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Research paper

Vertical variations in wood CO₂ efflux for live emergent trees in a Bornean tropical rainforest

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Difficult access to 40-m-tall emergent trees in tropical rainforests has resulted in a lack of data related to vertical variations in wood CO₂ efflux, even though significant variations in wood CO₂ efflux are an important source of errors when estimating whole-tree total wood CO₂ efflux. This study aimed to clarify vertical variations in wood CO₂ efflux for emergent trees and to document the impact of the variations on the whole-tree estimates of stem and branch CO₂ efflux. First, we measured wood CO₂ efflux and factors related to tree morphology and environment for seven live emergent trees of two dipterocarp species at four to seven heights of up to ~40 m for each tree using ladders and a crane. No systematic tendencies in vertical variations were observed for all the trees. Wood CO₂ efflux was not affected by stem and air temperature, stem diameter, stem height or stem growth. The ratios of wood CO₂ efflux at the treetop to that at breast height were larger in emergent trees with relatively smaller diameters at breast height. Second, we compared whole-tree stem CO₂ efflux estimates using vertical measurements with those based on solely breast height measurements. We found similar whole-tree stem CO₂ efflux estimates regardless of the patterns of vertical variations in CO₂ efflux because the surface area in the canopy, where wood CO₂ efflux often differed from that at breast height, was very small compared with that at low stem heights, resulting in little effect of the vertical variations on the estimate. Additionally, whole-tree branch CO₂ efflux estimates using measured wood CO₂ efflux in the canopy were considerably different from those measured using only breast height measurements. Uncertainties in wood CO₂ efflux in the canopy did not cause any bias in stem CO₂ efflux scaling, but affected branch CO₂ efflux.

Keywords: carbon allocation, dipterocarp, scaling, stem respiration.

Introduction

Plant respiration plays an important role in carbon cycling in forest ecosystems. Most of the carbon assimilated during photosynthesis is used for respiration (DeLucia et al. 2007, Litton et al. 2007), and plant respiration regulates productivity and carbon balance, i.e., net ecosystem exchange (NEE; Ryan 1991, Piao et al. 2010). Although many studies based

on eddy covariance measurements found large variations in NEE at a global scale (Luyssaert et al. 2007), the cause of the variations is still unknown because the variations in each component of carbon cycling are poorly understood (Malhi 2012). To understand the variations in NEE, it is necessary to estimate respiration for each component at the stand scale for various forest ecosystems and to understand how respiration for each component varies with biotic and abiotic factors.

Chamber-based measurements are often used to estimate CO₂ efflux for each component, such as soil, root and woody tissue. Although chamber-based measurements are useful for estimates of each type of CO₂ efflux, clarification and consideration of the spatial variation in scaling from point measurements to stand scale is required (e.g., Katayama et al. 2009). Woody tissue CO₂ efflux, which is the amount of carbon released from stems and branches, is an important component in plant respiration because it accounts for ~20–47% of total CO₂ released from plant tissue in forest ecosystems (Chambers et al. 2004, da Costa et al. 2013, Malhi et al. 2013, Doughty et al. 2014). Despite this importance, uncertainties remain related to the variations in wood CO₂ efflux in scaling to stand or whole-tree estimates.

Previous studies found that wood CO₂ efflux varied vertically within an individual (Yoda et al. 1965, Damesin et al. 2002, Araki et al. 2010). Most studies have shown that wood CO₂ efflux increased with stem height (Yoda et al. 1965, Damesin et al. 2002, Cavaleri et al. 2006, Araki et al. 2010), although other studies have also shown that wood CO₂ efflux did not vary with stem height (Ryan et al. 1996). In tropical rainforests, emergent trees often have a diameter at breast height (DBH, cm) >60 cm and heights often exceed 40 m. Vertical variations in wood CO₂ efflux for emergent trees in tropical rainforests are expected to be higher than those reported in previous studies for relatively smaller trees, because of the large vertical variations in temperature observed in tropical rainforests (Kumagai et al. 2001) and the large variation in diameter (Yoda et al. 1965, Damesin et al. 2002). However, previous studies related to vertical variations in wood CO₂ efflux in tropical rainforests used relatively small live trees with heights of 25 m (Cavaleri et al. 2006) and excised samples of woody parts (Yoda et al. 1965). The effects of several factors such as temperature and stem growth on vertical variations in wood CO₂ efflux for emergent trees are still unknown.

Whole-tree stem and branch CO₂ efflux have often been estimated using wood CO₂ efflux measured at breast height based on the assumption that wood CO₂ efflux does not vary with stem height (e.g., Chambers et al. 2004, Robertson et al. 2010), although significant vertical variations in wood CO₂ efflux have caused errors in scaling for smaller trees (Damesin et al. 2002, Araki et al. 2010). In Bornean tropical rainforests, emergent trees with DBH >60 cm accounted for about half of the total aboveground biomass and biomass increment (Paoli et al. 2008). Because biomass and stem growth were related to wood CO₂ efflux at the individual scale (e.g., Ryan 1990, Ryan et al. 1994, Mori et al. 2010), emergent trees may create a serious bias in stand-scale wood CO₂ efflux estimates.

