temperature. The reference respiration rate (E_{23}) was defined as E_s at the averaged stem temperature ($23\,°C$) in order to analyze the significant differences between two seasons during the study period. E_{23} was calculated as:

$$E_{23} = E_i \times Q_{10}^{[(23-T_s)/23]} \tag{4}$$

Where E_i is the measured E_s at T_s stem temperature.

According to Levy and Jarvis (1998), stem volume per unit ground area was defined as stem volume index (SVI) in this paper. Stem volume per sample tree was calculated with DBH and under-branch height. Stem volumes of other trees were calculated from

an allometric equation developed using stem volume of sample tree and DBH. Stem volume per unit ground area (SVI) was determined from stem volume per tree and number of trees per unit ground area.

3 Results

3.1 Seasonal changes of microclimate parameters in the experimental site

Means of air humidity and air temperature were 76.3 % and 31.3 °C in August, 62.7 % and 15.1 °C in December, respectively. Air temperature changed diurnally, typically reaching the maximum at about 16:00 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. 3). 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/dry season dynamics in our study site.

3.2 Temperature response of stem CO_2 efflux

There was a linear increase in stem CO_2 efflux (E_s) per unit surface area with diameter at the breast height (Fig. 4a, $r^2 = 0.40$, $n = 10$, $P < 0.05$), but no relationship between reciprocal of diameter and stem CO_2 efflux per unit volume (Fig. 4b). Thus the data indicated that E_s was proportional to stem volume and the major respiratory source was volume related according to Levy and Jarivs (1998). Therefore, the stem volume contributed more to E_s and was the better unit for expressing E_s in our study.

As showed in Fig. 5 that E_s presented a distictive daily dynamic. SE of E_s was larger than that of stem temperature (T_s), indicating that E_s values showed a larger coeffient 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, 104.6 µmol m^{-3} s^{-1} and 15.9 °C in Decmber, respectively. Mean daily E_s at 23 °C (E_{23}) was 205.1 and

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121.1 μmol m^{-3} s^{-1} in August and December, respectively. Statistical analysis showed that mean daily E_{23} was higher in August than in December ($P < 0.05$). There was an obvious seasonal variation in E_s at a given T_s. The exponential relationship between E_s and T_s was established (Fig. 6). 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 ($n = 3$, $P > 0.05$), indicaitng the similar responses of E_s to T_s and the similar proportional increase in E_s derived from the increase of T_s in the different seasons during our study period.

3.3 Stem CO$_2$ efflux at the stand level

The 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 did not vary by the same amounts among the individuls ranging from 1.2 to 3.1. To 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 are needed. Stem volume per unit ground area (SVI) in this study was 0.015 m^3 m^{-2}. As a result, averaged E_s per unit ground area was 3.36 and 1.26 μmol m^{-2} s^{-1} in August and December, respectively (Fig. 7). The stand-level E_s was estimated based on the assumption that E_s was constant along the stem (Araki et al., 2010). However, in this study the vertical variation in E_s was observed, which would lead to mis-calculation of the real stem respiraiton based on such assumption.

4 Discussion

4.1 Unit for expressing stem CO$_2$ efflux

Ryan (1990) pointed out that stem growth or the amount of living cells did not vary directly with surface area or biomass and thought that surface area or biomass could

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not be used to estimate the stand-level stem respiration. In our study, the stem volume as unit for expressing stem CO_2 efflux was determined using the relationship between stem CO_2 efflux and stem size, indicating that the contribution from volume to stem CO_2 efflux was more important and the major stem CO_2 efflux source was volume re-
5   lated according to Levy and Jarvis (1998). Additionally, it suggested that the respiring tissue was associated with the xylem cell (Meir and Grace, 2002). This may be ba-cause that (1) the xylem tissue in thickness contributed to about 90 % of the stem and (2) the living cells of the xylem tissue were very active in this *S. superba* plantation due to the high transpiration rates under the condition of sufficient water supply which was
10 reflected by the sap velocity of 0.83 and 0.41 g s^{-1} in the wet and dry season, respec-tively (Zhu et al., 2011). Cavaleri et al. (2006) found that CO_2 efflux of woody tissue from trees of small daimeter was correlated with surface area in a primary tropical rain forest. Meir and Grace (2002) drew a similar conclusion that the contribution from woody tissue volume was more important for the woody tissue respiration at high di-
15 ameter. Levy and Jarvis (1998) studied stem CO_2 fluxes in two Sahelian shrub species (*Guiera senegalensis* and *Combretum micranthum*) and pointed out that the inconsis-tent relationship between the stem CO_2 flux and surface area or volume resulted from the different stem size and that sapwood volume played a greater role on stem respi-ration with diameter increases. Besides, the unit of stem respiration for scaling to the
20 forest depended on the source of respiratory CO_2. Teskey et al. (2008) indicated 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 live cell volume could be only 20–25 % of the stem live cell volume (Stockfors and Linder, 1998), while the study of Ceschia et al. (2002) indicated that the live cell of the xylem was almost
25 equivalent to that of the entire stem with diameters up to 16 cm from *Fagus sylvatica*. 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. Therefore, estimation of the stand-level stem CO_2 efflux using the stem volume was adopted in our study.

Cavaleri et al. (2006) estimated growth and maintenance respiration using stem diameter and volume, respectively. Their results indicated that growth respiration was related to diameter and maintenance respiration had a close relationship with volume. Ryan et al. (1994) found maintenance respiration was 54 % and 82 % of the total woody tissue respiration for two tropical wet forest trees (a fast-growing and a slow-growing tree species), respectively. Carey et al. (1997) estimated that the maintenance respiration in the desert trees was greater than in the montane trees and thought the difference resulted from the higher temperature and the more allocation of biomass to sapwood in the desert habit. Based on the diameter data from 2007–2011, the annual diameter growth rate of *S. superba* stand averaged 0.48 cm. Therefore, we concluded that *S. superba* tree had a slow growth rate in this experimental site. Although maintenance and growth respirations were not separated in our study, the dependence of stem CO$_2$ efflux on volume revealed that maintenance respiration might be higher than growth respiration.

4.2 Vertical variation of CO$_2$ efflux along the stem

Generally, carbon loss estimation of woody tissue at ecosystem level from a point-measured respiration in the field was based on a assumption that stem respiration was constant along the stem (Damesin et al., 2002). However, some studies had showed the variation of stem respiration with height (Ryan et al., 1996; Ceschia et al., 2002; Araki et al., 2010). Edwards et al. (2002) demonstrated that the younger locations of the stem had higher respiration rates than the older locations and stem respiration rates in the upper trunk were four times higher than in the lower trunk. Stockfors (2000) predicted the whole-tree respiration by measuring stem temperature at different heights. Araki et al. (2010) found the vertical variation in daily stem CO$_2$ efflux of *Chamaecyparis obtusa* tree was more evident in the growing season than in the dormant season. In our study, mean E_s was found 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. Therefore, differences in stem temperature with height could not explain why stem CO$_2$ efflux doubled (and

more) with increased height on the stem. 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 was mainly de-
5 rived from the more physiologically active cells. We thought that there were more newly produced tissue cells at the higher location of the stem and therefore a higher sapwood volume/stem volume value might increase the source of respiratory CO_2. The higher respiration rates in the upper-canopy leaves were attributed to the higher maintenance respiration for the more photosynthetic activity (Turnbull et al., 2003; Whitehead et al.,
10 2004). The rate of stem photosynthesis was higher due to the higher irradiance at the upper of stems than at the lower (Cerasoli et al., 2009), also resulting in the higher requirements for maintenance respiration. Such explanation indirectly well interpreted our findings.