In this study, we measured vertical variations in wood CO₂ efflux for seven live emergent trees with diameters of 60–148 cm and heights of >37 m in a Bornean tropical rainforest including two dominant species at the site described

below. We measured wood CO₂ efflux up to 43 m in stem height, using ladders and a crane to conduct ecological observations in the canopy (e.g., Kenzo et al. 2007). The objectives of this study are (i) to clarify vertical variations in wood CO₂ efflux for live emergent trees in a Bornean tropical rainforest and to elucidate possible factors controlling the vertical variations and (ii) to assess how the vertical variations in wood CO₂ efflux affect whole-tree stem and branch CO₂ efflux estimates.

Materials and methods

Study site

The study was carried out in Lambir Hills National Park, Sarawak, Malaysia (4°12'N, 114°02'E) on the island of Borneo, situated ~20 km southwest of Miri, Sarawak. Lowland mixed-dipterocarp forest, which is a typical mature lowland tropical rainforest type in Southeast Asia (e.g., Ashton and Hall 1992, King et al. 2009), covers 85% of this 6949-ha park. At this site, the mean annual temperature was 25.8 °C and rainfall was distributed throughout the year with a mean annual rainfall of 2600 mm between 2000 and 2009 (Kume et al. 2011). The monthly rainfall between 1958 and 2001 averaged >100 mm (Kumagai et al. 2005).

An 85-m crane facility was constructed in the park for long-term ecological studies. Measurements in this study were conducted around a 4-ha study plot centered on the crane. Previously, we performed carbon cycling measurements at this site including measures of eddy covariance-based CO₂ flux (Kumagai et al. 2006), soil respiration (Ohashi et al. 2008, Katayama et al. 2009) and carbon allocation (Katayama et al. 2013).

Sample design

Two typical dominant species in Malaysian lowland forests in the Dipterocarpaceae were selected for this study (Ashton 1982): four individuals of *Dryobalanops aromatica* (Trees a1, a2, a3 and a4) and three *Shorea beccariana* (Trees b1, b2 and b3). These two species are large evergreen trees that grow up to 50–70 m tall (Itoh et al. 1997), are widely distributed over the Malay Peninsula, Sumatra and Borneo (Ashton 1982), and are dominant canopy species in the 4-ha plot (1.7 and 1.1% in number, 8.8 and 11.7% in aboveground biomass of trees with DBH >10 cm in the plot, respectively). The DBH of sample trees ranged from 60.0 to 148.0 cm (Figure 1 shows Tree a2). Ladders were set up reaching to almost the top of the canopies and were used for measurements of wood CO₂ efflux for six of the seven trees. The crane was used for wood CO₂ efflux measurements for Tree b3. Wood CO₂ efflux was measured at the main trunk with diameters ranging from 14 to 148 cm at four to seven heights for each tree (Table 1). The measurements were conducted six times for six trees and three times for one tree (b3) between 22 August and 11 September 2011.



Figure 1. Photograph of Tree a2. DBH and tree height of emergent trees often exceed 100 cm and 50 m, respectively, in Lambir Hills National Park.

To examine circumference variations at breast height, wood CO₂ efflux was measured at four places at breast height for the six sample trees with the exception of b3, which was measured three times. Additionally, to examine the representativeness of our sample trees, wood CO₂ efflux at breast height for another 41 trees with DBH ranging from 10 to 155 cm on the same plot was measured during the one-measurements campaign plus the seven trees for vertical measurements (for a total of 48 trees) in January 2012. All wood CO₂ efflux measurements were conducted between 8:30 and 15:00 h using measurements from randomly selected trees. Clear diurnal

Table 1. Size characteristics and stem height for wood CO₂ efflux measurements of each tree. Trees (Dipterocarpaceae) were named a1–a4 for *D. aromatica* and b1–b3 for *S. beccariana*.

No.	DBH (cm)	Tree height (m)	Height of the lowest live branch (m)	Stem height of wood CO ₂ efflux measurements (m)
<i>D. aromatica</i>				
a1	95.7	44.4	25	38 ¹ , 35 ¹ , 30 ¹ , 20 ¹ , 10 ¹ , 1.3 ¹
a2	148.0	53.1	31	40 ¹ , 35 ¹ , 30, 20, 10, 2 ¹
a3	60.0	37.8	21	34 ¹ , 30 ¹ , 20 ¹ , 10 ¹ , 2 ¹
a4	98.4	44.9	25	38 ¹ , 37 ¹ , 35 ¹ , 30 ¹ , 20 ¹ , 10 ¹ , 2 ¹
<i>S. beccariana</i>				
b1	69.0	44.0	34	40 ¹ , 35 ¹ , 30 ¹ , 20 ¹ , 10 ¹ , 1.3 ¹
b2	95.2	51.0	33	40 ¹ , 35 ¹ , 30 ¹ , 20 ¹ , 10 ¹ , 2 ¹
b3	95.3	50.3	38	43 ¹ , 38, 30, 15, 1.3 ¹

¹Diameter was measured.

variations were not detected by preliminary measurements of vertical wood CO₂ efflux for a single tree for 2 days during daylight hours. Additionally, six replications taken at a random time scale during the day were made for most measurements, and these suggested that mean wood CO₂ efflux at each measurement point was affected less by diurnal variations in this study than by other factors. However, the Discussion section considers uncertainty related to diurnal variations in wood CO₂ efflux.

Measurements

Wood CO₂ efflux was measured using a closed-static system with an infrared gas analyzer (GMP343, Vaisala, Helsinki, Finland) attached inside a chamber. The chamber and collars were made of polyvinyl chloride. A small 12-V battery-operated fan was installed to circulate air inside the chamber. The collars were attached to stems using glue and silicon sealant; leakage between the stem and the collar was prevented with nondrying clay. Leakage was checked by breathing around the chamber after all measurements. All measurements for each point were conducted using the same collar. A sampling time ranging from 60 to 120 s was used. CO₂ concentration within the chamber was measured every 5 s and recorded by a monitor (M170, Vaisala). Wood CO₂ efflux (R_{wood} , $\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated using Eq. (1):

$$R_{\text{wood}} = \frac{V}{22.4 \times A} \left(\frac{273.2}{273.2 + q} \right) \frac{dc}{dt}, \quad (1)$$

where V is the chamber volume ($1.087 \times 10^{-3} \text{ m}^3$), q is the air temperature inside the chamber ($^{\circ}\text{C}$), A is the projected area of the chamber ($7.854 \times 10^{-3} \text{ m}^2$) and dc is the increment of CO₂ concentration during the incubation time (dt). Equation (1) assumes that efflux rate is measured under standard barometric pressure. All measurements at each point were replicated two or three times and averaged. To check the accuracy of the system, we measured wood CO₂ efflux of some trees with the

closed-static system and used a commercial respirometer (LI-6400, Li-Cor, Inc., Lincoln, NE, USA) at the same points using the same collars. The relationship between observed wood CO₂ efflux determined using the closed-static system (R_{system}) and using LI-6400 (R_{LI6400}) was a linear regression ($n = 53$, $R_{\text{LI6400}} = 0.890 \times R_{\text{system}}$, $r^2 = 0.95$). We obtained wood CO₂ efflux corrected from R_{system} using this equation.

To examine factors related to vertical variations in wood CO₂ efflux, stem and air temperature, stem height, diameter and stem growth were measured at each wood CO₂ efflux measurement point. Air temperature and stem surface temperature were measured with a thermometer (TR-52i; T&D Co. Ltd, Nagano, Japan). Stem heights at all wood CO₂ efflux measurement points were checked using a measuring tape. In September 2011, dendrometer bands were placed at each measurement height around the collars except for some heights of Trees a2 and b3 in which the stem diameters were too large to install dendrometers using ladders set on only one side (Table 1). Stem growth rate (cm year⁻¹) at each measurement point was obtained by measuring the circumference in January 2012 and September 2012, and calculating the annual growth rate assuming constant growth.

Analysis of vertical variations

Relationships of wood CO₂ efflux to diameter, height and stem growth were examined. To eliminate the effects of temperature, wood CO₂ efflux measurements were corrected to a reference temperature of 25 °C using Eq. (2) and the value of Q_{10} ,

$$R_{25} = R(t)Q_{10}^{(25-t)/10}, \quad (2)$$

where R_{25} is wood CO₂ efflux at 25 °C, $R(t)$ is wood CO₂ efflux at the stem surface temperature of t (°C) and Q_{10} is a temperature coefficient of wood CO₂ efflux. Because Q_{10} was not calculated from the data in this study, it was assumed that Q_{10} was equal to 2.0, the same value as used in a study by Cavaleri et al. (2006) in tropical rainforests in La Selva, Costa Rica. In this study, wood CO₂ efflux is used as R_{25} , that is, the measured value was not used directly, except for the analysis of the effects of temperature. To examine the gradient of vertical variations in wood CO₂ efflux, the ratio of wood CO₂ efflux at the top of a tree against wood CO₂ efflux at breast height (k) was calculated for each tree.

Scaling woody tissue respiration

Total wood CO₂ efflux at the whole-tree scale was estimated based on vertical wood CO₂ efflux measurements by summing whole-tree stem and branch CO₂ efflux. Note that whole-tree wood CO₂ efflux in this study was limited to aboveground woody tissue and did not include coarse woody roots. Whole-tree surface area of woody tissue (m² tree⁻¹) was used for scaling wood CO₂ efflux in this study. Surface area and sapwood

volume have often been used as scaling parameters in previous studies. The use of surface area is more convenient in tropical forests (Chambers et al. 2004, Robertson et al. 2010) because sapwood area is poorly defined in the wood of tropical trees and interspecific variations are present in species-diverse tropical rainforests.

Whole-tree surface area of the main stem was estimated using the concept of a truncated cone (Yoneda 1993), which was applied to calculate each segment's surface area separately based on wood CO₂ efflux measurements at various heights. Each section's surface area was calculated using the radii (r_i) and height (h_i) of each truncated cone. Whole-tree surface area of the main stem was calculated by summing each separated surface area using Eq. (3):

$$A_{\text{stem}} = \sum_{i=0}^n \pi (r_i + r_{i+1}) \sqrt{(h_{i+1} - h_i)^2 + (r_i - r_{i+1})^2}, \quad (3)$$

where A_{stem} is stem surface area (m² tree⁻¹). The number of separate segments corresponds to the number of wood CO₂ efflux measurement points (n). Each segment was separated at intermediate height (h_i) between higher and lower wood CO₂ efflux measurement points. h_0 and h_n were the assumed ground-level and the highest wood CO₂ efflux measurements taken, respectively. r_i is the radius at h_i . r_0 and r_n are the assumed radii at breast height and the top of wood CO₂ efflux measurement points, respectively. Except for r_0 and r_n , r_i was interpolated using measured diameter at lower and higher wood CO₂ efflux measurement points. Wood CO₂ efflux of each individual segment was obtained by multiplying wood CO₂ efflux by the individual stem surface area measurements at each measurement point. Whole-tree stem CO₂ efflux was calculated by summing wood CO₂ efflux for each separate segment of each tree.