4.3 Stem CO_2 efflux in relation to stem temperature

15 Ryan et al. (1995) reported that the maintenance respiration rates of three pines and western hemlock were between 6.4 and 11.5 $\mu mol\,m^{-3}\,s^{-1}$ at 15 °C. Carey et al. (1997) estimated stem respiration rate of ponderosa pines grown in contrasting climates and found that the maintenance respiration rate per unit sapwood volume at 15 °C was 6.39 ± 1.14 $\mu mol\,m^{-3}\,s^{-1}$, while Sprugel (1990) found the maintenance respiration rate
20 was 86 $\mu mol\,m^{-3}\,s^{-1}$ at 15 °C for young *Abies amabilis*. Ryan et al. (1994, 1996) esti-mated woody-tissue maintenance respiration rate of 15–39 $\mu mol\,m^{-3}\,s^{-1}$ in *Pinus radi-ata*, and in two tropical wet forest trees it was 39.6 $\mu mol\,m^{-3}\,s^{-1}$ at 24.6 °C which was roughly two times that of temperate conifers. Ryan et al. (1997) further estimated the annual carbon cost of autotrophic respiration in boreal forest and obtained stem respi-
25 ration rate ranging from 73 to 203 $\mu mol\,m^{-3}\,s^{-1}$ during June–August and found that the differences of stem respiration rate among the tree species were significant. To sum up, there were great differences in stem CO_2 efflux at different study sites. Meir and Grace (2002) indicated that the differences in stem CO_2 efflux between sites resulted

from the discrepancy in metabolic activity. 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 were close to the values for boreal forest but higher than the values reported for tropical forest. Zha et al. (2004) concluded that the variations of stem respiration rate in different for-
est tree species reflected the physiological adjustments to temperature changes and the metabolic activity. Additionally, to the best of our knowledge autotrophic respiration was strogly influenced by photosynthetic substrate supply. In our experimental site, *S. superba* trees growed all the year round. The high temperature and soil moisture pro-moted the metabolic activity and increased the transpiration rate which transported the
CO_2 from the soil upwards increasing the stem CO_2 efflux at the monitored positions (Zhu et al., 2011). On the other hand, annual mean LAI in this *S. superba* planta-tion reached 4.3 which could provide sufficient substrate for stem respiration and then resulted in more CO_2 diffusion into the atmosphere.

Acosta et al. (2008) pointed out Q_{10} of stem and branch respiration was the highest
in the start of the growing season and decreased with the increase of temperature. Tjoelker et al. (2001) found the higher temperature sensitivity of Q_{10} in cold-grown plants. Zha et al. (2004) studied the seasonal and annual stem respiration of Scots pine and concluded that Q_{10} in the growing season was greater than in the non-growing season, but the differences between the seasons were small ranging from 1.88 to 1.91.
Damesin et al. (2002) estimated Q_{10} for the stem of beech, and it was 1.7 at the stand level which was relatively constant throughout the year. Zach et al. (2008) measured the elevational change in woody tissue CO_2 efflux in a tropical mountain and indicated the consistent temperature sensitivity across the differing growth environments. Ryan (1991) obtained a varying Q_{10} between 1.5 and 2.5. Levy and Javis (1998) found the
Q_{10} for tropical species between 1.6 and 2.2. Our result fell within this range, and was close to the mean Q_{10} for tropical species. Although a slightly higher Q_{10} in the wet season than in the dry season was observed, it was not significant. Therefore, in our study the temperature response of stem CO_2 efflux was similar in both August and December. We obtained a stable Q_{10} calculated with stem temperature which showed

the greater inertia relative to air temperature (Damesin et al., 2002). In accordance with Meir and Grace (2002), the non-significant variation in Q_{10} resulted from the similar underlying biochemical process.

Levy and Jarvis (1998) concluded that the seasonal changes in stem respiration were attributed to the growth. Cavaleri et al. (2006) did not find the seasonal variations of wood CO$_2$ efflux in a primary tropical rain forest over 2 years which resulted from the unobvious wet/dry season dynamics. 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). Damesin et al. (2002) estimated the stand-level stem and branch respiration of beech and found that the volume-based respiration rate at 15 °C showed a great seasonal variation between the dormant and growth periods. In our experimental site, wet/dry season dynamic was pretty significant with the higher air temperature and humidity in wet season and relatively lower air temperature and humidity in 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 of stem CO$_2$ efflux mainly resulted from the variations in stem temperature between the seasons. On the seasonal scale, the differences in mean stem temperature 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 very strong positive relationship between annual above-ground woody tissue respiration rate and leaf area index (LAI) when studying the woody tissue respiration in two tropical rain forests. Edwards et al. (2002) suggested a key role of substrate availability on the woody tissue respiration. Based on the data from LAI and stem CO$_2$ efflux, our result was consistent with their conclusion. The LAI of *S. superba* stand was significantly higher in August (4.9 m^2 m^{-2}) than in December (4.2 m^2 m^{-2}) during our study period ($n=3$, $P < 0.05$). 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.