Whole-tree surface area of branches was calculated using the pipe-model theory (Shinozaki et al. 1964) applied to the frequency distribution of diameter of tree branches (Yoneda 1993), which has often been used for scaling of branch CO₂ efflux (Chambers et al. 2004, Robertson et al. 2010), as seen in Eq. (4):

$$A_{\text{branch}} = 4 \times \frac{\pi w_b}{\pi \times \rho \times (d_{\text{max}} - d_{\text{min}})} \times \ln \left(\frac{d_{\text{max}}}{d_{\text{min}}} \right), \quad (4)$$

where A_{branch} , w_b , ρ , d_{max} and d_{min} are the branch surface area (m² tree⁻¹), the dry weight of the branches, the wood density (kg dry mass m⁻³), and the maximum and minimum diameters of branches, respectively. w_b was estimated by allometric equations developed by Yamakura et al. (1986) for East Borneo Island in Indonesia where the forest type was similar to this study site. d_{max} was measured directly using ladders for five trees (a1, a3, a4, b1 and b2). For Trees a2 and b3,

d_{\max} was not measured because access was not feasible, and in fact was nearly impossible. For these two trees, d_{\max} was estimated by stem diameter at the lowest live branch height (d_b) based on the relationship between d_{\max} and d_b for the other five trees ($d_b = 0.77 \times d_{\max}$, $r^2 = 0.77$). d_{\min} was assumed to be 2 mm, similar to previous studies (e.g., Yoneda 1993, Chambers et al. 2004). ρ was 0.796 for *D. aromatica* and 0.531 for *S. beccariana* and was calculated from measurements for each of three trees at this study site (Y. Inoue, unpublished data). Because we did not measure branch CO₂ efflux, mean wood CO₂ efflux measured in the canopy was multiplied by branch surface area to estimate branch CO₂ efflux. Note that 'the canopy' was defined as the area above the lowest living branch in this study.

To evaluate the impact of ignoring vertical variations in wood CO₂ efflux on whole-tree scaling, whole-tree stem and branch CO₂ efflux estimated using vertical measurements were compared with those calculated using only breast height measurements.

Results

Vertical variations in wood CO₂ efflux

Wood CO₂ efflux at breast height for each tree ranged from 1.00 to 2.10 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with a mean (\pm SD) of

$1.58 \pm 0.35 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the seven trees. The mean wood CO₂ efflux at breast height in four different directions for the six trees was $1.58 \pm 0.38 \mu\text{mol m}^{-2} \text{s}^{-1}$, while the mean wood CO₂ efflux at breast height at the collar for vertical measurements was $1.52 \pm 0.26 \mu\text{mol m}^{-2} \text{s}^{-1}$. The mean wood CO₂ efflux at breast height was 29.3% higher than that including the other 41 trees with DBH ranging from 10 to 155 cm. Wood CO₂ efflux at the highest point ranged from 0.50 to 3.38 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with a mean (\pm SD) of $2.04 \pm 1.05 \mu\text{mol m}^{-2} \text{s}^{-1}$. Wood CO₂ efflux averaged in the canopy ranged from 0.62 to 2.85 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with a mean (\pm SD) of $1.72 \pm 0.76 \mu\text{mol m}^{-2} \text{s}^{-1}$. Figure 2 shows the vertical variations in wood CO₂ efflux, which were the average of all measurements at each stem height for each tree. Vertical variations in wood CO₂ efflux were different for each tree and no systematic tendency in the variations was observed. Wood CO₂ efflux at some measurement points in the canopy for a1, b1 and b2 was significantly higher than wood CO₂ efflux at breast height (Tukey–Kramer's method; a1: $P < 0.1$; b1 and b2: $P < 0.05$). Wood CO₂ efflux at the two highest points of a2 was significantly lower than wood CO₂ efflux at breast height ($P < 0.05$). For Trees a3, a4 and b3, wood CO₂ efflux at all points was not different from each measured wood CO₂ efflux at breast height ($P > 0.1$). Significant differences in wood CO₂ efflux from wood CO₂ efflux at breast height were only observed in the canopy, and not below the canopy. These

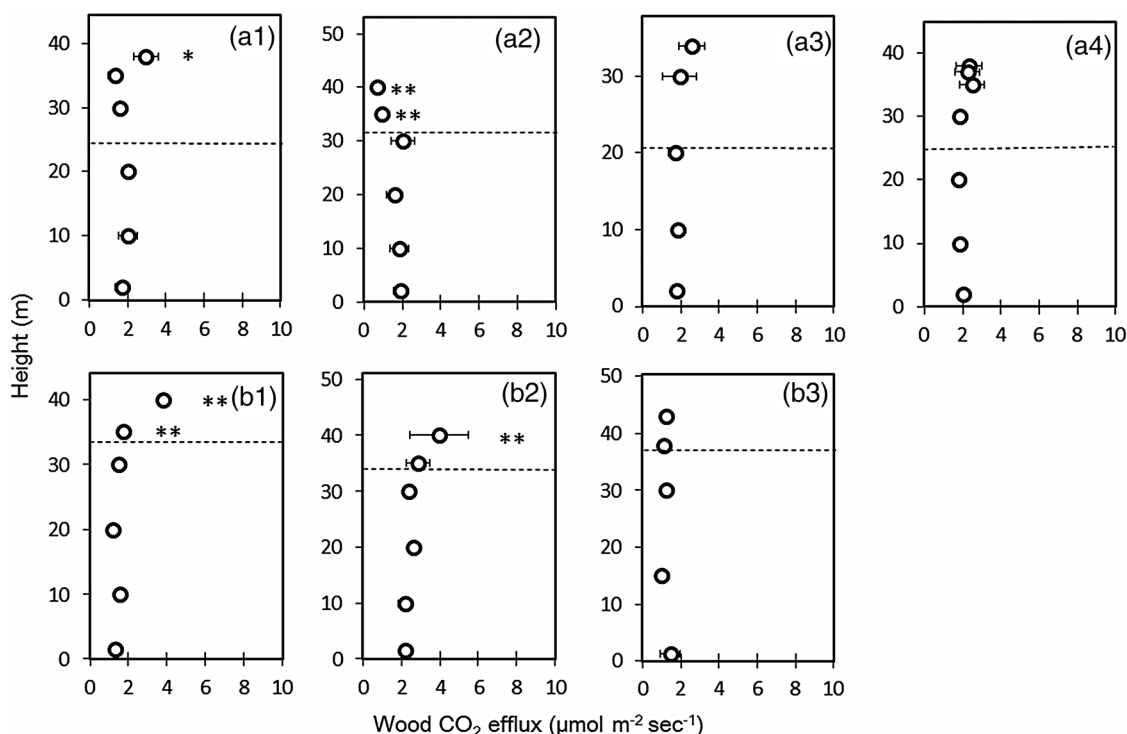


Figure 2. Vertical variations in wood CO₂ efflux of each tree. a1–a4 indicate four trees of *D. aromatica* (Dipterocarpaceae) and b1–b3 indicate three trees of *S. beccariana* (Dipterocarpaceae). The y-axis indicates the height for each tree. The dashed lines show the positions of the lowest live branches. Error bars represent standard deviation. Some very small error bars were hidden by symbols. An asterisk indicates a significant difference in wood CO₂ efflux between breast height and each stem height (** $P < 0.05$, * $P < 0.1$).

significant differences did not change when analyzing wood CO₂ efflux before correcting to a reference temperature of 25 °C, except that the difference at the second highest point for b1 was not significant.

Mean (±SD) air and stem temperature among all measurement points were 28.03 ± 0.86 and 27.38 ± 1.09 °C, respectively. The difference between maximum and minimum values for air and stem temperature of each tree averaged 2.11 and 2.76 °C, respectively. No significant relationships of wood CO₂ efflux with stem temperature, diameter, stem height and stem growth rate were observed for all measurements ($P > 0.1$). Wood CO₂ efflux measured in the canopy was negatively

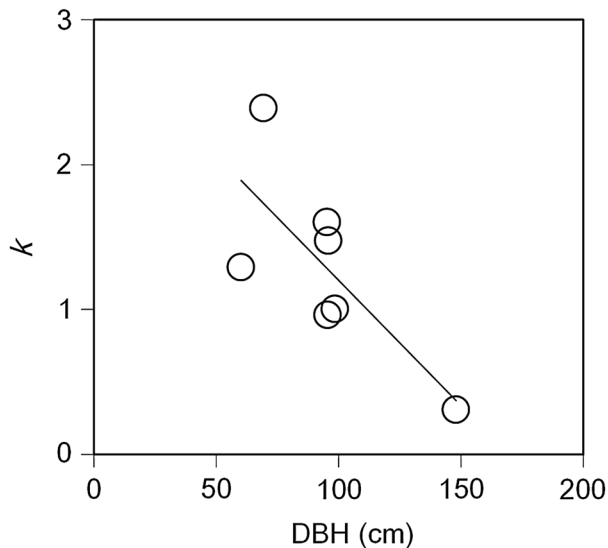


Figure 3. Relationship between DBH and k , which is the ratio of wood CO₂ efflux at breast height to that at the top of the tree. k was negatively correlated with DBH ($y = -0.017x + 2.925$, $P < 0.1$, $R^2 = 0.56$).

correlated with canopy depth (i.e., length from the canopy top, $P < 0.1$), but not with diameter. Although wood CO₂ efflux was significantly related to air temperature ($P < 0.05$, $R^2 = 0.02$), the slope was very small ($-0.07 \mu\text{mol m}^{-2} \text{s}^{-1} \text{ } ^\circ\text{C}^{-1}$).

k ranged from 0.31 to 2.39, with a mean of 1.29. k was negatively correlated with DBH; that is, k was greater or less for smaller or larger DBH trees, respectively (Figure 3, $P < 0.1$, $R^2 = 0.56$).