4.4 Stem CO$_2$ efflux at the stand level

Cavaleri et al. (2006) studied the woody tissue CO$_2$ efflux in a primary tropical rain forest comprising trees, *Pentaclethra macroloba*, palms and lianas and estimated the CO$_2$ efflux per unit ground area of $1.34 \pm 0.36\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ with data for 23 months. Ryan et al. (1996) estimated the aboveground respiration per unit ground area of higher than $2\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in a boreal forest ecosystem. Araki et al. (2010) found that the annual whole-stem respiration from a point-measured respiration was smaller than the respiration rate considering the vertical variations and indicated that the differences between two estimation methods were correlated with tree height and crown length. In this *S. superba* plantation, mean stem CO$_2$ efflux per unit ground area based on data for two months was $2.31\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ which was close to the values for boreal forest, and stem CO$_2$ efflux from trees of large diameter (DBH>14 cm) contributed to 90 % and 71 % of the estimated total stem CO$_2$ efflux in August and December, respectively. That may be because that 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. On the other hand, some studies took the stem photosynthesis into consideration when estimating the 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. In our experimental site stem photosynthesis was thought to be negligible considering the high LAI and the closed canopy.

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Individual- and stand-level Stem CO_2 efflux

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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

Table 2. Diameter (d, cm), mean stem CO$_2$ efflux ($\bar{E}_s$, µmol m^{-3} s^{-1}) and mean stem temperature ($\bar{T}_s$, °) of the stems at two heights of sample trees. Meansurements positions were at 1.3 and 2 m above the ground, respectively.

Height above the ground (m)	Tree 3			Tree 4			Tree 8			Tree12		
	d	$\bar{E}_s$	$\bar{T}_s$	d	$\bar{E}_s$	$\bar{T}_s$	d	$\bar{E}_s$	$\bar{T}_s$	d	$\bar{E}_s$	$\bar{T}_s$
1.3	14.9	115.5[**]	19.7[**]	25.6	24.5[**]	18.5[**]	9.3	23.2[**]	19.1[**]	17.0	47.2[**]	–
2	14.2	125.0	20.4	23.9	75.4	19.6	8.9	40.4	19.3	16.2	62.9	–

[**] value significantly different from 2-m height at $P < 0.01$.
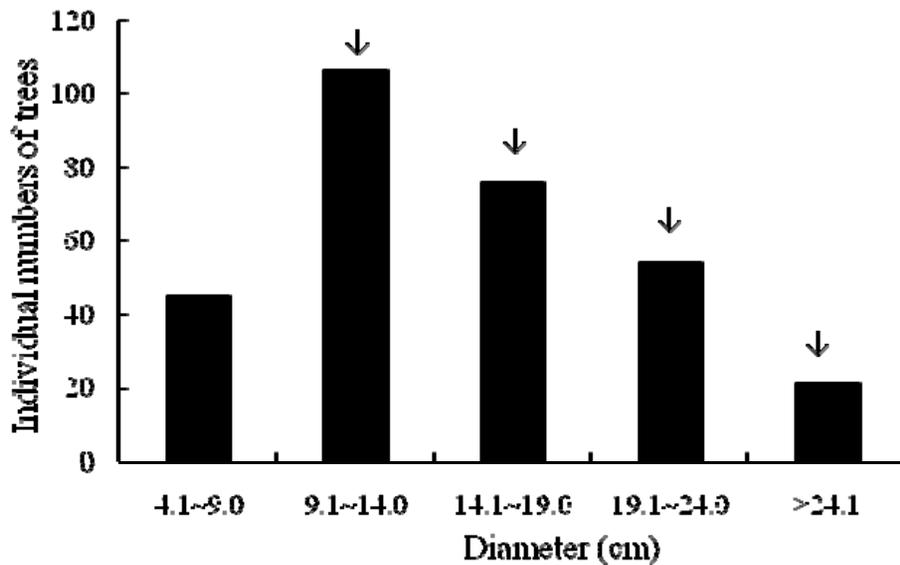
Fig. 1. Distribution of tree stem diameters at the experimental site. All diameters were measured at 1.3 m height. The arrows indicate the diameters of sample trees used for stem CO$_2$ efflux measurements.