Scaling whole-tree stem and branch CO₂ efflux

Most stem surface area was distributed below the canopy, accounting for 0.81 of the total stem surface area in the seven samples; because the canopy area was defined above as any area at or higher than the first live branch, branch surface area was distributed only in the canopy as defined here. The relationship between whole-tree stem CO₂ efflux using vertical measurements and that using only breast height measurements was significantly positively correlated ($P < 0.01$, $R^2 = 0.94$, Figure 4a) with a slope of nearly 1. Ratios of whole-tree stem CO₂ efflux using only breast height measurements to those using vertical measurements were 0.89–1.23 with a mean (±SD) of 1.07 ± 0.13 . The relationship between whole-tree branch CO₂ efflux using vertical measurements and those using only breast height measurements was not clear ($P > 0.1$, Figure 4a) and the ratio of whole-tree branch CO₂ efflux using only breast height measurements to those using vertical measurements ranged from 0.56 to 2.56 with a mean (±SD) of 1.18 ± 0.68 . Whole-tree branch CO₂ efflux using vertical measurements accounted for 0.61 ± 0.14 of whole-tree total wood CO₂ efflux as the sum of total stem and branch CO₂ efflux. The relationship between whole-tree total wood CO₂ efflux using vertical measurements and those using only breast height

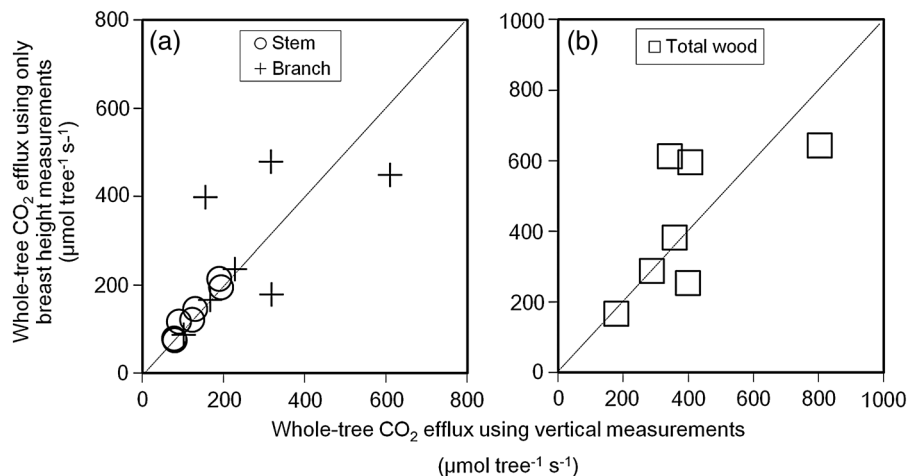


Figure 4. Relationship between whole-tree (a) stem and branch CO₂ efflux, and (b) total wood CO₂ efflux estimated using vertical measurements and that estimated using only breast height measurements. The regression line for whole-tree stem CO₂ efflux using vertical measurements of wood CO₂ efflux was significantly correlated with that using only breast height measurements ($y = 1.06x + 2.36$, $P < 0.01$, $R^2 = 0.94$). The differences between the regression lines for whole-tree branch and total wood CO₂ efflux were not significant ($P > 0.1$).

measurements was also not clear ($P > 0.1$, Figure 4b). The ratio of whole-tree total wood CO₂ efflux using only breast height measurements to those using vertical measurements ranged from 0.64 to 1.70 with a mean (\pm SD) of 1.09 ± 0.37 . The ratios of whole-tree stem, branch and wood CO₂ efflux using only breast height measurements to those using vertical measurements were negatively correlated with k ($P < 0.1$, $R^2 = 0.46$; $P < 0.05$, $R^2 = 0.76$; $P < 0.01$, $R^2 = 0.83$, respectively; Figure 5). The slope of the relationships was the steepest for branch data and relatively shallow for stem data. Although the ratios of whole-tree stem CO₂ efflux using only breast height measurements to that using vertical measurements were not related to DBH ($P > 0.1$, Figure 6a), the ratios of whole-tree branch and total wood CO₂ efflux using only breast height measurements to that using vertical measurements were positively correlated with DBH

($P < 0.01$, $R^2 = 0.77$; $P < 0.05$, $R^2 = 0.65$; Figure 6). The similar relationships shown in Figures 4–6 were observed even if wood CO₂ efflux measurements taken before temperature correction were used for the calculations.

Discussion

Possible factors related to the vertical variations in wood CO₂ efflux

Patterns of vertical variations in wood CO₂ efflux for emergent trees in this tropical rainforest were different in different individuals (Figure 2). Wood CO₂ efflux at the top of the canopy in this study (0.50 – $3.38 \mu\text{mol m}^{-2} \text{s}^{-1}$, with a mean of $2.04 \mu\text{mol m}^{-2} \text{s}^{-1}$) is comparable to the results of the highest wood CO₂ efflux in the canopy reported by previous studies. Earlier findings include $\sim 3 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Pinus radiata*

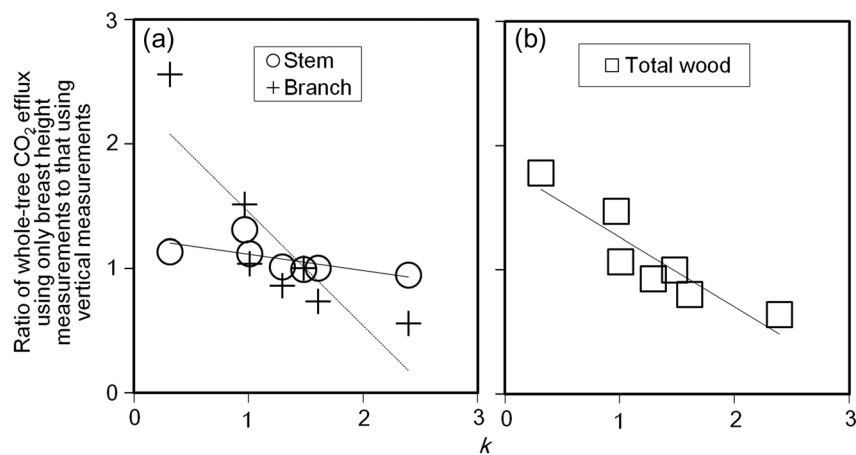


Figure 5. Relationship of k with the ratio of (a) whole-tree stem and branch CO₂ efflux using only breast height measurements to that using vertical measurements, and (b) whole-tree total wood CO₂ efflux using only breast height measurements to that using vertical measurements. The ratios for stem, branch and woody tissue were negatively correlated with k ($y = -0.13x + 1.24$, $P < 0.1$, $R^2 = 0.46$; $y = -0.91x + 2.34$, $P < 0.05$, $R^2 = 0.76$; $y = -0.56x + 1.82$, $P < 0.01$, $R^2 = 0.83$, respectively).

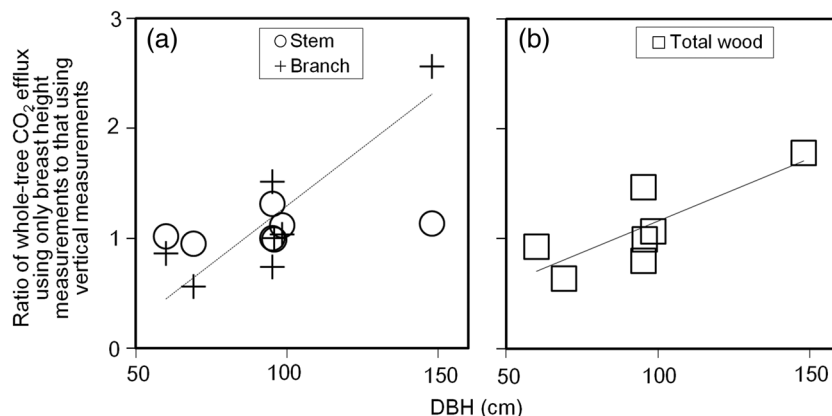


Figure 6. Relationship of DBH with the ratio of (a) whole-tree stem and branch CO₂ efflux using only breast height measurements to that using vertical measurements, and (b) whole-tree total wood CO₂ efflux using only breast height measurements to that using vertical measurements. The ratios for branch and woody tissue were positively correlated with DBH ($y = 0.021x - 0.818$, $P < 0.01$, $R^2 = 0.77$; $y = 0.011x + 0.018$, $P < 0.05$, $R^2 = 0.65$, respectively).

at 16 m height (Ryan et al. 1996), $\sim 5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for beech at 15 m height (Damesin et al. 2002), $\sim 4 \mu\text{mol m}^{-2} \text{s}^{-1}$ in tropical rainforests at ≥ 25 m height (Cavaleri et al. 2006) and $\sim 2.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Chamaecyparis obtusa* at 14 m height (Araki et al. 2010). Values of k (0.31–2.39 with a mean of 1.29) were also within the range of the maximum k value of previous studies (~ 1.6 , Ryan et al. 1996 and Damesin et al. 2002; ~ 1 –4.67, Araki et al. 2010). These results suggest that the emergent trees (>40 m tall) in our study do not have larger vertical variations in wood CO_2 efflux than small trees (<25 m tall).

The gradient of wood CO_2 efflux at breast height and at the top of the canopy (i.e., k) was related to DBH (Figure 3). This suggests that DBH was probably related to vertical variations in wood CO_2 efflux. Previous studies reporting an increase in wood CO_2 efflux with stem height used relatively small trees, having a DBH of <30 cm, for their measurements (Damesin et al. 2002, Araki et al. 2010), while no vertical variations were reported for relatively large trees with DBH >30 cm (Ryan et al. 1996). However, whether the threshold for this type of vertical variation is 30 cm DBH is unknown, because our results showed that wood CO_2 efflux increased according to stem height even for the large trees with a DBH of >60 cm.

In this study, no obvious effects of temperature on vertical variations in wood CO_2 efflux were detected. If wood CO_2 efflux at the top of the canopy is calculated by applying the maximum vertical difference in stem temperature between the treetop and that at breast height ($4.4 \text{ }^\circ\text{C}$ for a1) using Q_{10} (Eq.(2)), then wood CO_2 efflux at the top should increase by only 1.36-fold, however, measured wood CO_2 efflux at the top of the canopy was 1.83-fold of wood CO_2 efflux at breast height. Damesin et al. (2002) also observed large vertical variations in wood CO_2 efflux and mentioned that differences in temperature with height (the maximum observed was $6 \text{ }^\circ\text{C}$) could not explain why respiration doubled (and more) as stem height increased. No clear relationship between wood CO_2 efflux and stem growth was observed, although previous studies showed that stem growth was related to vertical variations in wood CO_2 efflux (Araki et al. 2010). Other studies reported that causes of vertical variations in wood CO_2 efflux were higher respiratory potential (Pruyn et al. 2002, Bowman et al. 2005) and an increase of diffused CO_2 transported upwards by flowing sap through the thin bark to the atmosphere in the canopy (e.g., Negisi 1979, Bowman et al. 2005), which might influence vertical variations in this study. Previous studies reported that ~ 15 – 55% of CO_2 respired by woody cells can remain within the tree on a daily basis (Teskey et al. 2008) and the proportion varied within a day (Teskey and McGuire 2007), suggesting that this contributes considerably to variations in wood CO_2 efflux. Vertical and circumferential variations in bark depth may also have an impact on wood CO_2 efflux as a result of the effects of diffused CO_2 . Additionally, larger temporal variations in stem temperature can