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Fig. 2. Photograph of stem respiratory chamber.
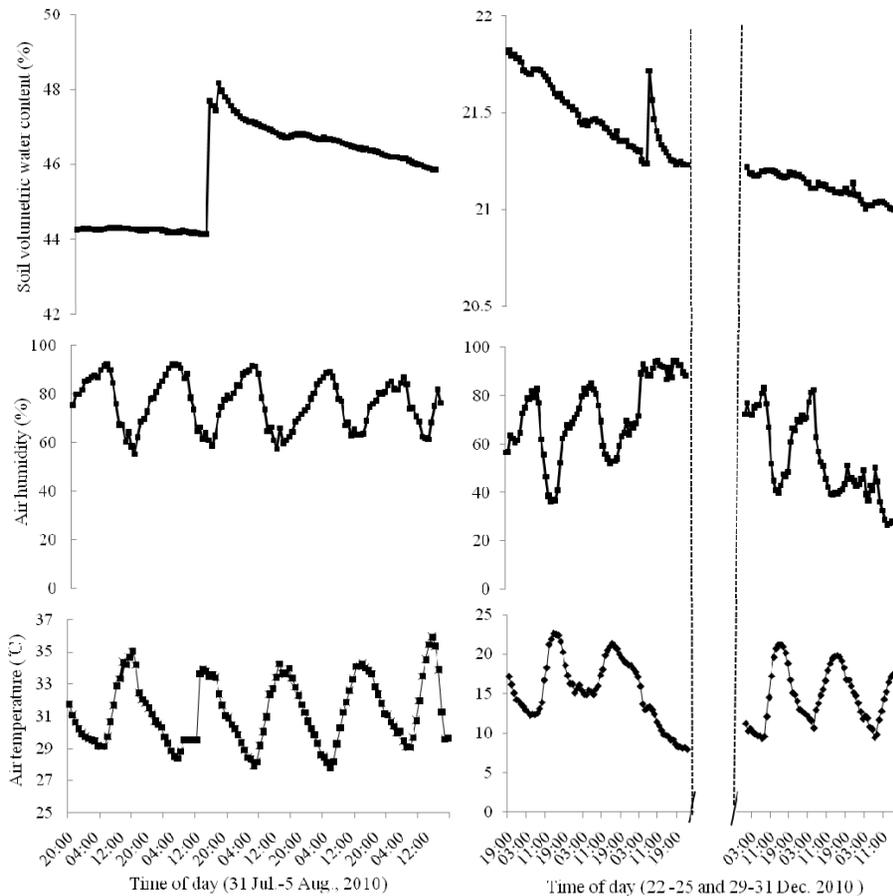
Fig. 3. Diurnal variation in soil volumetric water content, air humidity and air temperature during the study period. Abnormality of data from 09:00 to 19:00 on 2 August was due to the power failure. A large fluctuation occurred because it rained from 03:00 to 05:00 on 25 December.
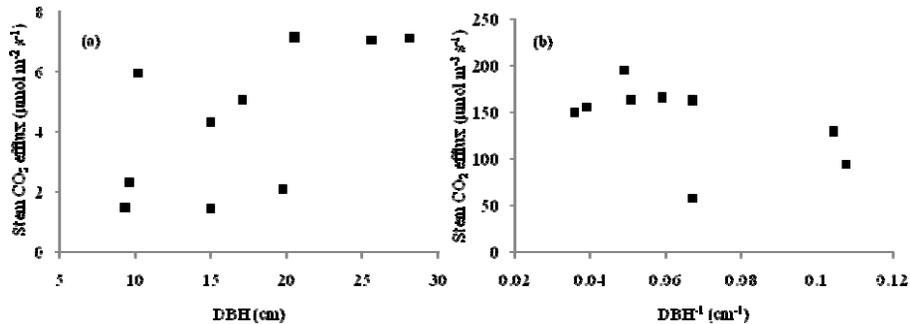
Fig. 4. Relationship between stem CO$_2$ efflux and diameter at the breast height (DBH). **(a)** surface-based stem CO$_2$ efflux and DBH; **(b)** stem volume-based stem CO$_2$ efflux and 1/DBH.
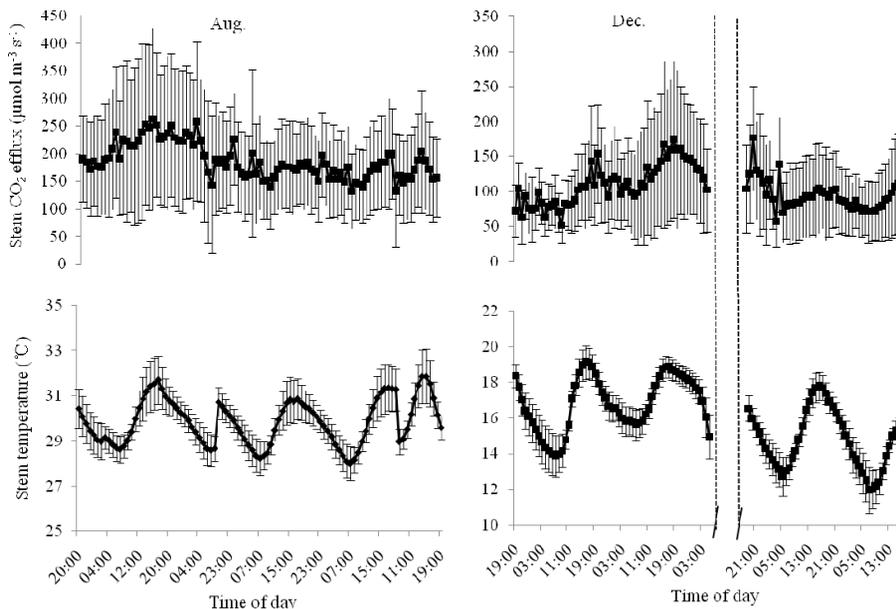
Fig. 5. Diurnal variation in mean stem CO$_2$ efflux and mean stem temperature of sample trees in August and December, 2010. Error bars show SE. Uncontinuos data were due to poor weather condition or instruments failure.