have a greater effect on stem tissue respiration in the canopy than those at breast height, resulting in wider range and greater standard deviations in wood CO_2 efflux at the top of the canopy than those at breast height. In reality, the mean temporal range of stem temperature at the top of the canopy for the seven trees ($4.3 \text{ }^\circ\text{C}$) was higher than that at breast height ($2.2 \text{ }^\circ\text{C}$). Higher temporal variations in the water content of bark in the canopy caused by direct solar radiation may also affect temporal variations in diffused CO_2 , resulting in higher variations in wood CO_2 efflux in the canopy when compared with measurements taken at breast height. Further studies such as analyses of the vertical variations in sap flux, bark thickness measurements and the partitioning of CO_2 will aid our understanding of factors related to these vertical variations.

Impact of the vertical variations on whole-tree total wood CO_2 efflux estimates

Errors in estimates caused by vertical variations in wood CO_2 efflux were different between stems and branches. Vertical variations in wood CO_2 efflux did not cause large errors in whole-tree stem CO_2 efflux estimates when only breast height measurements were used (Figure 4a) because the surface area in the canopy (19%) was very small compared with that below the canopy (81%). Additionally, whole-tree branch CO_2 efflux estimates using measurements at breast height resulted in large errors (Figure 4a) because wood CO_2 efflux varied in the canopy; therefore, the variations directly affected the estimates of whole-tree branch CO_2 efflux. Thus, measurements at only breast height are adequate for making estimates of whole-tree stem CO_2 efflux, but a problem still exists related to how whole-tree branch CO_2 efflux should be estimated.

The distribution of surface area and CO_2 efflux of woody tissue can vary based on diameter (Damesin et al. 2002, Ryan et al. 2009). The lack of measurements of wood CO_2 efflux at branch and surface area according to diameter can cause error in estimating whole-tree branch and total wood CO_2 efflux in this study. Additionally, Ryan et al. (2009) showed that whole-tree total wood CO_2 efflux based on vertical measurements was comparable to that based on measurements taken at only breast height when branch photosynthesis for *Eucalyptus* trees was considered, suggesting that the contribution of bark photosynthesis to branch CO_2 efflux should be examined. It is necessary to examine how these uncertainties can impact estimates of whole-tree branch CO_2 efflux, even though this process is very complicated and difficult to understand.

One important issue is determining whether surface area or volume should be used as a scaling parameter. The test of Levy and Jarvis (1998) is often used to determine the scaling parameter (e.g., Cavaleri et al. 2006). Although surface area was used for scaling in this study according to the test, whole-tree stem and branch CO_2 efflux were also estimated using volume. In the present study, the results documenting

whole-tree stem CO₂ efflux using vertical measurements were similar regardless of the scaling method used, either surface area or volume. However, whole-tree branch CO₂ efflux based on vertical measurements using volume was 60% lower than that using surface area in this study. These results showed that the decision as to which scaling parameter to use (i.e., surface area or volume) is also more important for branch than for stem CO₂ efflux estimates.

The ratio of whole-tree total wood CO₂ efflux determined using only breast height measurements to that using vertical measurements increased with decreasing k (Figure 5) and increasing DBH (Figure 6). Therefore, estimates of whole-tree total wood CO₂ efflux measured using only breast height measurements can result in a greater underestimation when compared with those derived using vertical measurements in emergent trees with a smaller DBH; this occurs because of their larger k values. Additionally, in one case k was <1 (Tree a2), for the tree with the largest DBH, resulting in overestimates in whole-tree total wood CO₂ efflux when using only breast height measurements. These results show that a comparison of wood CO₂ efflux at the stand scale between forests with different DBH distributions (such as those caused by differences in age) may cause errors in whole-tree total wood CO₂ efflux estimates.

Uncertainties

Estimates of stem and branch CO₂ efflux are important because they accounted for a large portion of plant respiration, and we found that vertical variations caused little bias in whole-tree stem CO₂ efflux estimates. However, we still have considerable problems on scaling because of the scarcity of information on spatial variations in wood CO₂ efflux for various diameters in different directions, temporal variations according to height caused by respired and diffused CO₂, CO₂ transported by sap flow, and potential variations in Q_{10} value according to heights and diameters. These variations may also differ from species to species. These uncertainties may introduce some unknown bias into scaling of wood CO₂ efflux. Therefore, additional studies are needed not only to clarify temporal variations in wood CO₂ efflux at various heights and diameters for various species, but also to clarify the sources of wood CO₂ efflux for reasonable scaling.

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Conflict of interest

None declared.

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