Fig. 6. Dependence of stem CO_2 efflux for all measured trees on stem temperature in August and December, 2010.
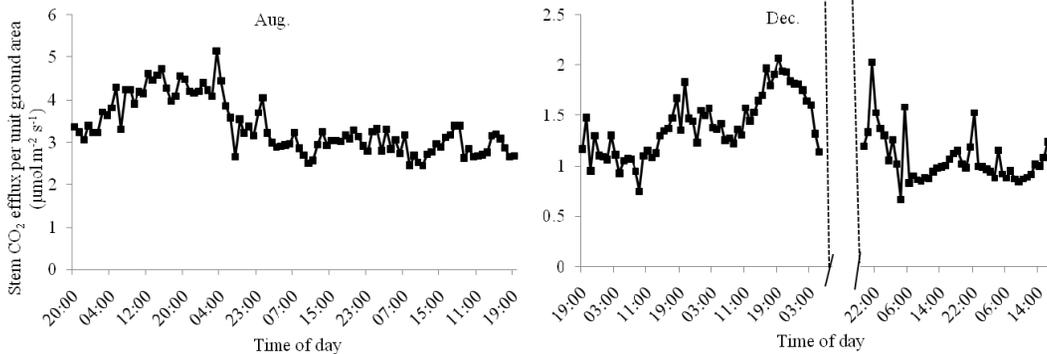
Fig. 7. Diurnal variation in mean stem CO$_2$ efflux per unit ground area in August and December, 2010.